Forest ecosystems and global change:

The functional importance of biodiversity and ecological continuity

Cover photo: Unmanaged, ancient beech forest (i.e. a forest associated with a long ecological continuity), Lohn (Lower Saxony). Photo: Andreas Fichtner

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Andreas Fichtner

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SUMMARY

- Global environmental change induced by people’s actions and the subsequent loss in biodiversity has raised concerns over the consequences for the functioning of ecosystems and the sustainable provisioning of ecological services that humanity depends upon. This is particularly relevant for forest ecosystems, as they host a huge proportion of the Earth’s terrestrial biodiversity and play a vital role in nature-based solutions to climate change (e.g. they sequester and store immense amounts of carbon). Ongoing global forest loss, in particular in the tropical and subtropical forest biomes, alongside with overexploitation are amongst the most significant threats to biodiversity and related ecosystem services. Although ecological research has advanced our understanding on biodiversity-ecosystem functioning relationships over the last decades, the mechanisms underlying those relationships are not well understood – in particular in long-lived plant communities such as forests. Moreover, it remains unclear how forest ecosystems will respond to multiple environmental changes and how this response is altered by legacies of past human interventions.

- The present thesis aims at providing new mechanistic insights for the previously reported positive effects of tree diversity on forest productivity and aims at exploring how this functional role is affected by climate change. The thesis also addresses the overlooked role of ecological continuity – meaning not altering ecological interactions that drive ecosystem functioning by land-use change and forest management – in mediating the response of forest ecosystems to global environmental changes. In this context, the thesis addresses further important gaps in knowledge by exploring how trees respond to simultaneous effects of different global change drivers and how potential interactions are affected by forest history. The thesis include experimental studies conducted in tropical, subtropical and temperate tree communities as well as observational studies conducted in temperate forest stands. The studies focus on key ecosystem functions such as primary productivity and nutrient cycling.

- Results from large-scale tree diversity experiments provide strong support that local neighbourhood tree species richness can enhance and stabilise productivity in higher diversity communities by competitive reduction via resource partitioning in canopy space – induced by shifts in branch morphology and enhanced biomass allocation to branches – and facilitation via (e.g.) microclimate amelioration. Focal tree functional traits, however, largely generate the mode (competitive reduction or facilitation) of diversity-mediated neighbourhood interactions. Neighbourhood tree diversity can also increase the resistance of forest ecosystems to drought by locally supporting drought-sensitive species in the community – most likely via soil water partitioning among local neighbours – and thereby strengthening the weakest components of the system. These are important findings, because they suggest that mechanisms operating at the local neighbourhood scale are a key component for regulating forest productivity and the response of forest ecosystems to climate change. Moreover, the studies presented in this thesis provide first support for the hypothesis that forests associated with a long ecological continuity, such as ancient forests (forest sites that have been continuously wooded for at least more than two centuries) and long-term unmanaged forests, are less sensitive to climate change than recent forests (forest sites that are afforested during the last two centuries on former agricultural land) and (intensively) managed forests. Shifts in fine root traits and fine root biomass due to persistent soil legacies of former land use (e.g. altered nutrient cycling due to changes in soil microbial community composition) as well as management-induced changes in crown morphology are some of the mechanisms that explain ecological continuity-ecosystem functioning relationships in forests under global change. However, further findings of the thesis indicate that the mitigation effects of ecological continuity may diminish when forests experience multiple drivers of global change simultaneously. Similarly, the thesis show that combined effects of multiple global change drivers are non-additive. The combined effects of nitrogen enrichment and drought increase the sensitivity of European beech (*Fagus sylvatica*) across life-history stages with

potential negative implications on development cycles of temperate beech forests. Overall, these findings emphasise the need to advance our understanding of the complex interrelationships between biodiversity, multiple drivers of global change and ecosystem functioning and how they are affected by the ‘ecological memory’ of an ecosystem.

- The findings of the thesis encourage an ecosystem-based perspective that prioritise the integrity of ecological functions and biome-specific forest biodiversity over economic interests and high-impact management options to meet various international agreements such as biodiversity conservation and climate-change mitigation. This in turn would benefit synergies among multiple forest ecosystem services and might be a promising way for the development of effective conservation measures and sustainable land-use strategies where the functionality of forest ecosystems is maximised and the risks for humanity are minimised.

Chapter 1

Introduction

BACKGROUND, MAIN OBJECTIVES AND STRUCTURE OF THE THESIS

1.1 Background

Global environmental change induced by people's actions can trigger tipping points in marine and terrestrial ecosystems with far reaching consequences for humanity (IPCC 2018; Lenton et al. 2019). Similarly, ongoing loss of biodiversity have triggered increasing concern on the stable provisioning of benefits that people obtain from nature (ecosystem services; IPBES 2019). During the last decades, evidence is mounting that changes in ecological communities have detrimental impacts on the functioning of ecosystems and their ability to simultaneously provide a wide range of ecosystem services (Loreau et al. 2001; Cardinale et al. 2012; Hooper et al. 2012; Naeem et al. 2012; Isbell et al. 2017; Fanin et al. 2018; Manning et al. 2018). Halting biodiversity loss has therefore become a central prerequisite for meeting the United Nations Sustainable Development Goals, because biodiversity underpins many of them (Griggs et al. 2013; CBD 2019).

Forest ecosystems cover c. 30% of the Earth's land surface (FAO 2018), host a huge proportion of the world's biodiversity, and play a central role in providing important ecosystem services (MEA 2005). This includes climate and water regulation, carbon sequestration and storage (e.g. forests contain about 50% of the world's terrestrial global carbon stocks; Bonan et al. 2008; Pan et al. 2011), wood production as well as cultural services. However, species go extinct at an 'unprecedented' rate (Butchart et al. 2010; Barnosky et al. 2011; IPBES 2019; Seibold et al. 2019) due to various drivers of global environmental change such as land-use change, overexploitation of natural resources (land-use intensification), changes in biogeochemical cycles (pollution), climate change and invasive alien species (Sala et al. 2000; Scherer-Lorenzen 2014; Maxwell et al. 2016). For example, the ongoing dramatic loss of forest area, that applies to tropical rain forests in particular, constitute the most important threat to global biodiversity (Giam 2017) and critically shifts the global carbon cycle, with unprecedented consequences for humanity (Betts et al. 2017, Erb et al. 2018; Lenton et al. 2019). These drivers of global environmental change can alter forest ecosystem functioning and related ecosystem services either directly by changing species' metabolism and demography or indirectly by altering communities' functional composition and diversity (Fichtner & Härdtle 2020; cf. also Díaz et al. 2007; De Laender et al. 2016). Hence, understanding the complex interdependence between biodiversity, ecosystem functioning and multiple environmental change drivers is of vital importance to secure the stable delivery of forest ecosystem services in future (McCann 2010; Griggs et al. 2013; Isbell et al. 2017).

Over the past 25 years, hundreds of experimental and observational studies have demonstrated that forest ecosystem functioning increases with the taxonomic and functional diversity of the species within a community (van der Plas 2019). Moreover, there is evidence that biodiversity simultaneously enhances multiple functions provided by forest ecosystems (i.e. ecosystem multifunctionality) for human well-being (Gamfeldt et al. 2013; Ratcliffe et al. 2017; Schuldt et al. 2018; van der Plas et al. 2018). For key ecosystem functions, such as primary productivity, mixed-species forests have been shown to be more productive than monocultures across a wide range of forest biomes (Paquette & Messier 2011; Zhang et al. 2012; Liang et al. 2016; Huang et al. 2018), resulting in higher wood supply as well as higher rates of carbon accumulation and higher amounts of carbon stored above- and belowground in species-rich forests (Chen et al. 2018; Liu et al. 2018). For example, in a large-scale subtropical tree experiment, Huang et al. (2018) have demonstrated that highly diverse tree communities (i.e. 16-species mixtures) had accumulated over twice the amount of aboveground carbon found in average monocultures after eight years. Consequently, a 10% decline of tree species richness is predicted to reduce forest productivity by 2-3% on average at the global scale (Liang et al. 2016; Huang et al. 2018), which corresponds to an estimated monetary value of tree species richness in maintaining commercial forest productivity of $166 billion to $490 billion per year (Liang et al. 2016). Such biodiversity-mediated effects on ecosystem functioning can result from species interactions that lead to competitive reduction via resource partitioning or facilitation (Wright et al.

2017; Barry et al. 2019). Positive net biodiversity effects can also arise through biotic feedbacks that decrease host-specific damage by herbivores and pathogens (natural enemy partitioning) or selection effects (i.e. the increased likelihood of including dominant and well-performing species in diverse communities; Loreau & Hector 2001; Barry et al. 2019). Yet, our understanding of mechanisms driving biodiversity-ecosystem functioning (BEF) relationships and how these relationships are altered by environmental changes is still limited.

Global environmental changes, such as land-use change and intensification, might also modulate the functioning of ecosystems by disrupting ecological continuity. Here, I use the term 'ecological continuity' in an ecosystem-based sense, meaning the continuity in biotic and abiotic forest ecosystem processes that develop without land-use change, forest management or significant silvicultural interventions. A long ecological continuity is therefore commonly associated with a high integrity in habitat structures, species composition, species interactions, soil conditions and biogeochemical cycles typical for a given forest type (Fichtner & Härdtle 2020). Importantly, ecological continuity refers to three different aspects that determine how forests mature: forest continuity, stand maturity and continuity in natural stand dynamics (Fichtner & Lüderitz 2013; Fichtner & Härdtle 2020). Forest continuity refers to the temporal extend of how long a given site is wooded (i.e. the maintenance of the forest cover over time including soil development). For example, forest sites that have been continuously wooded for at least more than two centuries have been described as 'ancient forests' (Peterken 1977; Rackham 1980) in contrast to 'recent forests' that are afforested during the last two centuries on former agricultural land. The reference date for 'ancientness', however, is still on debate (see Bergès & Dupouey 2020). Stand maturity is associated with tree and stand aging, and thereby with processes regulating the availability, continuity and diversity of habitat structures (Janssen et al. 2019; Fichtner & Härdtle 2020). The continuity in natural stand dynamics refers to the duration of stand development without anthropogenic disturbances, which depends on the length of forest management cessation or the frequency and intensity of silvicultural interventions (e.g. thinning or commercial harvesting). Note that a long-term forest continuity does not necessarily imply a high stand maturity or long-term natural stand dynamics, although each aspect determines the conservation value and ecological integrity of a forest (Watson et al. 2018; Janssen et al. 2019; Bergès & Dupouey 2020)[1].

Numerous studies have shown that the abundance and richness of forest species on average are higher in ancient than in recent forests due to dispersal and recruitment limitations (Brunet & von Oheimb 1998; Hermy et al. 1999; Flinn & Vellend 2005; Flensted et al. 2017). Likewise, primeval, long-term unmanaged and 'old-growth' forests (i.e. forests associated with a high degree of stand maturity and the presence of late forest development phases) offer habitat structures required for many species of conservation concern, and thus often host a higher diversity of stenotopic forest species (Heilmann-Clausen & Christensen 2004; Fritz et al. 2008; Moning & Müller 2009; Brunet et al. 2010; Paillet et al. 2010; Müller et al. 2014; Kaufmann et al. 2018). There is consensus about the conservation value (i.e. in terms of biodiversity conservation) of forests associated with a long ecological continuity, but the role of forest history in driving forest ecosystem functioning remains unclear (but see Johnstone et al. 2016; Perring et al. 2016; Bürgi et al.2017). Thus, an important next step is to explore how legacy effects of past land use and management modulate key forest functions and how such legacy effects interact with (multiple) drivers of global environmental change (see Q23, Q34, Q39 in Ammer et al. 2018).

1.2 Main objectives and structure of the thesis

Global environmental change alters forest ecosystem functioning and service provisioning, but the mechanisms underlying these changes are poorly understood. The overall aim of the thesis is to improve mechanistic insights into how biodiversity and ecological continuity modulate key ecosystem functions, such as primary productivity and nutrient cycling, and how biodiversity-ecosystem functioning and ecological continuity-ecosystem functioning relationships are altered by drivers of global environmental change (Fig. 1). In this context, the thesis addresses further important gaps in knowledge by exploring how trees respond to simultaneous effects of different global change drivers. Additionally, the thesis explores how ecosystem-based management strategies can

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[1] Paragraph taken from Fichtner & Härdtle (2020) and authored by Andreas Fichtner.

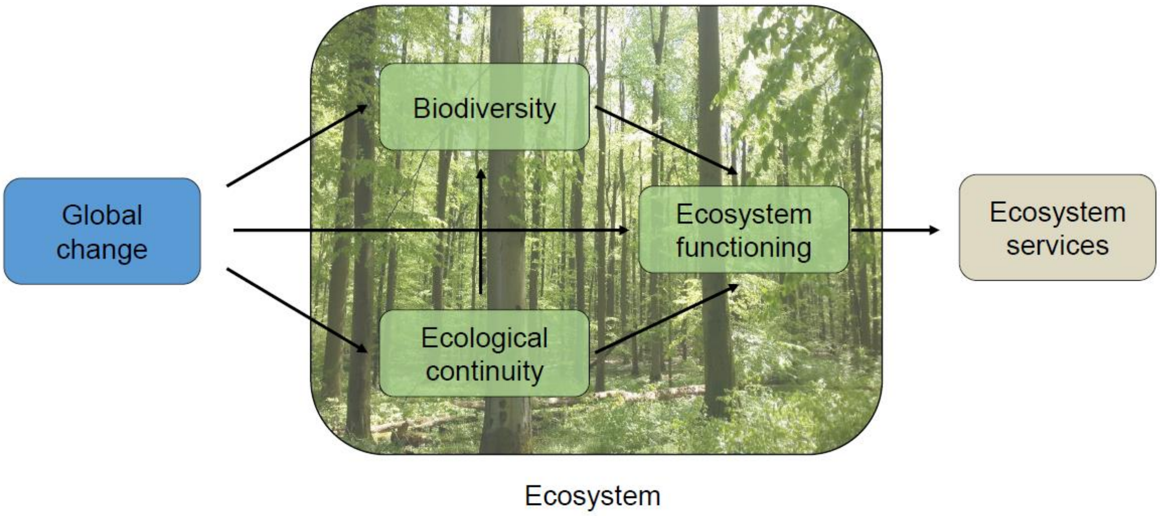

Figure 1 | Human dependence on nature. The stable provisioning of ecosystem services (the benefits that nature provides to people) is the vital basis for human well-being. Drivers of global environmental change, however, can have detrimental impacts on the functioning of ecosystems and related services either directly or indirectly via altering biodiversity and/or ecological continuity. Alternatively, biodiversity and ecological continuity jointly drive ecosystem functioning. Disruption of ecological continuity due to land-use change or land-use intensification can also translate into biodiversity loss, which in turn can negatively affect the functioning of ecosystems. Figure taken from Fichtner & Härdtle (2020) and designed/authored by Andreas Fichtner.

promote the supply of multiple forest ecosystem services and the conservation of forest biodiversity, in particular of those species that are associated with a special conservation interest.

The studies provided in this thesis are grouped into four parts: biodiversity and global change (**Part I**), forest continuity and global change (**Part II**), forest management and global change (**Part III**), and conservation biology (**Part IV**).

Part I (Biodiversity and global change) consists of six chapters that address BEF relationships and includes experimental studies from tropical and subtropical tree communities. BEF experiments offer a unique opportunity to unravel diversity effects from other confounding factors, and thus to identify mechanisms for the positive effects of tree diversity on forest productivity. Chapter 2–4 and 6–7 take the advantage of doing research in the world's largest biodiversity experiment with trees, the so-called 'BEF-China' experiment (Fig. 2a). The joint Chinese-German-Swiss research project was launched in May 2008 in subtropical China. Two experimental sites, each of which *c.* 25 ha in size, were planted with more than 400,000 trees and shrubs. Based on a species pool of 40 native broad-leaved tree species and two commercial coniferous species (*Pinus massoniana* and *Cunninghamia lanceolata* that were planted in monocultures only), a long diversity gradient was created by manipulating the number of tree species within a plot (monocultures and mixed-species communities of 2, 4, 8, 16 and 24 tree species), where species and tree species diversity levels were randomly assigned to planting positions and plots. For more detailed information see Bruelheide et al. (2014). Moreover, one study included in this thesis is based on data from the oldest BEF experiment in the tropics, the so-called 'Sardinilla' experiment that was established in 2001 in central Panama (Fig. 2b; Chapter 5). Here, more than 5000 tree seedlings of six native tree species were planted in a pasture of *c.* 5 ha (monocultures and mixed-species communities of three and six tree species). For more detailed information see Potvin and Gotelli (2008).

Local species interactions are considered a main cause for the positive effects of biodiversity on forest productivity, because physical complementarity and most facilitative effects come about only by immediate neighbours (Stoll & Weiner 2002; Uriarte et al. 2004; Wright et al. 2017). Although this hypothesis has received increasing attention in BEF forest research, the relative importance of such tree-tree interactions in driving biodiversity-productivity relationships at the community scale remains unclear. For this reason, it is important to understand how diversity-mediated neighbourhood interactions translate into the previously reported positive relationship between tree diversity and forest productivity. In this context, **Chapter 2** quantifies the contribution of local species interactions to biodiversity effects at larger scales and investigates how the relative importance of neighbourhood interactions varies across biodiversity levels in highly diverse tree communities.

Functional traits have been increasingly used in BEF research, as they are closely related to the ecological strategy of component plant species (Wright et al. 2004; Reich 2014; Díaz et al. 2016). Hence, the way how neighbours interact should be strongly related to their functional traits (Kunstler et al. 2016). Combining a local neighbourhood scale and functional trait approach, **Chapter 3** analyses shifts the mode and intensity of tree-tree interactions along an experimentally manipulated gradient of local neighbourhood tree species richness to unravel central mechanisms (competitive reduction and facilitation) underlying biodiversity effects on forest productivity, and thus to provide a mechanistic explanation why tree species mixtures can yield higher productivity compared to monocultures. **Chapter 4** follows up on the findings of the preceding chapter and investigates how net biodiversity effects at local neighbourhood scale vary over time. This chapter also aims at providing a mechanistic explanation for the previously reported importance of crown complementarity in biodiversity-productivity relationships using terrestrial laser scanning (TLS) technology.

Figure 2 | Tree diversity experiments. Experimental study plots of the **(a)** BEF-China (Photo: Werner Härdtle) and **(b)** 'Sardinilla' experiment (Photo: Matthias Kunz).

Based on the findings of the previous chapters, a critical next step is to understand how climate change affects BEF relationships in forests. Although tree diversity is supposed to play an important role in mitigating adverse climate change impacts on forest ecosystem functioning, such as drought-induced decline in forest productivity (Hisano et al. 2018, Ammer 2019; González de Andrés 2019; Grossiord 2019), results remain controversial and experimental evidence is rare. For example, there is no consensus on the degree to which tree diversity mitigates climate change impacts on forest productivity, particularly in highly diverse forests. This might be partly attributed to the fact that only very few studies investigated the role of tree diversity at the relevant scale at which species interact, that is, the local neighbourhood. In this context, **Chapter 5** analyses trait-mediated changes in biodiversity-productivity relationships at the local neighbourhood scale along an experimentally manipulated gradient of neighbourhood diversity in response to interannual fluctuations in climate over a six-year period. This approach allows us to explore the response of forests to drought and to contribute to a deeper understanding on the functional consequences of tree diversity loss for forest productivity in the context of climate change. **Chapter 6** shifts the focus from the local neighbourhood scale to the community scale and aims at understanding how tree diversity contribute to buffer interannual fluctuations in forest productivity in the context of climate change. The 'insurance hypothesis' predicts that biodiversity stabilises community productivity to fluctuating environmental conditions (Yachi & Loreau 1999) via three principle processes: (i) Species asynchrony (the negative response of some species can be compensated for by the positive response of others), (ii) overyielding (higher productivity in mixtures relative to monocultures) and (iii) favourable species interactions that increase the temporal stability of productivity of individual tree species (Jucker et al. 2014). However, evidence for forests remained scarce (but see results from natural forests: Jucker et al. 2014; Morin et al. 2014; del Rio et al. 2017). To test the insurance hypothesis in a controlled tree diversity experiment, this chapter is based on data from tropical tree communities over a ten-year period ranging from extremely dry to extremely wet conditions (see Hutchison et al. 2018).

More recently, BEF research has stressed the importance of multitrophic approaches (e.g. Eisenhauer et al. 2019). In the context of ongoing global insect decline (Dirzo et al. 2014; Hallmann et al. 2017; Leather 2018), **Chapter 7** explores how plant communities' taxonomic and functional diversity and their related structural diversity affect the abundance and richness of insects across trophic levels and ecosystems by using data from two of the world's largest biodiversity-ecosystem functioning experiments in temperate grasslands (Jena Experiment) and subtropical forests (BEF China). This is particularly relevant for developing scientific-based management and restoration strategies in agricultural and forest ecosystems.

Part II (Forest continuity and global change) consists of six chapters that address ecological continuity-ecosystem functioning relationships with a focus on forest continuity. This part includes observational studies from temperate Sessile oak (*Quercus petraea*; hereafter: oak) and European beech (*Fagus sylvatica*; hereafter: beech) forests as well as experimental studies on temperate tree species that differ in key functional traits and are assumed to be ecologically and/or economically important from an European perspective (Leuschner & Ellenberg 2017; Leuschner & Meier 2018).

In Central Europe, forest area has substantially increased during the last 200 years due to afforestation measures on formerly cultivated land (Leuschner & Ellenberg 2017). As a result, the vast majority of Central European forests are characterised by legacies of past land use. Such legacy effects have been shown to have lasting impacts on contemporary species diversity and community composition (Flinn & Vellend 2005; Hermy & Verheyen 2007; Fraterrigo et al. 2006; De la Peña et al. 2016) as well as on forest soil chemical properties (Koerner et al. 1997; Compton & Boone 2000; von Oheimb et al. 2008; Leuschner et al. 2014; Blondeel et al. 2019). Overall, land-use changes result in a disruption of ecological continuity, which in turn might alter biogeochemical cycles and important ecosystem services (e.g. timber production and carbon sequestration) under ongoing changes in environmental conditions. To address this issue, **Chapter 8** explores the impact of land-use history on soil microbial community composition and nutrient cycling (enzymatic activity levels) in oak forests after more than 110 years of forest regrowth on former arable land and heathland in relation to ancient forests (>235 years of forest continuity). This approach differs from the majority of previous work by using a past land-use intensity gradient that account for different historical land-use systems (arable farming, heathland farming and forest use) and long-term responses (more than a century; see Bergès & Dupouey 2020). Moreover, it remains unclear whether forest continuity buffers forest ecosystems against adverse impacts of climate change. Based on these findings, the following chapters hypothesise that forest continuity attenuates the effects of interannual fluctuations in climate on tree growth (**Chapter 9**) and increases the resistance of forest ecosystems to drought (**Chapter 10**) indirectly via modulating the size and morphology of the fine root system, which in turn is crucial for a trees' nutrient and water uptake.

Chapter 11–13 focus on the response of forests to multiple changes in environmental conditions such as simultaneous effects of drought and elevated atmospheric nitrogen (N) deposition. There is ample evidence from studies that have quantified the response of forests to single drivers of global environmental change, but how multiple drivers interactively affect ecosystem functions remains poorly understood. For example, the impact of co-occurring drivers of environmental change on forest productivity may differ depending on tree species identity and diversity as well as on land-use legacies. In a first step, **Chapter 11 and 12** investigate the response of three functional different tree species to combined effects of N fertilisation and summer drought by focusing on tree regeneration: saplings (*F. sylvatica*: 1-2 years; **Chapter 11**) and young trees (*F. sylvatica*, *Q. petraea*, *Pseudotsuga menziesii*; 6.5 years; **Chapter 12**). Additionally, **Chapter 12** explores how biodiversity-productivity relationships at the community scale are altered by co-occurring global change drivers. **Chapter 13** extends the analyses of the preceding chapters by adding a historical dimension to simultaneous effects of different global change drivers. This chapter analyses how combined effects of spring and summer water deficits and variable amounts of airborne N deposition affect radial growth of adult beech trees growing on forest sites with a different forest history.

Part III (Forest management and global change) consists of four chapters and addresses further aspects of ecological continuity, which critically depend on management intensity: stand maturity and continuity in natural stand dynamics.

Next to deforestation, the intensification of forest management is a major threat for biome-specific biodiversity (Lelli et al. 2019; Fichtner & Härdtle 2020) and the potential of forests to store carbon in the long term (Erb et al. 2018). In this context, primeval and long-term unmanaged forests offer a great opportunity for improving our understanding of management-induced changes in forest structure and functions and how these changes affect forests' responses to global change. There is consensus in ecology and nature conservation that unmanaged forests play a vital role for biodiversity, but their importance for carbon sequestration and long-term carbon storage is still under debate. In this context, **Chapter 14** tests the hypothesis that silvicultural interventions increase the susceptibility of trees to drought by using individual tree-ring chronologies from managed, short-term and long-term unmanaged beech forests. **Chapter 15** is based on the same management intensity gradient and investigates the effects of forest management cessation on tree morphology and radial growth of beech.

Crown size is considered an important morphological trait that affect trunk wood volume, as crown size is closely related to leaf area, and thus photosynthetic carbon gain (Niinemets 2010). In this context, thinning is assumed to promote the growth and quality of residual trees by reducing neighbours, and thereby allowing for crown expansion of focal trees (Pretzsch 2009). Moreover, past research has shown that crown traits depend on tree diversity (monocultures vs. mixed-species stands; Bayer et al. 2013; Pretzsch 2014). Yet, it remains largely unclear how (long-term) management cessation and tree species richness interactively affect trunk and crown morphological traits. **Chapter 16** extends the analyses of the previous chapter by investigating how the intensity and importance of competition effects on tree growth varies with tree size across a gradient of abiotic stress. This study is based on inventory data from managed and unmanaged beech forests and aims at testing, whether the efficiency of thinning interventions (i.e. the trade-offs between individual tree growth acceleration and ecological integrity loss, individual tree growth acceleration and stand productivity loss, individual tree growth acceleration and cutting damages) depend on tree maturity and abiotic site conditions.

Large-diameter trees are important determinants of forests' structural heterogeneity (Lutz et al. 2013), carbon sequestration (Stephenson et al. 2014) and storage (Lutz et al. 2018). Thus, old forests continue to sequester carbon for many centuries (Luyssaert et al. 2008) and have been shown to be more stable in carbon sequestration (Mustavi et al. 2017). However, the functional role of old and large-diameter trees in shaping tree-tree interactions is not well understood. **Chapter 17** takes advantage of a long-term unmanaged beech forests to explore how the spatial aggregation of large-diameter trees regulates neighbourhood interactions (in terms of their mode and intensity) in tree communities associated with a long continuity of anthropogenic undisturbed population dynamics.

Part IV (Conservation biology) consists of two chapters that address ecological continuity-biodiversity relationships. Using observational studies from temperate forest communities of the alliances *Fagion*, *Carpinion* and *Alno-Ulmion* (sensu Leuschner & Ellenberg 2017; Fig. 3), this part focuses on the link between forest continuity, biodiversity and conservation management, taking a globally rare spring geophyte – *Gagea spathacea* (Liliaceae) – as an example. *G. spathacea* mainly occurs in ancient deciduous forests of northern Central Europe (Wulf 1997; Schmidt et al. 2014) and is considered a 'priority species' according to the list of Central European vascular plant species requiring priority conservation measures (Schnittler & Günther 1999).

The 'Convention on Biological Diversity' (CBD) is an important political commitment to counteract global biodiversity loss. Limitations of

Figure 3 | Taking responsibility. *Gagea spathacea*, a species of special conservation interest, is a spring geophyte with a short annual developmental cycle of c. three months. The species relies on vegetative propagation by means of daughter bulbs, thus it is associated with an extremely low proportion of individuals flowering (inset photo). The photo shows a study plot in a highly diverse alder-ash forest. Photos: Andreas Fichtner.

insufficient ecological knowledge about target species, however, often hamper the implementation of efficient conservation strategies (Balmford et al. 2005; Chandra & Idrisova 2011; Joppa et al. 2013). This also applies to *G. spathacea* for which Germany has a particular responsibility for the long-term protection of its populations (Schnittler & Günther 1999). However, to date, there is no scientific-based information on the habitat requirements of this species of special conservation interest. To address these limitations, **Chapter 18** aims at evaluating the relative importance of abiotic habitat characteristics to identify main threats for the conservation of the large, remaining global populations. Given that *G. spathacea* is a highly stenoecious woodland species, its occurrence is often associated with a high diversity of forest species (Härdtle et al. 2003; Nordén et al. 2014; Stefańska-Krzaczek et al. 2016).Thus, strategies for safeguarding *G. spathacea* would co-benefit the conservation of forest biodiversity, in particular the conservation of rare and threatened forest species. **Chapter 19** aims at providing further comprehensive insight into the autecology of *G. spathacea* by conducting a ^{15}N tracer experiment. This chapter tests the hypothesis that *G. spathacea* exhibits a highly efficient N (re)cycling strategy that is characterised by an efficient N resorption from senescing leaves and reallocation to bulbs at the end of the growing season.

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Part I

Biodiversity and global change

Chapter 2

Neighbourhood interactions drive overyielding in mixed-species tree communities

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Neighbourhood interactions drive overyielding in mixed-species tree communities

Andreas Fichtner [1], Werner Härdtle [1], Helge Bruelheide [2,3], Matthias Kunz [4], Ying Li [5] & Goddert von Oheimb [3,4]

Theory suggests that plant interactions at the neighbourhood scale play a fundamental role in regulating biodiversity–productivity relationships (BPRs) in tree communities. However, empirical evidence of this prediction is rare, as little is known about how neighbourhood interactions scale up to influence community BPRs. Here, using a biodiversity–ecosystem functioning experiment, we provide insights into processes underlying BPRs by demonstrating that diversity-mediated interactions among local neighbours are a strong regulator of productivity in species mixtures. Our results show that local neighbourhood interactions explain over half of the variation in observed community productivity along a diversity gradient. Overall, individual tree growth increased with neighbourhood species richness, leading to a positive BPR at the community scale. The importance of local-scale neighbourhood effects for regulating community productivity, however, distinctly increased with increasing community species richness. Preserving tree species diversity at the local neighbourhood scale, thus seems to be a promising way for promoting forest productivity.

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[1] Institute of Ecology, Leuphana University of Lüneburg, Universitätsallee 1, 21335 Lüneburg, Germany. [2] Institute of Biology/Geobotany and Botanical Garden, Martin Luther University Halle-Wittenberg, Am Kirchtor 1, 06108 Halle (Saale), Germany. [3] German Centre of Integrative Biodiversity Research (iDiv), Halle-Jena-Leipzig, Deutscher Platz 5E, 04103 Leipzig, Germany. [4] Institute of General Ecology and Environmental Protection, Technische Universität Dresden, Pienner Straße 7, 01737 Tharandt, Germany. [5] School of Soil and Water Conservation, Beijing Forestry University, 35 Qinghua E Rd, Haidian District, 100083 Beijing, China. Correspondence and requests for materials should be addressed to A.F. (email: fichtner@leuphana.de) or to G.v.O. (email: Goddert_v_Oheimb@tu-dresden.de)

Tree species richness has been shown to foster ecosystem functions such as forest productivity[1–3], and biodiversity loss is expected to have negative implications for forest productivity worldwide[4]. Multiple studies in forests analysed biodiversity–productivity relationships (BPRs) at the scale of tree communities and found that tree species mixtures can yield higher productivity compared to monocultures (overyielding). Although positive BPRs were demonstrated by recent tree biodiversity experiments at both the community[5–8] and local neighbourhood scale[7,9,10], the mechanisms underlying BPRs are hardly understood. Specifically, it remained unclear, how tree interactions at the local neighbourhood level—the crucial scale of species interactions[11]—drive community BPRs. Exploring the way how individuals respond to changing neighbourhood conditions (e.g., neighbour diversity and abundance)[10,12,13] and how these neighbourhood interactions scale up to influence the community response, is therefore fundamental to understand the mechanisms underlying BPRs in tree communities[14].

The effect of species mixing on productivity (i.e., the net biodiversity effect) can result from multiple mechanisms, such as (1) selection effects, (2) resource partitioning, leading to competitive reduction, (3) facilitation and (4) natural enemy (e.g., pathogens or herbivores) partitioning, resulting in reduced Janzen–Connell effects (dilution effects)[15,16]. Statistically, the net biodiversity effect at the community scale can be partitioned in complementarity and selection effects[17]. While selection effects account for increased likelihood of including dominant and well-performing species in diverse communities, all other mechanisms of net biodiversity effects are summarised by the term 'complementarity'. Findings from tree biodiversity experiments provide support that positive BPRs result mostly from selection effects rather than complementarity effects[5]. However, there is also empirical evidence that tree mixtures enable higher canopy packing by means of niche differentiation in crown heights among species and intraspecific crown plasticity[18–21], which, in turn, contributes to increasing productivity of the community. Similarly, experimental and observational studies have shown that neighbourhood diversity increases individual tree growth through competitive reduction or facilitation[9,10,22–24]. Moreover, tree growth was found to be negatively related to damage of leaf fungal pathogens, which in turn decreased with tree species richness, thus showing a negative density dependence[25]. Such processes leading to overyielding in species mixtures can act at both the community[26] and neighbourhood[27] scale.

Mixed-species plant communities are the sum of co-occurring individuals of different species. As such, they can be considered as a network of locally interacting individuals[28]. Consequently, the response of tree communities to species mixing should be—at least to a certain extent—the result of aggregated small-scale variations in neighbourhood interactions[7,9,21,29]. Such neighbourhood interactions can either enhance or reduce individual tree growth, and are largely shaped by simultaneously operating positive (e.g., niche differentiation or facilitation) and negative (e.g., competition for resources) processes among neighbouring trees[30,31]. For example, simulation models revealed that neighbourhood interactions can induce positive BPRs in tree communities[24], but the extent to which locally interacting neighbours contribute to BPRs at the community scale is still poorly understood[32]. Specifically, empirical tests of the relationship between biodiversity effects at different spatial scales remain rare (but see ref. [33]), and the importance of neighbourhood interactions for enhancing productivity in mixed-species forests has not been quantified so far.

Here, we used tree communities of an early successional subtropical forest planted at two spatially explicit experimental sites—site A and B of a large-scale biodiversity–ecosystem functioning experiment in subtropical China (BEF-China)[34]—to quantify the contribution of neighbourhood interactions to biodiversity effects (using species richness as a measure for biodiversity) at the community scale (i.e., at the plot level). Our tree communities comprise 40 native broad-leaved species and cover a long diversity gradient, ranging from monocultures to 24-species mixtures. We hypothesise that positive BPRs in tree communities largely depend on how trees interact at the neighbourhood scale, and that the importance of neighbourhood interactions for BRPs increases as community species richness increases. To test these hypotheses, we applied a four-step approach: first, we used a neighbourhood modelling framework in which the annual wood volume growth (our measure for productivity) of a focal tree was expressed as a function of its initial size (wood volume) and the effects of neighbourhood competition (NCI), conspecific neighbour density (CND) and neighbourhood species richness (NSR). This analysis was based on 3962 focal trees growing at site A and allowed us to quantify individual-based biodiversity effects at the neighbourhood scale. In this study, we define the term 'individual-based biodiversity effect' as the net effect of all intra- and interspecific interactions within the neighbourhood of a focal tree (sensu ref. [17]), while neighbourhoods are defined as the total number of closest trees surrounding a focal tree with a maximum of eight neighbours (i.e., the local neighbourhood). Second, we predicted the annual wood volume growth of 3018 focal trees growing at site B, using parameter estimates obtained from the neighbourhood model of site A. Third, we calculated standardised plot-level aboveground wood productivity (AWP; hereafter community productivity) by summing size-standardised growth rates (separately for observed or predicted values) of all focal trees within a plot for site B. This allowed us to obtain and compare measures for observed ($\mathrm{AWP}_{\mathrm{obs}}$) and predicted community productivity ($\mathrm{AWP}_{\mathrm{nbh}}$), based on neighbourhood interactions. Finally, we applied a community-modelling framework in which $\mathrm{AWP}_{\mathrm{obs}}$ was expressed as a function of community species richness (CSR), $\mathrm{AWP}_{\mathrm{nbh}}$ and topography to account for variation in biotic and abiotic growing conditions. We then quantified the amount of variation in observed community productivity explained by neighbourhood interactions ($\mathrm{AWP}_{\mathrm{nbh}}$) along the diversity gradient, which allowed us to explore the link between biodiversity effects at the neighbourhood and community scale. Importantly, our function-derived growth rates were based on different data sets (site A data: neighbourhood model, site B data: community model) that represent different species pools (Supplementary Table 1), and thus ensure independence when examining the relationship between biodiversity effects at different spatial scales. Our study demonstrates that positive effects of biodiversity on community productivity are largely driven by interactions among local neighbours, highlighting the need to promote tree species diversity at the local neighbourhood scale for enhancing forest productivity.

Results

Biodiversity effects at the local neighbourhood scale. Overall, we found positive effects of neighbourhood species richness (NSR) on individual tree growth (G), but the magnitude of biodiversity effects was determined by the focal trees' size (i.e., initial wood volume) and neighbourhood competition (NCI; Fig. 1 and Supplementary Table 2). Conspecific neighbour density was not significantly related to G (χ^2: 0.37, $P = 0.540$). Importantly, results from neighbourhood models fitted for focal trees growing at sites A and B, and based on different species sets, were qualitatively the same (Supplementary Table 3), suggesting that our estimates of $\mathrm{AWP}_{\mathrm{nbh}}$ had an adequate power to explore the link between $\mathrm{AWP}_{\mathrm{obs}}$ and $\mathrm{AWP}_{\mathrm{nbh}}$.

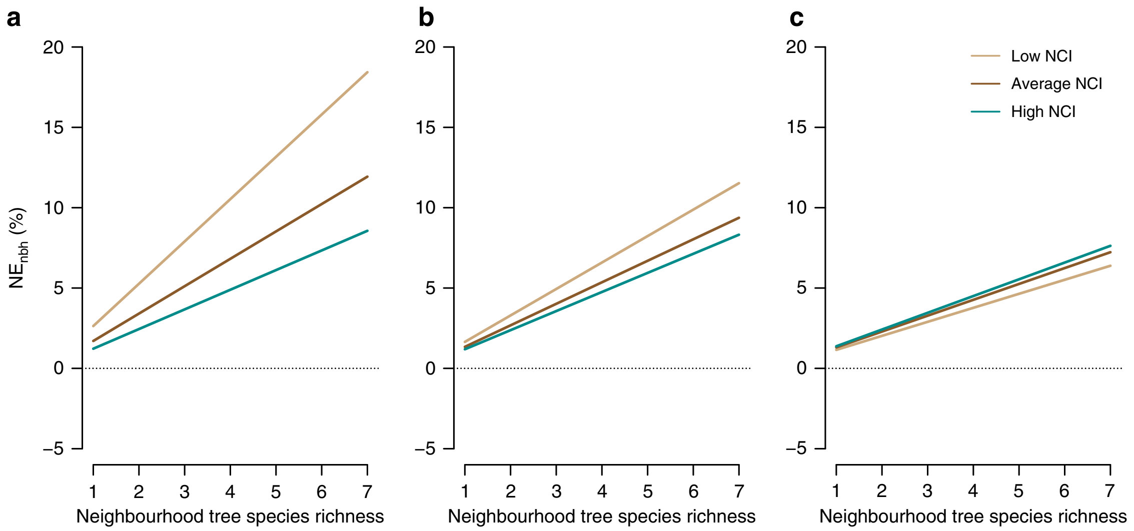

Fig. 1 Biodiversity effects on individual tree growth. Size-dependent variation in net biodiversity effects at the neighbourhood scale (NE_{nbh}) with neighbourhood competition and neighbourhood tree species richness (NSR). NE_{nbh} indicates the predicted change (%) in individual tree growth (annual growth rate of wood volume of a focal tree growing with heterospecific compared to growing with conspecific neighbours) in response to neighbourhood tree species richness at low, average and high value of neighbourhood competition index (NCI) for **a** small-sized, **b** medium-sized and **c** large-sized trees. Lines represent mixed-effects model fits for each size and competition level, respectively. Tree size, NCI and NSR explained 48% of the variation in individual tree growth

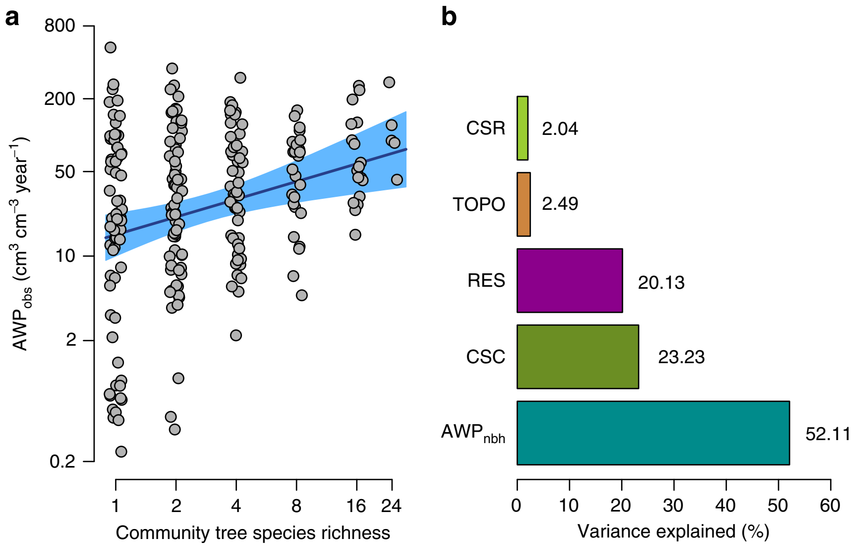

Fig. 2 Biodiversity effects on community productivity. **a** Biodiversity–productivity relationship at the community scale. The solid blue line corresponds to the fitted relationship of a mixed-effects model, with the shaded area representing the 95% confidence interval of the prediction. Points represent observed values of standardised aboveground wood productivity (AWP_{obs}) for each individual plot ($n = 234$; site B). Plot-specific values are jittered to facilitate visibility, and axes are logarithmic. **b** Biotic and abiotic drivers of the community biodiversity–productivity relationship. Variance partitioning for four predictors: community (i.e., at the plot level) tree species richness (CSR) and composition (CSC, specified as random effect), community productivity based on neighbourhood inteactions (AWP_{nbh}) and heterogeneity in topography (i.e., variation in elevation, TOPO). Bars and numbers next to the bars correspond to the fraction of variance explained by each predictor of a linear mixed-effects model, and the variance not explained by the model (the residual, RES)

Biodiversity effects at the community scale. As expected, NSR was positively and strongly related to community species richness (CSR; $r^2 = 0.66$, $P < 0.001$; Supplementary Fig. 1), whereby positive neighbourhood-scale biodiversity effects translated into positive effects at the community scale. Consequently, observed community productivity increased with CSR (AWP_{obs}; $t = 3.25$, $P < 0.01$). On average, AWP_{obs} of highly species-rich communities (24-species mixtures) was more than twice as high (+122%) as those of monocultures (Fig. 2a). AWP_{obs} of monocultures was highly variable and was on average higher for species with low wood density ($t = −3.08$, $P < 0.01$) and leaf toughness ($t = −5.58$, $P < 0.001$; Supplementary Fig. 2). Particularly, slow-growing species (i.e., species in the 25% quantile of species-specific AWP_{obs} in monoculture) benefited the most from growing in species-rich communities (16-/24-species mixtures; Supplementary Figure 3).

Importance of neighbourhood interactions. The best-fitting community productivity model included positive effects of

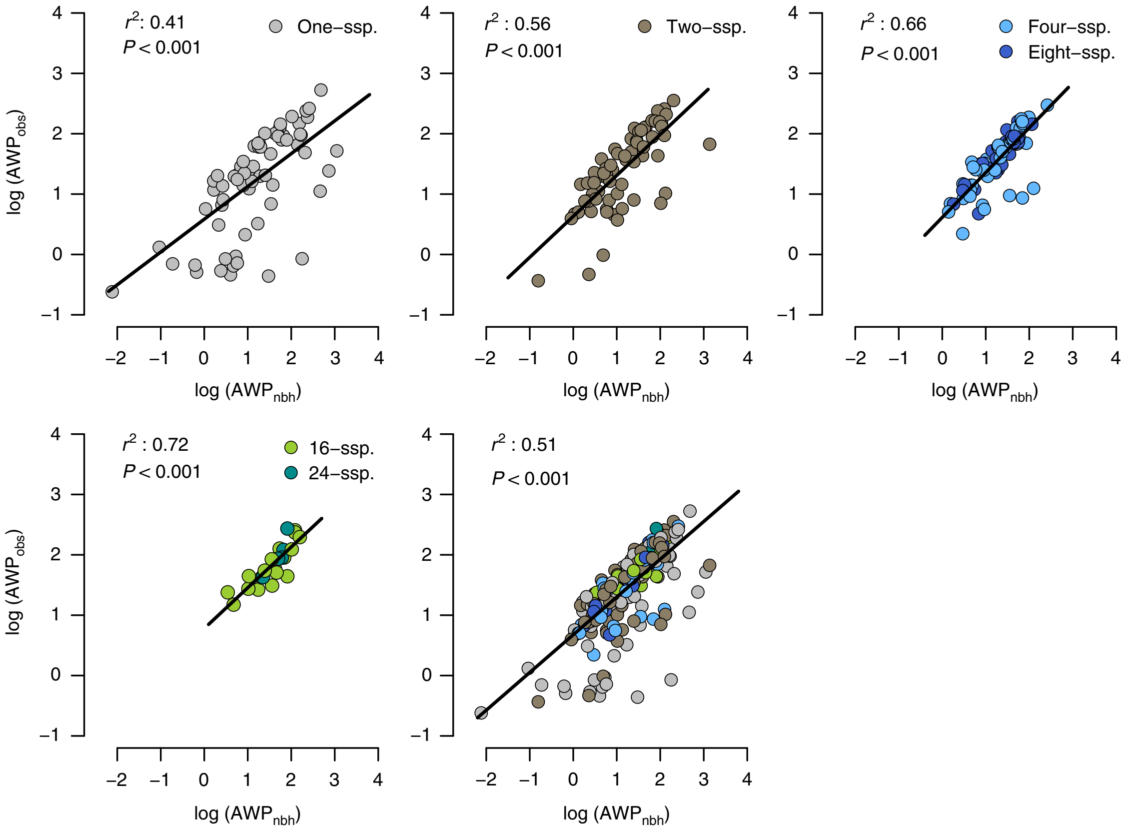

Fig. 3 Variation in the effects of neighbourhood interactions on community productivity between species mixtures. Standardised aboveground wood productivity (AWP, $cm^3\ cm^{-3}\ year^{-1}$) is based on observed (AWP_{obs}) and predicted (AWP_{nbh}) annual wood volume growth of all focal trees within a plot. Note that AWP_{nbh} represents the net effect of aggregated neighbourhood interactions on community productivity as predicted by a neighbourhood model. Lines represent mixed-effects model fits for monocultures, species mixtures and across all monocultures and species mixtures: low (two-species mixture), medium (four- and eight-species mixtures) and high (16- and 24-species mixtures) level of community species richness (CSR). Marginal r^2 values (fixed effects only) are shown for each CSR level

neighbourhood interactions (AWP_{nbh}) and CSR, and a negative effect of elevation (Supplementary Fig. 4). Both fixed and random effects accounted for a large proportion of the variance in AWP_{obs} (fixed effects: 57% fixed and random effects: 80%; Supplementary Table 4). We found that the vast majority of the variance in AWP_{obs} was explained by AWP_{nbh} (52.1%), followed by community species composition (CSC; 23.2%), which was specified as a random effect in the model (see 'Methods'). In contrast, the explanatory power of log-CSR (2.0%) and heterogeneity in topography (2.5%) was extremely low (Fig. 2b). Note that the amount of variance explained by our predictors reflects partial effects, meaning the fraction attributable to each variable in the model after accounting for the effects of the other variables in the model. Interestingly, the importance of neighbourhood interactions as the predictor of community productivity was distinctly higher in species-rich (i.e., four/eight and 16-/24-species mixtures) than in species-poor communities (i.e., monocultures and two-species mixtures). This was reflected by the coefficients of determination (r^2), which increased consistently with CSR and ranged between 0.41 and 0.72 (values for monocultures and 16-/24-species mixtures, respectively; Fig. 3).

Discussion

This study provides insights into processes that generate BPRs in tree communities. First, our findings provide experimental evidence that neighbourhood interactions play a fundamental role in regulating BPRs in young subtropical forests, and confirm predictions from simulation models for tropical forests[24]. Second, we found that the importance of neighbourhood interactions in regulating community productivity increased with increasing tree species richness at the community scale. Overall, these results suggest that the positive effects of biodiversity on forest productivity are primarily associated with local neighbourhood species interactions rather than processes operating at the community scale.

We found that the positive effects of species richness on community productivity were primarily driven by species interactions at the neighbourhood scale. Neighbourhood interactions might not only be related to the diversity of neighbouring trees, but also to the abundance of local competitors and focal tree characteristics (i.e., tree size and functional traits), which in turn determine its sensitivity to competition by local neighbours[35,36]. Indeed, our results demonstrate that the magnitude of positive biodiversity effects at the neighbourhood scale largely varied with initial focal tree size and NCI, where the benefits of growing in heterospecific neighbourhoods were most evident for smaller trees experiencing low competitive neighbour effects (i.e., low level of NCI; Fig. 1b). This response is most likely the result of competitive reduction due to niche differentiation among neighbours[24,35], which is particularly relevant for small individuals with a relatively low competitive tolerance[37]. Size-mediated competition tolerance is particularly evident for aboveground tree interactions, meaning that larger trees capture disproportionally greater amounts of light relative to their size when interacting with smaller ones (asymmetric competition)[38]. Given that NCI captures the net competitive effects of neighbours larger than the focal tree in our study (asymmetric neighbourhood competition, see Methods), the main effect of an increasing NCI is most likely an increasing degree of competition for light[37,39]. However, it should be noted that larger neighbours may also have negative effects on belowground growth of a focal tree, brought about by, e.g., water and nutrient pre-emption, due to the neighbours' disproportionate advantage to access available soil resources[40]. The fact that for smaller trees, positive neighbourhood-scale biodiversity effects declined as NCI increased are therefore an indication that the relative competition intensity via (light) resource depletion becomes stronger and counteracts the positive effects of competitive reduction via, e.g., niche partitioning of canopy space[21,41], and thus, shapes the net effect of co-occurring interactions. This interpretation is supported by findings that identified competition for light as a key determinant in shaping the outcome of BPRs in forests[42,43], and that revealed stronger complementarity effects for smaller than for larger trees[43,44]. Next to competitive reduction, species may benefit from heterospecific facilitation[16,45]. For example, facilitative neighbour effects, via an improvement of microclimate conditions, were identified as a key mechanism for positive diversity effects of conservative species (e.g., species with high leaf toughness and low specific leaf area)[10]. This could explain the observed positive effect of NCI on the magnitude of neighbourhood-scale biodiversity effects as trees were larger in size (Fig. 1c), although our results reflect an across-species response. These results illustrate that both competitive reduction and facilitation—brought about by heterospecific neighbours—are fundamental mechanisms that regulate BPRs at the community scale.

The second largest proportion of variance in community productivity was explained by community species composition. Although overyielding in species mixtures was mainly driven by neighbourhood interactions, selection effects seemed to be a further important determinant of BPRs in young tree communities[5]. In contrast, the relatively low explanatory power of CSR on community BPR, after accounting for the effects of neighbourhood interactions, suggests that processes driving community BPRs, such as positive aboveground–belowground interactions[46,47] or negative density dependence of pathogens and herbivores[48,49] are particularly important at the local neighbourhood scale. Similarly, heterogeneity in topography (i.e., variation in elevation) was a weak determinant of the observed community overyielding. This is consistent with findings from site A of the experiment, where environmental variation in topography and soil chemical properties jointly only explained at maximum 4% of tree growth rates (i.e., radial crown increment) [50]. Finally, part of the unexplained variance in community BPR might be associated with litter-mediated tree interactions[51,52] or variation in leaf bacterial diversity[53], all mechanisms that have been proposed to drive overyielding, but were not considered in this study. Moreover, small-scale spatial heterogeneity in nutrient and water supply potentially affects BPRs[54]. However, given the large number of plots with varying species and species combinations in our experiment, it is less likely that the spatial configuration of plots strongly influences the outcome of BPRs. Additionally, species and species richness levels were randomly assigned to planting positions and plots[34]; thus, the likelihood that biodiversity effects were confounded with differences in belowground resource availability is relatively small.

A further important finding was that the explanatory power of neighbourhood interactions for community productivity increased with community species richness. Unsurprisingly, neighbourhood species richness tended to be higher in species-rich communities (Supplementary Fig. 1). In this case, however, it is important to note that neighbourhood species richness effects were both size- and competition-dependent in our study (three-way interaction: $t = 2.68$, $P = 0.007$; Supplementary Table 2). Thus, the role of neighbourhood interactions in regulating overyielding at the community scale cannot be entirely attributed to the number of heterospecific neighbours. Instead, diverse neighbourhoods can modulate the mode (competition or facilitation) and intensity of local tree interactions, and thereby the strength of positive (facilitative) and negative (competitive) neighbour effects[10]. In this context, our results suggest that neighbourhood interactions become increasingly important in explaining community BPRs as CSR increases, meaning that processes leading to competitive reduction and/or facilitation at the local neighbourhood scale are fundamental in regulating the productivity of (highly) diverse tree communities.

Our results have important implications for understanding and predicting forest productivity in response to global biodiversity loss. A meta-analysis has shown positive BPRs in forests at the global scale[4]. Here, we show that tree interactions at the neighbourhood scale largely determine the growth response of tree communities to species mixing. This implies that diversity-mediated interactions among local neighbours are highly relevant for enhancing productivity in mixed-species forests— particularly in highly diverse forest communities such as subtropical or tropical ecosystems. This also highlights the importance of mixing tree species at the smallest spatial scale (i.e., the local neighbourhood level) instead of mixing monospecific patches or forest stands at the stand or landscape scale, respectively. Overall, this underlines the functional importance of local-scale species interactions in plant communities.

Methods

Study site and experimental design. In this study, we used data from two spatially explicit experimental sites (site A and site B, each ~25 ha in size and ~5 km apart from each other) established in southeast subtropical China (29.08°–29.11° N, 117.90°–117.93° E) as part of the BEF-China tree diversity experiment[34]. The study sites are located on a sloped terrain (average slope 27.5° for site A and 31° for site B) between 100 and 300 m a.s.l.; the mean annual temperature is 16.7 °C and mean precipitation is 1821 mm year^{-1}. The predominant soil types are Cambisols, Regosols and Colluvissols[55], and the natural vegetation in the study area is characterised by subtropical mixed broad-leaved forests with a high abundance of evergreen species[56].

The experiment covers a long diversity gradient ranging from monocultures to 24-species mixtures, which were planted based on a total species pool of 40 native broad-leaved tree species (Supplementary Table 1). To ensure that all species were equally represented along the species richness gradient, species compositions of the mixtures were selected using one random (based on a 'broken-stick' design) and two non-random (based on either rarity or SLA of the species) extinction scenarios (see ref. [34]). In total, we used 474 (site A: $n = 240$, site B: $n = 234$) study plots (25.8 × 25.8 m), which were established on sites of a former *Pinus massoniana* Lambert and *Cunninghamia lanceolata* (Lamb.) Hook commercial plantation that was harvested at a rotation age of 20 years. Plots were planted in March 2009 (site A) and 2010 (site B) with 400 trees (20 × 20 individuals) using a planting scheme with equal projected distances of 1.29 m. At the time of planting, all saplings had the same age between 1 and 2 years[34]. Replanting of saplings that died during the first growing season was conducted in November 2009 (deciduous species) and March 2010 (evergreen species) at site A and 1 year later at site B. Weeding was conducted twice (2009–2011) and later once a year (since 2012) during the growing season (May–October), where all herbaceous and non-planted woody species, as well as resprouts of the previously planted *P. massoniana* and *C. lanceolata* were carefully removed[34]. Study plot species richness ranged from monocultures ($n =$ 150) to mixtures of 2 ($n = 134$), 4 ($n = 91$), 8 ($n = 52$), 16 ($n = 37$) and 24 ($n = 10$) species. Species and species richness levels were randomly assigned to planting positions and plots, respectively[34].

Tree data. Tree measurements started in autumn 2010 (site A) and 2011 (site B) to avoid confounding effects between experimental treatments and planting. For all trees within a plot, species identity, stem diameter (measured 5 cm above the ground) and tree height (measured from the stem base to the apical meristem) were recorded in 2010 (site A) or 2011 (site B) and each subsequent year (September–October; Supplementary Table 5). To account for edge effects, growth analyses were focused on 6980 trees in the centre of the 474 study plots (hereafter: focal trees; site A: $n = 3962$, site B: $n = 3018$) that survived during the 5-year (2011–2016) study period (i.e., tree measurements were available in 2011 and

2016). The number of recorded focal trees depended on species mixture and varied between 16 (monocultures and two-species mixtures) and 100 individuals (for 4-, 8-, 16- 24-species mixtures; Supplementary Fig. 5). In 2016, a subset of 23% (site B) to 26% (site A) of the study plots were treated according to the procedure described above, while in all other plots and species mixtures, respectively, 16 central trees were used as focal trees. Trees of the outermost row of the centre within a study plot were regarded as neighbour-only trees ($n = 6793$; site A: $n = 3708$, site B: $n = 3085$; Supplementary Fig. 5). Aboveground tree–tree interactions were obvious already after 2 years of planting[57].

Calculation of individual tree growth. We used the annual aboveground wood volume growth (G; cm^3 year^{-1}) as a measure for individual tree growth. For each focal tree, we approximated the wood volume (V) by using a fixed value of 0.5 for form factor (i.e., a reduction factor that reduces the theoretical volume of a cylinder to tree volume[58]), which is an average value for young subtropical trees obtained from terrestrial laser scan data (Kunz et al., unpublished data; $V = (\pi D^2/4) * H * f$, where D is the measured ground diameter, H is the measured tree height and f is a cylindrical form factor). G was calculated from diameter and tree height measurements recorded in 2011 and 2016 (i.e., the common census interval for sites A and B)

$$G = \frac{V_2 - V_1}{t_2 - t_1} \tag{1}$$

where V_1 and V_2 are the tree wood volumes at the beginning (t_1) and end (t_2) of the study period 2011–2016. To avoid potential biases in tree-level and plot-level estimates, we excluded trees with negative growth rates in the subsequent analyses (site A: 1.7%, site B: 2.1%) that can result from, e.g., measurement errors, different measurement positions between the censuses (e.g., due to trees with trunk irregularities) or mechanical tree damage (e.g., due to falling large-sized branches)[59].

Neighbourhood-scale model. We used linear mixed-effects models to explore how local biodiversity patterns were modified by initial focal tree size (wood volume) and local neighbourhood conditions. The latter were characterised as the abundance of competitors (expressed as the neighbourhood competition index, NCI) and number of heterospecific (different species identity as the focal tree) tree species (NSR) in the local neighbourhood of a focal tree. The effect of NSR on individual tree growth may also depend on the number of conspecific neighbours[60]. As the number of conspecific (same species identity as the focal tree) neighbours varied within a given NSR level in our study, we used conspecific neighbour density (CND) as an additional predictor to separate the effects of CND and NSR on focal tree growth. For each focal tree i, NCI was calculated as the total basal area of closest neighbours j with a larger stem diameter than the focal tree ($\sum_{j \neq i} \pi D_j^2/4$, where D is the measured ground diameter), CND as the total number of closest conspecific neighbours and NSR as the total number of closest heterospecific neighbour species ($\sum_{j \neq i} N_j$, where N is the recorded species number). Both NCI, CND and NSR represent the net effect of neighbouring trees on the growth of a focal tree. Although neighbour effects can be size-symmetric (i.e., summed basal area of all neighbours) or size-asymmetric (i.e., summed basal area of neighbours with a larger stem diameter than the focal tree)[61], preliminary analysis indicated that NCI based on asymmetric competition provided a significant better fit to the data compared to the size-symmetric NCI ($\Delta\text{AIC} = 426.5$, $P < 0.001$). Given the close correlation between neighbour tree diameter (D) and height (H) in this study (Pearson correlation: $r = 0.91$, $P < 0.001$; Supplementary Fig. 6), larger neighbours were assumed to be taller. On this basis, we examined the changes in annual wood volume growth of a focal tree as a basic function of its size and local interactions with neighbouring trees based on NCI, CND and NSR. Tree size and NCI were $\log_{10}$-transformed to linearise their relationship with annual growth rate (see ref. [36] for a related approach). The basic model had the form

$$\begin{aligned} \log\left(G_{i,j,s,k,p}\right) = \; & \alpha + \beta_1 \log\left(V_{i,j,s,k,p}\right) + \beta_2 \log\left(\text{NCI}_{i,j,s,k,p} + 1\right) + \beta_3\, \text{CND}_{i,j,s,k,p} \\ & + \beta_4\, \text{NSR}_{i,j,s,k,p} + \gamma_j + \varphi_s + \upsilon_k + \tau_p + \varepsilon_{i,j,s,k,p} \end{aligned} \tag{2}$$

where G is the annual wood volume growth over a 5-year interval of focal tree i of species j growing in neighbourhood condition s (species composition) and k (total number of neighbours) in plot p; α is the intercept and $\beta_{1,2,3,4}$ are parameters adjusting the effects of initial focal tree wood volume (V), neighbourhood competition (NCI), conspecific neighbour density (CND) and neighbourhood tree species richness (NSR); γ, φ, υ and τ denote crossed random effects of focal trees' species identity, neighbourhood species composition, neighbour density and plot identity, respectively, and ε is the residual error—assuming a normal distribution with mean 0 and variance σ^2 of all variance components. We included plot, species identity and neighbourhood species composition in the random structure to account for variation in abiotic growing conditions within a study site (e.g., small-scale differences in topography) and species-specific effects. We also tested for a random effect that allowed the effects of NSR to vary among species, but found no statistical support for such a random slope model, demonstrating that the shape of the G-NSR relationship was consistent across species ($\chi^2 = 2.00$, $P = 0.367$). Due to mortality of re-planted trees, we used the average values of NCI, CND and NSR in the study period (2011–2016), as they most accurately reflect the neighbourhood conditions experienced by a focal tree during the observation period[37]. The average mortality rate across study species in the study period (focal and neighbour-only trees) ranged between 17% (site A) and 23% (site B).

First, we determined the optimal random-effects structure based on restricted maximum likelihood (REML) estimation, including all covariates and possible interaction terms. Second, we determined the optimal fixed-effects structure by using the maximum likelihood (ML) method[62]. Different competing models (including all possible combinations of covariates and two- and three-way interaction terms with NSR) were evaluated by sequential comparison based on the Akaike information criterion (AIC). The model with the lowest AIC and highest Akaike weights (i.e., the likelihood of being the best-fitting model based on AIC values)[63], respectively, was chosen as the most parsimonious model (Supplementary Table 6). We further simplified the model with the lowest AIC by removing all terms that were not significant according to likelihood ratio tests[62]. Parameter estimates of the best-fitting model were based on restricted maximum likelihood (REML) estimation[62] and are presented in Supplementary Table 2. All predictors were standardised (divided by their standard deviations) before analysis. Models were fitted for each study site separately. There was no critical correlation between covariates (collinearity), as indicated by the variance inflation factors (all VIFs <2.7). Model assumptions (including spatial independence) were checked and confirmed according to ref. [62].

Quantifying neighbourhood-scale net biodiversity effects. To examine how local biodiversity effects were related to neighbourhood species richness, we used growth predictions (based on fixed-effects estimates) from our best-fitting model (Supplementary Table 2). The individual-based net biodiversity effect at the neighbourhood scale (NE_{nbh}) for a given NSR-level j was calculated as the relative change in annual wood volume growth (G) of a focal tree growing in conspecific ($\text{NSR} = 0$) compared to heterospecific neighbourhoods ($\text{NSR} = 1,\ldots,7$)

$$\text{NE}_{\text{nbh},j} = 100\,\frac{G_{\text{h},j} - G_{\text{c}}}{G_{\text{c}}} \tag{3}$$

where c indicates conspecific and h heterospecific neighbours with $j = 1,\ldots,7$ species. $\text{NE}_{\text{nbh},j}$ was then related to species richness of the local neighbourhood, separately for low, average and high NCI. For each focal tree, we predicted G at low (20% quantile of log-transformed NCI), average (50% quantile) and high (80% quantile) abundance of competitors in its local neighbourhood. We did this for every level of NSR, while keeping the tree size fixed at a specific value using the 20% (small trees), 50% (medium-sized trees) and 80% (large-sized trees) quantile of log-transformed initial wood volume. In this way, our function-derived growth rates allowed us to analyse how neighbourhood-scale biodiversity effects vary with NSR.

Sensitivity analysis. Given the negative correlation between NSR and CND in our study ($r = -0.76$), neighbourhoods with a high number of heterospecific species are associated with fewer conspecific neighbours. We therefore compared the relative importance of NSR and CND effects by fitting a series of candidate models for each predictor separately. We found strong statistical support that NSR is an important driver regulating individual tree productivity rather than CND, because CND was not significant (Supplementary Table 7).

To assess whether our results depend on the calculation of the neighbourhood competition index (NCI), we run a series of candidate models either using size-symmetric (i.e., summed basal area of all neighbours) or size-asymmetric (i.e., summed basal area of neighbours with a larger stem diameter than the focal tree) NCIs. We found qualitatively similar results (Supplementary Tables 6 and 8), but the inclusion of size-asymmetric NCI effects into the best-fitting model resulted in a substantial drop of AIC (size-asymmetric NCI: 6352.7; size-symmetric NCI: 6536.8), and the Akaike weights indicated that the model including size-asymmetric NCI effects has a relative likelihood being the best-fitting model of 100% compared to the model including size-symmetric NCI effects.

Calculation of community productivity. In this study, communities are defined as the total number of focal trees within a given plot. For each plot of site B, the aboveground wood productivity (AWP) was calculated based on individual tree growth (annual wood volume growth; G) of all focal trees within a plot. The contribution of a given tree to AWP strongly depends on its initial size[64]. Thus, differences in size structure among species mixtures might cause spurious correlations between community productivity and species richness when individual tree growth rates are scaled up to plot-level productivity. We therefore considered the relative importance of each focal tree in terms of its contribution to the total mean wood volume (see ref. [65] for a related approach). We used the total mean wood volume (2011–2016) instead of the total initial wood volume (2011) to account for potential bias associated with differences in tree density (i.e., the number of trees per plot that can vary with the sampling scheme or mortality; see sections above). Observed community productivity (AWP_{obs}) was quantified as

$$\text{AWP}_{\text{obs}} = \frac{\sum_{i=1}^{N} \left(G_{\text{obs},i} * V_i\right)}{\sum_{i=1}^{N} \overline{V}_i} \tag{4}$$

where $\mathrm{AWP}_{\mathrm{obs}}$ is the observed annual standardised aboveground wood productivity ($\mathrm{cm}^3\ \mathrm{cm}^{-3}\ \mathrm{year}^{-1}$) of a given plot, and $G_{\mathrm{obs},i}$, V_i and $\overline{V}_i$ are the observed annual wood volume growth, initial wood volume (2011) and mean wood volume in the study period 2011–2016 of focal tree i, respectively. Similarly, we calculated community productivity based on predictions from our neighbourhood model ($\mathrm{AWP}_{\mathrm{nbh}}$). Here, we used parameter estimates obtained from our best-fitting neighbourhood model for trees growing at site A (Supplementary Table 2) to predict the annual wood volume growth (G) of all focal trees growing at site B, meaning that we related parameter estimates—derived from site A—directly to observed focal tree and neighbour data of site B

$$\mathrm{AWP}_{\mathrm{nbh}} = \frac{\sum_{i=1}^{N}(G_{\mathrm{nbh},i} * V_i)}{\sum_{i=1}^{N}\overline{V}_i} \qquad (5)$$

where $\mathrm{AWP}_{\mathrm{nbh}}$ is the predicted standardised annual aboveground wood productivity ($\mathrm{cm}^3\ \mathrm{cm}^{-3}\ \mathrm{year}^{-1}$) of a given plot based on tree interactions at the neighbourhood scale. $G_{\mathrm{nbh},i}$ is the predicted annual wood volume growth of focal tree i using parameter estimates of a neighbourhood model (site A), and V_i and $\overline{V}_i$ are the observed initial wood volume (2011) and mean wood volume in the study period 2011–2016 of focal tree i, respectively. Note that mean mortality rates across species did not substantially differ among species richness levels (Supplementary Table 9).

Community-scale model. We used linear mixed-effects models to determine drivers of the biodiversity–productivity relationship (BPR) at the community scale. To account for variation in tree species composition among study plots, plot species composition was used as a random effect. $\mathrm{AWP}_{\mathrm{obs}}$ was used as a response variable and fixed effects were included for community tree species richness (CSR), community productivity based on neighbourhood inteactions ($\mathrm{AWP}_{\mathrm{nbh}}$) and for small-scale variation in topography (elevation, slope and 'northness') among study plots within a study site. For each plot, data on mean elevation (m), slope (°) and 'northness' (cosine-transformed radian values of the aspect) were extracted from a 5-m digital elevation model (DEM) based on differential GPS measurements. The overall quality of the DEM was high, with an explained variance of 98% and a root mean square error (RMSE) of 1.9 m (10-fold cross-validation) in an elevation range of 112 m (see ref. [57]). Model selection was based on the procedure as described above for the neighbourhood models. The response variable, CSR and $\mathrm{AWP}_{\mathrm{nbh}}$ were $\log_{10}$-transformed to meet model assumptions. All predictors were standardised (divided by their standard deviations) before analysis. There was no indication for collinearity (all VIFs < 1.2). Model assumptions were checked and confirmed according to ref. [62].

To quantify the contribution of fixed- and random-effects variables in explaining variation in community productivity along the species richness gradient, we conducted a variance-partitioning analysis using the method of ref. [66] that computes the fraction of variation attributable to each variable in a regression model. Variance partitioning was performed with the best-fitting model. This analysis allowed us to quantify the importance of neighbourhood interactions in driving BPRs in young tree communities.

All analyses were conducted in R (version 3.3.1)[67] using the packages lme4[68], lmerTest[69], MuMIn[70] and variancePartition[66].

Data availability. Data that support the findings of this study have been deposited in the BEF-China project database (http://china.befdata.biow.uni-leipzig.de/) and are available from the corresponding authors on reasonable request.

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Author contributions

G.v.O., W.H. and H.B. designed the research. Y.L. and M.K. collected and compiled the data. A.F. analysed the data and wrote the manuscript. All authors contributed to revisions.

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Chapter 3

From competition to facilitation: how tree species respond to neighbourhood diversity

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From competition to facilitation: how tree species respond to neighbourhood diversity

Andreas Fichtner[1*], Werner Härdtle[1], Ying Li[1], Helge Bruelheide[2,3], Matthias Kunz[4] and Goddert von Oheimb[3,4]

[1]*Leuphana University of Lüneburg, Institute of Ecology, Scharnhorststr. 1, 21335 Lüneburg, Germany;* [2]*Martin Luther University Halle-Wittenberg, Institute of Biology / Geobotany and Botanical Garden, Am Kirchtor 1, 06108 Halle (Saale), Germany;* [3]*German Centre of Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5E, 04103 Leipzig, Germany;* [4]*Technische Universität Dresden, Institute of General Ecology and Environmental Protection, Pienner Straße 7, 01737 Tharandt, Germany*

*Correspondence: A. Fichtner, fichtner@leuphana.de

Abstract

Studies on tree communities have demonstrated that species diversity can enhance forest productivity, but the driving mechanisms at the local neighbourhood level remain poorly understood. Here we use data from a large-scale biodiversity experiment with 24 subtropical tree species to show that neighbourhood tree species richness generally promotes individual tree productivity. We found that the underlying mechanisms depend on a focal tree's functional traits: For species with a conservative resource-use strategy diversity effects were brought about by facilitation, and for species with acquisitive traits by competitive reduction. Moreover, positive diversity effects were strongest under low competition intensity (quantified as the total basal area of neighbours) for acquisitive species, and under high competition intensity for conservative species. Our findings demonstrate that net biodiversity effects in tree communities can vary over small spatial scales, emphasising the need to consider variation in local neighbourhood interactions to better understand effects at the community level.

Keywords: BEF-China, biodiversity, complementarity, ecosystem functioning, forests, functional traits, productivity, species interactions

INTRODUCTION

Most studies of diversity-productivity relationships (DPRs) in forests analysed biodiversity effects at the community scale (Paquette & Messier 2011; Zhang *et al.* 2012; Vilà *et al.* 2013; Forrester & Bauhus 2016; Liang *et al.* 2016; Tobner *et al.* 2016), and inevitably neglected mechanisms caused at smaller scales, such as interactions among neighbouring trees. Species interactions at the neighbourhood level, however, are crucial to understand effects at the community level (Scherer-Lorenzen 2014), because positive (facilitative) and negative (competitive) plant interactions emerge at small spatial scales (Stoll & Weiner 2000). Studies that have assessed the impact of local neighbourhood diversity on individual tree productivity have shown that an increase in heterospecific neighbours can lead to positive or neutral effects (Potvin & Dutilleul 2009; von Oheimb *et al.* 2011; Ratcliffe *et al.* 2015; Chen *et al.* 2016; Chamagne *et al.* 2017). By contrast, it remains unclear how neighbourhood interactions change along diversity gradients or how they translate into diversity effects.

Competition for light is a key determinant that shapes the outcome of DPRs in forests (Morin *et al.* 2011; Jucker *et al.* 2014), and the competitive ability of a tree is strongly related to both its size and its functional traits. There is consensus that competition for light among terrestrial plants is size-asymmetric, such that larger trees capture disproportionally greater amounts of light relative to their size when interacting with smaller ones (Freckleton & Watkinson 2001). Additionally, certain functional traits induce competitive hierarchies, meaning that the trees' sensitivity to competition largely depends on favourable traits (i.e. competitive imbalance; Kunstler *et al.* 2012). Key traits in competitive hierarchies are wood density and specific leaf area, with conservative species (e.g. species with high wood density) being less sensitive to competition than species with fast resource acquisition (e.g. species with high specific leaf area; Kunstler *et al.* 2016). Functional traits are often associated with the so-called fast–slow continuum (Reich 2014), where light-demanding pioneer species are associated with a high specific leaf area or leaf nitrogen content and shade-tolerant late successional species with a high wood density or leaf toughness (Wright *et al.* 2007; Valladares & Niinemets 2008). Moreover, trait-related niche differences can alter the strength of competitive interactions by promoting niche partitioning, and thus, reduce interspecific competition among neighbouring plants (i.e. competitive reduction; Lasky *et al.* 2014). As a result, light exploitation can become more efficient in mixed forests due to complementary use of canopy space (Sapijanskas *et al.* 2014; Jucker *et al.* 2015; Schmid & Niklaus 2017; Williams *et al.* 2017), which in turn promotes productivity at the community level (Zhang & Chen 2015). Beside competitive reduction, positive diversity effects can arise from facilitation, for example through enhancement of resource availability (e.g. nitrogen fixation, hydraulic lift, common mycorrhizal networks or modification of soil microbiota) or amelioration of abiotic stress (e.g. alteration of microclimate due to shading; Brooker *et al.* 2008; Montgomery *et al.* 2010; McIntire & Fajardo 2014; Klein *et al.* 2016; Rodríguez-Echeverría *et al.* 2016). Both competitive reduction and facilitation are major mechanisms underlying DPRs in forests (Forrester & Bauhus 2016). Thus, competitive or facilitative interactions should have a major influence on the community response to changing tree diversity. Assessing the importance of species diversity for forest productivity therefore requires an understanding of how species interactions vary along spatial gradients (Bravo-Oviedo *et al.* 2014; Forrester 2014). As community responses are – at least to a large extend – the result of aggregated small-scale variations in neighbourhood interactions (Potvin & Dutilleul 2009), it is crucial to analyse diversity mechanisms at the level of tree individuals in order to understand diversity-related changes in forest productivity (Potvin & Gotelli 2008; Chen *et al.* 2016). However, little is known about the role of neighbourhood diversity in modulating tree interactions. Therefore, the separation of mechanisms that drive tree species coexistence in mixtures (i.e. competitive reduction and facilitation) remains challenging.

Here we used experimental tree communities of an early-successional subtropical forest to determine the mechanisms underlying DPRs at the local neighbourhood level. Our tree communities cover a long diversity gradient, ranging from monocultures to 24-species mixtures, allowing us to quantify diversity effects (using species richness as a measure for biodiversity) on tree productivity in relation to various levels of local neighbourhood tree species richness with a maximum of eight heterospecific neighbours. The effect of species mixing on community productivity (i.e. the net biodiversity effect) can be statistically partitioned in complementarity and selection effects (Loreau & Hector 2001). Niche partitioning or facilitation are considered the main components causing a statistical complementarity effect, whereas the increasing likelihood of including well-performing species in diverse communities induces a statistical selection effect at the community level (Loreau 2000). The outcome of diversity effects at the local neighbourhood level, however, is assumed to be largely driven by simultaneously operating positive (e.g. niche partitioning, facilitation and trophic interactions) and negative (e.g. competition for resources) species interactions (Potvin & Dutilleul 2009; Wright *et al.* 2014). In this study, we therefore define the term 'diversity effect' as the net effect of all intra- and interspecific interactions within the local neighbourhood of a focal tree (sensu Loreau & Hector 2001). We hypothesised that the underlying mechanisms of positive diversity effects largely depend on how neighbours interact and how these local interactions change along diversity gradients (Fig. 1 and Fig. S1 in Appendix S1 in Supporting Information). To assess these hypotheses, we applied a two-step approach: First, we estimated diversity effects based on neighbourhood models (i.e. how tree productivity varied with the presence of heterospecific neighbours). Second, we quantified the mode and intensity of tree interactions (i.e. the relative difference in tree productivity with and without local neighbours) using a relative interaction index (RII) and predicted tree size- and diversity-related changes in RII. The combination of both approaches allowed us to identify mechanisms that underlie positive effects of local species richness on tree productivity.

METHODS

Study site and experimental design

In this study, we used data from a 26.6 ha experimental site (site A) established in southeast subtropical China (29°08'–29°11' N, 117°90'–117°93' E; elevation 105–275 a.s.l.) as part of the BEF-China tree diversity experiment (Bruelheide *et al.* 2014). The mean annual temperature is 16.7 °C and mean precipitation is 1821 mm year^{-1}. The predominant soil types are Cambisols, Regosols and Colluvissols (Scholten *et al.* 2017) and the natural vegetation in the study area is characterised by subtropical mixed broad-leaved forests with a high abundance of evergreen species (Bruelheide *et al.* 2011).

The experiment covers a long diversity gradient ranging from monocultures to 24-species mixtures, which were planted based on a total species pool of 40 native broad-leaved tree species. Species compositions of the mixtures were selected using one random and two non-random (direct or trait-based) extinction scenarios. The random extinction scenario was replicated three times based on different species pools and likewise each non-random extinction scenario was replicated three times with different species compositions. We selected 236 study plots (25.8 x 25.8 m), which were established on the site of a former *Pinus massoniana* Lambert and *Cunninghamia lanceolata* (Lamb.) Hook. commercial plantation that was harvested at a rotation age of 20 years. Plots were planted in March 2009 with 400 trees (20 x 20 individuals) using a regular planting distance of 1.29 m. Replanting of saplings that died during the first growing season was conducted in November 2009 (deciduous species) and March 2010 (evergreen species). Weeding was conducted twice (2009–2011) and later once a year (since 2012) during the growing season (May–October), where all herbaceous and non-planted woody species as well as resprouts of the previously planted *P. massoniana* and *C. lanceolata* were carefully removed (Bruelheide *et al.* 2014). Study plot species richness ranged from monocultures ($n = 81$) to mixtures of two ($n = 66$), four ($n = 40$), eight ($n = 26$), 16 ($n = 19$) and 24 ($n = 4$) species. Species and species richness levels were randomly assigned to planting positions and plots, respectively. All species were equally represented at each richness level. For detailed information on species richness and species composition manipulation see Bruelheide *et al.* (2014).

Tree measurements started in autumn 2010 to avoid confounding effects between experimental treatments and planting. For all trees within a plot, species identity, stem diameter (measured 5 cm above ground), tree height (measured from the stem base to the apical meristem), crown diameter along two directions (north–south and east–west) and crown position (height of crown base) were recorded in 2010 and each subsequent year (September–October; see Table S1 in Appendix S2). To account for edge effects, the central 16 trees (for monocultures and 2-species mixtures) or central 100 trees (for 4-, 8-, 16-, 24-species mixtures) were used as focal trees ($n = 5677$), and all other individuals in the immediate neighbourhood of a focal tree were regarded as neighbour-only trees ($n = 6856$; Fig. S2 in Appendix S1). A detailed description of the sampling scheme is provided in Li *et al.* (2014).

We used the relative growth rate (RGR) of wood volume as a measure for tree productivity. For each focal tree, we approximated the wood volume (V) by using a fixed value of 0.5 for form factor, which is an average value for young subtropical trees (Kunz, Härdtle & von Oheimb, unpublished data; $V = (\pi D^2 / 4) * H * f$, where D is the measured ground diameter, H the measured tree height and f is a cylindrical form factor). Relative growth rate of wood volume was computed as

$$\mathrm{RGR} = \frac{\log(V_2 / V_1)}{t_2 - t_1}$$

where V_1 and V_2 are the tree wood volumes at the beginning (t_1) and end (t_2) of census interval 2010–2014. We used RGR instead of absolute growth rate, because initial tree size varied considerably among focal trees (range: 5–500 cm; mean: 70.3 cm; SD: 51.4 cm), and RGR is less sensitive towards differences in initial tree size (Mencuccini *et al.* 2005).

Neighbourhood models of tree productivity

We used linear mixed-effects models to explore how local diversity patterns were modified by tree size and neighbourhood conditions. The latter were characterised as the abundance of competitors (expressed as the neighbourhood competition index, NCI) and number of tree species (NSR) in the local neighbourhood of a focal tree. For each focal tree i, NCI was calculated as the total basal area of immediate neighbours j ($\sum_{j \neq i} \pi D_j^2 / 4$, where D is the measured ground diameter) and NSR was calculated as the total number of immediate

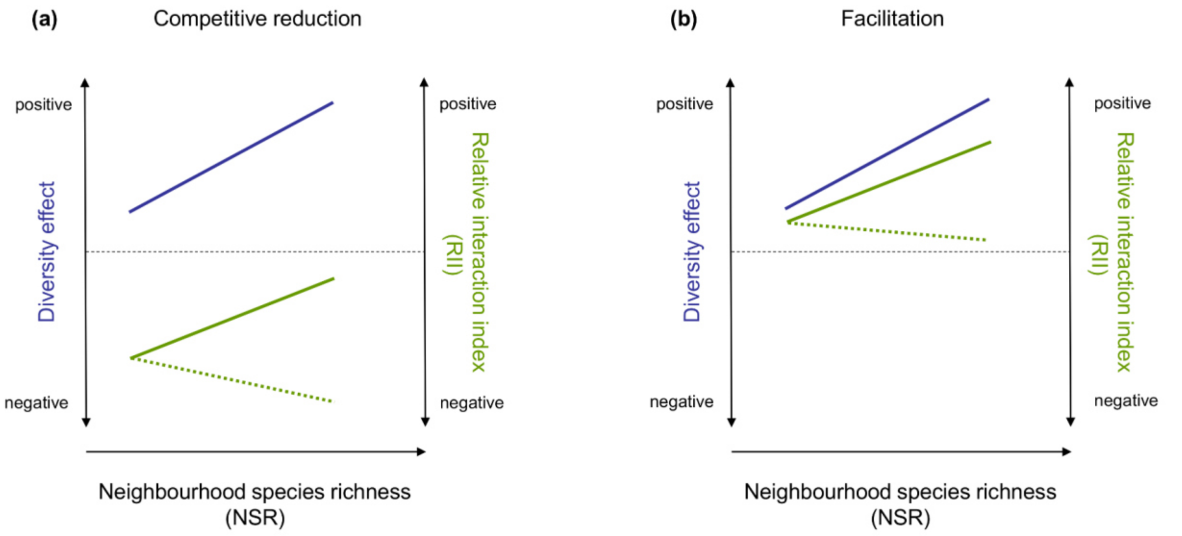

Figure 1 Possible mechanisms that induce positive diversity effects at the local neighbourhood level. Neighbourhood tree species richness (NSR) can promote individual tree productivity. This positive effect (blue line) can arise from (a) competitive reduction or (b) facilitation, depending on how neighbours interact: Neighbour interactions are competitive (negative relative interaction index; RII) when tree productivity is higher in the absence rather than in the presence of neighbours. In the case of facilitative interactions (positive RII), productivity is higher with neighbours than without. Moreover, the intensity of neighbour interactions (absolute value of RII) corresponds to the importance of competitive reduction or facilitation in inducing positive diversity effects. For example, (a) competitive reduction can prevail when competition intensity decreases (i.e. processes leading to competitive reduction, such as canopy stratification, will become less important; solid green line) or increases (i.e. processes leading to competitive reduction will become increasingly important; dotted green line) with NSR. Similarly, (b) facilitation can prevail when facilitation intensity either decreases (i.e. processes leading to facilitation will become less important; dotted green line) or increases (i.e. processes leading to facilitation will become increasingly important; solid green line) with NSR (see Figure S1 in Appendix S1 for further illustration).

heterospecific neighbour species ($\sum_{j \neq i} N_j$, where N is the recorded species number). On this basis, we examined changes in annual wood volume growth of a focal tree as a basic function of its size and local interactions with neighbouring trees based on NCI and NSR. Tree size and NCI were log-transformed to linearise their relationship with annual wood volume growth (see Rüger *et al.* 2011; Kunstler *et al.* 2016 for related approaches). The basic model had the form:

$$\mathrm{RGR}_{i,s,k,p} = \alpha + \beta_1 \log(H_{i,s,k,p}) + \beta_2 \log(\mathrm{NCI}_{i,s,k,p} + 1) + \beta_3\, \mathrm{NSR}_{i,s,k,p} + \gamma_s + \varphi_k + \upsilon_p + \varepsilon_{i,s,k,p}$$

where RGR is the relative growth rate of wood volume of focal tree i of species s growing in neighbourhood species composition k in plot p; α is the overall mean RGR and $\beta_{1,2,3}$ are parameters adjusting the effects of initial tree height (H), neighbourhood competition (NCI) and neighbourhood tree species richness (NSR); γ, φ and υ denote crossed random effects of focal trees' species identity, neighbourhood species composition and plot identity, respectively, and ε is the residual error - assuming a normal distribution with mean 0 and variance σ^2 of all variance components. We included plot, species identity and neighbourhood species composition in the random structure to account for variation in abiotic growing conditions within the study site and species-specific effects. We also tested for a random effect that allowed the effects of NSR to vary among species, but found no statistical support for such a random slope model, demonstrating that the shape of the RGR-NSR relationship was consistent across species (see Table S2 in Appendix S2). Due to mortality of re-planted trees, we used the average values of NCI and NSR in the census interval (2010–2014), as they more accurately reflect the neighbourhood conditions experienced by a focal tree (Coomes & Allen 2007). The average mortality rate of the study species (focal and neighbour-only trees) in the census interval was 12% (see Table S3 in Appendix S2)

First, we determined the optimal random-effects structure based on restricted maximum likelihood (REML) estimation, including all covariates and possible interaction terms. Second, we determined the optimal fixed-effects structure by using the maximum likelihood (ML) method (Zuur *et al.* 2009). Different competing models (including all possible combinations of covariates and interaction terms) were evaluated by sequential comparison based on the Akaike Information Criterion (AIC). Only models with an AIC difference (ΔAIC) ≤ 2 (compared with the best-fitting model) were considered to be models with substantial support (Burnham & Anderson 2002) and the model with the highest Akaike weight (i.e. the likelihood of being the best-fitting model based on AIC values) was chosen as the most parsimonious model (see Table S4 in Appendix S2). Parameter estimates of the best-fitting model were based on restricted maximum likelihood (REML) estimation (Zuur *et al.* 2009) and are presented in Table S5 in Appendix S2. There was no correlation between covariates (collinearity), as indicated by the variance inflation factors (all VIFs < 2; Zuur *et al.* 2010).

Assessing trait-mediated effects on tree productivity and tree interactions along species richness gradients

To examine the role of functional traits of a focal tree in regulating the effects of neighbourhood species richness and tree interactions, we selected four key traits (specific leaf area, SLA; leaf nitrogen content, LNC; leaf toughness, LT; wood density, WD) which are linked to productivity and shade tolerance, and which thus reflect tree ecological strategies (Poorter *et al.* 2008; Valladares & Niinemets 2008; Lasky *et al.* 2014). This allowed us to rank the tree species according to acquisitive (high SLA, LNC) and conservative (high WD, LT) trait values (Wright *et al.* 2007; Díaz et al. 2016). We used this classification, because niche differences among species, and hence neighbourhood complementarity are assumed to be driven by a combination of functional traits, rather than a specific single trait (Kraft *et al.* 2015, Chen *et al.* 2016). We first conducted a principal component analysis (PCA) on standardised values of leaf (SLA, LNC, LT) and wood (WD) traits. The first two axes explained 77% (axis 1: 50%, axis 2: 27%) of the overall trait variation among species (see Fig. S3 in Appendix S1). Three functional traits were closely related to the first axis (Pearson correlation SLA: $r = -0.87$; LNC: $r = -0.62$; LT: $r = 0.90$, all $P < 0.001$), while WD was significantly related to the second axis ($r = -0.93$, $P < 0.001$). The deviation of WD in our study is likely the result of the three oak species (*Quercus acutissima*, *Q. fabri*, *Q. serrata*) that had comparatively high WD values and leaf traits more common in acquisitive species (Kröber *et al.* 2015). We then used the first axis scores and determined significant changes in RGR with functional trait composition of focal trees by applying a recursive partitioning approach (Hothorn *et al.* 2006). The resulting splits (i.e. threshold values) indicate a significant shift in the trait-productivity relationship among species. Here, we used the first-order threshold ($P < 0.001$; see Fig. S3 in Appendix S1) to classify the study species into two functional groups: acquisitive species and conservative species. This classification was primarily based on species' differences in leaf traits (SLA, LNC, LT). Trait data were extracted from trait assessments conducted at our study site (Kröber *et al.* 2015).

Assessing changes in tree productivity and tree interactions along species richness gradients

To examine how diversity and tree interaction effects were related to neighbourhood species richness, we used growth predictions (based on fixed-effects estimates) from our best-fitting models (see Table S5 in Appendix S2). We fitted separate models for acquisitive and conservative species, which allowed us to estimate trait-dependent responses. The diversity effect (DE) for a given NSR-level j was calculated as the relative change in predicted RGR of a focal tree growing in conspecific compared to heterospecific neighbourhoods:

$$\mathrm{DE}_j = 100\ \frac{\mathrm{RGR}_{h,j} - \mathrm{RGR}_c}{\mathrm{RGR}_c}$$

where c indicates conspecific and h heterospecific neighbours with $j = 1,\ldots,8$ species. DE_j was then related to species richness of the local neighborhood, separately for acquisitive and conservative species and for high and low NCI.

Changes in the net effect of all ongoing tree interactions (intra- and interspecific) were quantified using the relative interaction index (RII; Armas *et al.* 2004). RII was calculated for each focal tree as

$$\mathrm{RII} = \frac{\mathrm{RGR}_{+N} - \mathrm{RGR}_{-N}}{\mathrm{RGR}_{+N} + \mathrm{RGR}_{-N}}$$

where RGR denotes the relative growth rate of a focal tree either in absence (–*N*) or presence (+*N*) of local neighbours, obtained from our best-fitting models. The index is standardised, symmetrical around zero (allowing for unbiased comparisons between competition and facilitation) and bounded between +1 and –1. Negative values indicate competition, while positive values imply that tree interactions are facilitative. For each focal tree, we predicted RGR at low (RGR_{-N}) or high (RGR_{+N}) abundance of competitors in its local neighbourhood. We did this for every level of NSR, while varying the focal trees' size (using 10 cm intervals; across-size approach). Similarly, we varied NSR, while keeping tree size fixed at a specific value (initial height of 20 cm, 50 cm, 100 cm or 150 cm; size-dependency approach). In the case of RGR_{-N}, NCI was set at 10% and for RGR_{+N} we used the 90% quantile of NCI of each functional group, taking into account potential effects of functional traits (acquisitive versus conservative) on competitive responses (see Kunstler *et al.* 2011 for a related approach). In this way, our function-derived growth rates allowed us to analyse how RIIs vary with NSR.

All analyses were conducted in R (version 3.3.1; R Core Team 2016) using the packages lme4 (Bates *et al.* 2015), lmerTest (Kuznetsova *et al.* 2016), MuMIn (Bartón 2016), party (Hothorn *et al.* 2006), plot3D (Soetaert 2016) and vegan (Oksanen *et al.* 2016).

RESULTS

Relative growth rates (RGR) largely varied among species, with mean values ranging from 0.65 (± 0.02) for *Triadica sebifera* (acquisitive species) to 1.86 (± 0.12) for *Daphniphyllum oldhamii* (conservative species). This corresponds with RGRs that were 0.5-fold larger in conservative than in acquisitive species (t = 5.96, P < 0.001; see Fig. S4 in Appendix S1).

For both functional groups (i.e. acquisitive and conservative species), average tree productivity (RGR) across tree sizes was positively related to NSR, and mean positive diversity effects (i.e. the relative increase in RGR in heterospecific compared to conspecific neighbourhoods) of conservative species were 54% higher than that of acquisitive species. However, we found that the magnitude and direction of diversity effects were strongly context-dependent (see Table S4 in Appendix S2), as shown by a significant interaction between tree size, competition and species richness (acquisitive species: t = 3.41, P < 0.001; conservative species: t = 3.73, P < 0.001; see Table S5 in Appendix S2). First, the effect of NCI on the magnitude and direction of diversity effects was trait-dependent (Fig. 2; Fig. S5 in Appendix S1). Acquisitive species benefited from decreasing competition intensity in their local neighbourhood. At low NCI, mean RGR of acquisitive species increased continuously with NSR (2–14%; Fig. 2a), but at high NCI, RGR was consistently lower in heterospecific than in conspecific neighbourhoods. In contrast, conservative species benefited from increasing neighbourhood competition intensity, with increasing positive diversity effects along the species richness gradient under high NCI (3– 22%; Fig. 2b). Second, the effect of NSR on the mode and intensity of tree interactions was determined by the functional traits and size of the focal trees (Fig. 3), as the sensitivity to competition varied markedly along the species richness gradient (see Fig. S6 in Appendix S1). Averaged across tree sizes, tree interactions varied from competition to facilitation, with interaction intensities being strongest in species-rich neighbourhoods (as indicated by the highest absolute values of RII). RII decreased with NSR for acquisitive species (i.e. competitive effects of heterospecific neighbours on the focal tree increased) and increased with NSR for conservative species (i.e. facilitative effects of heterospecific neighbours on the focal tree increased). Particularly for smaller trees with acquisitive traits, competition became more intense in species-rich neighbourhoods, while for large-sized (initial height: 150 cm) individuals interactions became neutral (Fig. 3a). For conservative species, neighbourhood interactions shifted from competition to facilitation, and this pattern emerged more clearly as trees were larger in size (Fig. 3b).

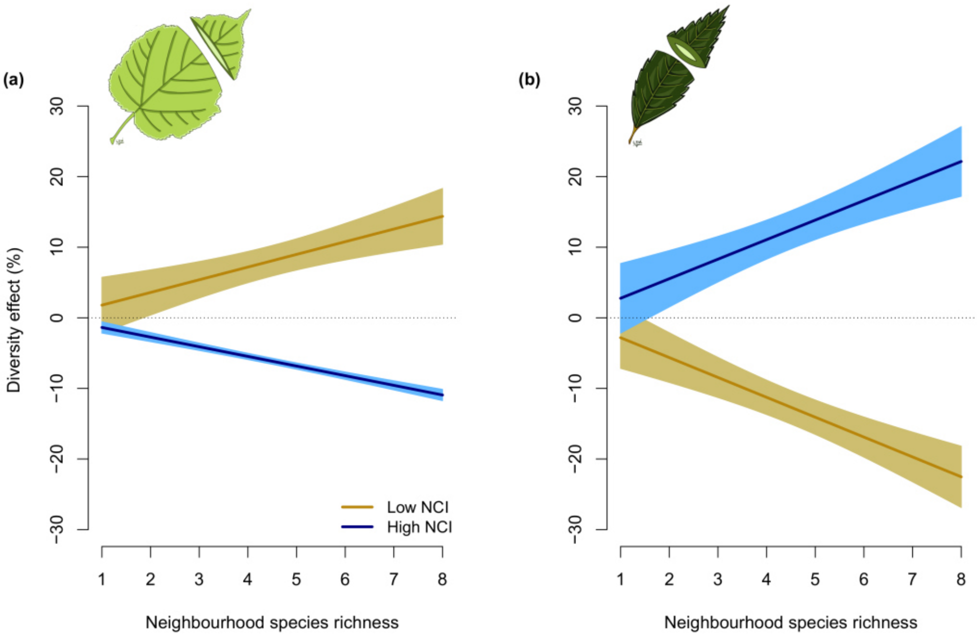

Figure 2 Trait-dependent variation in diversity effects with neighbourhood competition and tree species richness. Diversity effects indicate the change (%) in individual tree productivity (relative growth rate of wood volume of a focal tree growing with heterospecific compared to growing with conspecific neighbours) in response to neighbourhood species richness at low and high value of neighbourhood competition index (NCI; computed as the 10% and 90% quantile of NCI for (a) acquisitive and (b) conservative species, as defined by groups in a PCA on functional traits). Lines represent the mean response across tree sizes (initial tree height: 20–150 cm) as predicted by mixed-effects models. The shaded areas represent the 95% confidence interval range. Leaf illustrations by Carolina Levicek.

DISCUSSION

Our results demonstrate that diversity effects on tree growth need to be assessed in the context of a focal tree's local competitive environment in order to better understand mechanisms underlying DPRs at the community level. By identifying the mode of tree interactions in response to neighbourhood species richness we found that diversity mechanisms are regulated largely by the species' functional traits: Acquisitive species benefited primarily from a more diverse neighbourhood when competition intensity was low, leading to competitive reduction, while conservative species drew most benefit from a more diverse neighbourhood when competition intensity was high, leading to facilitation. Hence, the way how focal trees responded to neighbourhood diversity was largely determined by the ability to tolerate competition (Fortunel *et al.* 2016) and the benefit that some species may gain from heterospecific facilitation (Montgomery *et al.* 2010).

Positive (facilitation) and negative (competition) neighbour interactions often occur simultaneously in plant communities, and the net effect is likely the result of jointly operating processes (Holmgren *et al.* 1997; Bruno *et al.* 2003). The strength and direction (competition or facilitation) of neighbour interactions can also shift with plant ontogeny (Miriti 2006; Wright *et al.* 2014). As a result, the outcome at the neighbourhood level can arise through multiple co-occurring factors (Wright *et al.* 2014). Crown traits play a central role for light-related tree interactions, which in turn affect carbon assimilation (Pretzsch 2014). Given the close correlation between neighbourhood basal area (NCI) and neighbourhood crown projection area (Pearson correlation: $r = 0.92$, $P < 0.001$; see Fig. S7 in Appendix S1) in this study, we may assume that the main effect of an increasing NCI is an increasing degree of shading. Shading by neighbours, however, can affect plant growth either negatively by reducing light availability (Freckleton & Watkinson 2001) or positively by ameliorating microclimate conditions (McIntire & Fajardo 2014), and these effects can be species-specific (Valladares *et al.* 2008). Tree diversity studies have shown that competition

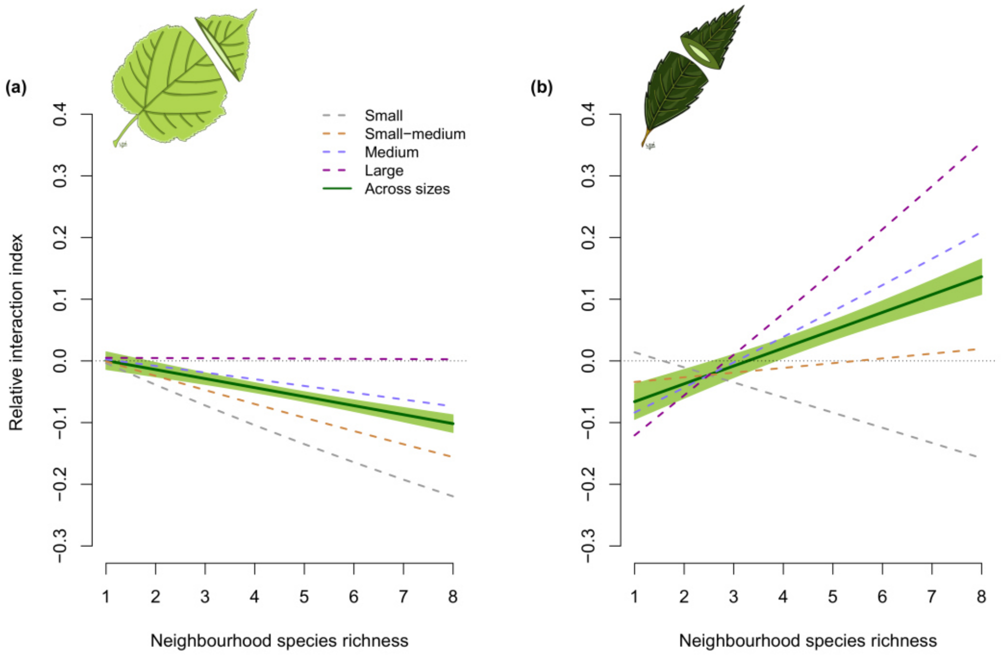

Figure 3 Size-mediated effects of local neighbourhood tree species richness on tree interactions. (a) Acquisitive species and (b) conservative species, as defined by groups in a PCA on functional traits. The relative interaction index (RII) quantifies the mode and intensity of tree interactions. It is symmetrical around zero (neutral interactions) and ranges from +1 (strong facilitation) to –1 (strong competition). The solid green line represents the mean response across tree sizes (initial tree height: 20–150 cm) as predicted by mixed-effects models. The shaded areas indicate the 95% confidence interval range. Dashed lines represent mixed-effects model fits for trees of different sizes (small: 20 cm, small-medium: 50 cm, medium: 100 cm, large: 150 cm). Local neighbourhood species richness (NSR) indicates heterospecific neighbour effects (both intra- und interspecific tree interactions). Leaf illustrations by Carolina Levicek.

for light is less prevalent in mixtures compared to monocultures (Morin *et al.* 2011), because spatial complementarity in tree crowns and intraspecific crown plasticity enable trees to reduce competitive pressure from neighbours, and thus improve their light interception (Sapijanskas *et al.* 2014; Jucker *et al.* 2015; Williams *et al.* 2017). In this context, Jucker *et al.* (2014) showed that light-demanding species (e.g. those with high SLA) and smaller individuals primarily benefited from competitive reduction and an associated increase in light availability. This is consistent with our finding of increasing positive diversity effects of acquisitive species with decreasing neighbourhood competition intensity, particularly for smaller individuals (Fig. S6a in Appendix 1). Conversely, the positive relationship between diversity effects and neighbourhood competition intensity we observed for conservative species is most likely the result of facilitative interactions at higher neighbourhood diversity brought about by an improvement of microclimate conditions (Montgomery *et al.* 2010; Wright *et al.* 2014). Such facilitative neighbour effects have been shown to decrease excess irradiance (i.e. decreasing the degree of photoinhibition) and to reduce air and soil surface temperature extremes as well as vapour pressure deficits at the leaf surface and the evaporative demand of whole trees, particularly for shade-tolerant species (Montgomery *et al.* 2010). Additionally, positive effects of heterospecific neighbours on tree productivity may be caused indirectly by a reduction of species-specific pathogens (dilution effects, Keesing *et al.* 2006; reduced Janzen-Connell effects; Wright 2002).

Next to microclimate amelioration, heterospecific neighbours can modify plant interactions positively by altering microhabitat complexity (e.g. the spatial and temporal heterogeneity created by the physical presence of benefactor species or the species' size and architecture; McIntire & Fajardo 2014). Our results also suggest that neighbour size structure (height inequality) favours facilitation, as almost half (43%) of the species-specific variation in RII of taller individuals of conservative species was explained by the height variation of neighbouring trees (see Fig. S8 in Appendix S1). Studies on shrubs and tree seedlings have shown that facilitation is particularly important for smaller individuals, because they generally experience a high level of stress with regard to resource acquisition (light, water, nutrients). In contrast, taller individuals have an improved access to resources and a higher resource demand. Therefore the relative impact of competition may increase as plants grow (Miriti 2006; Wright *et al.* 2014). Our results further imply that facilitative interactions are important even for taller individuals at later ontogenetic stages. This interpretation is consistent with findings for young trees in two-species mixtures (Forrester *et al.* 2011). Similarly, Lasky *et al.* (2015) reported that taller trees drew most benefit from growing in diverse neighbourhoods, although they had the greatest access to light resources. The observed size-related variation in facilitation intensity of species with conservative traits might be partly explained by the relative low competitive tolerance of smaller individuals (Coomes & Allen 2007). For small trees relative competition intensity via resource depletion is stronger and counteracts facilitative effects via microclimate amelioration of heterospecific neighbours, and thus, dominates the net effect of co-occurring interactions. Similarly, neighbour effects on taller individuals of acquisitive species were neutral, possibly due to a trade-off between maximum resource capture and competitive tolerance as trees grow taller (Lasky *et al.* 2015). This illustrates that facilitative effects may become increasingly apparent during stand development (Cavard *et al.* 2011).

Averaged across tree sizes, both mechanisms (competitive reduction and facilitation) were most effective in species-rich neighbourhoods, and translated into increasing diversity effects either with low (for acquisitive species) or high (for conservative species) neighbourhood competition (see Fig. 2). Thus, the interplay between trait-mediated competition response of a focal tree and species richness of neighbouring trees should act as a fundamental driver in regulating the magnitude of local diversity effects. This is in agreement with previous studies which demonstrate that specific functional traits determine a tree's competition tolerance and competitive effects (Kunstler *et al.* 2016), and that neighbourhood multi-trait dissimilarity is positively associated with individual tree growth (Chen *et al.* 2016). The fact that competition intensity was most pronounced for (smaller) acquisitive species and facilitation intensity for (taller) conservative species supports the idea that functional traits largely regulate competitive and facilitative responses to species diversity at the local scale (Butterfield & Callaway 2013) and that changes in resource requirements during ontogeny additionally shape the outcome of local species interactions (Lusk *et al.* 2008; Lasky *et al.* 2015). Here it is important to emphasise that our findings arise from even-aged tree communities planted in a controlled field experiment. Thus, effects of neighbourhood conditions on tree interactions may also result from differences in abiotic conditions (e.g. resource supply). However, we did not assume serious confounding effects for several reasons. First, we used plot as a random factor in our neighbourhood models, and thus accounted for abiotic heterogeneity within the study site (the variance explained by plot random effects was 15% for acquisitive species and 11% for conservative species). Second, given the large number of plots with varying species and species combinations in our experiment, it is less likely that the spatial configuration of plots with a specific-species combination and richness level strongly influences the outcome of tree interactions (see Healy *et al.* 2008). Third, species and species richness levels were randomly assigned to plots and planting positions (Bruelheide *et al.* 2014); thus, the likelihood that diversity effects were confounded with differences in the abiotic environment (Healy *et al.* 2008) is relatively small. This interpretation is supported by the findings of Kröber *et al.* (2015), who found that environmental variation in slopes, aspect and soil conditions jointly only explained at maximum 4% of crown width growth rate at site A of the experiment.

Niche differentiation among neighbours is considered a fundamental driver for positive biodiversity-productivity relationships at the community level (Chen *et al.* 2016). In this study, we demonstrate that the role of biodiversity in modulating forest productivity requires a better understanding of species interactions at the local neighbourhood level. Our findings show that the driving mechanisms (competitive reduction or facilitation) of diversity effects at the local neighbourhoood level depend on a focal tree's resource-use strategy. Moreover, the abundance of competitors in the local neighbourhood of a focal tree regulates the efficiency of mechanisms underlying complementarity, which, in turn, determines the strength of local diversity effects and emphasises the importance of neighbourhood interactions in shaping diversity-productivity relationships at the community level. Analyses of local-scale species interactions are therefore crucial to advance our mechanistic understanding of both neighborhood- and community-level diversity effects. Our results also have important forest resource management implications for the conservation of highly diverse forests in the face of global biodiversity loss by suggesting that tree species richness at the local neighbourhood level is a strong regulator of forest productivity.

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Chapter 4

Neighbour species richness and local structural variability modulate aboveground allocation patterns and crown morphology of individual trees

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LETTER

Neighbour species richness and local structural variability modulate aboveground allocation patterns and crown morphology of individual trees

Matthias Kunz,[1]*
Andreas Fichtner,[2]
Werner Härdtle,[2]
Pasi Raumonen,[3]
Helge Bruelheide[4,5] and
Goddert von Oheimb[1,5]

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Abstract

Local neighbourhood interactions are considered a main driver for biodiversity–productivity relationships in forests. Yet, the structural responses of individual trees in species mixtures and their relation to crown complementarity remain poorly understood. Using a large-scale forest experiment, we studied the impact of local tree species richness and structural variability on above-ground wood volume allocation patterns and crown morphology. We applied terrestrial laser scanning to capture the three-dimensional structure of trees and their temporal dynamics. We found that crown complementarity and crown plasticity increased with species richness. Trees growing in species-rich neighbourhoods showed enhanced aboveground wood volume both in trunks and branches. Over time, neighbourhood diversity induced shifts in wood volume allocation in favour of branches, in particular for morphologically flexible species. Our results demonstrate that diversity-mediated shifts in allocation pattern and crown morphology are a fundamental mechanism for crown complementarity and may be an important driver of overyielding.

Keywords

BEF-China, biodiversity, crown complementarity, ecosystem functioning, forests, productivity, terrestrial laser scanning.

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INTRODUCTION

Forests play a central role in hosting global terrestrial biodiversity and providing important ecosystem services, such as carbon sequestration or timber production (FAO 2010; Watson *et al*. 2018). This role, however, can be critically altered by ongoing dramatic global declines in biodiversity (IPBES 2019), as biodiversity has been demonstrated to enhance forest multifunctionality (Gamfeldt *et al*. 2013; van der Plas *et al*. 2016; Schuldt *et al*. 2018). During the last decade, numerous studies provided evidence for a positive net biodiversity effect on primary productivity (overyielding) in forests (Morin *et al*. 2011; Paquette & Messier 2011; Zhang *et al*. 2012; Liang *et al*. 2016; Tobner *et al*. 2016; Grossman *et al*. 2017; Fichtner *et al*. 2018; Huang *et al*. 2018). Although local tree–tree interactions are considered an important driver for such biodiversity–productivity relationships at the scale of tree communities (Stoll & Weiner 2000; Uriarte *et al*. 2004), empirical evidence of diversity-mediated processes at the local neighbourhood scale is sparse. For example, a recent study showed that interactions among local neighbours accounted for more than 50% of the variation in above-ground wood production of highly diverse subtropical tree communities (Fichtner *et al*. 2018), indicating the need to focus on individual trees and their local neighbourhood to elucidate the mechanisms that bring about overyielding in mixed-species forests.

The arrangement of the crown is decisive for light-related tree interactions and, thus, for the carbon balance of an individual tree (Ishii & Asano 2010). Spatial complementarity in tree crowns, which is physical niche partitioning in canopy space (hereafter ‘crown complementarity’), is thought to be an important biological mechanism underlying the positive mixture effects in forests (Pretzsch 2014; Sapijanskas *et al*. 2014; Niklaus *et al*. 2017; Williams *et al*. 2017; Barry *et al*. 2019). Crown complementarity can also arise in monocultures, but it is usually greater in mixtures (Pretzsch 2014; Jucker *et al*. 2015; Williams *et al*. 2017). Hence, for several reasons a thorough understanding of spatial aboveground complementarity in tree species mixtures is still lacking. Previous studies supposed inherent species-specific differences in crown architecture and neighbourhood-driven crown plasticity to be the main drivers for crown complementarity (Jucker *et al*. 2015; Niklaus *et al*. 2017; Williams *et al*. 2017). This view, however, considered inadequately the nature of crown plasticity: it is an important response in the feedback system between current tree structure, the local environment and tree growth

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[1] *Institute of General Ecology and Environmental Protection, Technische Universität Dresden, PF 1117, 01735 Tharandt, Germany*

[2] *Institute of Ecology, Leuphana University Lüneburg, Universitätsallee 1, 21335 Lüneburg, Germany*

[3] *Department of Mathematics, Tampere University, FI-33014 Tampere University, Tampere, Finland*

[4] *Institute of Biology/Geobotany and Botanical Garden, Martin Luther University Halle- Wittenberg, Am Kirchtor 1, 06108, Halle, Germany*

[5] *German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5E, 04103 Leipzig, Germany*

**Correspondence: E-mail: matthias.kunz@tu-dresden.de*

(Schröter *et al.* 2012; Pretzsch 2014). Crown plasticity, i.e. the dynamic morphological adjustments of tree individuals to diversity-induced environmental variability (here: variability in canopy space), may therefore strongly enhance the intraspecific variation of crown architecture in species mixtures compared to monocultures. As a result, it is difficult to properly separate the effects of inherent species-specific differences and crown plasticity. A better mechanistic understanding of how tree species mixing impacts crown complementarity may be achieved by directly analysing what is the ultimate foundation of crown complementarity (both in monocultures and mixtures): the variation in crown size and crown shape among tree individuals (Pretzsch 2009; Williams *et al.* 2017).

Another important element of tree–tree interactions related to canopy space use is the spatial constellation of neighbouring trees. Generally, neighbourhood conditions experienced by an individual tree are expressed in size- and distance-related abundance measures (also known as competition indices). However, a high value of a local neighbourhood abundance measure *per se* may not restrict canopy space filling of a respective target tree if the spatial distribution is uneven or heterogeneous, allowing to make use of gaps and spaces in the canopy. It is therefore crucial to use a spatially explicit measure for both the size *and* the structural variability of the local neighbourhood to better understand crown complementarity. Furthermore, trees may exhibit an exceptional plasticity in crown size and shape, because they record their recent growth and interaction history in woody biomass allocation and tree architecture, which is an important prerequisite for further adjustments in growth and carbon allocation (Liu *et al.* 2018). Initial differences in size and shape are modified over time through structural crown adjustments, in response to light-related tree interactions. Thus, the three-dimensional (3D) appearance of tree crowns emerges through time, and spatial complementarity analyses need to consider the temporal dynamics of crown development. Finally, the complex 3D nature of tree crowns makes detailed investigations inherently demanding. So far quantifying crown characteristics of individual trees up with a very high resolution over a prolonged period of time has been logistically unfeasible, but such knowledge may be key to understand the biological mechanisms underlying crown complementarity.

In this study, we made use of terrestrial laser scanning (TLS) technology to analyse non-destructively the two basic elements of crown complementarity, size and shape variation, at a very high spatial resolution over five years in a large-scale forest biodiversity – ecosystem functioning (BEF) experiment. Crown size and shape ultimately depend on the differential aboveground biomass allocation within a tree, in particular the trunk-to-branch ratio. Thus, current crown characteristics are the result of complex mechanisms operating at different levels of organization, including the differential investments among branches of different orders, the mode of ramification and branch morphology (Niinemets 2010; Lang *et al.* 2012; Van de Peer *et al.* 2017a). While first order branches largely define the crown contour, second and higher order branches characterise the inner crown structure. Typical morphological adjustments in response to locally favourable light conditions are an increase in branching rate or the formation of longer and thicker branches (Stoll & Schmid 1998). By such morphological changes at the branch level, trees modularly respond to micro-environmental light heterogeneity (Kawamura 2010), resulting in plasticity in crown characteristics among tree individuals within species and within tree individuals.

Previous studies varied in their support for the assumption that greater crown complementarity promotes productivity. Whereas Jucker *et al.* (2015) did not find a relationship between canopy packing and growth, Niklaus *et al.* (2017) and Williams *et al.* (2017) reported that crown complementarity was positively associated with biomass overyielding. In this study, we tested the impact of neighbourhood tree species richness on crown complementarity and its relationship to individual-tree growth. Specifically, we hypothesised that (1) crown complementarity increases with increasing neighbourhood tree species richness; (2) both crown size and crown shape variation contribute to crown complementarity, but the latter being more important in mixtures than in monocultures; (3) spatiotemporal tree diversity effects occur at different hierarchical levels, i.e. in trunk to branch allocation pattern, in branch morphology, and in crown architecture; and (4) higher crown complementarity promotes individual-tree growth.

MATERIAL AND METHODS

Study site and experimental design

The study was conducted in the BEF-China tree experiment, which is located near Xingangshan, Jiangxi Province in south-east subtropical China (29.08°-29.11°N, 117.90°-117.93°E, 100–300 m above sea level; Bruelheide *et al.* 2014). The experimental design is thoroughly described in the Supplementary Methods. Briefly, the experiment consists of two sites (A and B) established in 2009 and 2010, respectively. A total of 566 study plots of each 666.7 m^2 were randomly assigned to monocultures and two-, four-, eight-, 16-, and 24-species mixtures (derived from a pool of 40 tree species; Table S1). Each plot was planted with 400 (20 × 20) saplings in a raster pattern at equal projected distances of 1.29 m (Figure S1). Thus, each tree has potentially eight direct neighbours, which we here refer to as 'the local neighbourhood'. Species were randomly assigned to planting positions within a plot, by which a large number of intra- and interspecific interactions were implemented. Local neighbourhood tree species richness (NSR) therefore ranged from zero (monoculture) to eight (all neighbours consists of different species).

Terrestrial laser scanning data and tree inventory data

Using TLS we sampled 30 plots on site A including eight tree species (Table S2). The richness levels of these plots ranged from monocultures to two-, four-, and eight-species mixtures. TLS data was collected annually in the years 2012 to 2016. We used a standardized sampling scheme that captured each tree in the central area of the plots from multiple positions to ensure sufficient coverage (Figure S1). For each tree individual we manually extracted a high-resolution 3D point cloud (with a resolution of at least the 3 mm level, Figure S2). In total we extracted point clouds for 1554 tree individuals, resulting in 5861 tree point clouds across all years (Table S2).

For technical information, scan registration and tree extraction procedure see Supplementary Methods.

To test whether the results from the selected 30 plots agree well with those from all plots of site A and B, we used inventory data from direct measurements of tree height and ground diameter which were taken annually between September and October from 2010 to 2016 in site A and from 2011 to 2016 in site B. The aboveground wood volume was estimated for a total of 37184 trees (site A: 17856, site B: 19328, further details in Supplementary Methods).

Characterisation of crown size and shape

To quantify and compare the sizes and shapes of tree crowns we derived a range of simple to more complex structural characteristics from the individual-tree point clouds (Figure S2). These included: crown length, crown projection area (CPA), crown width, crown displacement, crown volume, crown surface area, crown sinuosity (Martin-Ducup *et al.* 2016), crown compactness, the Gini coefficient (Cowell 2011) of crown volumes per strata, as well as ratios of crown-width-to-crown-length, crown-length-to-tree-height, crown-width-to-tree-height, crown-surface-area-to-crown-volume and crown-displacement-to-tree-height. CPA, crown volume and crown surface area were computed using 2D and 3D alpha-shapes. For further details on crown structure metrics see Supplementary Methods.

Quantitative structure models from TLS data

From the point clouds quantitative structure models (QSMs) were used to quantify tree compartments (i.e. trunk and branches) and their respective wood volumes. QSMs are hierarchical geometric primitive models that accurately approximate the tree branching structure, geometry, and volume from a point cloud (Raumonen *et al.* 2013; Calders *et al.* 2015). The method first segments the tree into stem and individual branches and simultaneously defines its topological branching structure (e.g. branching order). In the second step the method creates a surface and volume model of the segments by fitting cylinders. Finally, the tree characteristics of interest (i.e. wood volumes of the trunk and branches of the different orders, branch diameters and lengths, etc.) are available from the cylinder model (Figure S2a). We used *TreeQSM* software (Åkerblom 2017) to derive the QSMs. For the specific QSM modelling parameters see Supplementary Methods.

Crown complementarity analysis

We computed the crown complementarity of a target tree with its neighbours according to Williams *et al.* (2017). Crown complementarity (CC) between two trees (i and j) was defined as "the difference among trees in crown volume within strata from the ground to the top of the canopy." It is computed as follows:

$$CC_{ij} = \frac{\sum |V_{ik} + V_{jk}|}{V_i + V_j}$$

where V_i and V_j are the crown volume in each strata k and of the whole tree i and j. In our study, we compute a local crown complementarity index (CCI_l) as the mean crown complementarity of a target tree i with all its direct neighbours (n):

$$CCI_l = \frac{\sum_j CC_{ij}}{n}$$

CCI_l can range between 0 (no complementarity) and 1 (complete complementarity). At the local neighbourhood scale elevation differences between planted trees did not affect CCI_l results.

To separate the effects of size and shape variation on the CCI_l we computed two neighbourhood measures that express each component. Local variation in crown size was computed as Rao's Q (Rao 1982, see Supplementary Methods) of all trees within the local neighbourhood. Local variation in crown shapes was computed as functional dispersion (Laliberté & Legendre 2010) using six crown characteristics (crown compactness, Gini coefficient of crown volume per strata, and the ratios crown-width-to-crown-length, crown-length-to-tree-height, crown-displacement-to-tree-height, crown-sinuosity-to-tree-height) of all trees in the local neighbourhood. These characteristics were selected because they were independent of tree size.

Species grouping based on tree (crown) morphology

To analyse groups of species in more detail we classified the eight tree species in our TLS study with regard to their ability for morphological flexibility (MF), i.e. the overall potential of a tree to respond with crown plasticity to changing environmental or competitive conditions. We considered a species as morphologically rigid when there is only little variation in morphological traits. In contrast, morphologically flexible species are characterised by a large variation in (crown) size and shape. To capture the complex nature of crown sizes and shapes, MF was quantified by a wide range of crown traits: crown sinuosity, crown compactness, Gini coefficient of crown strata volume, and the ratios of crown-width-to-crown-length, crown-length-to-tree-height, crown-surface-area-to-crown-volume, crown-displacement-to-tree-height, and crown-sinuosity-to-tree-height (Figure S3). To avoid possible effects of neighbourhood species richness on crown attributes, we only used trees from monoculture plots to compute species specific MF values (further details are provided in Supplementary Methods). Based on the morphological crown traits we derived a MF score for each tree species, which allowed to unequivocally assign each species to one of two groups: (1) morphologically flexible species (*Castanea henryi* (Skan) Rehder & E. H. Wilson, *Choerospondias axillaris* (Roxburgh) B. L. Burtt & A. W. Hill, *Quercus serrata* Murray and *Sapindus saponaria* L.), and (2) morphologically rigid species (*Liquidambar formosana* Hance, *Castanopsis sclerophylla* (Lindley & Paxton) Schottky, *Triadica sebifera* (L.) Small and *Nyssa sinensis* Oliver).

Neighbourhood competition index

To account for the local neighbourhood conditions experienced by a target tree, size and spatial patterns of neighbouring trees have to be considered (Radtke *et al.* 2003). Therefore, neighbourhood conditions cannot be expressed as a simple quantity, e.g. neighbour basal area, but also directional aspects of neighbourhood pressure have to be taken into account.

We regard a neighbourhood as highly competitive when: (1) neighbourhood basal area is high, (2) all neighbours are larger or equal in size compared relatively to the target tree, (3) competitive pressure on the target tree is formed from all directions, and (4) little variation in crown structural attributes exists. Largest competition intensity is then assumed to exist within a structurally homogeneous neighbourhood with a large number of strong competitors. Contrary, low levels of neighbourhood competition are expressed by fewer (and less strong) competitors and a structurally heterogeneous neighbourhood that enables better conditions for growth, e.g. through niche complementarity (Chen *et al*. 2016; Van de Peer *et al*. 2017b). We developed a neighbourhood competition index (NCI) which takes all these elements into account (for a detailed NCI description see Supplementary Methods).

Statistical analyses

To disentangle the effects of variation in crown size and shape of a local neighbourhood as drivers of local crown complementarity (CCI_l) in monocultures and species mixtures we used linear mixed-effects models with TLS data from 2015. For time-series analyses (2012 to 2016) we also applied linear mixed-effects models to test whether tree size and shape variables depended on NSR and NCI, and how these effects changed through time (i.e. years). In the models including time, we considered all possible two-way and three-way interactions. Moreover, we used the initial wood volume (inventory data from 2010) of a target tree as additional fixed effect. The target tree and study plot were used as nested random effects (tree nested in plot). Target trees' species identity and neighbourhood species composition were used as crossed random effects. The following response variables were used: aboveground wood volume, trunk wood volume, branch wood volume, ratio of trunk to branch wood volume, branch length, number of first and second order branches, diameter of first order branches, relative branch length (length/volume), crown volume, CPA, crown sinuosity and crown displacement.

For each model conditional and marginal r-squared values were computed to assess the amount of variance explained by both fixed (marginal) and random (conditional) effects. Response variables were log-transformed (except for CCI_l) as this resulted in an improved linear model fit and reduced residual variance. All predictors were standardised (divided by their standard deviation) before analysis. Parameter estimates of the models were based on restricted maximum likelihood (REML) estimation and are presented in Tables S3–S19. Variance inflation factors indicated no critical correlation (all VIFs < 1.5) between covariates. Model assumptions, including spatial independence, of our models were tested and confirmed according to Zuur *et al*. (2009). Residuals showed no significant sign of heteroscedasticity and were normally distributed around a zero mean. Effect size was computed as Cohen's d (Cohen 1988).

To explore how crown complementarity effects scale up from the local neighbourhood level to the plot level, we first calculated the net diversity effect (NE) at the stand level according to Loreau & Hector (2001) and distinguished statistical selection effects (SE) from statistical complementarity effects (CE). We further weighted NE by the mean CCI_l of a given plot: $\mathrm{NE}_{CCI} = \mathrm{NE} * \overline{CCI_l}$, where NE_{CCI} is the crown complementarity-weighted net diversity effect at the plot level and CCI_l the local crown complementarity index of a target tree.

Statistical analyses were performed with R 3.3.0 (R Core Team 2016) using the R packages lme4 (Bates *et al*. 2014), lmerTest (Kuznetsova *et al*. 2016), MuMIn (Barton 2016) and variancePartition (Hoffman & Schadt 2016).

RESULTS

We found a positive relationship between neighbourhood tree species richness (NSR) and local crown complementarity (CCI_l) (Fig. 1). The lower boundary of CCI_l increased with increasing NSR, whereas the upper boundary was near to or equal to the maximum value of 1.0 along the NSR gradient. Thus, CCI_l displayed a larger variation of values in less diverse neighbourhoods (between 0.25 and 0.99 in monocultures). Both crown size and shape variation significantly contributed to the variation in CCI_l, but the explanatory power of shape variation was higher than that of size (Fig. 1, Table S3). The importance of crown shape variation as a predictor of CCI_l increased in mixtures, whereas the opposite was observed for size.

On the individual-tree level, we found a significant three-way interaction between NSR, neighbourhood competition (NCI) and time in 11 of the 12 response variables (Table 1).

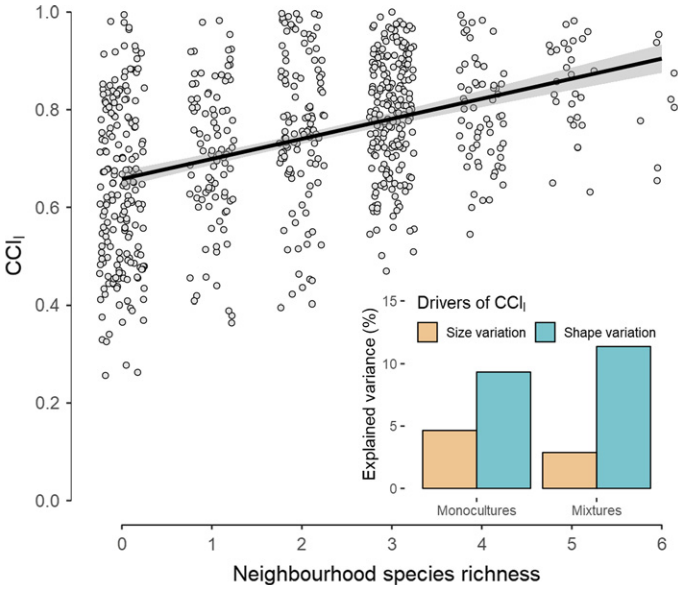

Figure 1 Neighbourhood species richness and crown complementarity. Gray dots represent crown complementarity (CCI_l) of a target tree with its local neighbours. Higher CCI_l values indicate higher complementarity. CCI_l computation was based on tree measurements in 2015 derived from point clouds (site A). The black line is a linear model fit (R^2 = 0.17, $P < 0.001$). Inset panel shows variance partitioning (based on a linear mixed model, see Methods) for the effects of crown size (size variation) and crown shape (shape variation) on CCI_l in monocultures and mixtures. Points are jittered for better clarity.

The effect of NSR on total wood volume and wood volume increment of individual trees strengthened through time with effects being modulated by NCI and focal trees' size, i.e. initial wood volume. The results were qualitatively the same based on inventory data from all plots at the two sites and for the subset of plots (site A) that were measured using TLS (Fig. 2a, Tables S4–S8, Figures S4–S5). The increase in wood volume was found for trunks and for branches, showing that both tree compartments benefitted from increased NSR (Tables S9–S10). The trunk-to-branch volume ratio increased with time and shifted in favour of branches at increased NSR, more so at low NCI, while promoting the trunk at high NCI (Fig. 2b, Table S11). At the branch level, we found a higher number of first and second order branches, greater lengths and diameters as well as lower relative branch lengths in more species-rich and less competitive neighbourhoods (Tables S12–S15). At the whole crown level, we observed a significant increase in crown volume and crown projection area as well

Table 1 Mixed-effects models (ANOVA, type III sum of squares) for effects of initial tree wood volume (initial size), neighbourhood tree species richness (NSR), neighbourhood competition (NCI), year, and interactions on individual tree wood volumes and crown architecture ($n = 2773$)

	Above-ground wood volume (log)				Trunk wood volume (log)				Branch wood volume (log)			
Fixed effect	$\mathrm{df}_{\mathrm{num}}$	$\mathrm{df}_{\mathrm{den}}$	*F*	*P*	$\mathrm{df}_{\mathrm{num}}$	$\mathrm{df}_{\mathrm{den}}$	*F*	*P*	$\mathrm{df}_{\mathrm{num}}$	$\mathrm{df}_{\mathrm{den}}$	*F*	*P*
Initial size	1	724.1	756.04	< 0.001	1	723.9	767.41	< 0.001	1	721.6	623.68	< 0.001
NCI	1	2581.4	49.35	< 0.001	1	2595.3	70.88	< 0.001	1	2526.1	28.07	< 0.001
NSR	1	1812.5	10.16	< 0.01	1	1842.2	5.15	< 0.05	1	1839.8	7.16	< 0.01
Year	1	2106.1	135.28	< 0.001	1	2107.3	238.76	< 0.001	1	2117.2	42.59	< 0.001
NCI*NSR	1	2676.8	13.75	< 0.001	1	2697.6	7.33	< 0.01	1	2673.2	10.03	< 0.01
NCI*Year	1	2058.2	9.78	< 0.01	1	2059.6	33.35	< 0.001	1	2069.0	0.81	0.370
NSR*Year	1	2135.6	15.60	< 0.001	1	2154.7	1.68	0.196	1	2166.2	24.41	< 0.001
NCI*NSR*Year	1	2129.4	20.28	< 0.001	1	2144.5	3.99	< 0.05	1	2153.4	26.58	< 0.001

	Trunk volume/ branch volume (log)				Branch length (log)				Number of branches (1st and 2nd order) (log)			
Fixed effect	$\mathrm{df}_{\mathrm{num}}$	$\mathrm{df}_{\mathrm{den}}$	*F*	*P*	$\mathrm{df}_{\mathrm{num}}$	$\mathrm{df}_{\mathrm{den}}$	*F*	*P*	$\mathrm{df}_{\mathrm{num}}$	$\mathrm{df}_{\mathrm{den}}$	*F*	*P*
Initial size	1	695.283	66.19	< 0.001	1	728.8	682.97	< 0.001	1	721.9	578.13	< 0.001
NCI	1	2137.4	0.84	0.361	1	2522.9	43.58	< 0.001	1	2337.5	40.55	< 0.001
NSR	1	1745.3	5.65	< 0.05	1	1845.5	1.83	0.176	1	1743.8	2.41	0.121
Year	1	2218.1	25.58	< 0.001	1	2119.2	109.72	< 0.001	1	2149.8	80.56	< 0.001
NCI*NSR	1	2337.2	6.91	< 0.01	1	2663.4	4.43	< 0.05	1	2533.7	7.39	< 0.01
NCI*Year	1	2173.7	13.54	< 0.001	1	2069.8	14.70	< 0.001	1	2097.3	5.66	< 0.05
NSR*Year	1	2262.0	24.99	< 0.001	1	2165.7	3.41	0.065	1	2186.1	9.00	< 0.01
NCI*NSR*Year	1	2253.3	21.37	< 0.001	1	2154.8	3.89	< 0.05	1	2178.5	12.46	< 0.001

	Diameter 1st order branches (log)				Relative branch length (log)				Crown volume (log)			
Fixed effect	$\mathrm{df}_{\mathrm{num}}$	$\mathrm{df}_{\mathrm{den}}$	*F*	*P*	$\mathrm{df}_{\mathrm{num}}$	$\mathrm{df}_{\mathrm{den}}$	*F*	*P*	$\mathrm{df}_{\mathrm{num}}$	$\mathrm{df}_{\mathrm{den}}$	*F*	*P*
Initial size	1	636.1	194.66	< 0.001	1	632.6	170.37	< 0.001	1	700.7	552.49	< 0.001
NCI	1	1888.1	0.78	0.378	1	1979.6	0.06	0.802	1	2367.8	41.52	< 0.001
NSR	1	1748.2	7.95	< 0.01	1	1672.4	13.97	< 0.001	1	1842.4	2.09	0.148
Year	1	2240.1	3.44	0.064	1	2213.2	6.45	< 0.05	1	2107.9	59.56	< 0.001
NCI*NSR	1	2157.6	8.27	< 0.01	1	2222.5	12.89	< 0.001	1	2564.7	4.15	< 0.05
NCI*Year	1	2209.3	6.24	< 0.05	1	2178.5	11.36	< 0.001	1	2062.0	7.06	< 0.01
NSR*Year	1	2223.5	20.85	< 0.01	1	2266.3	32.83	< 0.001	1	2143.0	4.55	< 0.05
NCI*NSR*Year	1	2231.2	21.32	< 0.01	1	2260.0	34.29	< 0.001	1	2134.3	4.58	< 0.05

	Crown projection area (log)				Crown sinuosity (log)				Crown displacement (log)			
Fixed effect	$\mathrm{df}_{\mathrm{num}}$	$\mathrm{df}_{\mathrm{den}}$	*F*	*P*	$\mathrm{df}_{\mathrm{num}}$	$\mathrm{df}_{\mathrm{den}}$	*F*	*P*	$\mathrm{df}_{\mathrm{num}}$	$\mathrm{df}_{\mathrm{den}}$	*F*	*P*
Initial size	1	703.6	590.36	< 0.001	1	727.1	127.37	< 0.001	-	-	-	-
NCI	1	2528.1	90.60	< 0.001	1	2408.3	5.11	< 0.05	1	2356.2	88.96	< 0.001
NSR	1	150.9	0.53	0.464	1	1874.5	2.27	0.132	1	2525.1	19.32	< 0.001
Year	1	2182.9	99.68	< 0.001	1	2114.5	7.45	< 0.01	1	2232.9	28.78	< 0.001
NCI*NSR	-	-	-	-	1	2535.2	1.10	0.296	1	2598.8	15.14	< 0.001
NCI*Year	1	2150.6	5.86	< 0.05	1	2071.6	1.76	0.185	1	2203.2	42.22	< 0.001
NSR*Year	1	2082.5	14.61	< 0.001	1	2173.1	10.26	< 0.01	1	2266.7	20.29	< 0.001
NCI*NSR*Year	-	-	-	-	1	2158.6	4.67	< 0.05	1	2248.6	11.24	< 0.001

All tree parameters were derived using TLS based analyses. $\mathrm{df}_{\mathrm{num}}$, numerator degrees of freedom; $\mathrm{df}_{\mathrm{den}}$, denominator degrees of freedom. *F* and *P* indicate *F* ratios and the *P* value of the significance test, respectively. "-" indicates that terms were not included in the model.

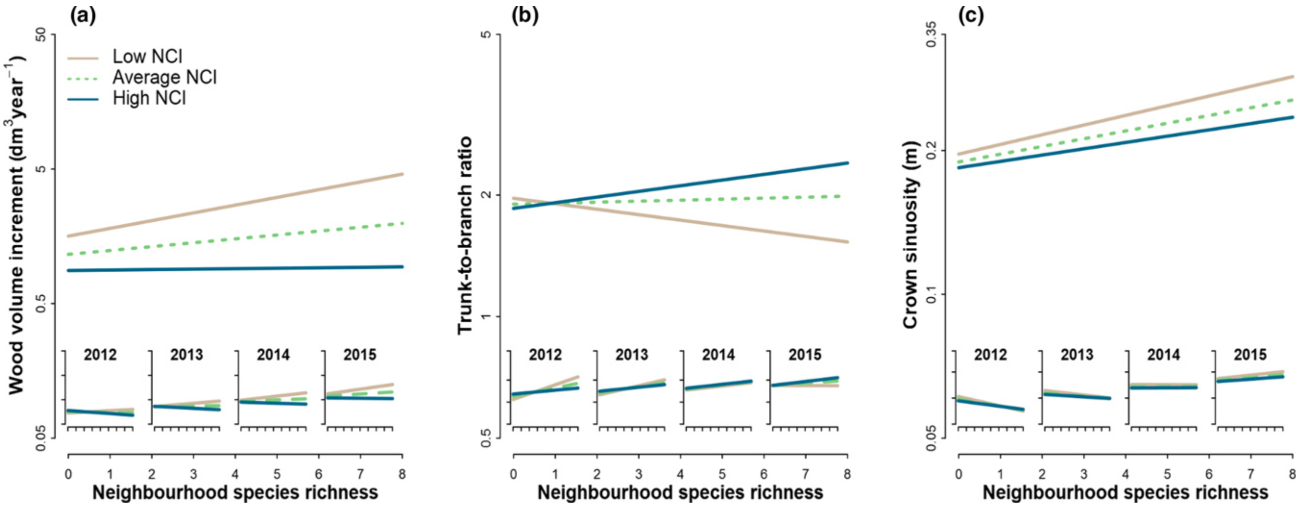

Figure 2 Interplay between neighbourhood species richness and competition over time. (a) Diversity-productivity relationship in relation to various intensities of neighbourhood competition (NCI). Lines correspond to the predicted response based on linear mixed-effects models for field observations ($n = 36556$ over 6 years) at experimental site A. Average NCI corresponds to mean NCI value, low and high NCI correspond to the lower (25%) and upper (75%) quartiles. Inset panel displays the temporal development during 2012 and 2015, while main panels display the growth response in 2016. Species richness corresponds to the number of heterospecific neighbours. Y-axis is logarithmic. Initial wood volume was kept at its mean. (b) Change of wood volume allocation pattern between trunk and branch (trunk-to-branch ratio) in relation to species richness under three different scenarios of competition (NCI) at the local neighbourhood scale. Lines correspond to the predicted response based on linear mixed-effects models for TLS-based observations ($n = 5861$ over 5 years) at experiment site A. Average NCI corresponds to mean NCI value, low and high NCI correspond to the lower (25%) and upper (75%) quartiles. Inset panel displays the temporal development during 2012 and 2015, while main panels display the growth response in 2016. Species richness corresponds to the number of heterospecific neighbours. Y-axis is logarithmic. Initial wood volume was kept at its mean. (c) Change of crown sinuosity, as a measure of crown plasticity, in relation to species richness under three different scenarios of competition (NCI) at the local neighbourhood scale. Lines correspond to the predicted response based on linear mixed-effects models for TLS-based observations ($n = 5861$ over 5 years) at experiment site A. Average NCI corresponds to mean NCI value, low and high NCI correspond to the lower (25%) and upper (75%) quartiles. Inset panel displays the temporal development during 2012 and 2015, while main panels display the growth response in 2016. Species richness corresponds to the number of heterospecific neighbours. Y-axis is logarithmic. Initial wood volume was kept at its mean.

as a greater crown displacement and sinuosity in more diverse neighbourhoods (Fig. 2c, Tables S16–S19). The latter two increased on average by 10% and 8%, respectively, compared to monocultures, indicating that crown plasticity of individual trees was higher in mixtures. This is in alignment with a greater importance of crown shape variation for CCI_l.

The power of the NSR effect for the 12 response variables was trait-dependent, with morphologically flexible species showing a stronger and morphologically rigid species a weaker effect (Fig. 3). These plasticity-driven differences translated into differences in crown complementarity, with higher CCI_l values for morphologically flexible species compared to rigid species (Figure S6).

Individual trees experiencing a low crown complementarity in the local neighbourhood showed an intermediate growth rate whereas a high crown complementarity was associated with both, very high and very low growth rates (data not shown). In our study with eight species, the four species in each of the two morphological trait groups showed different height growth rates (Figure S7). Therefore, to avoid simple size related effects on CCI_l and growth, we compared this relation only for two species each with similar high growth rates (morpohologically flexible: *Choerospondias axillaris, Castanea henryi*; morphologically rigid: *Nyssa sinensis, Liquidambar formosana*). Trees in neighbourhoods of high CCI_l growing at low NCI showed higher growth rates compared to those growing at high NCI, and the relation changed from negative to slightly positive/ neutral in morphologically flexible species in mixtures (Fig. 4).

At the stand level we observed a significant overyielding - mainly driven via statistical complementarity effects - with increasing species richness (Fig. 5, Figure S8). Therefore, the positive NSR and *CCI* effects at the local neighbourhood scale translated into stand-level effects over time.

DISCUSSION

Our study shows that crown complementarity increases with neighbourhood tree species richness, as diverse neighbourhoods allowed trees to optimize their crown morphology (crown size and shape) with effects being stronger for crown shape. This neighbourhood-driven plasticity was mainly brought about by enhanced biomass allocation to branches and changes in branch morphology, suggesting that diversity-mediated biomass allocation may be a fundamental mechanism of positive biodiversity-productivity relationships in forest ecosystems. These processes developed over time in the young experimental plantation, and differed between morphologically flexible and rigid species.

Our finding of higher crown complementarity in species mixtures coincides with our first hypothesis and was previously shown in observational and experimental studies (Jucker *et al.* 2015; Niklaus *et al.* 2017; Williams *et al.* 2017). In addition, our results denote the high importance of the level of

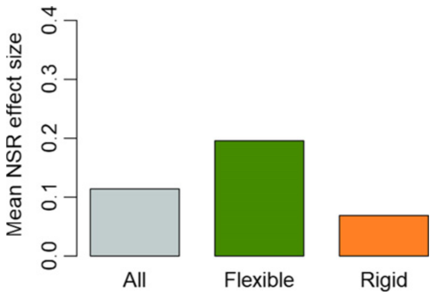

Figure 3 NSR effect size for species groups (based on morphological traits). Mean absolute effect size (Cohen's d) of neighbourhood species richness (NSR) for all trees and species groups was computed as the mean of the individual NSR effect size in each model across the 12 studied TLS-based tree parameters. Species are classified according to their variability in morphological traits: flexible (*Castanea henryi, Choerospondias axillaris, Quercus serrata, Sapindus saponaria*) and rigid (*Liquidambar formosana, Castanopsis sclerophylla, Triadica sebifera, Nyssa sinensis*). Samples size of target trees with full information on all neighbours: all = 2773, flexible = 1534, rigid = 1239.

species richness at the local neighbourhood, which had a strong impact on the minimum CCI_l values. The large range of CCI_l values in monocultures is only due to architectural differences within species. In conspecific neighbourhoods, size variation can solely stem from differences among tree individuals within a species, whereas shape variation can occur both among individuals within a species and within individuals. Even in monocultures a large variability in crown shapes is an important prerequisite for attaining a high crown complementarity. The considerable increase of lowest CCI_l values in mixtures shows that differences among species add an important amount of crown size and shape variation. The increased proportion of variance explained by crown shape compared to size, confirming our second hypothesis, suggests that diversity-driven shape plasticity of tree crowns is of great importance in mixtures, and that the relevance of crown plasticity might have been underestimated by the approaches used in previous studies (Jucker *et al.* 2015; Niklaus *et al.* 2017; Williams *et al.* 2017). Our analysis thus suggests that species diversity induces trait variability, here a high variability of crown architectural traits of individual trees in mixed-species stands.

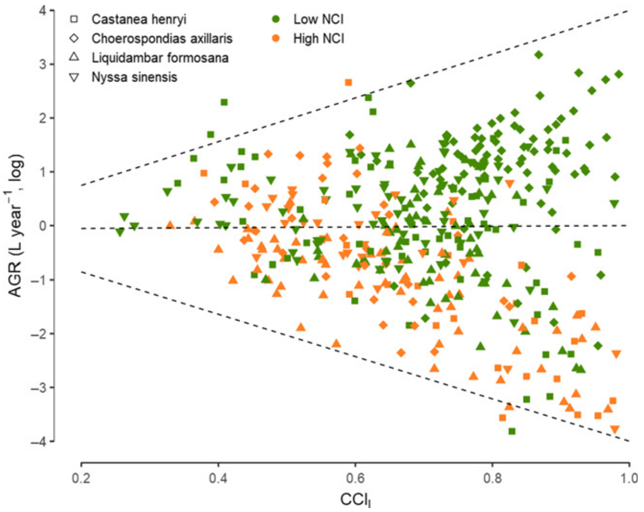

Figure 4 Crown complementarity and absolute growth rate. Data shows observed absolute growth rate per year (AGR, 2010 to 2015) of total wood volume in relation to local crown complementarity (CCI_l) for four species (indicated by different shapes) with similar height growth. Colours indicate low and high local neighbourhood competition (NCI). Horizontal dashed line displays median AGR. Sloped dashed lines indicate that, both, positive and negative crown complementarity–growth relationship can occur with increasing CCI_l.

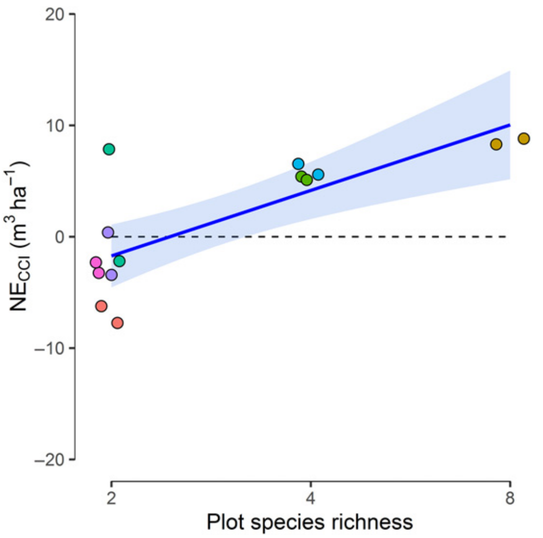

Figure 5 Relationship between the crown-complementarity-weighted net diversity effect (NE$_{CCI}$) and tree species richness at the plot level. Data points show crown-complementarity-weighted net diversity effect in the year 2015 for species mixtures in relation to their respective monocultures (R^2 = 0.56, F = 15.17, $P < 0.01$). The analysis is based on 30 plots that were surveyed using TLS. Colours indicate equal species combinations of the plots. The y-axis is square root-transformed. Points are slightly jittered for better visibility.

The biological foundation for the diversity-mediated modifications in individual-tree crown architecture are mechanisms operating at different hierarchical levels of organisation, including differential aboveground biomass allocation within trees as well as the ramification mode and morphology of branches. At all levels we observed significant neighbourhood diversity effects, which supported our third hypothesis. For the BEF-China experiment it has been found that tree species richness increased productivity both at the individual-tree (Fichtner *et al.* 2017, 2018) and at the stand-level (Huang *et al.* 2018). Our analysis indicates that both main aboveground woody compartments, i.e. trunks and branches, benefitted from increased local neighbourhood species richness. Carbon investments in the trunk drive height primary growth with apical meristems and radial secondary growth. Because competition for light is typically size-asymmetric, height increment has the highest priority for biomass allocation when light is limiting growth (Falster & Westoby 2003; Pretzsch 2009). Preferential carbon investments in primary growth are, therefore, to be expected in the young tree communities at the study site, which is confirmed by the rapid height increments observed by Li *et al.* (2017) in this experiment. Crown dimensions and crown shape plasticity, however, critically depend on the proportion of biomass allocated to the branches. The trunk-to-branch volume ratio undergoes ontogenetic changes, leading to increased values over time because of higher growth rates in trunks than in branches (Niklas 1995; Silveira *et al.* 2012). In our study, however, we found that tree species richness modifies this trend in favour of branches, indicating that neighbourhood effects can compensate for age-related shifts in aboveground biomass partitioning patterns. These shifts in allocation might form an important mechanistic basis underlying enhanced crown plasticity in mixtures.

The observed diversity-driven responses at the branch level do not only facilitate an increased crown size (e.g. higher crown projection area and crown volume due to higher numbers and greater length of first order branches), but in particular lead to differences in the crown shape, including the inner crown properties. Our results confirm findings from Bayer *et al.* (2013) who reported that mature European beech (*Fagus sylvatica* L.) trees growing in mixture with Norway spruce (*Picea abies* (L.) H. Karst) had significantly more branches of the first three orders and a higher sum of branch lengths compared with those in monocultures. Finally, at the whole crown level, we found that crowns were more displaced and more sinuous in mixtures than in monocultures, demonstrating the ability of these young trees for lateral crown expansion away from the stem base position. The development of asymmetric crowns may be caused by branch expansion towards high light conditions (phototrophic growth) and by inhibition of branch growth and survival under unfavourable light conditions (correlative inhibition; Stoll & Schmid 1998). These results support the assumption that both vertical and lateral expansion of the crowns contribute significantly to physical niche partitioning in canopy space (Longuetaud *et al.* 2013; Forrester & Bauhus 2016; Martin-Ducup *et al.* 2016; Barbeito *et al.* 2017).

The response of all architectural variables to species richness was affected by neighbourhood competition (NCI) and varied over time. Our NCI can be interpreted as a spatially explicit standardised competition index of the local neighbourhood. The spatial arrangement of neighbouring trees is an important dimension in the competition for canopy space. For a target tree it might make a great difference whether neighbours are equally distributed around the tree or only occur in particular directions. Structural heterogeneity can modulate competition and biodiversity (McElhinny *et al.* 2005; Sabatini *et al.* 2015) and vice versa. Furthermore, the temporal impact is likely a consequence of the compensatory feedback loop "Structure → Environment → Growth → Structure" operating in the forest ecosystems (Pretzsch 2014; Martin-Ducup *et al.* 2016). A tree's stature and structure captures the effects of local neighbourhood interactions and growth responses of the past, and morphological adjustments in the 3D tree architecture need time to emerge. This might explain the differences between our findings and those of other studies using only a single measurement (Lang *et al.* 2012; Van de Peer *et al.* 2017a), according to which tree diversity approved to be a poor predictor for aboveground biomass allocation and tree architecture. And it also provides an explanation for the finding that, in contrast to observations in grassland BEF-experiments, the positive biodiversity effects in tree communities emerge with time (Reich *et al.* 2012; Huang *et al.* 2018).

Functional traits largely regulate the local neighbourhood interactions (Butterfield & Callaway 2013). Fichtner *et al.* (2017) demonstrated that the driving mechanisms of diversity effects at the local neighbourhood scale depend on the target tree's resource-use strategy: these effects were brought about by competitive reduction for species with acquisitive traits, and by facilitation for species with a conservative resource-use strategy. In our study we used a subset of the species included by Fichtner *et al.* (2017), but seven of the eight species were acquisitive, and only one species conservative (namely *Castanopsis sclerophylla*). We therefore assume that competitive neighbour interactions prevailed in the present study, and target tree's ability for morphological flexibility largely determine its response to local neighbourhood tree species richness.

Moreover, we hypothesized that higher crown complementarity promotes individual-tree growth, which was only partly supported due to the large variation in growth rates at higher levels of crown complementarity. In part, these findings contrast those of Williams *et al.* (2017) who reported that crown complementarity at the plot level was positively related to stem biomass overyielding. This might be explained by the fact that in their study of very young tree communities crown complementarity was largely driven by species identity (selection effects) rather than statistical complementarity effects or by differences in the biomes (temperate vs. subtropical). Our findings, however, are in line with the conceptional model on the influence of stand structural attributes on forest functioning, which ranges from positive over neutral to negative (Ali 2019). A positive effect would be attributable to the enhancement of the resource use partitioning, whereas negative effects would result from asymmetric competition. Note that crown complementarity, measured as *CCI*, does not inevitably provide information on the competitiveness of a tree. Small or growth-inhibited trees can exhibit very high levels of *CCI*. Given that in our study species are mainly associated with an acquisitive resource-use strategy, smaller individuals and/or those experiencing a high NCI suffered from a high CCI_I. In these communities, high crown complementarity may result in competitive reduction in some cases and in increased competition in other cases. Nonetheless, altogether, species mixtures more frequently provide higher crown complementarity and structural variability leading to reduced competitive pressure that allowed trees to increase their productivity. This translated into overyielding at the stand level and is consistent with findings of Fichtner *et al.* (2018).

We are aware that we could not account for physiological responses, diversity-mediated effects of herbivory and pathogens, or belowground interactions which have been shown to be additional important factors for tree growth (Ishii & Asano 2010; Bu *et al.* 2017; Schuldt *et al.* 2017). Variation in topography and soil conditions may also effect tree growth but those factors were found to be of weak explanatory power in the BEF-China experiment (Kröber *et al.* 2015; Fichtner *et al.* 2018). We also note the limitation to generalize results from juvenile tree field-experiments to adult tree communities. However, overall, our results provide evidence that the temporal variation in tree productivity strongly depends on species richness and structural variability of the local neighbourhood of a target tree. Promoting high taxonomic and structural diversity at the local neighbourhood scale is therefore an important goal for enhancing forest productivity. Moreover, we showed that trees are highly flexible in their morphology due to increased investment into trunk and branch wood under favourable neighbourhood conditions (i.e. species-rich and structurally less competitive neighbourhoods). Given the temporal importance of crown complementarity development, our study suggest that exploring neighbourhood diversity-mediated responses of carbon allocation and partitioning is a critical next step to deepen our understanding of the functional role of tree diversity in providing forest-based ecosystem services in future.

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AUTHORSHIP

MK and GvO conceived the idea of this study. HB, WH and GvO designed the research. GvO, WH and MK compiled the data and performed the literature search. MK, AF, HB and PR analysed the data. MK wrote the first draft of the manuscript and all the authors contributed substantially to the submitted version.

DATA AVAILABILITY STATEMENT

Inventory data sets are deposited in the BEF-China data portal under dataset numbers 593/594 (http://china.befdata.biow.uni-leipzig.de/) and under Dryad Digital Repository (https://doi.org/10.5061/dryad.0gb5mkkwk). Additional Supporting Information may be downloaded via the online version of this article at Wiley Online Library (www.ecologyletters.com).

DATA DEPOSIT STATEMENT

Inventory data sets are deposited in the BEF-China data portal under dataset number 593/594 (http://china.befdata.biow.uni-leipzig.de/).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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Chapter 5

Neighbourhood diversity mitigates drought impacts on tree growth

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Neighbourhood diversity mitigates drought impacts on tree growth

Andreas Fichtner[1] | **Florian Schnabel**[2,3] | **Helge Bruelheide**[3,4] | **Matthias Kunz**[5] | **Katharina Mausolf**[6] | **Andreas Schuldt**[7] | **Werner Härdtle**[1] | **Goddert von Oheimb**[3,5]

[1]Institute of Ecology, Leuphana University of Lüneburg, Lüneburg, Germany; [2]Systematic Botany and Functional Biodiversity, Leipzig University, Leipzig, Germany; [3]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany; [4]Institute of Biology/Geobotany and Botanical Garden, Martin Luther University Halle-Wittenberg, Halle (Saale), Germany; [5]Technische Universität Dresden, Institute of General Ecology and Environmental Protection, Tharandt, Germany; [6]Institute of Ecosystem Research, Kiel University, Kiel, Germany and [7]Faculty of Forest Sciences, Forest Nature Conservation, Georg-August-University Göttingen, Göttingen, Germany

Correspondence
Andreas Fichtner
Email: fichtner@leuphana.de

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Abstract

1. Biodiversity is considered to mitigate detrimental impacts of climate change on the functioning of forest ecosystems, such as drought-induced decline in forest productivity. However, previous studies produced controversial results and experimental evidence is rare. Specifically, the biological mechanisms underlying mitigation effects remain unclear, as existing work focuses on biodiversity effects related to the community scale.
2. Using trait-based neighbourhood models, we quantified changes in above-ground wood productivity of 3,397 trees that were planted in a large-scale tree diversity experiment in subtropical China across gradients of neighbourhood diversity and climatic conditions over a 6-year period. This approach allowed us to simultaneously assess to what extent functional traits of a focal tree and biodiversity at the local neighbourhood scale mediate the growth response of individual trees to drought events.
3. We found that neighbourhood tree species richness can mitigate for drought-induced growth decline of young trees. Overall, positive net biodiversity effects were strongest during drought and increased with increasing taxonomic diversity of neighbours. In particular, drought-sensitive species (i.e. those with a low cavitation resistance) benefitted the most from growing in diverse neighbourhoods, suggesting that soil water partitioning among local neighbours during drought particularly facilitated most vulnerable individuals. Thus, diverse neighbourhoods may enhance ecosystem resistance to drought by locally supporting drought-sensitive species in the community.
4. *Synthesis*. Our findings demonstrate that mechanisms operating at the local neighbourhood scale are a key component for regulating forests responses to drought

and improve insights into how local species interactions vary along stress gradients in highly diverse tree communities.

KEYWORDS
biodiversity, climate change, drought resistance, ecosystem functioning, forest, functional traits, species interactions, stress-gradient hypothesis

1 | INTRODUCTION

Forests store immense amounts of carbon (Pan et al., 2011), and carbon sequestration by trees is assumed to be an important measure to remove carbon dioxide from the atmosphere (Griscom et al., 2017). However, the expected increase in severity and frequency of drought events (IPCC, 2018) might have detrimental impacts on forest ecosystem functions (e.g. biomass production), services (e.g. carbon sequestration), species composition and diversity (Choat et al., 2018; Zhang, Niinemets, Sheffield, & Lichstein, 2018). Conversely, biodiversity has a positive effect on forest productivity (Duffy, Godwin, & Cardinale, 2017), as mixed-species forest communities have been demonstrated to be more productive (Huang et al., 2018; Liang et al., 2016) and more consistent in productivity over time than monocultures (del Río et al., 2017; Jucker, Bouriaud, Avacaritei, & Coomes, 2014; Morin, Fahse, de Mazancourt, Scherer-Lorenzen, & Bugmann, 2014; Schnabel et al., 2019), resulting in higher amounts of carbon stored above- and below-ground in species-rich forests (Liu et al., 2018). Yet, despite advances in our understanding of biodiversity–productivity relationships (BPRs), the role of biodiversity in mitigating adverse effects of climate change on the functioning of forest ecosystems remains controversial (Ammer, 2019; González de Andrés, 2019; Grossiord, 2019; Hisano, Chen, Searle, & Reich, 2019; Hisano, Searle, & Chen, 2018), making predictions of ecosystem responses to climate change challenging. For example, it has been shown that the strength of BPRs at the community scale was higher in forest types or at forest sites associated with adverse climatic conditions (Jucker et al., 2016; Paquette & Messier, 2011), but the opposite response was revealed for forest sites along a global precipitation gradient (Jactel et al., 2018). In contrast, a recent study showed that functional tree diversity enhanced community productivity during normal, but not during warmer climatic conditions (Paquette, Vayreda, Coll, Messier, & Retana, 2018). Similarly, interannual variation in climate has been demonstrated to have no consistent effect on the strength of community BPRs within a given forest site (Jucker et al., 2016). This indicates that we currently lack a general understanding of mitigation effects (i.e. the potential of biodiversity in attenuating climate change impacts on ecosystem functioning, such as drought-induced decline in growth) in long-lived plant communities, such as forests.

Biodiversity-mediated effects on ecosystem functioning can result from species interactions, leading to competitive reduction or facilitation, thereby promoting ecosystem functions (Barry et al., 2019). The existing controversies regarding mitigation effects might therefore be reconciled when considering the relevant scale for species interactions, that is, the local neighbourhood (Stoll & Weiner, 2000). Such biodiversity-mediated interactions among local neighbours are a key component for regulating productivity in diverse tree communities (Fichtner et al., 2018), suggesting that the potential of biodiversity in mitigating the impact of drought on tree growth largely depends on how species interact at the local neighbourhood scale. In this context, the stress-gradient hypothesis (SGH) predicts that competitive plant–plant interactions become less important in favour of facilitative ones with increasing environmental stress (Bertness & Callaway, 1994). Consequently, BPRs at the local neighbourhood scale should become stronger during periods of water deficits, meaning that the relative importance of biodiversity effects increases during drought (Figure 1a,b). The few evidence on climate–growth relationships in response to local neighbourhood conditions comes from observational studies performed in less diverse temperate forests with a limited taxonomic tree diversity (Jourdan, Kunstler, & Morin, 2019), and most of these studies accounted for neighbourhood diversity using a contrast of neighbourhood composition (conspecific vs. heterospecific neighbours; Mölder & Leuschner, 2014; Vitali, Forrester, & Bauhus, 2018) or neighbourhood competition (intraspecific vs. interspecific competition; Aussenac, Bergeron, Gravel, & Drobyshev, 2019). Similarly, one recent experimental study explored drought resistance of tropical tree seedlings in response to neighbourhood composition (conspecific vs. heterospecific neighbours; O'Brien, Reynolds, Ong, & Hector, 2017). Improving mechanistic insight into mitigation effects therefore requires experimental evidence on how local neighbourhood interactions alter the response of individual trees to drought across biodiversity levels (i.e. along a gradient of neighbourhood diversity), particularly in highly diverse tree communities.

Refined versions of the SGH additionally suggest that the outcome of local neighbourhood interactions may depend on the stress tolerance and diversity of the interacting species (Maestre, Callaway, Valladares, & Lortie, 2009; Soliveres, Smit, & Maestre, 2015). In a previous study, we showed that the mode (competitive reduction and facilitation) and intensity of biodiversity-mediated neigbourhood interactions in subtropical tree communities is closely related to the functional traits of the focal species (Fichtner et al., 2017). Moreover, there is evidence that the diversity in hydraulic traits of component trees within a community play an important role for regulating forest ecosystem resilience to drought (Anderegg et al., 2018). Thus, it is further conceivable that functional traits

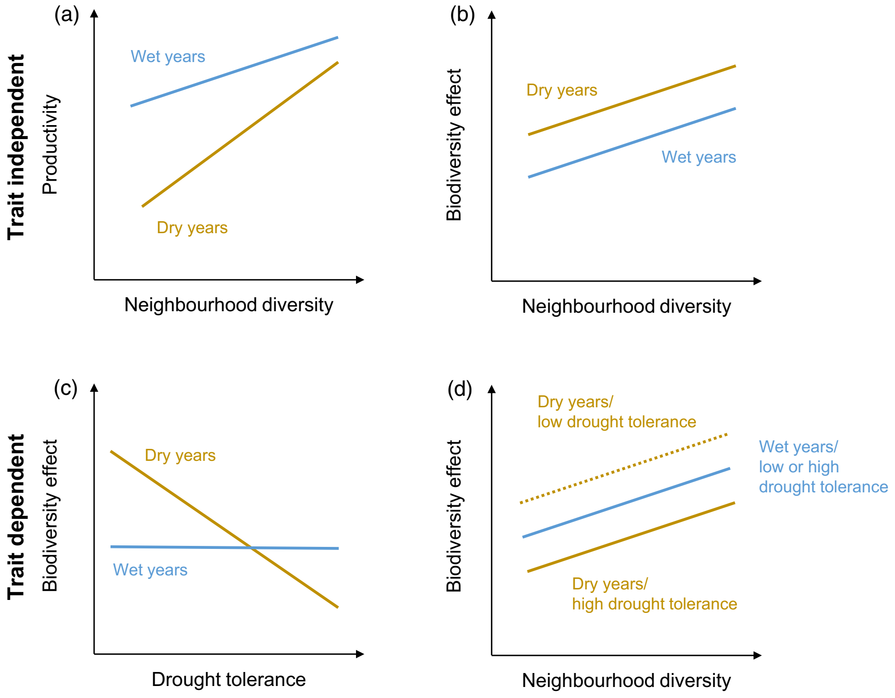

FIGURE 1 Neighbourhood interactions and climate change. (a) Across different tree species (trait-independent response), neighbourhood diversity is assumed to mitigate negative impacts of climate change on individual tree productivity, resulting in a positive biodiversity–productivity relationship during drought. Moreover, the relative importance of neighbourhood diversity in mitigating drought-induced growth decline is expected to increase during drought, thus (b) the magnitude (effect size) of biodiversity effects should become stronger. (c) Alternatively, the magnitude of biodiversity effects might depend on the species' functional traits associated with drought tolerance (trait-dependent response). (d) Biodiversity effects are, thus, expected to become stronger for drought-sensitive species during unfavourable climatic conditions (in dry years), while they should become stronger for drought-tolerant species during favourable climatic conditions (in wet years). Consequently, the relative importance (effect size) of neighbourhood diversity in modulating climate change impacts should critically depend on species' functional traits

that predict the species' response to water limitations and therefore its drought tolerance mediate the magnitude of biodiversity effects (effect size) at the local neighbourhood scale during drought (Figure 1c,d).

Here, we used growth and trait data of young subtropical trees planted in a large-scale biodiversity–ecosystem functioning experiment in China (BEF-China; Bruelheide et al., 2014) to explore how climate variability (years with and without water deficits) modulates biodiversity effects on tree growth at the local neighbourhood scale (using species richness as a measure for biodiversity). In this study, we define the term 'biodiversity effect' as the net effect of all intra- and interspecific interactions within the neighbourhood of a single focal tree, while the neighbourhood is defined as the total number of closest trees surrounding the focal tree (i.e. the local neighbourhood). Note that this definition differs from the one in Loreau and Hector (2001), where the diversity effect refers to the whole community. Our tree communities cover a long diversity gradient, ranging from monocultures to 24-species mixtures and from conspecific neighbourhoods to species-rich neighbourhoods with a maximum of eight heterospecific neighbours. Specifically, we quantified growth responses of 3,397 focal trees, belonging to 25 species, to climate events along an experimentally manipulated gradient of local neighbourhood diversity over a 6-year period. Using trait-based neighbourhood models, we tested whether neighbourhood diversity mitigates drought-induced growth decline. We hypothesized (a) that positive biodiversity effects become stronger during years with water deficits and (b) that the focal trees' drought tolerance (using cavitation resistance as a key physiological trait that predicts the species' response to water limitations) mediate the importance of biodiversity effects at the local neighbourhood scale.

2 | MATERIALS AND METHODS

2.1 | Study site and experimental design

In this study, we used data from 228 study plots (25.8 × 25.8 m^2) of a 26.6-ha experimental site (site A; 29.125°N, 117.908°E) established in southeast subtropical China as part of the BEF-China tree diversity experiment (Bruelheide et al., 2014). The study site is located on sloped terrain (average slope 27.5°) between 105 and 275 m above sea level. The climate of the study area is characterized as subtropical summer monsoon (mean annual temperature of 16.7°C and mean precipitation of 1,821 mm/year, averaged from 1971 to 2000; Yang et al., 2013) with the wet season lasting from April to August. The mean annual temperature for the study period (2010–2016; based on available data from the closest weather station Jingdezhen, CMA, 2019) was 18.4°C and the mean precipitation was 2,111 mm/year. The mean monthly temperatures ranged from 2.9°C (winter) to 34.8°C (summer) and the mean monthly precipitation ranged from 25 mm/month (winter) to 492 mm/month (summer). Prevailing soil types are Cambisols, Regosols and Colluvissols (Scholten et al., 2017). In March 2009, each study plot was planted with 400 1- to 2-year-old tree saplings (20 × 20 individuals) with a horizontal planting distance of 1.29 m (Bruelheide et al., 2014). Based on a species pool of 40 native broad-leaved tree species, a long diversity gradient was created by manipulating the number of tree species within a plot (monocultures and mixed communities of 2, 4, 8, 16 and 24 tree species), where species and tree diversity levels were randomly assigned to planting positions and plots. All saplings that died during the first growing season were replanted in November 2009 (deciduous species) and March 2010 (evergreen species). More detailed information on the experimental design is provided by Bruelheide et al. (2014).

2.2 | Tree data

For all trees within a plot, species identity, stem diameter (measured 5 cm above-ground) and tree height (measured from the stem base to the apical meristem) were recorded. To avoid confounding effects between experimental treatments and planting, tree measurements started in autumn (September–October) 2010. Here, we used growth data of 3,397 trees that were assigned to the central planting positions within a plot (hereafter: focal trees) and that survived during the 6-year (2010–2016) study period (i.e. tree measurements were available in each year; Table S1). All other trees within a plot were treated as neighbour-only trees (Figure S1). For each focal tree, above-ground wood volume was calculated by multiplying the arithmetic product of tree basal area and tree height with a factor of 0.5412 (an average value for young subtropical trees obtained from our study species; Huang et al., 2018) to account for the deviation of the theoretical volume of a cylinder from actual tree volume (Pretzsch, 2009). Annual growth rates were calculated for each year of the study period as $V_t - V_{t-1}$, where V is the above-ground wood volume in a specific year (t) with t = 2010, ..., 2016. To avoid potential bias in model estimates, we excluded those trees that exhibited negative growth rates in a given census intervals (7.3%) that can result from stochastic processes (e.g. mechanical tree damage due to falling large-sized branches or falling stones or browsing) or measurement errors (e.g. different measurement positions between the censuses due to trees with trunk irregularities). Note that the likelihood of such processes increases with time. To account for variation in tree size, growth rates were standardized by dividing annual above-ground wood productivity by the initial volume of the focal tree in the respective annual census interval (AWP; $\text{cm}^3\ \text{cm}^{-3}\ \text{year}^{-1}$).

2.3 | Climate data

We used the standardized precipitation-evapotranspiration index (SPEI) to identify climate events. The drought index captures the monthly climatic water balance (precipitation minus potential evapotranspiration), where negative values indicate periods with water deficits (negative climatic water balance) and positive values conditions with ample water supply (positive climatic water balance; Vicente-Serrano, Beguería, & López-Moreno, 2010). We considered annual water balances (calculated for a 12-month timescale, $\text{SPEI}_{12\text{-Oct}}$) to link observed annual growth rates with interannual variation in climatic conditions, as they have been shown to capture well variation in tree demography in response to climate events in humid biomes (Hutchison, Gravel, Guichard, & Potvin, 2018; Vicente-Serrano et al., 2013). SPEI data with a 0.5° (latitude/longitude) resolution were calculated with the R code for generating the global SPEI database (Beguería, 2017) based on updated precipitation and potential evapotranspiration data (CRU TS v4.03; Harris, Jones, Osborn, & Lister, 2014) to cover the study period (Figure S2).

2.4 | Functional trait data

Functional trait data for our study species were obtained from trait assessments conducted at our study site (Kröber, Zhang, Ehmig, & Bruelheide, 2014). We focused on hydraulic traits, as they allow for an advanced mechanistic understanding of plant responses to changes in water availability (Griffin-Nolan et al., 2018). To examine the role of inter-specific trait variation in regulating neighbourhood interactions during climate events, we used the water potential at which 50% of xylem hydraulic conductivity is lost (Ψ_{50}; Figure S3) as an indicator for species' drought tolerance (Choat et al., 2012). Vulnerability to cavitation is considered a key physiological trait determining species' response to water limitations, where increasing (less negative) Ψ_{50} values indicate a higher risk of cavitation (Choat et al., 2018; Maherali, Pockman, & Jackson, 2004). In our study, drought-tolerant species (those with lower Ψ_{50} values) were associated with a high leaf toughness (r: −.58, p = .002) and leaf thickness (r: −.41, p = .041). In contrast, specific leaf area (r: .37, p = .070) and wood density (r: −.12, p = .555) were not significantly related to Ψ_{50}.

2.5 | Data analysis

We used linear mixed-effects models to test the effects of local neighbourhood conditions, climatic fluctuations (expressed as the drought index, SPEI) over a 6-year study period (2010–2016) and focal tree's drought tolerance (DT) on individual tree productivity. We were primarily interested to explore changes in local biodiversity-mediated neighbourhood interactions along climatic gradients independently from temporal changes in growth rates (note that in general, growth rates of young trees increase through time; thus, annual growth variation might not inevitable be linked to changes in annual climatic conditions). To avoid confounding effects between year (i.e. the calendrical interval of a census) and drought index (SPEI), we therefore removed the temporal trend in AWP ($\mathrm{cm}^3\ \mathrm{cm}^{-3}\ \mathrm{year}^{-1}$) by dividing AWP of a given focal tree (i) in a specific census interval (k) by the average AWP (using the 50% quantile of AWP) of the respective census k:

$$\mathrm{SAWP}_{i,k} = \left(\mathrm{AWP}_{i,k} \Big/ \overline{\mathrm{AWP}_k}\right), \tag{1}$$

where SAWP denotes the standardized annual above-ground wood productivity (dimensionless) of a focal tree in an annual census interval.

Neighbourhood conditions were characterized as the relative abundance of neighbours (expressed as the neighbourhood competition index, NCI) and number of heterospecific (different species identity as the focal tree) tree species (NSR) in the local neighbourhood of a focal tree. For each focal tree i, NCI was calculated as the focal trees' basal area relative to the total basal area of closest neighbours j ($\sum_{j \neq i} \pi D_j^2/4$, where D is the measured ground diameter) in a given study year. NSR was calculated as the total number of closest heterospecific neighbour species ($\sum_{j \neq i} N_j$, where N is the recorded species number) in given study year. NSR represents the net effect of neighbouring trees on the growth of a focal tree and is, as expected, positively related to log-tree species richness at the community level ($r = .82$, $p < .001$). We excluded the maximum of NSR (8), as this level was only realized once across study years.

The focal trees' species identity (to account for effects of species identity), neighbourhood species composition (to account for compositional differences of neighbouring trees), total number of living neighbours (to account for effects of neighbour mortality) and the focal tree nested in study plot (to account for small-scale variation in abiotic site conditions and repeated measurements) were used as crossed random effects. To allow for temporal variation in species identity effects, we additionally included a random slope of study year (continuous variable corresponding to the six consecutive census intervals) depending on species identity, which significantly improved the fit of the initial model (ΔAIC: 334.22; $\chi^2 = 337.39$, $p < .001$).

First, we determined the optimal random-effects structure based on restricted maximum likelihood (REML) estimation, considering additive and interactive effects. Second, we determined the optimal fixed-effects structure using the maximum likelihood (ML) method (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). In this study, we were primarily interested to understand how net biodiversity effects at the local neighbourhood scale vary in the magnitude and direction of their responses to drought and how these effects are mediated by the focal trees' functional traits. To test for trait-independent and trait-dependent responses, we therefore considered the three-way interaction among NSR, SPEI and DT, where a significant three-way interaction would indicate a trait dependency of the NSR-SPEI relationship and vice versa. Additionally, we included NCI as a main effect in our neighbourhood model to account for the impacts of neighbour abundance on individual tree productivity. To simplify the model structure, and thus allowing for a biologically plausible interpretation of parameter estimates, we did not include interaction terms with NCI in the subsequent analyses (note that the difficulty of interpreting interactions increases with the number of predictors involved; Zuur, Ieno, & Smith, 2007). Importantly, results from a neighbourhood model accounting for a three-way interaction between NCI, SPEI and DT were qualitatively the same (Table 1; Table S2), suggesting that our parameter estimates had an adequate power to explore the link between NSR, SPEI and DT. Different competing models were evaluated by sequential comparison based on the Akaike Information Criterion (AIC). The model with the lowest AIC and highest Akaike weights (i.e. the likelihood of being the best-fitting model based on AIC values; Burnham & Anderson, 2002) was chosen as the most parsimonious model (Table S3). Parameter estimates of the best-fitting model were based on restricted maximum likelihood (REML) estimation (Zuur et al., 2009). For each census interval (2010–2011, 2011–2012, 2012–2013, 2013–2014, 2014–2015, 2015–2016), we used the initial values of NCI and NSR. All predictors were standardized ($M = 0$, $SD = 1$) before analysis; SAWP and NCI were log-transformed (using the natural logarithm) to meet model assumptions. There was no critical correlation between

TABLE 1 Best-fitting mixed-effects model of the effects of neighbourhood conditions, drought index and drought tolerance on individual tree growth (standardized above-ground wood productivity, SAWP). Regression coefficients are standardized and significant terms ($p < .05$) are highlighted in bold. See Table S5 for variance components

	Estimate	*SE*	*df*	*t* value	*p* value
Intercept	0.136	0.126	15.9	1.08	.295
Neighbourhood competition index (NCI, log)	−0.258	0.008	4,970.0	−33.30	**<.001**
Neighbourhood tree species richness (NSR)	0.026	0.013	1,134.0	2.02	**.043**
Drought index (SPEI)	0.008	0.007	10,800.0	1.13	.261
Drought tolerance (DT)	−0.143	0.066	20.8	−2.17	**.042**
NSR × SPEI	0.003	0.005	15,500.0	0.53	.598
NSR × DT	0.023	0.008	2,869.0	2.76	**.006**
SPEI × DT	−0.020	0.007	8,892.0	−2.83	**.005**
NSR × SPEI × DT	−0.015	0.006	15,590.0	−2.74	**.006**

Abbreviations: *df*, degrees of freedom; *SE*, standard error.

covariates (collinearity), as indicated by the variance inflation factors (all VIFs <1.03). Model assumptions were checked and confirmed according to Zuur et al. (2009). In addition, we fitted an alternative model that accounted for variation in topography (slope and elevation) to test the robustness of our parameter estimates (Table 1; Table S4). This was confirmed and is in line with the previously reported weak impacts of topography and soil chemical properties on tree growth rates (Kröber et al., 2015) and community productivity (Fichtner et al., 2018) at our study site.

To assess the impact of climate on biodiversity effects, we used growth predictions (based on fixed-effects estimates) from our best-fitting model (Table 1). Specifically, we quantified climate-induced changes in annual tree productivity of a focal tree growing in conspecific (NSR = 0) compared to heterospecific neighbourhoods (NSR ≥ 1). Changes in the net biodiversity effect (NE) for a given NSR-level *j* were quantified using a measure of relative effect sizes (i.e. neighbour-effect index with additive symmetry; Díaz-Sierra, Verwijmeren, Rietkerk, de Dios, & Baudena, 2017):

$$\mathrm{NE}_j = 2\frac{\left(\mathrm{SAWP}_{h,j} - \mathrm{SAWP}_c\right)}{\mathrm{SAWP}_c + \left|\left(\mathrm{SAWP}_{h,j} - \mathrm{SAWP}_c\right)\right|}, \qquad (2)$$

where SAWP denotes the predicted annual standardized above-ground wood productivity (back-transformed from logarithmic scale) of a focal tree and *c* indicates conspecific and *h* heterospecific neighbours with *j* = 1, ..., 7 species. The effect size measure is standardized, symmetrical around zero and bounded between −1 and +2. Negative values indicate underyielding (higher SAWP in conspecific relative to heterospecific neighbourhoods), while positive values imply overyielding (higher SAWP in heterospecific relative to conspecific neighbourhoods). NE was then related to species richness of the local neighbourhood, for each species (across species approach; trait-independent response) or separately for low, average and high drought tolerance (DT; trait-dependent response). For each focal tree, we predicted SAWP at low (80% quantile of species-specific Ψ_{50}; note that Ψ_{50} values are negative), average (50% quantile) and high (20% quantile) DT. We did this for every level of NSR, while keeping NCI fixed at its mean and keeping SPEI fixed at values of −1.5 (severely dry), −0.8 (moderately dry), 0.8 (moderately wet) or 1.5 (severely wet). In this way, our function-derived growth rates allowed us to explore how neighbourhood-scale biodiversity effects vary in the mode and intensity during climate events. All analyses were conducted in R (version 3.5.1; R Core Team, 2018) using the packages lme4 (Bates, Maechler, Bolker, & Walker, 2015), lmerTest (Kuznetsova, Brockhoff, & Christensen, 2016) and MuMIn (Bartón, 2016).

3 | RESULTS

Across species, neighbourhood tree species richness (NSR) promoted individual tree growth (standardized above-ground

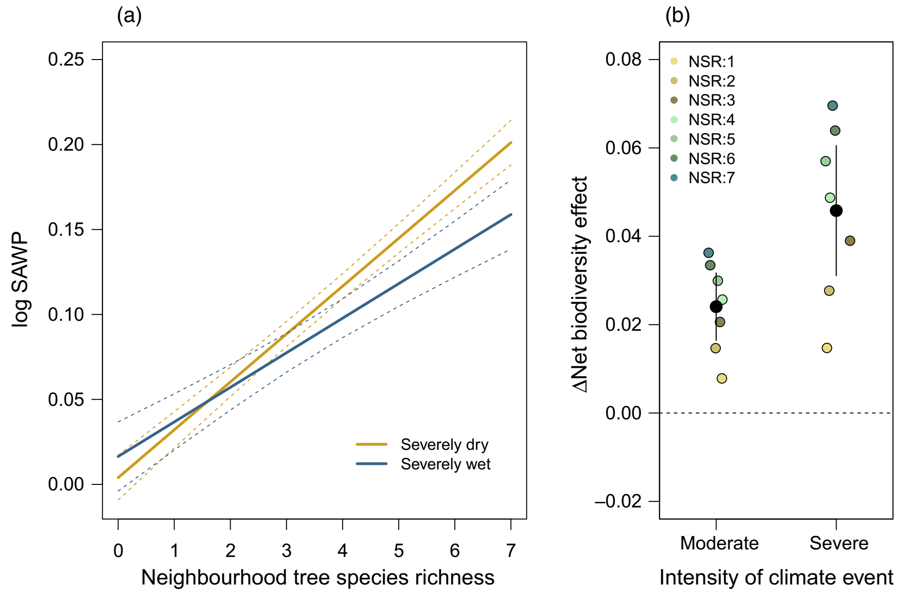

FIGURE 2 Variation in trait-independent (averaged across species) biodiversity effects at the local neighbourhood scale on individual tree growth (standardized above-ground wood productivity, SAWP) with neighbourhood tree species richness (NSR) and climate conditions. (a) Changes in local biodiversity–productivity relationships (BPRs). Lines correspond to the fitted BPRs of a mixed-effects model, with dotted lines representing the 95% confidence interval of the prediction. NSR = 0 indicate conspecific and NSR ≥ 1 heterospecific neighbourhoods. (b) Changes in the magnitude (standardized effect size) of net biodiversity effects (Δ net biodiversity effects; mean and 95% confidence interval) on SAWP with the intensity of climate events. Severe event: difference in Δ net biodiversity effects between severely dry (SPEI = −1.5) and severely wet (SPEI = 1.5) years; moderate event: difference in Δ net biodiversity effects between moderately dry (SPEI = −0.8) and moderately wet (SPEI = 0.8) years. Positive values indicate higher biodiversity effects in dry relative to wet years and negative values indicate higher biodiversity effects in wet relative to dry years. Transparent points represent Δ net biodiversity effects predicted for each NSR level. NSR-specific values are jittered to facilitate visibility

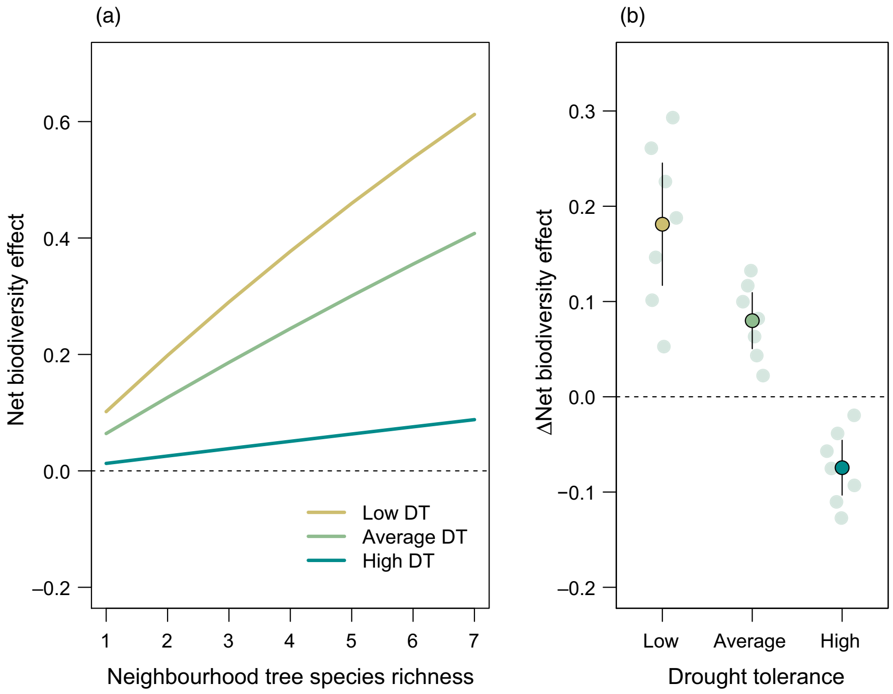

FIGURE 3 Trait-mediated biodiversity effects during climate events. (a) Variation in the magnitude (standardized effect size) of net biodiversity effects on individual tree growth (standardized above-ground wood productivity, SAWP) with neighbourhood tree species richness (NSR) and the focal trees' drought tolerance (DT) during a severe drought (SPEI = −1.5). Lines are mixed-effects model fits for each drought tolerance category. Positive values of the standardized effect size indicate overyielding (higher productivity in heterospecific; NSR ≥ 1, relative to conspecific, NSR = 0, neighbourhoods) and negative values indicate underyielding (higher productivity in conspecific relative to heterospecific neighbourhoods). (b) Trait-dependent differences in net biodiversity effects (Δ net biodiversity effects, mean and 95% confidence interval) between severely dry (SPEI = −1.5) and severely wet (SPEI = 1.5) years. Transparent points represent Δ net biodiversity effects predicted for each NSR level. NSR-specific values are jittered to facilitate visibility. See Figure 2 for further information

wood productivity, SAWP) both in dry and wet years (Figure 2a; Figure S4). Overall, positive biodiversity effects increased with increasing NSR (Figure S5), but were on average 15% (moderate event) and 30% (severe event) stronger in dry compared to wet years (severe event: $t = 6.10$, $p < .001$; moderate event: $t = 6.18$, $p < .001$; Figure 2b). Importantly, the magnitude of biodiversity effects (and thus their potential for climate change mitigation) critically depended on the focal trees' hydraulic traits, as indicated by the significant three-way interaction between NSR, drought index and drought tolerance (DT; Table 1). Specifically, drought-sensitive species benefitted the most from growing with heterospecific neighbours during drought, with biodiversity effects here being on average about 0.5 and 6 times higher than for species with an average or high DT, respectively (Figure 3a). In contrast, differences in drought tolerance of the focal tree had little impact on the magnitude of biodiversity effects during favourable conditions (wet years; Figure S6). As a result, the magnitudes of biodiversity effects promoting growth of drought-sensitive species and those with average DT were significantly higher in dry than wet years (low DT: $t = 5.53$, $p = .001$; average DT: $t = 5.33$, $p = .002$). Contrarily, drought-tolerant species benefitted less from growing in diverse neighbourhoods in dry compared to wet years ($t = −5.07$, $p = .002$; Figure 3b). This was consistent with significantly higher SAWP for species with low and average DT during drought, while the opposite was evident for species with high DT (low DT: $t = 3.23$, $p = .014$; average DT: $t = 2.71$, $p = .030$; high DT: $t = −4.98$, $p = .002$; Figure S7).

4 | DISCUSSION

We found that positive biodiversity effects at the local neighbourhood scale persist and became stronger in years with water deficits, indicating that neighbourhood diversity has a strong potential to mitigate adverse impacts of climate change on tree growth. This confirms our first hypothesis and theoretical considerations of positive species interactions and biodiversity effects becoming more important during adverse climatic conditions (Brooker, 2006; Hisano et al., 2018; Wright, Wardle, Callaway, & Gaxiola, 2017). There are multiple mechanisms by which tree–tree interactions could mitigate drought-induced growth decline. Overall, tree responses to drought largely depend on the amount of plant-available soil water remaining during a drought event, but soil water availability, in turn, is strongly altered by species interactions (Forrester, 2014). Species interactions can lead to higher water availability and water-uptake efficiency via competitive reduction or facilitation and thereby mitigate trees' water stress (Forrester & Bauhus, 2016). For example, reduced competition for water among heterospecific neighbours was recently shown as a mechanism maintaining growth rates of tropical tree seedlings under drought (O'Brien et al., 2017). Thus, trees might be more productive in diverse neighbourhoods during periods of water deficits by benefitting from enhanced fine root growth and interspecific variation in rooting strategies, and hence from an improved access to soil water (Brassard et al., 2013; Sun et al., 2017). Moreover, soil water availability is determined by the water use behaviour of coexisting species. It is therefore conceivable that the observed mitigation effects of neighbourhood diversity additionally result from interspecific differences in stomatal regulation strategies (Forrester, 2017; Kröber & Bruelheide, 2014). Next to resource partitioning, microclimate amelioration via facilitative neighbourhood interactions might act as a further mechanism by which the water demand of a focal tree growing in diverse neighbourhoods is decreased. For example, increasing tree species diversity at the local neighbourhood scale allows for more complex structured and densely packed canopies by shifts in wood volume allocation in favour of branches over time (Kunz et al., 2019). This, in turn, can reduce irradiance, air and soil surface temperature as well as vapour pressure deficits at the leaf surface and the evaporative demand of whole trees (Montgomery, Reich, & Palik, 2010), therefore improving abiotic growing conditions during drought. Biotic facilitation via mycorrhizal networks might be a further reason why trees growing with functional diverse neighbours are more resistant to drought. For example, such common mycorrhizal mycelium links the roots of trees by which coexisting tree species can transfer substantial amounts of carbon below-ground (Klein, Siegwolf, & Körner, 2016), suggesting that below-ground transfers of water and nutrients become increasingly important in a changing climate (Simard et al., 2012). Our finding of consistently higher biodiversity effects in more diverse neighbourhoods during drought suggests that positive neighbourhood interactions can improve the local soil water availability or microclimate for a given focal tree, thereby becoming particularly important during periods of water deficits. Positive neighbourhood interactions can also arise through biotic feedbacks (Barry et al., 2019). Reduced conspecific neighbour density and the presence of heterospecific neighbours can decrease host-specific damage by herbivores and pathogens (Barbosa et al., 2009; Hantsch et al., 2014; Johnson, Beaulieu, Bever, & Clay, 2012). These effects might be particularly pronounced during dry conditions (e.g. Lin, Comita, Zheng, & Cao, 2012), and beneficial effects of a diverse neighbourhood might therefore be more notable, because drought stress can weaken trees and make them particularly susceptible to enemy attack (Jactel et al., 2012). Although we were not able to assess the importance of potential mechanisms underlying mitigation effects, our results indicate that processes operating at the local neighbourhood scale are a key component that contribute to the role of biodiversity in mitigating impacts of drought on forest ecosystems.

Based on a large-scale biodiversity experiment, our study shows mitigation effects of neighbourhood diversity on drought-induced growth decline, but the magnitude of mitigation was dependent on the focal trees' hydraulic traits. This supports our second hypothesis of changes in trait-mediated neighbourhood interactions across biodiversity levels during climatic events. Given that a focal trees' drought tolerance was negatively related to the magnitude of biodiversity effects, the relative importance of neighbourhood diversity was higher for drought-sensitive species, but lower for species with a high drought tolerance in dry compared to wet years. Thus, our results suggest that both neighbourhood diversity and the focal trees' traits related to hydraulic function have a dominant role in mediating drought responses of individual trees. In our study system, neighbourhood tree species richness promotes individual tree productivity of species with an acquisitive resource-use strategy by competitive reduction (Fichtner et al., 2017), and those species with the lowest cavitation resistance are associated with acquisitive functional traits (Figure S3). We therefore conclude that shifts in neighbourhood interactions towards less intense competition for soil water among local heterospecific neighbours largely explain why drought-sensitive species benefitted the most from growing with diverse neighbours during drought. Our results are in contrast to findings from temperate forests, where Jucker, Bouriaud, Avacaritei, Dănilă, et al. (2014) demonstrated the strongest decline in biodiversity effects (relative to community tree species richness) during dry years for species associated with the lowest drought tolerance. Similarly, the proportion of heterospecific neighbours was shown to positively affect drought resilience of drought-tolerant species (*Quercus pubescens*), while a neutral (*Fagus sylvatica*) and negative (*Abies alba*) effect was evident for less drought-tolerant species (Jourdan et al., 2019). These differences might be largely attributed to differences in biomes (level of tree species diversity, climate and soil conditions). Finally, favourable light- or nutrient-related species interactions are assumed to become more important in wet years or at sites associated with high precipitation (Jactel et al., 2018), which could explain why trees with favourable traits to tolerate drought benefitted more from growing in species-rich neighbourhoods in wet than in dry years.

The strong effects of neighbourhood diversity in mediating individual tree productivity has important consequences for climate-change mitigation, as our experimental findings clearly show that more diverse neighbourhoods are able to mitigate the negative impacts of drought on individual tree productivity. Importantly, we observed a stronger biodiversity effect for drought-sensitive species in dry years. This implies that water-related neighbourhood relationships are primarily beneficial for trees with unfavourable traits to tolerate drought. In this way, diverse local neighbourhoods can act as a 'welfare net' by providing greatest support for most vulnerable individuals in the community. Our results suggest that neighbourhood diversity can increase ecosystem resistance against adverse impacts of climate change via strengthening the weakest components of the system. Although there might be trade-offs between mixed-species forest productivity and high-quality timber production or harvesting systems (Coll et al., 2018), our findings emphasize the importance of promoting tree species richness at the local neighbourhood scale in current afforestation and forest restoration strategies to secure high forest productivity and carbon sequestration even during periods of drought.

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AUTHORS' CONTRIBUTIONS

G.v.O., W.H. and H.B. conceived and designed the study; M.K., K.M. and F.S. compiled the data; A.F. analysed the data with support of F.S. and H.B. A.S. contributed to the discussion of the results. A.F. wrote the manuscript with substantial input from all co-authors.

DATA AVAILABILITY STATEMENT

All data are available on the BEF-China project database: https://china.befdata.biow.uni-leipzig.de/datasets/614 (Fichtner et al., 2020).

ORCID

Andreas Fichtner https://orcid.org/0000-0003-0499-4893
Florian Schnabel https://orcid.org/0000-0001-8452-4001
Helge Bruelheide https://orcid.org/0000-0003-3135-0356
Matthias Kunz https://orcid.org/0000-0002-0541-3424
Katharina Mausolf https://orcid.org/0000-0002-4925-9828
Andreas Schuldt https://orcid.org/0000-0002-8761-0025
Werner Härdtle https://orcid.org/0000-0002-5599-5792
Goddert von Oheimb https://orcid.org/0000-0001-7408-425X

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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Chapter 6

Drivers of productivity and its temporal stability in a tropical tree diversity experiment

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Drivers of productivity and its temporal stability in a tropical tree diversity experiment

Florian Schnabel[1,2,3] | Julia A. Schwarz[1] | Adrian Dănescu[4] | Andreas Fichtner[5] | Charles A. Nock[6] | Jürgen Bauhus[1] | Catherine Potvin[7,8]

[1]Chair of Silviculture, Institute of Forest Sciences, University of Freiburg, Freiburg, Germany

[2]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany

[3]Systematic Botany and Functional Biodiversity, University of Leipzig, Leipzig, Germany

[4]Thünen Institute of Forest Ecosystems, Eberswalde, Germany

[5]Institute of Ecology, Leuphana University of Lüneburg, Lüneburg, Germany

[6]Department of Renewable Resources, Faculty of Agricultural, Life and Environmental Sciences, University of Alberta, Edmonton, AB, Canada

[7]Department of Biology, McGill University, Montreal, QC, Canada

[8]Smithsonian Tropical Research Institute, Panama City, Panama

Correspondence

Florian Schnabel, German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany.
Email: florian.schnabel@idiv.de

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Abstract

There is increasing evidence that mixed-species forests can provide multiple ecosystem services at a higher level than their monospecific counterparts. However, most studies concerning tree diversity and ecosystem functioning relationships use data from forest inventories (under noncontrolled conditions) or from very young plantation experiments. Here, we investigated temporal dynamics of diversity–productivity relationships and diversity–stability relationships in the oldest tropical tree diversity experiment. Sardinilla was established in Panama in 2001, with 22 plots that form a gradient in native tree species richness of one-, two-, three- and five-species communities. Using annual data describing tree diameters and heights, we calculated basal area increment as the proxy of tree productivity. We combined tree neighbourhood- and community-level analyses and tested the effects of both species diversity and structural diversity on productivity and its temporal stability. General patterns were consistent across both scales indicating that tree–tree interactions in neighbourhoods drive observed diversity effects. From 2006 to 2016, mean overyielding (higher productivity in mixtures than in monocultures) was 25%–30% in two- and three-species mixtures and 50% in five-species stands. Tree neighbourhood diversity enhanced community productivity but the effect of species diversity was stronger and increased over time, whereas the effect of structural diversity declined. Temporal stability of community productivity increased with species diversity via two principle mechanisms: asynchronous responses of species to environmental variability and overyielding. Overyielding in mixtures was highest during a strong El Niño-related drought. Overall, positive diversity–productivity and diversity–stability relationships predominated, with the highest productivity and stability at the highest levels of diversity. These results provide new insights into mixing effects in diverse, tropical plantations and highlight the importance of analyses of temporal dynamics for our understanding of the complex relationships between diversity, productivity and stability. Under climate change, mixed-species forests may provide both high levels and high stability of production.

KEYWORDS
biodiversity, drought, ecosystem functioning, neighbourhood, overyielding, Sardinilla experiment, structural diversity, tree species diversity, tropical plantation forest

1 | INTRODUCTION

Forest restoration has been identified as the most important natural solution for climate change mitigation (Griscom et al., 2017). For example, the Bonn Challenge advocates for +150 Mil ha of restored forests by 2020. Tropical and subtropical regions, where ongoing deforestation and forest degradation have left extensive areas of degraded land, provide a unique opportunity for restoring productive forests (Bauhus, van der Meer, & Kanninen, 2010). Planted forests can provide many of the ecosystem functions and services of natural tropical forests, albeit some at a lower level (Bauhus et al., 2010; Pawson et al., 2013), while making a substantial contribution to satisfy the increasing demand for global roundwood (Kanninen, 2010). Planted forests are, however, in most cases still established as monocultures, often with non-native tree species (Verheyen et al., 2016), despite the fact that mixed-species forests (either planted or from natural regeneration) are considered important for adaptation of forests in the face of global change (Messier, Puettmann, & Coates, 2013; Pawson et al., 2013). Tree species mixtures can provide multiple ecosystem services at higher levels than their monospecific counterparts, although this may not be the case for all ecosystem services (Gamfeldt et al., 2013; van der Plas et al., 2016). The strongest evidence for such positive mixing effects exists for productivity and C sequestration (e.g. Forrester & Bauhus, 2016; Paquette & Messier, 2011; Piotto, 2008). While there is some evidence regarding higher ecological stability and resilience of mixed-species stands in relation to specific stress and disturbance factors (Bauhus, Forrester, Gardiner, et al., 2017; Hutchison, Gravel, Guichard, & Potvin, 2018; Jactel et al., 2017), there are very few long-term analyses of stability of productivity in relation to tree diversity.

Understanding the mechanisms behind the relationship of biodiversity with ecosystem functioning (BEF) is crucial for designing and implementing diverse, resilient and productive planted forests. Studies of BEF relationships in forests have employed various approaches over the last two decades, ranging from analysis of forest inventories to experimental plantations specifically designed to test BEF relationships (Bauhus, Forrester, & Pretzsch, 2017; Nock et al., 2017). While each approach has its specific strengths and drawbacks, experiments provide the strongest test of BEF effects by controlling for underlying environmental effects and directly comparing tree performance in monocultures and in mixtures (see Bauhus, Forrester, & Pretzsch, 2017). Given experiments are generally inventoried more frequently than forest plots, they offer unique opportunities to study temporal developments of diversity effects (Huang et al., 2018), as well as the buffering effects of diversity from disturbance and environmental variation (Isbell et al., 2015). To date, few such analyses have been conducted, as most forest BEF experiments are still young. One exception is 'Sardinilla' in Panama, the oldest BEF experiment in the tropics (Scherer-Lorenzen et al., 2005), which was used here to analyse diversity–stability relationships (DSRs) and the temporal development of diversity–productivity relationships (DPRs).

Net overyielding occurs when productivity in mixtures is higher than in monocultures. This can be attributed to the combined effect of competitive reduction (+) and facilitation (+) versus competition (−) and is also referred to as 'complementarity effect' (Forrester & Pretzsch, 2015). However, enhanced mixture productivity might also result from the dominance of one or few species caused by selection or mass ratio effects (Fotis et al., 2018; Grime, 1998). Indeed tree–tree interactions that scale up to community-level responses can be positive or negative, depending on species' assemblage and environmental influences (Forrester & Bauhus, 2016; Forrester & Pretzsch, 2015) with tree size and competition by neighbouring trees strongly influencing diversity effects on single-tree productivity (Dănescu, Albrecht, & Bauhus, 2016; Fichtner et al., 2018). Hence, to develop resilient plantations, it is crucial to clarify the context dependency of DPRs in forest ecosystems: under which climatic conditions, during which stage(s) of stand development and at what levels of diversity forest managers can expect beneficial effects of mixtures on productivity (Forrester & Bauhus, 2016).

In the face of future climatic stress and disturbances, it will become increasingly important to design plantations not only to increase productivity but also to stabilize it. The effects of tree species diversity on the resistance to drought, wind, fire, pests and pathogens appear equivocal and, in most cases, except for herbivorous insects, the evidence base is weak (Bauhus, Forrester, Gardiner, et al., 2017). Even less is known about the effects of diversity on the temporal stability (Lehman & Tilman, 2000; Tilman, 1999) of community productivity in forests, that is, the fluctuation of productivity around its long-term mean. In grassland ecosystems, there is abundant evidence that interannual fluctuations of community-level productivity are smaller in more diverse compared to less diverse communities, resulting in a net positive DSR (Hautier et al., 2014; Isbell et al., 2015). The few studies that have analysed temporal stability in temperate and boreal forest ecosystems support the hypothesis that diversity can stabilize community-level productivity (Aussenac, Bergeron, Gravel, & Drobyshev, 2019; del Río et al., 2017; Jucker, Bouriaud, Avacaritei, & Coomes, 2014; Morin, Fahse, de Mazancourt, Scherer-Lorenzen, & Bugmann, 2014). For seasonally dry tropics undergoing supraseasonal drought cycles, where the contrast between favourable and unfavourable growth conditions is likely stronger, there has been some evidence from the Sardinilla experiment that species mixing decreases the climatic sensitivity of tree growth and hence stabilizes productivity (Hutchison et al.,

2018) but no detailed analysis of the underlying drivers of this phenomenon exist.

The overall aim of this study was to test not only whether diversity increases productivity and its temporal stability in mixed stands but also to identify whether this might be driven by species diversity or structural diversity, whether stability was more influenced by overyielding or asynchronous growth of tree species (Jucker et al., 2014), and how these influences change with stand development. We expect that the strength of positive diversity effects and consequently overyielding in mixed species stands, which were reported for the first half of the experiment's lifespan (Potvin & Gotelli, 2008; Sapijanskas, Potvin, & Loreau, 2013), increases with stand development. Moreover, the period of development of the 'Sardinilla' plantation has been characterized by contrasting climatic conditions, including an exceptionally wet and an exceptionally dry La Niña and El Niño period, respectively (Detto, Wright, Calderón, & Muller-Landau, 2018; Hutchison et al., 2018). Here, we used this climatic variation to examine whether DPRs, as previously hypothesized (Forrester & Bauhus, 2016), change along a gradient of climate-induced water variability. Hutchison et al. (2018) showed that tree mortality in the monocultures of Sardinilla was modulated by extreme climatic events while species mixing buffered against this effect. We expect that lower climatic sensitivity of mixtures is driven by species asynchrony, that is, the fluctuating responses of species to contrasting climatic conditions (Jucker et al., 2014) and overyielding. We test whether these mechanisms translate into an overall positive DSR, expressed here as one aspect of stability, the single and intuitive metric 'temporal stability'.

While tree community-level analyses are common in forestry studies aiming to produce results for a management-relevant scale, it is increasingly recognized that community responses in mixed stands are driven by tree–tree interactions at the neighbourhood level (Dănescu et al., 2016; Fichtner et al., 2018; Potvin & Dutilleul, 2009). Importantly, neighbourhood analyses allow to accurately describe variability in stand density, mortality and stand structure (Forrester & Bauhus, 2016; Forrester & Pretzsch, 2015). Here, we employ a combined analysis of DPRs at both the community and tree neighbourhood scale to provide insight into the complex interplay of complementarity effects during stand development.

Finally, most studies on BEF relationships in forests simply use species richness or diversity as the measure of tree diversity (Forrester & Bauhus, 2016). However, structural diversity is increasingly recognized as another key attribute influencing productivity and stress tolerance of trees (Dănescu et al., 2016; Pretzsch, Schütze, & Biber, 2018). Applying this perspective, trees of different sizes occupy distinct niches and could behave, at least to a certain degree, like functionally different species (Dănescu et al., 2016). Recently, an indirect positive effect of species diversity on productivity via changes in size structure (Zhang, Chen, & Coomes, 2015) and also a direct positive, nonmediated, effect of structural diversity (Dănescu et al., 2016) have been described. In contrast, structural diversity had negative effects on productivity in monospecific, clonal eucalypt stands established through staggered planting to create structural diversity (Binkley, Stape, Bauerle, & Ryan, 2010; Ryan et al., 2010). In tree mixtures with highly divergent tree growth rates, effects of both components of diversity should be tested. This has not been done so far under controlled conditions. We are also not aware of any study that examined effects of structural diversity on temporal stability of tree growth.

Thus, this paper addresses the following hypotheses:

1. Overyielding increases with stand development and is highest in the most diverse tree neighbourhoods and stands (plots);
2. Both tree species diversity and structural diversity increase productivity and its temporal stability during a period with contrasting climatic features;
3. Temporal stability of productivity in mixtures is driven by species asynchrony and overyielding.

2 | MATERIALS AND METHODS

2.1 | Study design

The study was conducted in an experimental planted forest, that was established in Sardinilla (central Panama, 9°19′30″N, 79°38′00″W) in 2001. The climate at the site is tropical with an annual precipitation sum of 2,661 mm and annual mean temperature of 26°C and is characterized by a pronounced dry season from January until the beginning of May (BCI, Physical Monitoring Program of STRI). On average, only 12% of the annual precipitation falls during the dry season. Six native tree species were originally planted in monocultures and mixtures of different species richness levels. A total of 24 plots (45 × 45 m, each) were established on a former pasture including plots consisting of monocultures of all six species ($N = 12$), different three-species assemblages ($N = 6$) and mixtures of all six-species ($N = 6$) with an average of 233 individuals per plot (equalling 1,150 trees/ha; Potvin & Dutilleul, 2009; Scherer-Lorenzen et al., 2005). To ensure trait divergence in each mixture, species were allocated based on their relative growth rates. In each three-species mixture, one fast growing pioneer species, either *Luehea seemannii* (LS) or *Cordia alliodora* (CA), one light-intermediate species, either *Anacardium excelsum* (AE) or *Hura crepitans* (HC) and one slow-growing and shade-tolerant species, either *Tabebuia rosea* (TR) or *Cedrela odorata* (CO) were chosen randomly based on their relative growth rates in nearby natural forests (Scherer-Lorenzen et al., 2005). One species, CA, suffered mortality rates >90% in the first years after planting likely a result of site properties, possibly due to the compacted and undrained soil (Potvin & Gotelli, 2008; Sapijanskas et al., 2013) or root herbivory by beetle larvae (Healy, Gotelli, & Potvin, 2008), but not a diversity effect. We, therefore, excluded it from our analysis (for details see Appendix S2). In this study, we consequently refer to the 'realized' species richness levels in Sardinilla, which comprise monocultures ($N = 10$), two- ($N = 3$), three- ($N = 3$) and five-species mixtures ($N = 6$).

2.2 | Performance proxies of tree growth

At the time of analysis, trees in the plantation were 16 years old, with the tallest trees over 25 m, old enough, therefore, to examine diversity–stability relationships (DSRs) and the temporal development of diversity-productivity relationships (DPRs). We used two key response variables, diameter and height growth, as proxies of tree performance. Diameter and height were measured annually from 2002 to 2017 for all trees in the plantation at the end of each growing season (December–January). Diameter was measured at breast height (1.3 m) for trees with a total height >2 m for each stem (i.e. in case of multistemmed trees). We chose 2006, when 85% of all trees had reached a height of >2 m, as start year of our analysis to ensure a complete and consistent data set. Our inventory data set thus comprises a complete, spatially explicit, inventory of all trees measured annually from January 2006 to January 2017. Basal area increment (BAI) between successive years was used as a proxy for productivity and was calculated as:

$$\mathrm{BAI}_{\mathrm{tree}} = \sum_{j=1}^{n}\left(\frac{\pi}{4} * \mathrm{dbh}^{2}_{j(t+1)}\right) - \sum_{j=1}^{n}\left(\frac{\pi}{4} * \mathrm{dbh}^{2}_{j(t)}\right), \qquad (1)$$

where dbh is diameter at breast height, j is an index for the n stems of each tree (i.e. for multistemmed trees) and t is an index for the year of survey.

We corrected negative BAI values (e.g. caused by measurement errors or wind damage) in order to avoid biased model estimates. As described in the previous work, negative increments represent a common challenge in experiments utilizing inventory data sets with a high temporal resolution (Fichtner et al., 2018). The applied procedure included predicting basal area at dbh with additionally available basal diameter data via species-specific allometric relationships and the exclusion of wind-damaged trees, for example, as after the tropical storm 'Otto' in 2016 (see Appendix S2 for details). To avoid edge effects, we excluded the outer border row of trees of each plot for calculation of response variables. However, to best reflect the actual growing conditions of trees, we calculated all predictor variables (e.g. diversity indices) using data of all trees in the plantation including border trees.

2.3 | Community- and tree neighbourhood-level analyses

First, we analysed DPRs and DSRs at the community level in relation to community tree species richness, the most common diversity predictor in BEF research (Forrester & Bauhus, 2016; Jucker et al., 2014). Secondly, we used a wider set of diversity measures to assess the impact of species and structural diversity on productivity and its stability at the community level. We hypothesize that DPRs at the community level (here the plot) may be driven by tree–tree interactions in neighbourhoods. In a third step, we explored the underlying mechanisms of community-level DPRs through modelling the influence of the same set of candidate indices on growth of individual trees at the neighbourhood level (Figure 1).

At the community level we calculated annual productivity ($\mathrm{BAI}_{\mathrm{plot}}$, m^2 ha^{-1} year^{-1}) as the sum of BAI of all trees per plot or species that were alive in a particular year (N = 2,596). In contrast, at the neighbourhood level, we analysed single-tree growth ($\mathrm{BAI}_{\mathrm{tree}}$, cm^2/year) of all trees that were alive at the end of the observation

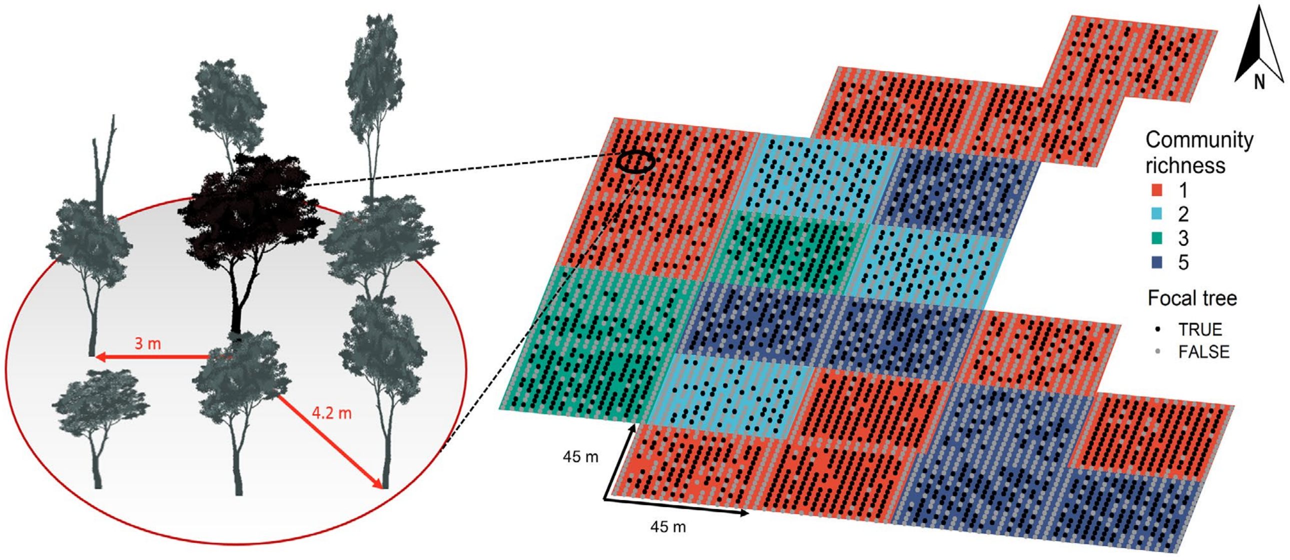

FIGURE 1 Design of the community and tree neighbourhood level analyses. On the right, the plots in the Sardinilla plantation are shown, coloured according to their species richness level (N = 22). The black points represent the position of individual, living focal trees (2006–2016) whose productivity was modelled in response to their immediate neighbours. Grey points show all trees planted in 2001 (including dead individuals and border trees). On the left, the design of the tree neighbourhood analysis is illustrated. The central black tree represents the focal tree with its immediate neighbours, up to a maximum of eight living trees. Community- and neighbourhood-level productivity and predictor variables (e.g. diversity indices) were calculated for each year (2006–2016) based on annually resolved values of tree basal areas and heights

period, hereafter called ‘focal trees’ (N = 2,159, Figure 1). Annually resolved values of species diversity and structural diversity were calculated for the whole community (each plot) and for each tree's neighbourhood.

The neighbourhood of focal trees comprised of its immediate neighbours, that is, all living trees within a radius of 5 m. This resulted in a maximum of eight neighbours, considering the fixed planting design of the plantation (3 × 3 m, Figure 1). Compared to Potvin and Dutilleul (2009) who analysed neighbourhood effects in Sardinilla for 2002–2006, we expanded the immediate neighbourhood from four to eight neighbours to account for larger tree dimensions and consequently larger interaction radii in later years of stand development.

2.4 | Measures of species and structural diversity

To improve our understanding of the processes that drive DPRs and DSRs in forests, we used a wide set of species diversity and structural diversity indices, because previous studies have shown that the choice of indices can strongly influence the outcome of analyses (Dănescu et al., 2016; Schnabel, Donoso, & Winter, 2017).

In other studies, species diversity has been considered a component of forest structure (Dănescu et al., 2016). Here, we quantified tree species diversity using three conventional indices: (a) species richness (i.e. the number of tree species), (b) the Shannon diversity index (Shannon, 1948) using relative basal area to quantify species proportions and (c) evenness, calculated as Shannon index divided by its theoretical maximum (Table 1).

To quantify diameter and height diversity we calculated widely used metrics of forest structural diversity: (a) standard deviation (sd), (b) coefficient of variation (CV) and (c) Gini coefficient (GC; Gini, 1912; Table 1). Higher index values reflect higher structural diversity for all indices (see Lexerød & Eid, 2006 for a detailed index comparison). Hereafter, we refer to these indices as measures of ‘species diversity’ and ‘structural diversity’. We acknowledge that these indices reflect only a small subset of all aspects of forest structure, namely species diversity and the variation in tree diameters and heights and measure different aspects of diversity (e.g. variation, diversity and inequality).

2.5 | Community-level overyielding

To quantify overyielding or underyielding of mixtures, we calculated the relative productivity (RP) of the two-, three- and five-species mixtures versus their respective monocultures, following Forrester and Pretzsch (2015; Equation 3). We used annually resolved productivity values calculated for the whole community ($\mathrm{BAI}_{\mathrm{plot}}$, $\mathrm{m}^2\ \mathrm{ha}^{-1}\ \mathrm{year}^{-1}$) and for each individual species ($\mathrm{BAI}_{\mathrm{plot\ species}}$, $\mathrm{m}^2\ \mathrm{ha}^{-1}\ \mathrm{year}^{-1}$).

$$\mathrm{RP}_{\mathrm{community}}\,(\%) = \left(\frac{\mathrm{BAI}_{\mathrm{mix}}}{m_1\mathrm{BAI}_{1\mathrm{mono}} + m_2\mathrm{BAI}_{2\mathrm{mono}} + \cdots + m_i\mathrm{BAI}_{i\mathrm{mono}}} - 1\right)100, \quad (2)$$

where $\mathrm{BAI}_{\mathrm{mix}}$ is the $\mathrm{BAI}_{\mathrm{plot}}$ of all species in the mixture, $\mathrm{BAI}_{\mathrm{mono}}$ is the $\mathrm{BAI}_{\mathrm{plot}}$ of the respective monoculture of species i and m_i is the proportion of species i in mixture corresponding to its initial planting density (N trees/ha).

TABLE 1 Summary of the species diversity and structural diversity indices used in this study. Data are for the community level (N = 22 plots × 11 years) and the tree neighbourhood level (N = 2,159 trees × 11 years)

			Community		Neighbourhood	
Component	**Index**	**Acronym and equation**	**Mean**	**Range**	**Mean**	**Range**
Species diversity	Species richness	$\mathrm{Richness}_s = N$	2	1–5	2	0–5
	Shannon index	$\mathrm{Shannon}_s = \sum_{i=1}^{N} P_i * \ln(P_i)$	0.58	0.00–1.73	0.42	0.00–1.59
	Shannon evenness	$\mathrm{Evenness}_s = \frac{\mathrm{Shannon}_s}{\ln(N)}$	0.40	0.00–0.97	0.38	0.00–1.00
Structural diversity (*ba*)	Standard deviation	$\mathrm{sd}_{\mathrm{d}} = \mathrm{sd}(ba)$	109.33	17.32–288.00	95.75	0.00–614.81
	Coefficient of variation	$\mathrm{CV}_{\mathrm{d}} = 100 * \frac{\mathrm{sd}_{\mathrm{d}}}{\bar{x}_{ba}}$	82.77	53.88–152.08	68.96	0.00–202.34
	Gini coefficient	$\mathrm{GC}_{\mathrm{d}} = \frac{\sum_{j=1}^{n}(2*j-n-1)*ba_j}{\sum_{j=1}^{n}(n-1)*ba_j}$	0.43	0.30–0.60	0.40	0.00–0.95
Structural diversity (*height*)	Standard deviation	$\mathrm{sd}_h = \mathrm{sd}(h)$	280.67	90.86–618.41	251.10	0.00–860.90
	Coefficient of variation	$\mathrm{CV}_h = 100 * \frac{\mathrm{sd}_h}{\bar{x}_{height}}$	31.73	14.68–52.08	27.71	0.00–97.35
	Gini coefficient	$\mathrm{GC}_h = \frac{\sum_{j=1}^{n}(2*j-n-1)*h_j}{\sum_{j=1}^{n}(n-1)*h_j}$	0.18	0.08–0.28	0.16	0.00–0.65

Note: All variables and indices were calculated for annually resolved values per plot (all living trees including border and snapped trees) and per tree neighbourhood (alive, immediate neighbours). *ba* is the basal area measured at 1.3 m (cm^2) and h is the height (cm) of tree i, P the proportion of *ba* for species i, $\bar{x}_{ba}$ and $\bar{x}_{height}$ are the mean tree *ba* and *height*, j is a tree's rank is ascending order from 1 to n, ba_j is the basal area and h_j is the height of the tree with rank j. Mean values show the temporal mean and range covers the respective minimum and maximum values for the observation period 2006–2016.

As already mentioned, the failure of CA led to a decrease in tree density in some mixtures, which resulted in more growing space for the remaining individuals as compared to the denser monocultures. To avoid an overestimation of diversity effects, we considered the realized richness by excluding CA individuals when calculating mixing proportions (i.e. m_i equal to 0.50 and not 0.33 in the former three- and now two-species mixtures). As m_i determines the monoculture productivity, here presented RP values should be considered as conservative estimates of overyielding.

RP of a given species *i* was calculated for each year as:

$$\mathrm{RP}_{\mathrm{species}}\,(\%) = \frac{\mathrm{BAI}_{i\,\mathrm{mix}}}{m_i \mathrm{BAI}_{i\,\mathrm{mono}}} \times 100, \tag{3}$$

where $\mathrm{BAI}_{i\,\mathrm{mix}}$ is the total BAI per plot for species *i* in the mixture and $\mathrm{BAI}_{i\,\mathrm{mono}}$ is the total BAI per plot for species *i* in the monoculture. Comparing the RP among species allowed us to disentangle the possibly contrasting mixing-effects of single species that translate into a net complementarity effect of the entire community. To calculate comparable productivity estimates per species, we used the mixing proportion m_i as $\mathrm{BAI}_{\mathrm{plot\ species}}/m_i$. A one-sample *t* test was used to compare the temporal mean $\mathrm{RP}_{\mathrm{community}}$ and $\mathrm{RP}_{\mathrm{species}}$ against 0 (the expected monoculture yield).

2.6 | Growth stability

We tested for DSRs at the community level by analysing the temporal stability of tree productivity, hereafter 'stability', following Jucker et al. (2014) as:

$$\mathrm{Stability} = \frac{\mu_{\mathrm{BAI}}}{\sigma_{\mathrm{BAI}}}, \tag{4}$$

where μ_{BAI} is the mean and σ_{BAI} is the standard deviation of annual community (=plot) productivity expressed as the sum of BAI increment per hectare and year between 2006 and 2016. According to Jucker et al. (2014), overyielding (higher productivity of mixtures vs. monocultures) would lead to higher stability by means of increasing μ_{BAI}, while higher species asynchrony (contrasting responses of species to environmental variability) should result in higher stability as a result of lowering σ_{BAI}.

We calculated species asynchrony at the community level using the species synchrony measure φ (Loreau & de Mazancourt, 2008) as 1 − φ:

$$\mathrm{Species\ asynchrony} = 1 - \frac{\sigma^2_{\mathrm{BAI}}}{\left(\sum_{i=1}^{n} \sigma_{\mathrm{BAI\ species}\ i}\right)^2}, \tag{5}$$

where $\sigma_{\mathrm{BAI\ species}\,i}$ is the standard deviation of productivity of species *i* in a community of *n* species (Hautier et al., 2014; Jucker et al., 2014). Asynchrony ranges between 1 (complete species asynchrony) and 0 (complete species synchrony) and is per definition 0 in monocultures, where plot variation is entirely the result of fluctuation of BAI within a single species (Jucker et al., 2014).

TABLE 2 Overview of response variables and the final set of nondiversity growth predictors used in the community- and tree neighbourhood-level models

Variables	Community level	Neighbourhood level
Response		
$\mathrm{BAI}_{\mathrm{plot}}$	✓	
$\mathrm{BAI}_{\mathrm{tree}}$		✓
Predictors without interaction with diversity		
relM	✓	✓
ba		✓
BAL		✓
Predictors in interaction with diversity		
Year	✓	
Period		✓
Relative size		✓

Note: Community-level productivity is per plot ($\mathrm{BAI}_{\mathrm{plot}}$, $\mathrm{m}^2\,\mathrm{ha}^{-1}\,\mathrm{year}^{-1}$) and neighbourhood-level productivity for individual trees ($\mathrm{BAI}_{\mathrm{tree}}$, $\mathrm{cm}^2\,\mathrm{ha}^{-1}\,\mathrm{year}^{-1}$) modelled with species-specific models for all five species (LS, AE, HC, TR, CO). relM = relative mortality of a plot or tree neighbourhood (0.0–1.0); *ba* = focal tree's basal area (cm^2); BAL = basal area of trees larger than the focal tree (m^2). Periods were chosen according to contrasting climatic conditions and represent: an intermediate (P1, 2006–2009), a particularly wet (P2, 2010–2012) and an exceptionally dry period (P3, 2013–2016; see Appendix S3 for details). Relative tree size classes are C1 = overtopped, C2 = intermediate, C3 = dominant (Equation 6). See Appendix S4 for details and summary statistics of response variables and nondiversity tree growth predictors.

2.7 | Modelling the drivers of diversity-productivity relationships

To understand the underlying drivers of DPRs, we modelled tree productivity at the community and tree neighbourhood level in relation to species and structural diversity (Table 1), while also accounting for other factors relevant for tree growth (Table 2). The latter included tree mortality at the community level and tree size and competition at the neighbourhood level (Dănescu et al., 2016; Fichtner et al., 2018; Hutchison et al., 2018; Potvin & Gotelli, 2008).

2.7.1 | Community-level growth models

At the community level, we accounted for the effect of tree mortality on productivity ($\mathrm{BAI}_{\mathrm{plot}}$) by considering relative mortality in plots (relM; Table 2). To model temporal trends in DPRs we incorporated year, its squared form and tested interactions between year and each candidate diversity index (Table 2). We did not include a stand density proxy like plot basal area due to the high correlation with year to avoid collinearity. Alternative model runs with this proxy produced similar results. Annually resolved values (2006–2016) were used for all response and predictor variables (Tables 1 and 2).

2.7.2 | Neighbourhood-level growth models

At the tree neighbourhood level, we built species-specific models to address differences among species. In addition to diversity indices, we included the following growth relevant factors (see Appendix S4 for details): (a) relative mortality (relM) of immediate neighbours to account for neighbourhood mortality, (b) a focal tree's log-transformed *ba* to account for the effect of tree size and (c) *ba* of the immediate neighbours *j* larger than the focal tree *i* (BAL) to account for competition calculated as $\sum_{j \neq i} ba_j$ (Table 2).

We modelled the mean annual $\mathrm{BAI}_{\mathrm{tree}}$ of individual trees during three observation periods chosen according to contrasting climatic regimes: a first intermediate period (2006–2009), a secondparticularly wet period (2010–2012) and a third exceptionally dry period (2013–2016; see Appendix S3 for details). All response and predictor variables were calculated as mean values per period. We chose periods rather than annual increments (like at the community-level), to factor out measurement inaccuracies between successive years, caused mainly by null or near-zero tree increments during the latter years of the observation period, marked by high water deficits. We checked the validity of zero increment values using a comparison with available basal diameter data (measured 10 cm from the ground) for the same trees, which confirmed our assumption of low increments. To assess changes in diversity effects during stand development and with climatic conditions, we tested for interactions between each candidate diversity index and the observation period. Finally, to test whether tree size influences DPRs, we tested for interactions between diversity indices and relative size of focal trees compared to their neighbours, calculated as:

$$\text{Relative size} = 1 - \left(\frac{1}{\text{BAN}} * \text{BAL}\right), \qquad (6)$$

where BAN is the sum of basal areas of neighbouring trees. We scored each tree's relative size according to three equally spaced classes to facilitate interpretation and to mitigate collinearity: overtopped (C1, 0.00–0.33), intermediate (C2, 0.34–0.66) and dominant trees (C3, 0.67–1.00). Relative size thus captures the combined effect of a focal tree's size and competitive status.

2.8 | Modelling framework

2.8.1 | Diversity–productivity relationships

We used linear mixed-effects models (LMMs) to gain insight into the temporal development of diversity-productivity relationships while accounting for the inherently correlated errors in our data. Factors identifying replication and spatial structure (tree species composition at the community and additional plots, subplots and focal tree identity at the tree neighbourhood level) were modelled as nested random effects. We followed the same model selection procedure at the community and neighbourhood level to ensure comparability of results. To test whether species diversity or structural diversity or a combination of both affect tree growth, we developed a null model of tree productivity without any diversity index and a series of models, each incorporating one diversity component. Model development involved the stages proposed by Zuur, Ieno, Walker, Saveliev, and Smith (2009):

1. Specifying a null model (i.e. excluding diversity variables) with a beyond-optimal selection of fixed effects.
2. Optimizing the random structure (random effects, temporal autocorrelation, variance structure) in the presence of the beyond-optimal model specification.
3. The optimal null model structure was chosen via removing all non-significant fixed effects (see Table 2 for the final set) and was kept fixed in the subsequent analysis.
4. Testing diversity indices: we included the species and structural diversity indices (Table 1) one by one and evaluated index performance via an information theoretic model selection framework based on Akaike weights (*w*; Burnham & Anderson, 2002; Whittingham, Stephens, Bradbury, & Freckleton, 2006).
5. Final diversity model: the highest ranking species diversity and structural diversity index determined in step four was included into one final model.

Due to the non-normal distribution of the response we applied a fourth root transformation at the community level and a Box–Cox transformation (Box & Cox, 1964) at the tree neighbourhood level. We only included predictors into the models that were not collinear (Spearman's rho < 0.6 and a variance inflation factor for mixed models <5, which is a conservative choice (Dormann et al., 2013).

2.8.2 | Diversity–stability relationships

We used linear regression to test our hypothesis that species and structural diversity stabilize productivity in mixtures via regressing community stability against diversity indices (Table 1). As described in the LMM framework above, Akaike weights were used to determine the best candidate diversity indices. To determine whether diversity effects on stability resulted from increased μ_{BAI} or decreased σ_{BAI}, we regressed both against the best-performing index. Finally, we tested for the effect of species asynchrony by regressing it against stability. If residuals were not normally distributed, we applied a log-transformation to the response variable. Simple linear regression was used to analyse stability, quantified as temporal means without repeated measurements.

All analysis were performed in R (version 3.5.0) using the packages nlme (Pinheiro, Bates, DebRoy, Sarkar, & R Core Team, 2018), piecewiseSEM (Lefcheck, 2016), AICcmodavg (Mazerolle, 2019) and ggplot2 (Wickham, 2016) for graphics. Validity of model assumptions was tested via graphical tools (quantile–quantile, residual, autocorrelation and partial autocorrelation plots). LMMs were fit with the package nlme to allow for the specification of variance functions, to address heteroscedasticity and to model temporal autocorrelation (see Appendix S4 for technical details on LMM development, structure and model evaluation). Finally, we explored whether the overlap between the considered tree neighbourhoods (Figure 1) might influence our results. We tested two alternatives: models based on a subset of data with strictly nonoverlapping neighbourhoods or with spatial instead of temporal autocorrelation, which yielded consistent results (see Appendix S7 for details).

3 | RESULTS

3.1 | Community-level overyielding and stability

All mixtures were more productive than monocultures and this overyielding increased with species richness (Figure 2a). Across all years, mean overyielding was 25%–30% in the two- and three-species mixtures and nearly 50% in the five-species mixtures. Overyielding was only significant for the two- and five-species mixtures. Calculating overyielding based on the 'initially planted species richness', in contrast to the here used 'realized species richness', increased overyielding estimates to ~80%–90% in the two- and five-species mixtures, while overyielding in the three-species mixtures remained unchanged (no CA individuals were planted in these plots; Figure S6).

Overyielding differed among the five tree species: the fastest growing species, LS (pioneer) and AE (light-intermediate) showed highly significant overyielding, while the two shade-tolerant species (CO, TR) did not (Figure 2b). In CO, the response was highly variable but tended to be positive (*p* = .08, Figure 2b). HC (intermediate) was the only species with significant underyielding in mixtures (Figure 2b).

Overyielding significantly increased (*p* = .0082) over time in the five-species mixtures, while no significant trend was detected in two- and three-species mixtures (Figure 3). An apparent decline in overyielding in three-species mixtures from high values in the first years (2006–2008) (Figure 3; Figure S7) was not significant. While we found overyielding for all richness levels and in most years between 2006 and 2016, it was lowest and even negative around 2010 (Figure S7). This drop, during a particularly wet period, coincided with a peak in monoculture productivity but no consistent change in mixtures (Figure 4; Figure S3). Differences in species productivity

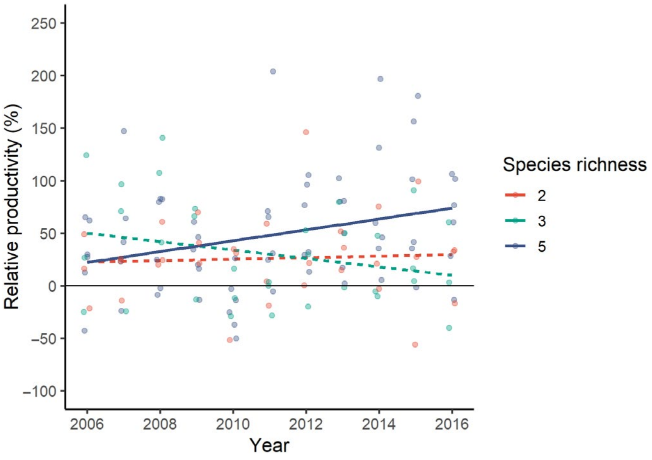

FIGURE 3 Temporal development of relative productivity (RP) according to the species richness levels of mixtures (2, 3 and 5 species) compared to monocultures. Fitted linear mixed-effects models exclusively account for the fixed effect of time on the development of RP and for repeated measurements through a random plot effect. Continuous lines indicate significant relationships while dashed lines indicate nonsignificant relationships. The zero line represents the monoculture yield. Points represent observed values of RP for each individual plot and 11 years (*N* = 22 × 11)

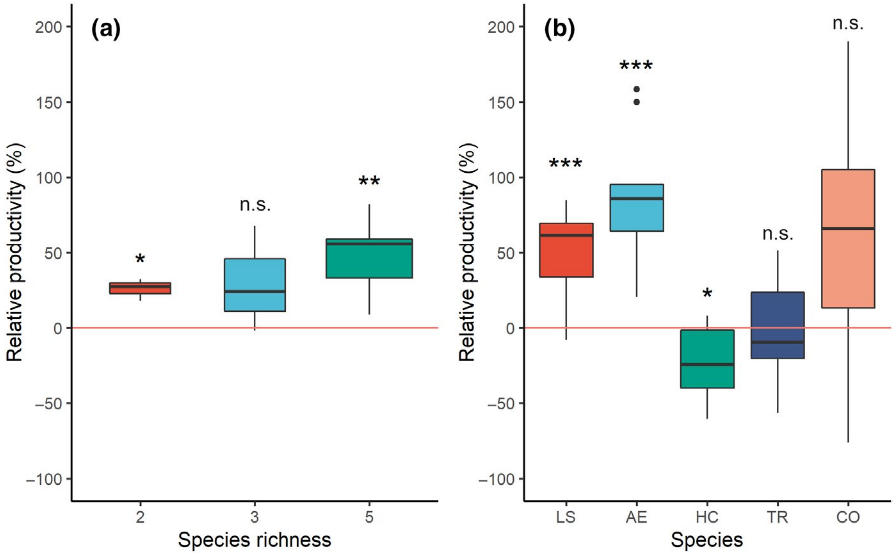

FIGURE 2 Temporal mean (2006–2016) relative productivity (RP) of mixtures compared to monocultures. RP was calculated based on community-level productivity (m^2 ha^{-1} year^{-1}) with Equations (2) and (3). RP is presented per realized species richness levels (a) and individual species (b). Species are ordered according to their relative growth rates in natural forests, from fast (left) to slow (right). The five species are *Luehea seemannii* (LS), *Anacardium excelsum* (AE), *Hura crepitans* (HC), *Tabebuia rosea* (TR) and *Cedrela odorata* (CO). The zero line represents the monoculture yield. Significant differences between mixtures and monocultures are shown as stars with *$p \le .05$, **$p \le .01$, ***$p \le .001$, n.s., not significant

in monocultures generally corresponded with their relative growth rates in natural forests (Figure 4), except for HC (intermediate in natural forests), which was consistently the slowest growing species in the experiment (Figure 4). The performance of those species that reacted positively to increasing diversity levels (LS and AE) fluctuated over time and varied with mixture type. The fast growing species LS had the highest productivity in the first years, especially in three-species mixtures, while the second fastest growing species AE reached similar levels of productivity at a later phase of stand development (Figure 4).

The stability of community-level productivity significantly increased with species richness (Figure 5a). The stabilizing effect of diversity resulted mainly from a significant positive effect of richness on the temporal mean of productivity (μ_{BAI}), while there was no significant effect on the temporal variation in productivity (σ_{BAI}; Figure S8). Species asynchrony had a strong and highly significant positive effect on stability, consistent with a trend towards higher asynchrony at higher richness levels (Figure 5b). μ_{BAI} had a positive and σ_{BAI} a negative relationship with asynchrony, albeit both relationships were not significant (results not shown). All candidate species diversity indices had a similar impact on stability, with the highest Akaike weight for species richness ($w = 0.31$), followed by the Shannon diversity ($w = 0.24$) and evenness index ($w = 0.15$; results not shown). We found no significant effect of structural diversity on stability and low Akaike weights for all structural diversity indices ($w = 0.03$ or below; results not shown).

3.2 | Drivers of community productivity

Species and structural diversity both had overall positive influences on productivity but displayed contrasting patterns over time. While the positive effect of species diversity significantly increased ($p = .0095$), the opposite was true for structural diversity. For the latter, the strong positive effect in the first years (tree age >5)

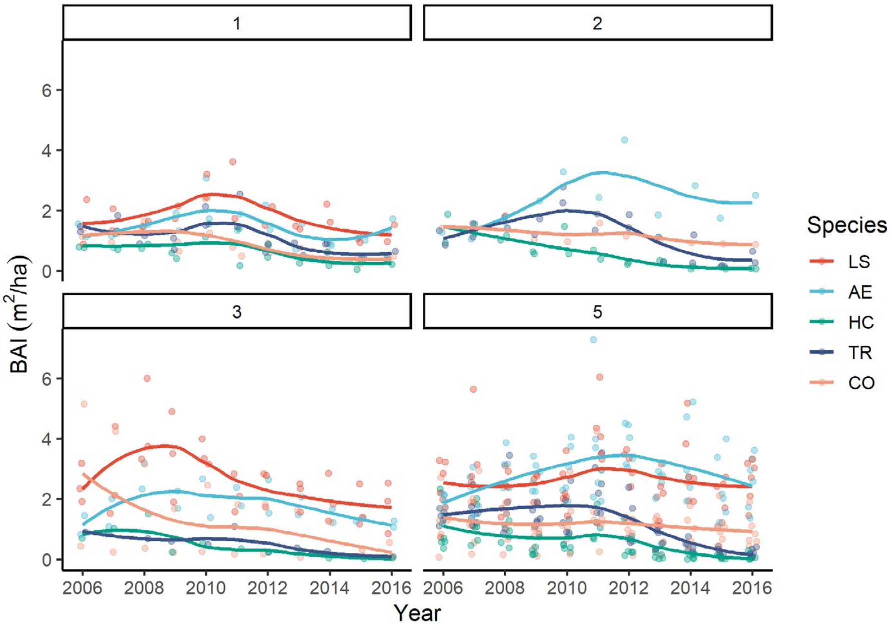

FIGURE 4 Temporal development of community-level productivity (BAI$_{\text{plot}}$, m^2/ha) per year and species, in connection with four levels of species richness (1, 2, 3 and 5 species; see boxes above panels). Temporal patterns are described by local polynomial regressions. Points represent observed values of productivity per plot for 11 years ($N = 10 \times 11$ for monocultures, $N = 3 \times 11$ for two- and three-species mixtures and $N = 6 \times 11$ for five-species mixtures). The productivity of species in mixtures was scaled to the monoculture yield with the mixing proportion m_i as BAI$_{\text{plot species}}/m_i$. In the legend, species are ordered according to their relative growth rates in natural forests, from fastest (LS) to slowest (CO). AE, *Anacardium excelsum*; CO, *Cedrela odorata*; HC, *Hura crepitans*; LS, *Luehea seemannii*; TR, *Tabebuia rosea*

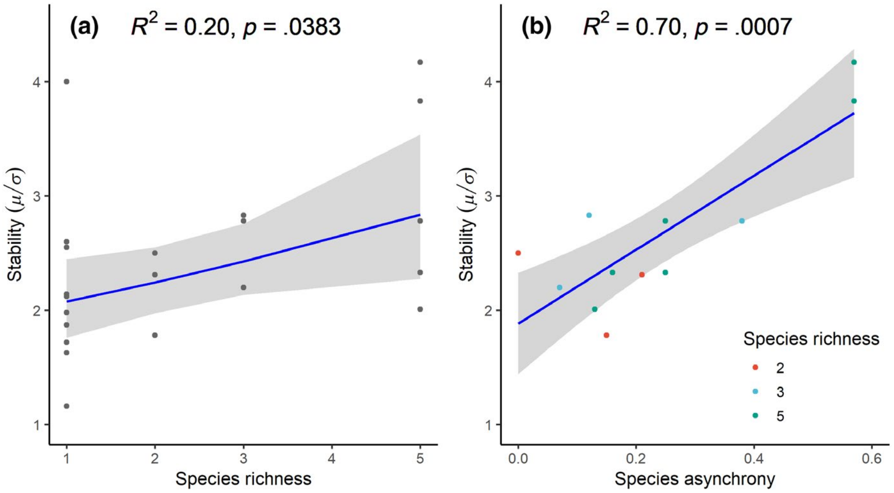

FIGURE 5 Temporal stability of community productivity as a function of species richness (a) and species asynchrony (b). Stability and species asynchrony were calculated with Equations (4) and (5) respectively. For (a) fitted values were back transformed from a log-scale to match the original values per plot (grey points). For (b) points represent values per plot and colours the respective species richness. The grey-shaded areas show a 95% confidence interval for the fitted models

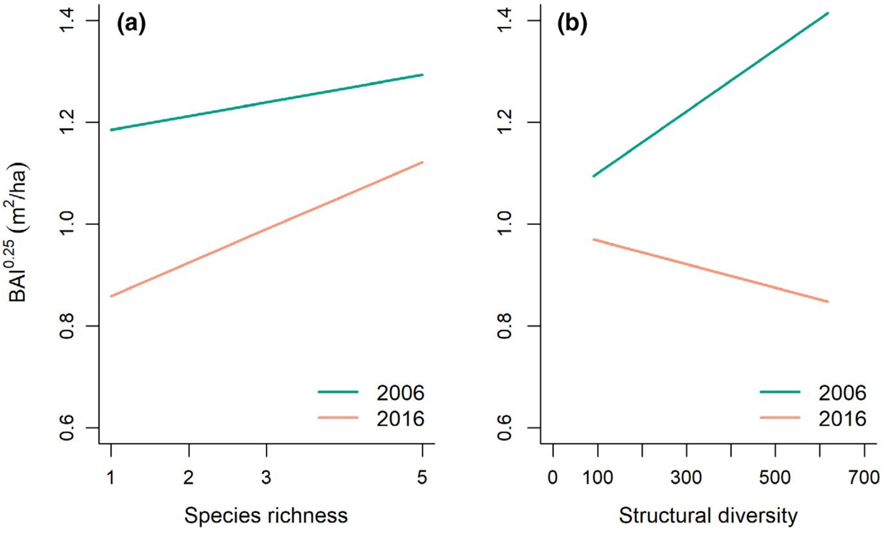

FIGURE 6 Changes in species diversity (a) and structural diversity (b) effects over time. Diversity effects show the change in community-level productivity (BAI$_{plot}$, m^2/ha) at the start (2006) and end (2016) of the observation period for the highest ranking species diversity (Richness$_s$) and structural diversity index (sd$_h$). Lines show linear mixed-effects model fits at intermediate levels of the other diversity component, that is, the species diversity effect at mean structural diversity and vice versa. Response values were fourth root transformed to normalize residuals. For linear mixed-effects model parameter estimates, see Table S3 and for a description of the diversity indices, Table 1

TABLE 3 Highest ranking species diversity (SR) and structural diversity (SD) index models for the community and tree neighbourhood level with respective model-fits, Akaike weights and correlation statistics

Response	SR index	SD index	Other fixed effects	w_{SR}	w_{SD}	Rho	R^2_m	R^2_c
Community								
BAI$_{plot}$	Richness$_s$	sd$_h$	relM, Year, Year^2	0.41	0.25	0.45	0.38	0.68
Neighbourhood								
LS (BAI$_{tree}$)	Shannon$_s$	CV$_d$	log(ba), relM, BAL, Period, Relative size	0.61	0.01	0.34	0.74	0.78
AE (BAI$_{tree}$)	Richness$_s$	CV$_d$	log(ba), relM, BAL, Period, Relative size	0.77	0.00	0.35	0.94	0.98
HC (BAI$_{tree}$)	Evenness$_s$	—	log(ba), relM, BAL, Period, Relative size	0.49	—	—	0.96	0.97
TR (BAI$_{tree}$)	Evenness$_s$	GC$_h$	log(ba), BAL, Period, Relative size	1.00	0.00	0.46	0.81	0.86
CO (BAI$_{tree}$)	Richness$_s$	sd$_h$	log(ba), relM, BAL, Period, Relative size	0.00	1.00	0.29	0.86	0.94

Note: Only the most parsimonious (highest Akaike weight) models with significant diversity components are presented (see Appendices S4 and S6 for detailed selection criteria and index ranking). Akaike weights (*w*) show the relative support for a candidate diversity model (with 0 for a low and 1 for the highest relative likelihood). Spearman's rho shows the correlation between the species and structural diversity indices. Marginal R^2 values (R^2_m) represent the variance explained by the fixed and conditional R^2 values (R^2_c) the variance explained by fixed and random effects (Nakagawa, Schielzeth, & O'Hara, 2013) of the final model. For a detailed description of the diversity indices, see Table 1 and for other variable names, Table 2.

significantly declined over time ($p = .0049$; Figure 6; Table S3). Stand-level productivity significantly decreased over time and with higher mortality of trees ($p \le .0001$; Figure 6, Table S3). All species diversity indices showed similar and significantly positive effects, but species richness led to the most parsimonious model (Table 3 and Table S2). The standard deviation of tree height led to the most parsimonious structural diversity index model (Table 3 and Table S2), but also the other diameter and height diversity indices that increased model performance had overall positive effects. Akaike weights and direct standardized effect sizes clearly supported the relative superiority of species diversity over structural diversity, but changes in productivity over time were stronger for structural diversity (Table 3; Table S3).

3.3 | Drivers of individual tree productivity at the neighbourhood level

All species-specific null models had a similar set of fixed effects. Significant nondiversity growth predictors unrelated to diversity were (in decreasing order of their effect size): (a) size of the focal tree with a positive effect on productivity; (b) competition (expressed as BAL), which had a negative effect on productivity; and (c) neighbour mortality that increased productivity of focal trees (Table 3; Tables S4–S8; see Appendix S6 for details). Importantly, single-tree productivity declined for all species from period 1 (2006–2009) over period 2 (2010–2012) to far lower productivity in period 3 (2013–2016; Tables S4–S8).

Indices of species and structural diversity were significantly related to individual tree productivity for three out of five species. Growth in the species HC and TR responded only to species diversity but not to structural diversity. To capture the partly contrasting effects of species and structural diversity on growth performance and to simultaneously focus on the most relevant effects, we report here only the highest ranking species and structural diversity index (see Table S2 for a detailed index ranking). All presented models explained high shares of the variation in tree productivity (marginal $R^2 \ge 0.74$; Table 3). Finally, as interactions of the diversity component

TABLE 4 Significant species diversity and structural diversity effects ($p \leq .05$) on individual tree productivity at the tree neighbourhood level

		Periods			Relative tree size		
Response (BAI$_{tree}$)	Diversity index	P1 2006–2009 Intermediate	P2 2010–2012 Wet	P3 2013–2016 Dry	C1 Overtopped	C2 Intermediate	C3 Dominant
Species diversity							
LS	**Shannon$_s$**	++		+			++
AE	**Richness$_s$**			++		+	++
HC	**Evenness$_s$**			−−			
TR	**Evenness$_s$**	+		−−			
CO	Richness$_s$			+			+
Structural diversity							
LS	CV$_d$			−−			
AE	CV$_d$			++			
HC	n.s.						
TR	n.s.						
CO	**sd$_h$**	++					

Note: The highest-ranking species-specific models of tree productivity at the tree neighbourhood level and their interactions with the period of observation and/or a tree's relative size are shown. Significant positive effects of diversity on productivity are shown with a +, ++ and negative effects with a −, −− (two scales of effect strength each) within a species-specific model. Sample size for the five species is: LS (N = 469 × 3), AE (N = 383 × 3), HC (N = 288 × 3), TR (N = 607 × 3), CO (N = 412 × 3) for individual trees and three observation periods. Periods were chosen according to contrasting climatic conditions and represent: an intermediate (P1, 2006–2009), a particularly wet (P2, 2010–2012) and an exceptionally dry period (P3, 2013–2016; see Appendix S3 for details). Relative size classes of focal trees are: C1 = overtopped, C2 = intermediate and C3 = dominant trees (see Equation 6). The diversity component (species diversity or structural diversity) with the higher Akaike weight (w) for each species is printed in bold (Table 3). For linear mixed-effects model parameter estimates, see Tables S4–S8. Species are ordered according to their relative growth rates in natural forests, from fastest (LS) to slowest (CO).
Abbreviations: AE, *Anacardium excelsum*; CO, *Cedrela odorata*; HC, *Hura crepitans*; LS, *Luehea seemannii*; n.s., not significant; TR, *Tabebuia rosea*.

with period and/or a tree's dominance class were significant ($p \leq .05$) for all species, we only report on these higher-order model terms (Table 4).

Neighbourhood diversity effects on individual tree productivity strongly varied between the examined periods (Table 4). We found the overall strongest species diversity and structural diversity effects in the third period. In contrast, in the second period, measures of diversity displayed an overall low, nonsignificant influence on tree productivity. In addition, relative size of focal trees modulated species diversity but not structural diversity effects on single-tree productivity (Table 4).

Productivity in focal trees of different species responded differently to species diversity, but overall positive effects prevailed (Table 4). Effects were consistently positive for the fast-growing species LS, the intermediate AE and the shade-tolerant CO that experienced the strongest effects in the first (LS) and third period (AE, CO) respectively. For these three species, positive species diversity effects on productivity increased with a focal tree's dominance (Table 4). Only the slow-growing species HC showed a consistently and increasingly negative relationship with species diversity (Table 4; Table S6). Interestingly, species diversity effects on productivity of the shade-tolerant TR were comparably variable over time (Table 4).

Effects of structural diversity on individual species changed over time and became more contrasting (Table 4). In the first period, effects were consistently positive for all species except HC (Tables S4–S8), but this effect was significant only for the shade-tolerant species CO (Table 4). In the third period, structural diversity had especially a positive effect on the intermediate species (AE), while the fast-growing species LS was negatively influenced. Finally, we found a moderate positive correlation among species and structural diversity for most species (LS, AE, TR, CO, Table 3).

4 | DISCUSSION

4.1 | Temporal dynamics of species diversity–productivity relationships

Results of this study clearly support our hypothesis of a positive diversity-productivity relationship (DPR) that increases in strength over time. While earlier studies in Sardinilla concluded that two- and three-species mixtures were the most productive (e.g. Healy et al., 2008; Potvin & Gotelli, 2008), our analysis of a longer temporal record shows that overyielding increased with stand development in the five-species mixtures, which overall outperformed the less diverse mixtures. Thus, if only early years of the experiment were analysed, very different conclusions would be drawn regarding optimal richness levels for the productivity of mixed-species plantations, that is, few versus many species.

Several processes could explain this finding: differences between species likely required time to develop into complementary interactions, for example to realize crown packing induced overyielding (Jucker, Bouriaud, & Coomes, 2015). Furthermore, species with similar growth rates were planted in direct adjacency in the five-species mixtures of Sardinilla, which likely caused an initial spatial dilution of complementary species characteristics (Sapijanskas et al., 2013; Scherer-Lorenzen et al., 2005). This would lead to the observed pattern of overyielding increasing with stand development as contrasting species started to interact. Finally, the fast-growing species LS likely benefitted from neighbourhood species diversity especially in the first years when it experienced no or little competition for light from slower growing competitors (Table 4; Figure 3). Community overyielding was consequently high in the three-species mixtures (one third of individuals are LS trees) in the first years (Figure S7).

Current knowledge on the mechanisms driving the temporal dynamics of DPRs in forests is so far based nearly exclusively on results from two-species mixtures (Forrester & Bauhus, 2016). Only very recently, a similarly increasing DPR over time has been reported for the BEF-China and FORBIO tree diversity experiments (Huang et al., 2018; van de Peer, Verheyen, Ponette, Setiawan, & Muys, 2018) and for a replacement-series mixture experiment in Costa Rica (Ewel, Celis, & Schreeg, 2015), while most other forest BEF experiments are still too young for such temporal analysis. Our results add to the increasing evidence that species diversity is a key tool to increase forest productivity (Huang et al., 2018; Jactel et al., 2018) and caution against conclusions drawn from early stages of experiments and afforestation trials, which cannot take into account the temporal dynamics of DPRs. The importance of long-term observations in diversity experiments is also supported by studies of commercial mixed-species plantations with native tree species in Costa Rica (Piotto, Craven, Montagnini, & Alice, 2010; Redondo-Brenes & Montagnini, 2006). Here, several species that grew well at a juvenile stage suffered high mortality with progressing stand development (Piotto et al., 2010).

To mechanistically explain our findings regarding overyielding, we modelled tree productivity as a function of species and structural diversity both at the community and tree neighbourhood level. In tree neighbourhoods, species and structural diversity effects on single-tree productivity varied (a) among species, (b) with progressing stand development, (c) according to contrasting climatic conditions and (d) with relative dominance of focal trees. The general patterns found for neighbourhoods, however, were consistent with those found at the community level. We conclude that tree–tree interactions in neighbourhoods are the principal drivers of diversity effects observed at the community level, confirming earlier results from Sardinilla (Potvin & Dutilleul, 2009) and other tree diversity experiments (Fichtner et al., 2018; van de Peer et al., 2018). In line with former results from Sardinilla (Potvin & Dutilleul, 2009; Sapijanskas et al., 2013), tree size was the strongest determinant of tree-level productivity, followed in our study by competition and mortality. Importantly, species diversity effects on productivity increased with dominance of individual trees for species with different shade-tolerances. This indicates that one important diversity effect is competitive reduction for fast growing tree species, while slower growing and shade-tolerant species may also benefit from species diversity if they are less suppressed by their neighbouring companion species. This is consistent with results from the BEF-China experiment, where small trees that experienced comparatively little competition benefitted most from neighbourhood species richness (Fichtner et al., 2018). The combined contribution of tree size and competition by neighbours to diversity effects highlights the increasingly recognized role of local tree neighbourhoods for understanding DPRs in forest ecosystems (Forrester & Pretzsch, 2015; Stoll & Newbery, 2005).

Here, we calculated the RP of mixed-species systems (compared to monocultures) for the whole community and for individual species to take into account selection versus complementarity effects (Forrester & Bauhus, 2016; Forrester & Pretzsch, 2015). Species of all ecological types—a fast-growing (LS), an intermediate (AE) and a slow-growing species (CO)—overall performed better in mixtures compared to their respective monocultures, while only one species (HC) consistently reacted negative. This clearly indicates an overall positive complementarity (i.e. ‘true’ mixing) effect driven by the relative dominance of competitive reduction and/or facilitation over competition. Former studies in Sardinilla provide some mechanistic insights into the processes and species-specific properties that likely contributed to the responses found in this study. For example, Zeugin, Potvin, Jansa, and Scherer-Lorenzen (2010) found higher nitrogen (N)- and phosphorus (P)-use efficiencies for the overyielding species (LS and AE) and Sapijanskas, Paquette, Potvin, Kunert, and Loreau (2014) showed that tree species diversity enhanced community-level light capture and hence productivity. Importantly, complementary water use was found in mixtures in Sardinilla, caused by three distinct water uptake depths of participating species (Schwendenmann, Pendall, Sanchez-Bragado, Kunert, & Hölscher, 2015), which could cause competitive reduction through niche differentiation (spatial segregation) and possibly also facilitation due to hydraulic redistribution of water from deeper to shallower soil layers (Forrester, 2017). This complementary water uptake may have driven overyielding, especially during drought conditions in the last observation period. It is important to note here that most of these studies used data from 2006 to 2009, while we report on the longer period 2006–2016. Hence, the described processes might have changed in strength and relative importance over time.

4.2 | Structural diversity effects on productivity

We showed for the first time that structural diversity is an important driver of ecosystem functioning in forests under the controlled conditions of a forest BEF experiment. The structural diversity indices used here may be regarded as measures of canopy complexity (Dănescu et al., 2016; McElhinny, Gibbons, Brack, & Bauhus, 2005), which is increasingly recognized as an important determinant of forest productivity, especially in mixed stands via light-mediated tree–tree interactions (Forrester & Bauhus, 2016). In Sardinilla, three processes were shown to increase light capture and hence productivity of trees growing in mixtures: (a) architectural niche separation, (b) plastic changes in crown shape and (c) temporal niche differentiation among species driven by different leaf phenologies (Sapijanskas et al., 2014). Our diameter and height diversity indices likely reflect architectural differences and to a certain degree plastic changes in crown shape, the two processes most often evoked as drivers of canopy complexity (Dănescu et al., 2016; Sapijanskas et al., 2014). Phenological differences among tree species played an important role in Sardinilla (Sapijanskas et al., 2014) but their species-specific contribution is likely better reflected through species diversity indices than through structural diversity indices. Consistent with theory, shade-tolerant (understorey) and light intermediate (mid-canopy) species benefitted most from an increase in structural diversity since they are further away from light saturation compared to canopy trees (Sapijanskas et al., 2014). Additionally, the light-intermediate species AE benefitted most during drought conditions which could be explained via protection from harsh climatic conditions (Pretzsch et al., 2018), a process that has been found to strongly determine DPRs especially of conservative species (Fichtner et al., 2017). In contrast, the negative neighbourhood structural diversity effects on productivity of fast-growing species (LS) might be caused by greater crown exposure to wind and radiation under dry conditions, which has been described for taller species in other mixtures (Vitali, Forrester, & Bauhus, 2018). Increasingly divergent effects of neighbourhood structural diversity on individual species may have led to the declining effect of structural diversity on community-level productivity.

Structural diversity had less influence on community productivity than species diversity. While species diversity leads to complementary above- and below-ground interactions, structural diversity effects on forest productivity likely result from above-ground niche partitioning, that is, a subset of the effects of species diversity. As suggested by work in natural forests (Jucker et al., 2015; Zhang et al., 2015), structural diversity effects in our species-rich but rather young tropical plantation are thus likely (partially) mediated effects of species diversity. Crown complementarity as result of intrinsic differences between species is such an effect, which was recently shown to strongly drive DPRs in young tree mixtures (Williams, Paquette, Cavender-Bares, Messier, & Reich, 2017). It is unlikely that at a certain point in time DPRs are driven either by species diversity or by structural diversity. Instead, our results support the idea that the relative contribution of these complementarity effects changes over time. This conclusion is consistent with recent theoretical work and results from many studies, even though the latter were almost exclusively based on two-species mixtures (Forrester, 2014, 2017; Forrester & Bauhus, 2016). In our study, all analysed mixtures consisted of tree species with clearly different shade tolerances (shade-tolerant, intermediate and light-demanding) that occupied different canopy positions. In other words, they display characteristics that should encourage crown complementarity (Williams et al., 2017) and thus enhance light capture and light-use efficiency (Forrester, 2017; Potvin et al., 2011). Similarly, structural diversity effects on productivity were positive in stands characterized by distinct vertical layering, species with different shade tolerances (Hardiman, Bohrer, Gough, Vogel, & Curtis, 2011; Zhang et al., 2015) or only shade-tolerant species (Dănescu et al., 2016) but negative for shade-intolerant *Eucalypt* species (Binkley et al., 2010; Ryan et al., 2010). Structural diversity may hence act as an important driver of positive DPRs if the above prerequisites are met.

4.3 | Tree diversity increases production stability

Under climate change, stability of production and other functions of forests are likely to become a key issue in the 21st century. Our results for the oldest tropical tree diversity experiment, like those of Hutchison et al. (2018), clearly support the idea that diversity exerts a positive influence on stability. Tropical mixed-species plantations showed a more stable productivity across periods of contrasting climatic conditions. Hutchison et al. (2018) reported that monoculture mortality in Sardinilla was strongly driven by climatic conditions and that mixing species buffered this effect. Whereas Hutchison et al. (2018) separated the influence of extreme climatic events on growth and mortality, we focussed on living trees to express stability as an integrated metric, 'temporal stability' (Tilman, 1999), over 10 years of growth. In agreement with our expectation, based on both ecological theory (Loreau & de Mazancourt, 2013) as well as results from the few studies that examined temporal stability (del Río et al., 2017; Jucker et al., 2014), we found species asynchrony to be the strongest predictor of stability. The complementary species interactions that have been described for the Sardinilla experiment (see above) provide the basis for niche differentiation among species and facilitate asynchronous species responses to changing environmental conditions (Loreau & de Mazancourt, 2008). Since asynchrony depends mostly on species characteristics, it may not surprise that we did not find a significant contribution of structural diversity to stability of productivity.

In addition to species asynchrony, stability increased through overyielding (higher mean productivity μ in mixtures) but not through reduced variation (σ) of productivity (Figure S8). Similarly, Jucker et al. (2014) found a consistent stabilizing effect of overyielding on growth stability across European forest biomes. The lack of a mixing effect on variability of productivity in our study might be partly attributable to the delayed complementarity effects in five-species mixtures, combined with the random positioning of the five-species plots on especially variable soils (Healy et al., 2008). Finally, species diversity can increase stability via enhanced growth in mixtures but also by reducing drought-induced mortality compared to monocultures (Hutchison et al., 2018).

Overyielding of mixed stands is expected to increase with harsher climatic conditions and more limited water resources, but only if species interactions increase water availability and/or water-use efficiency (Forrester, 2014; Forrester & Bauhus, 2016). In line with theory, we found the strongest effects of neighbourhood-level species diversity on productivity during a dry period, characterized by a strong and prolonged El Niño drought, while diversity effects were negligible during a wet climatic period. This pattern was apparent at the tree neighbourhood and the community level. The nonlinear drop in overyielding during the extremely wet climate period (P2) likely reflects the absence of a limiting resource (Forrester & Bauhus, 2016) and underlines the climate-induced water availability dependence of overyielding in Sardinilla. The influence of climate on overyielding in the most recent years, however, cannot be disentangled from the effect of increasing species interactions as trees grow. We, therefore, assume that the highest overyielding in the last years was attributable to both increasing strength of interactions with progressing stand development and amplified complementarity during drought. These climate-driven changes in complementary tree–tree interactions at the tree neighbourhood level are likely the principle mechanisms behind the community-level growth responses to contrasting climatic conditions that were reported by Hutchison et al. (2018). Complementary neighbourhood interactions for water are also the likely underlying reason for lower mortality in mixtures when compared to monocultures during the dry period (Hutchison et al., 2018). Complementary water uptake strategies (Schwendenmann et al., 2015) in addition to distinctly different leaf phenologies of the assembled species (Kunert, Schwendenmann, & Hölscher, 2010) may have allowed mixtures to outperform monocultures during drought.

In summary, we found that species and structural diversity enhanced both productivity and its stability in mixed compared to monospecific stands. We show that beneficial effects of diversity in this tropical tree plantation increased with stand development, were highest at the highest levels of diversity and strongest under drought conditions. Results of this study regarding increased productivity in mixtures are consistent with findings from tropical and boreal forests but may not similarly hold in temperate forests or at larger spatial scales, as competitive species interactions and environmental gradients can outweigh beneficial complementarity effects (Chisholm et al., 2013; Fotis et al., 2018; Paquette & Messier, 2011). Tree–tree interactions in local neighbourhoods were the principle drivers of these diversity effects. For forest restoration initiatives tree-by-tree mixing, compared to commonly used group planting, might, therefore, facilitate positive effects of mixed-species systems on productivity during early stages of stand development (van de Peer et al., 2018). These results support the idea that mixed plantations with species of complementary resource use are a promising strategy for combining high productivity and production stability in the face of unprecedented climate changes.

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ORCID

Florian Schnabel https://orcid.org/0000-0001-8452-4001
Julia A. Schwarz https://orcid.org/0000-0003-2610-3588
Adrian Dănescu https://orcid.org/0000-0002-2910-4976
Andreas Fichtner https://orcid.org/0000-0003-0499-4893
Charles A. Nock https://orcid.org/0000-0002-3483-0390
Jürgen Bauhus https://orcid.org/0000-0002-9673-4986

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Chapter 7

Multiple plant diversity components drive consumer communities across ecosystems

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Multiple plant diversity components drive consumer communities across ecosystems

Andreas Schuldt[1,2,3], Anne Ebeling[4], Matthias Kunz[5], Michael Staab[6,7], Claudia Guimarães-Steinicke[8], Dörte Bachmann[9], Nina Buchmann[9], Walter Durka[1,10], Andreas Fichtner[11], Felix Fornoff[6], Werner Härdtle[11], Lionel R. Hertzog[12], Alexandra-Maria Klein[6], Christiane Roscher[1,13], Jörg Schaller[14], Goddert von Oheimb[1,5], Alexandra Weigelt[1,8], Wolfgang Weisser[15], Christian Wirth[1,8], Jiayong Zhang[16], Helge Bruelheide[1,2] & Nico Eisenhauer[1,17]

Humans modify ecosystems and biodiversity worldwide, with negative consequences for ecosystem functioning. Promoting plant diversity is increasingly suggested as a mitigation strategy. However, our mechanistic understanding of how plant diversity affects the diversity of heterotrophic consumer communities remains limited. Here, we disentangle the relative importance of key components of plant diversity as drivers of herbivore, predator, and parasitoid species richness in experimental forests and grasslands. We find that plant species richness effects on consumer species richness are consistently positive and mediated by elevated structural and functional diversity of the plant communities. The importance of these diversity components differs across trophic levels and ecosystems, cautioning against ignoring the fundamental ecological complexity of biodiversity effects. Importantly, plant diversity effects on higher trophic-level species richness are in many cases mediated by modifications of consumer abundances. In light of recently reported drastic declines in insect abundances, our study identifies important pathways connecting plant diversity and consumer diversity across ecosystems.

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[1] German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, 04103 Leipzig, Germany. [2] Martin Luther University Halle-Wittenberg, Institute of Biology/Geobotany and Botanical Garden, Am Kirchtor 1, 06108 Halle, Germany. [3] Faculty of Forest Sciences, Forest Nature Conservation, Georg-August-University Göttingen, Büsgenweg 3, 37077 Göttingen, Germany. [4] Friedrich-Schiller-University Jena, Institute of Ecology and Evolution, Dornburger Strasse 159, 07743 Jena, Germany. [5] Institute of General Ecology and Environmental Protection, Technische Universität Dresden, PF 1117, 01735 Tharandt, Germany. [6] University of Freiburg, Nature Conservation and Landscape Ecology, Tennenbacher Straße 4, 79106 Freiburg, Germany. [7] University of Freiburg, Freiburg Institute of Advanced Studies (FRIAS), Albertstraße 19, 79104 Freiburg, Germany. [8] Systematic Botany and Functional Biodiversity, Leipzig University, Johannisallee 21-23, 04103 Leipzig, Germany. [9] ETH Zurich, Institute of Agricultural Sciences, Universitätsstrasse 2, 8092 Zurich, Switzerland. [10] Helmholtz Centre for Environmental Research - UFZ, Department of Community Ecology, Theodor-Lieser-Str. 4, 06120 Halle, Germany. [11] Leuphana University of Lüneburg, Institute of Ecology, Universitätsallee 1, 21335 Lüneburg, Germany. [12] Terrestrial Ecology Unit, Gent University, K.L. Ledeganckstraat 35, 9000 Gent, Belgium. [13] UFZ, Helmholtz Centre for Environmental Research, Physiological Diversity, Permoserstrasse 15, 04318 Leipzig, Germany. [14] University Bayreuth, Environmental Geochemistry, Bayreuth Center for Ecology and Environmental Research (BayCEER), Universitätsstraße 30, 95447 Bayreuth, Germany. [15] Technical University of Munich, Department of Ecology and Ecosystem Management, Terrestrial Ecology Research Group, Hans-Carl-von-Carlowitz-Platz 2, 85354 Freising, Germany. [16] Key Lab of Wildlife Biotechnology, Conservation and Utilization of Zhejiang Province, Zhejiang Normal University, 321004 Jinhua, Zhejiang Province, China. [17] Leipzig University, Institute of Biology, Deutscher Platz 5e, 04103 Leipzig, Germany. Correspondence and requests for materials should be addressed to A.S. (email: andreas.schuldt@forst.uni-goettingen.de)

Safeguarding biodiversity has become a key societal concern in the light of global environmental change[1–3] and declining numbers of insects and other organisms[4–6], particularly because biodiversity plays an important role in the provisioning of ecosystem services[7,8]. The nowadays common management of many ecosystems for only a few, selected species of primary producers contributes to changes in overall biodiversity that might prove detrimental to human well-being[6,9,10]. Managing for a higher diversity of plants has therefore been suggested as a way to mitigate such potentially negative consequences[11,12] and is expected to promote both biodiversity and ecosystem functioning at higher trophic levels[11,13]. This is because plant diversity provides essential resources and habitat for higher trophic-level organisms[14]. Yet, previous studies in forests, grasslands, and other ecosystems varied in their support for the assumption that plant diversity promotes the diversity of herbivores, predators, or parasitoids[13,15–18].

A thorough understanding of the extent to which biodiversity effects across trophic levels can be generalized is hampered by the fact that the underlying mechanisms are often not well resolved[14]. Previous studies have focused primarily on plant species richness as one component of plant diversity[13,15–17,19], although changes in the functional composition and functional diversity of plant communities may ultimately drive the effects of plant species richness on higher trophic levels[20]. Nevertheless, functional redundancy among plant species can lead to nonlinear or a lack of relationships between plant diversity and higher trophic levels[21,22]. In addition, the physical structure of plant communities has been shown to influence the spatial distribution and complexity of habitats, microclimates, and species interactions[23–25]. However, we still have a limited understanding of how the structural diversity of plant communities (both in terms of vertical distribution and horizontal variation across space) contributes to overall plant diversity effects on higher trophic levels and how it potentially interacts with the effects of plant functional diversity.

A better mechanistic understanding of how plant diversity affects the diversity and functioning of higher trophic levels may, therefore, be achieved by simultaneously considering and disentangling the relative contribution of plant functional and plant structural diversity to overall biodiversity effects[26,27]. Such an approach might also help to explain the variability in biodiversity effects among different ecosystems, such as grasslands and forests, if we were able to reduce complex plant diversity effects to basic principles related to plant structure and functional diversity. For example, differences in the vertical or horizontal distribution of structural diversity of grassland plants and trees affect gradients of light availability and temperature[28] that can strongly influence arthropod communities[23–25]. In this context, it may be particularly important to consider plant diversity effects on the abundances of higher trophic-level organisms, such as arthropods. The biomass and abundance of arthropods have recently been reported to decline significantly due to anthropogenic activities[4,6,29]. At the local scale, part of this decline may be due to changes in the structural and functional composition of plant communities[9,29]. However, the linkages between changes in plant diversity, changes in arthropod abundances, and the consequences for arthropod diversity (i.e., indirect effects of plant diversity that modify arthropod diversity via changes in arthropod abundances) at the scale of local communities are not yet well understood[5].

Here we disentangle the impact of changes in major components of plant diversity on species richness of herbivores, predators, and parasitoids for two different ecosystems. We make use of an extensive data set with 53 plant species and 34,060 individuals of 882 arthropod species of two large-scale biodiversity experiments, one in temperate grasslands[30,31] and one in subtropical forests[32]. This comparison can help us to obtain first insights into the extent to which effects of plant diversity might operate in similar ways in contrasting ecosystems. We use path models to analyze the relative contribution of direct and indirect effects of plant taxonomic diversity (species richness), functional diversity and composition, and structural diversity on overall arthropod species richness and the species richness of major trophic groups of arthropods. We quantified functional diversity as the variability among plant species in morphological and chemical leaf traits that were shown previously to affect arthropods[22,33,34]. Because plant traits can further influence arthropods via mass-ratio effects[35], we also tested for the effects of mean trait values on arthropod abundance and species richness. Vertical stratification and horizontal variation of plant height within study plots were used to quantify plant structural diversity. Importantly, we explicitly differentiated between direct and indirect plant diversity effects on arthropod species richness. We considered direct effects as those directly linking plant diversity to arthropod species richness (e.g., because plant diversity-mediated habitat diversity provides more niches that support a higher diversity of arthropods[36]). Because we hypothesized that arthropod species richness is influenced by changes in arthropod abundances (i.e., assuming that species richness is affected via more individuals[37]), we considered effects of plant diversity that modified arthropod abundances as indirect effects on arthropod species richness. Our study therefore provides important insights into the potential mechanisms linking changes in plant communities to consumer diversity via changes in abundances. We also tested the alternative hypothesis of reciprocal interactions between arthropod species richness and abundance[38], which might be better reflected by residual covariance terms than by a directional pathway in the path models. We show that the combination of plant functional and structural diversity mechanistically explains plant species richness effects on higher trophic levels in both ecosystem types. Although the relative effects of functional and structural diversity on arthropods differed among trophic levels and ecosystems, they operated in many cases via modifying arthropod abundances—indicating a high vulnerability of arthropod diversity to currently observed declines in arthropod numbers.

Results

Species composition across trophic levels. In total, we sampled 8075 arthropods belonging to 506 (morpho)species (excluding singletons, i.e., species that only occurred with one individual) in the BEF-China forest biodiversity experiment. Herbivores were the most abundant and species-rich of the trophic groups we considered in our analyses (2204 individuals [27% of total arthropod abundance], 233 species [46% of total arthropod species richness]), followed by predators (1739 individuals [22%], 171 species [34%]) and parasitoids (617 individuals [8%], 32 species [6%]). In the Jena Experiment in grassland, we sampled 25,985 arthropods belonging to 376 species (excluding singletons). Predators were the most abundant (15,702 [60% of total]) and species-rich (184 species [49% of total]) group, followed by herbivores (6099 individuals [23%], 129 species [34%]) and parasitoids (1171 individuals [5%], 26 species [7%]). In both experiments, Pearson correlations between abundance and/or richness values of herbivores, predators, and parasitoids were always positive when significant ($P \leq 0.05$; Supplementary Table 1).

Functional and structural diversity explain richness effects. In both ecosystem types, plant species richness promoted leaf trait

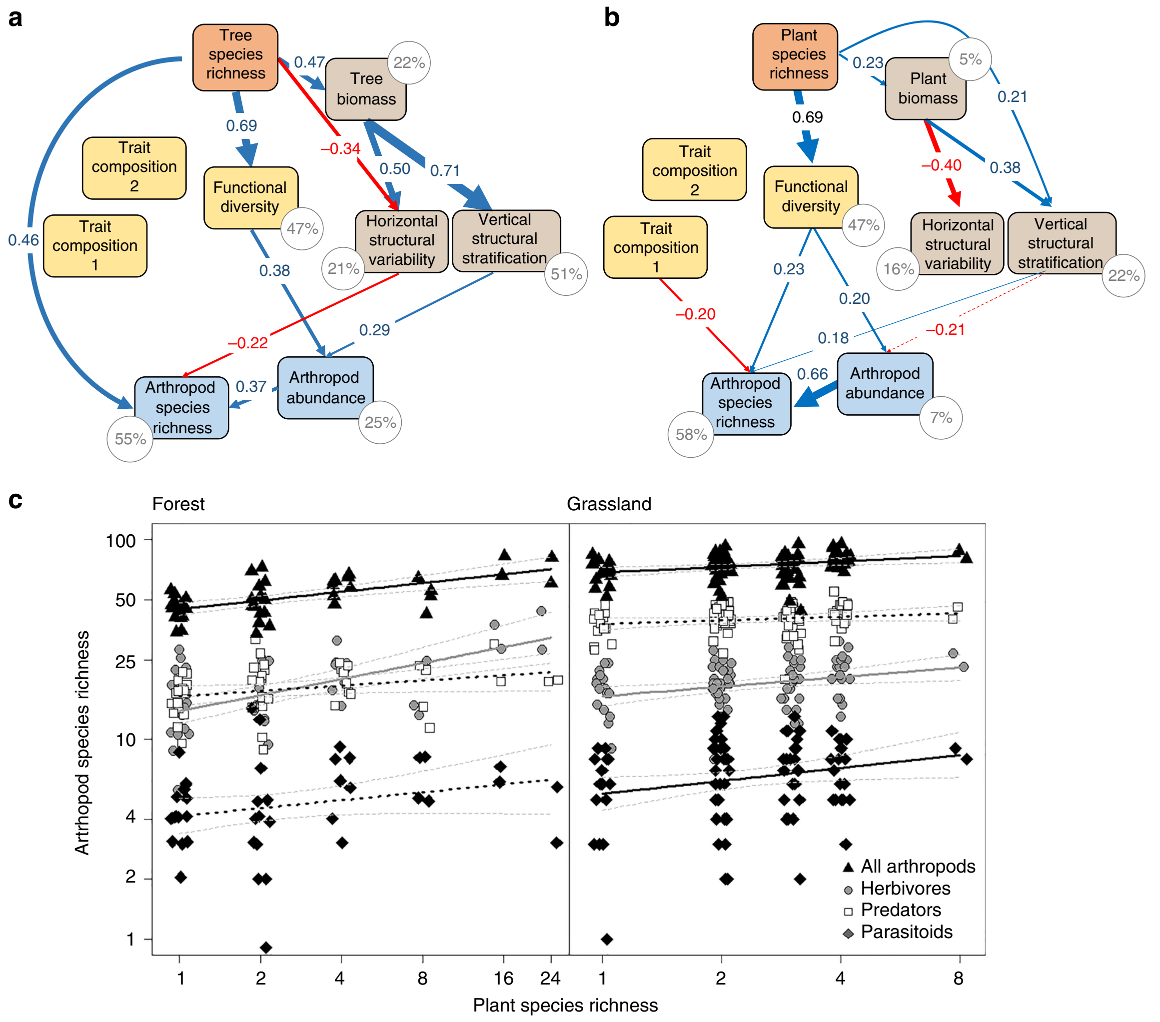

Fig. 1 Effects of plant diversity on arthropod species richness. Direct and indirect effects of plant species richness (orange), leaf trait functional diversity and composition (yellow), and structural characteristics (brown) of the plant communities on overall arthropod abundance and species richness (blue) for **a** the forest system ($\chi^2 = 6.96$, DF = 10, $P = 0.789$), and **b** the grassland system ($\chi^2 = 19.9$, DF = 14, $P = 0.185$) based on path model results. Trait compositions 1 and 2 represent the first two axes of a principal components analysis (PCA) on community-weighted means of five leaf traits; functional diversity is the mean pairwise dissimilarity (based on Rao's Q) of these traits among study plots. Vertical stratification (based on Rao's Q) and horizontal variability of plant structure (based on Moran's *I*) represent variability in plant height (grassland) or the first two axes of a PCA on the variability of tree height and crown projection area (forest) within the study plots. Positive and negative pathways and their corresponding standardized path coefficients in **a** and **b** are indicated in blue and red, respectively. Solid lines show significant relationships ($P \leq 0.05$ based on 1000 bootstrap draws; scaled by their standardized effect size), dotted lines show non-significant pathways (see Supplementary Tables 2, 3 for full results). For clarity, covariances between structural and functional diversity (see Fig. S4) were not plotted but are shown in Supplementary Tables 2 and 3. Percentage values show the explained variance of endogenous (dependent) variables. Effects of plant species richness on arthropod species richness **c** in the BEF-China forest experiment (left panel; values corrected for the number of trees sampled; $N = 46$ study plots), and in the Jena Experiment in grassland (right panel; $N = 92$). Solid regression lines indicate significant ($P < 0.05$) relationships, broken regression lines show marginally significant relationships ($P < 0.1$). Broken gray lines are 95% confidence intervals. Source data are provided as a Source Data file

functional diversity (calculated as mean pairwise trait dissimilarity; Fig. 1a, b). Plant species richness also increased plant biomass and influenced—either directly, or indirectly via effects on biomass—plant structural diversity (calculated as mean pairwise dissimilarity and spatial dispersion in height; Fig. 1a, b). Plant trait composition (based on community-weighted mean (CWM) trait values), in turn, was not significantly affected by plant species richness in either ecosystem (Fig. 1a, b).

In both ecosystem types, plant species richness showed a significantly positive relationship with overall arthropod species richness (forest: 0.14 ± 0.03 SE, $F_{1,44} = 26.2$, $P < 0.001$; grassland: 0.09 ± 0.03 SE, $F_{1,90} = 8.4$, $P = 0.005$ for a linear regression on log-transformed species richness data) and with the species richness of herbivores (forest: 0.27 ± 0.06 SE, $F_{1,44} = 20.2$, $P < 0.001$; grassland: 0.15 ± 0.06 SE, $F_{1,90} = 7.2$, $P = 0.009$ for a linear regression on log-transformed species richness data) (Fig. 1c). Likewise, predator and parasitoid species richness showed a marginally positive relationship with plant species richness in both the forest (0.09 ± 0.04 SE, $F_{1,44} = 3.9$, $P = 0.055$ and 0.14 ± 0.08 SE, $F_{1,44} = 3.0$, $P = 0.090$, for linear regressions on predator and parasitoid richness, respectively) and the grassland system (0.06 ± 0.03 SE, $F_{1,90} = 3.2$, $P = 0.076$ and 0.22 ± 0.10 SE, $F_{1,90} = 4.8$, $P = 0.030$, respectively) (Fig. 1c). The associations between plant species richness and arthropod species richness were to a large extent explained by plant functional and structural diversity in both ecosystems (Figs. 1a, b, 2, and 3). Only forest

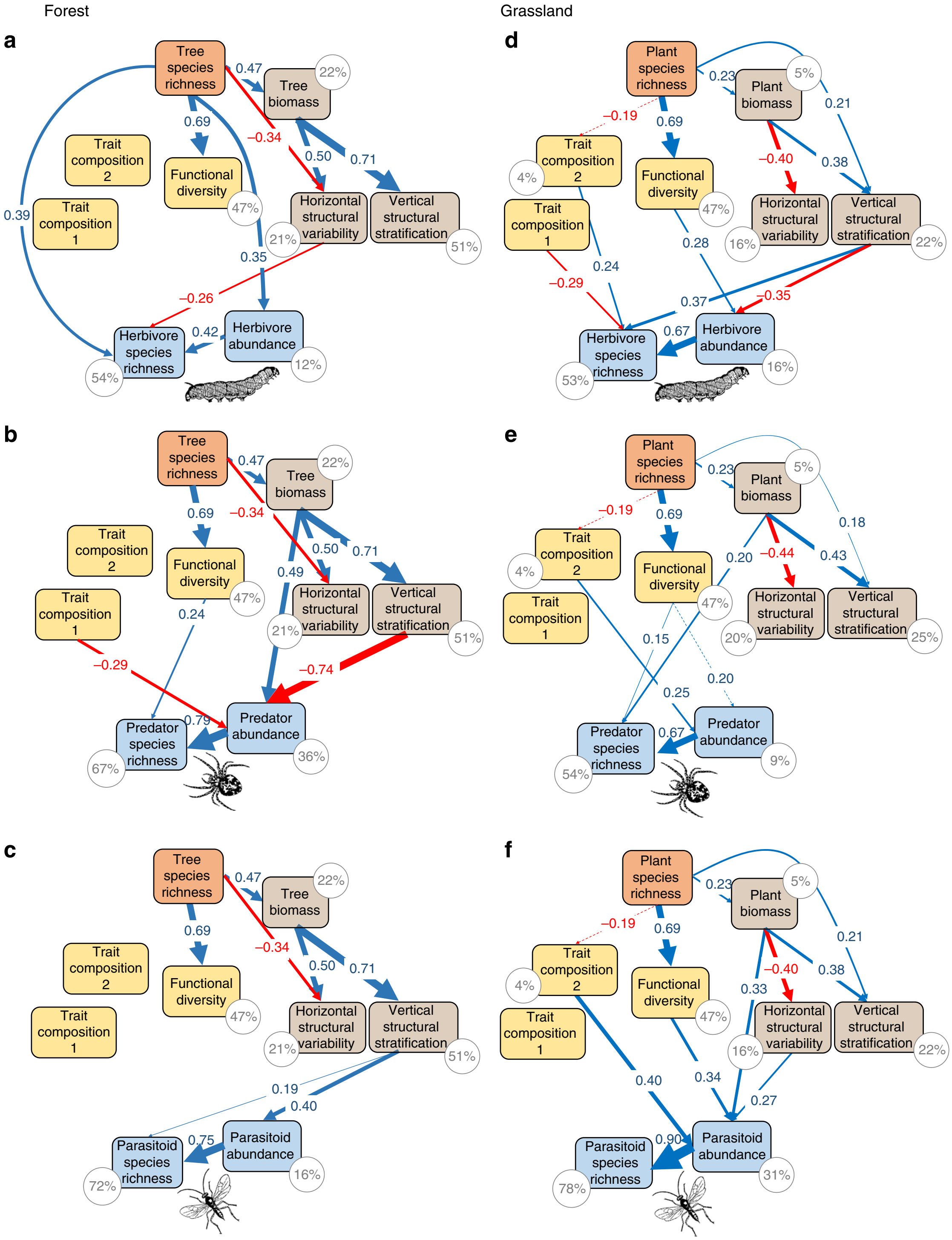

Fig. 2 Effects of plant diversity on arthropods across trophic levels. Direct and indirect effects of plant species richness (orange), leaf trait functional diversity and composition (yellow), and structural characteristics (brown) of the forest and grassland plant communities on arthropod abundance and species richness (blue) based on path model results. **a** Forest herbivores ($\chi^2 = 6.6$, DF = 11, $P = 0.796$), **b** forest predators ($\chi^2 = 13.4$, DF = 17, $P = 0.723$), **c** forest parasitoids ($\chi^2 = 7.7$, DF = 12, $P = 0.814$), **d** grassland herbivores ($\chi^2 = 25.3$, DF = 20, $P = 0.259$), **e** grassland predators ($\chi^2 = 14.8$, DF = 15, $P = 0.495$), **f** grassland parasitoids ($\chi^2 = 27.2$, DF = 21, $P = 0.302$). Trait compositions 1 and 2 represent the first two axes of a principal components analysis (PCA) on community-weighted means of five leaf traits; functional diversity is the mean pairwise dissimilarity (based on Rao's Q) of these traits among study plots. Vertical stratification (based on Rao's Q) and horizontal variability of plant structure (based on Moran's I) represent variability in plant height (grassland) or the first two axes of a PCA on the variability of tree height and crown projection area (forest) within the study plots. Positive and negative pathways and their corresponding standardized path coefficients in **c** and **d** are indicated in blue and red, respectively. Solid lines show significant relationships ($P \leq 0.05$ based on 1000 bootstrap draws; scaled by their standardized effects), dotted lines show non-significant pathways (see Supplementary Tables 4–9 for full results). For clarity, covariances between structural and functional diversity (see Fig. S4) were not plotted but are shown in Supplementary Tables 4–9. Percentage values show the explained variance of endogenous (dependent) variables. The animal icons (from www.openclipart.org) are licensed for use in the public domain without copyright (Creative Commons Zero 1.0). Source data are provided as a Source Data file

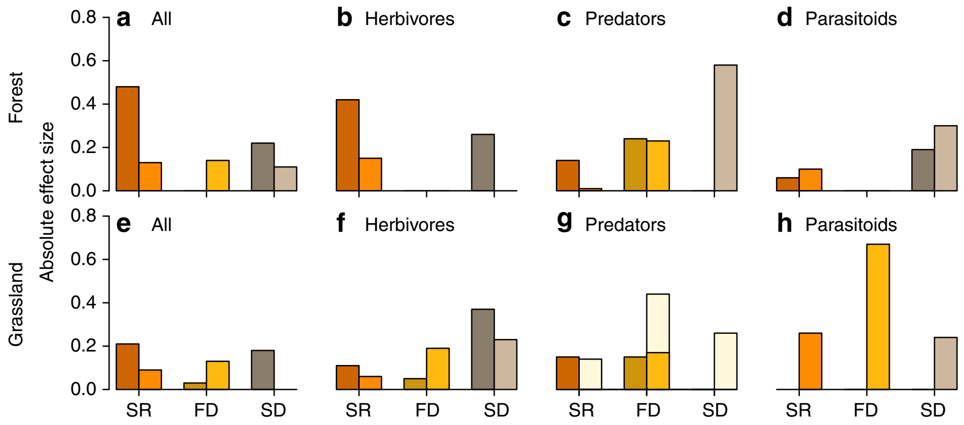

Fig. 3 Direct and indirect effects of plant diversity on arthropod species richness. Bars show summed effects of plant taxonomic (SR, orange color), functional (FD, yellow color), and structural (SD, brown color) diversity on arthropod species richness, obtained from the path models in Figs. 1 and 2. Absolute values are shown to enable better comparison of effect sizes among predictors. Effects are either direct (darker hues, left bar of each diversity component, connecting arthropod richness with plant diversity via direct paths) or indirect via arthropod abundance (lighter hues, right bar of each diversity component, effects of plant diversity on arthropod abundance, which in turn affected arthropod species richness). **a**–**d** show results for the forest experiment, **e**–**h** for the grassland experiment, with **a**, **e** featuring overall arthropod species richness, **b**, **f** herbivores, **c**, **g** predators, and **d**, **h** parasitoids. beige-colored bars in **g** show indirect effects of plant diversity on grassland predator species richness when restricting the analyses to arthropods directly sampled from the vegetation (i.e., excluding data from pitfall traps). Absolute effect size was calculated as the product of standardized path coefficients connecting each plant diversity component with arthropod species richness, summed over the individual predictors of each component (i.e., trait composition 1+trait composition 2+functional diversity for FD and horizontal structural variability+vertical structural stratification for SD). Note that direct and indirect effects of plant species richness (SR) on arthropod richness also include the effects via FD and SD (because SR influenced FD and SD, and effects of FD and SD on arthropod richness are therefore partial effects of SR). Source data are provided as a Source Data file

herbivores showed a direct relationship with plant species richness, a pattern that was also found for overall arthropod species richness because of the large proportion of herbivores (Figs. 1a and 2a, indicating mechanisms not addressed by our study design and selection of predictor variables).

In both study systems and for all trophic levels (herbivores, predators, parasitoids), arthropod abundances had strong positive effects on arthropod species richness (standardized path coefficients ranging between 0.42 and 0.90), and significant associations between plant diversity and arthropod species richness were often indirect via effects on arthropod abundances (Figs. 1, 2, and 3). However, the relative influence of plant functional and structural diversity on arthropod abundances and arthropod species richness differed between the two study systems (Fig. 2). Results for overall arthropod diversity in the forest ecosystem strongly reflected the impact of plant diversity on the abundance and species richness of the dominating herbivores (Figs. 1a and 2a). In contrast, results for overall arthropod diversity in the grassland ecosystem reflected a mix of the relationships between plant diversity and both predator and herbivore abundance and species richness (Figs. 1b and 2d, e). In general, directional effects of arthropod abundance on arthropod species richness were more strongly supported than interdependent effects (expressed as residual covariance terms) between abundance and species richness. In both ecosystems, second-order Akaike Information Criterion (AICc) values were lowest for models assuming that arthropod abundance drives patterns in arthropod species richness for overall, predatory, and parasitoid arthropods (Supplementary Tables 2–17). Only in the case of forest and grassland herbivores were models assuming more complex interdependencies between arthropod abundance and species richness equally likely (Supplementary Tables 11 and 15). Models based on rarefied arthropod species richness showed that when factoring out arthropod abundance, many of the indirect and direct relationships between plant diversity and arthropod species richness disappeared (Supplementary Tables 18–24), underpinning the role of arthropod abundance changes in modifying the relationships between plant and arthropod diversity.

Strength of diversity effects varies across trophic levels. In the forest system, herbivore species richness was not significantly related to the functional identity of the tree communities (as described by weighted trait means) and was only moderately related to plant structural diversity (negative effect of horizontal variation of tree structure; Fig. 2a). Instead, forest herbivore species richness and abundances showed a strong, positive relationship with tree species richness. Associations between structural diversity and arthropod abundance or species richness in the forest system became stronger at higher trophic levels (standardized path coefficients for herbivores −0.26 for horizontal structural variation, compared to −0.74 for vertical stratification for predators, and 0.19 (horizontal) and 0.40 (vertical) for parasitoids). The influence of structural diversity dominated the overall (direct and indirect) relationships between tree diversity and the abundance and species richness of predators and parasitoids (Fig. 3). The vertical stratification of tree height and crown size (based on crown projection area) was strongly negatively related to predator abundances and positively to parasitoid abundances (Fig. 2b, c). Moreover, forest parasitoid species richness increased with the horizontal variation of tree structure (Fig. 2c). Predator abundance strongly increased with tree biomass (Fig. 2b). Relationships between tree functional diversity or composition and arthropods in the forest system were weaker and most pronounced for predators: their species richness increased and their abundance decreased with increasing functional diversity and mean trait values (PC1 related to high leaf toughness and low specific leaf area (SLA) and leaf nitrogen concentration; Supplementary Table 25) (Fig. 2b).

In the grassland system, plant functional diversity was consistently positively related to arthropod abundances across trophic levels (Fig. 2d–f). Trait composition representing the dominance of plant species with high leaf toughness and silica concentrations and low leaf nitrogen concentrations (PC1; Supplementary Table 26) were associated with decreased grassland herbivore species richness. Trait composition related to the dominance of plant species with low SLA and leaf carbon concentrations (PC2; Supplementary Table 26) showed a positive relationship with herbivore species richness and both predator and parasitoid abundance in the grassland system (Fig. 2d–f). Plant biomass was directly associated with predator species richness and parasitoid abundance (Fig. 2e, f). Vertical stratification and horizontal variation in plant structure particularly influenced herbivores (Fig. 2d) and, to a lesser extent, parasitoids (Fig. 2f). Predators in grassland were only significantly related to plant structure when excluding the majority of ground-active species (i.e., focusing on suction samples: positive effect of vertical stratification of plant structure on predator abundance; Fig. 3g, Supplementary Fig. 1).

Discussion

Our study shows for two contrasting ecosystems that functional and structural diversity of the plant communities strongly contribute to explaining the positive relationships between plant species richness and the plot-level species richness of invertebrate consumers across trophic levels. The relative importance of plant functional and plant structural diversity differed across trophic levels and between ecosystems. Yet, many strong associations between plant diversity and arthropod species richness were consistently found to operate via relationships with arthropod abundances. These findings have important implications for attempts to develop a more detailed understanding of biodiversity relationships and the impact of global environmental change across trophic levels, and they highlight important avenues for the future of biodiversity research.

First, our results indicate that structural diversity metrics of plant communities are highly relevant mediators of plant diversity effects on arthropod diversity and that they strongly contribute to a mechanistic explanation of these effects. Recently, researchers have started to address the mechanisms underlying previously observed effects of plant species richness on higher trophic levels by testing for the potential role of plant functional diversity and composition[22,39,40]. However, structural diversity as an additional mediator of plant diversity effects on consumer diversity has received much less attention. This is despite the well-known fact that plant structure significantly affects herbivores, predators, and parasitoids by modifying environmental conditions and habitat space[23–25] and that plant species richness can influence the physical structure of plant communities[41,42].

Associations with plant structural diversity were particularly pronounced for forest arthropods. This might be explained by the size and longevity of trees compared to grassland plants. Trees function as keystone structures that ensure long-term habitat continuity for associated arthropods, while mowing of grasslands (two times per year in our grassland study system) leads to seasonal changes in vegetation structure (with consequences for arthropod community composition, as reflected by differences in the frequency and identity of dominant arthropod taxa; see Methods). Moreover, the large size of the trees compared to grassland plants results in spatially more extensive microclimatic gradients from light-exposed upper canopy parts to shaded interiors of the canopy[28]. These differences might explain why the resulting relationships with plot-level arthropod species richness were more important than differences in leaf functional characteristics in the forest system.

The consistent associations with leaf trait functional diversity at all trophic levels (herbivores, predators, parasitoids) in the grassland system might be indicative of bottom–up effects that propagate through the food web from plants via herbivores to predators and parasitoids, consistent with previous results reported for the effects of plant species richness in both study systems[16,22]. Differences in sampling methods between the study systems probably play a minor role: forest arthropods were all sampled directly from the vegetation (by beating), as were most grassland herbivores and parasitoids (primarily captured by suction sampling). Moreover, although most grassland predators were ground-active (sampled with pitfall traps), restricting the analyses to predators sampled from the vegetation (for which plant structure might be more important than for ground-active arthropods) did not change the relative importance of plant functional vs. structural diversity effects.

At the same time, however, the relative importance of functional and structural diversity on arthropods varied substantially across trophic levels in both ecosystems. While studies replicated across a wider range of environmental conditions and manipulative experiments will be required to verify the causal drivers and generality behind the observed effects, this variability across trophic levels provides indications of potential mechanisms. Negative relationships between vertical stratification or horizontal variation in plant structure and herbivore abundances could indicate a disruption of host-finding abilities or of herbivore dispersal in structurally more heterogeneous environments[27,43]. In contrast, direct positive associations with herbivore and parasitoid species richness might reflect a higher diversity of habitats and niches for different species[23,24].

While the lack of relationships between leaf trait functional diversity and forest herbivores could indicate that functional traits not considered in our study play a role, strong correlations between functional diversity and phylogenetic diversity (often used as a metric to capture unmeasured variability in functional traits[44], see Methods) suggest that the traits used in our analyses account for an important part of the overall trait space. In our case, the results might therefore suggest that tree functional trait effects on higher trophic levels did not primarily act via trophic linkages. This implies that tree diversity operated via direct effects on predators and parasitoids, and not via the modification of prey abundance and species richness[45]. This is in line with the assumption of the enemies hypothesis that effects of plant diversity on predator diversity can also operate via modifications of habitat structure or reduction of intra-guild predation[14,23].

In the case of plant functional characteristics, such direct effects might be related to fine-scale structures—expressed at the level of leaves—that correlate with functional traits[46]. Many of the forest predators were web-building spiders[22]. Differences in leaf toughness or SLA (as represented by principal components analysis (PCA) axis 1 of trait composition, which negatively affected forest predator abundance) might affect leaf structural attributes that are important for the diversity of possible web-attachment points and which therefore influence predator species richness[23]. Moreover, the abundances of these predators might be more strongly promoted by the total availability of habitat space, as indicated by the strong positive effects of tree biomass on forest predator abundance. Variability in tree size might reduce the overall availability of habitat space for dominant species with specific habitat requirements, which could explain the negative effect of vertical stratification of tree structure on forest predator abundance. Nevertheless, our finding that plant biomass effects on arthropods often worked indirectly via structural diversity shows that structural diversity can also be important for mechanistically understanding the consequences of diversity–productivity relationships for ecosystem functioning[47]. In the case of grassland herbivore species richness, the negative effect of leaf silica concentrations (represented by PCA axis 1 of trait composition) might be indicative of the previously suggested role of silica as a defense against herbivores[48].

Second, our finding that relationships between plant diversity and arthropod species richness were in many cases indirect via the modification of arthropod abundances has important consequences for our ability to predict biodiversity change in response to global environmental change. Strong and consistent effects of arthropod abundance on arthropod species richness suggest an important role of pathways related to the more-individuals hypothesis (i.e., more individuals allow for viable populations of more species[37,38]). The interesting finding is that of the many possible pathways and mechanisms that potentially link plant diversity to higher trophic level diversity (many of which are direct effects between plant and animal diversity, e.g., via modifications of habitat diversity that supports a higher diversity of animals[39,49]), those that influence species richness via changes in abundance made an important contribution to explaining overall diversity effects in both study systems. These effects were in many cases as strong as or even stronger than the direct effects of taxonomic, functional, or structural plant diversity on arthropod species richness. The important mediating role of arthropod abundances on the relationships between plant diversity and arthropod species richness also became evident when factoring out arthropod abundances by rarefaction and when comparing models with direct pathways vs. covariation between arthropod abundance and species richness.

Recently, scientists and society have become increasingly aware of drastic declines in arthropod biomass[5,6,29]. However, the linkages between these declines and ongoing changes in biodiversity remain less clear[5,29]. In this context, our study helps to disentangle important pathways connecting changes in the environment and in biodiversity via species abundances. Our results underscore the importance of more thoroughly considering these linkages. Explicitly incorporating changes in species abundance and how these changes are mediated by environmental change can be critical to understanding current and future changes of biodiversity and associated ecosystem functions. In our study, these effects would have stayed elusive without the inclusion of plant structural diversity, highlighting the benefits of simultaneously considering multiple components of plant diversity and the potential mechanisms discussed above. The same may be true for higher trophic-level diversity and the diversity of interactions among trophic levels, and we hope that our study stimulates future research exploring such interactions. In particular, the top–down effects of predators and parasitoids on herbivores[14], cascading effects of plant diversity via herbivores on secondary consumers[16], or effects of other functional groups (e.g., insectivorous birds[50]) are additional modifiers that deserve further research and that our models take into account only implicitly by analyzing the net effect of plant diversity on individual trophic levels. Our findings are particularly important in the light of ongoing habitat simplification and the loss of structural heterogeneity of ecosystems[51], and they support management recommendations that aim at maintaining and increasing the structural diversity of ecosystems (e.g., promoting uneven-aged forests[52] and grazing regimes in grasslands[53]). At the same time, the variability in effects of plant functional and plant structural diversity on arthropod abundance and species richness across trophic levels and ecosystem types cautions against overly simplistic generalizations and underscores the necessity of future research to take the ecological complexity of ecosystems into account.

Methods

Study sites and experimental design. We considered two large-scale and long-term plant diversity experiments representing a forest[32] and a grassland ecosystem[30], respectively.

The BEF-China forest experiment is located close to Xingangshan, Jianxi Province, China (29°08′–29°11′ N, 117°90′–117°93′ E, 100–300 m above sea level) and represents subtropical mixed evergreen broadleaved forest. The mean annual temperature at the study site is 16.7 °C, and mean annual precipitation is 1800 mm (ref. [32]). The experiment consists of two study sites (A and B) established in 2009 and 2010, respectively. It comprises 566 study plots of 25.8×25.8 m^2. Planted species richness, based on a pool of 40 broadleaved tree species, ranges from monocultures to mixtures of 2, 4, 8, 16, and 24 species. Trees were planted in a regular grid (20 rows and 20 columns) with 1.29 m planting distance among trees for a total of 400 trees per plot. Species were randomly assigned to individual planting positions within the plots, with the total number of individuals per plot divided equally among the species planted in a given plot[32].

Our analyses followed the design for a set of 64 (32 per site, randomly distributed across the sites) very intensively studied plots. Tree species composition of the mixtures was determined by randomly assigning (without replacement) each species of the 16-species mixtures to one 8-species mixture, subdividing these sets of 8 tree species to non-overlapping subsets of four species, and the 4-species subsets to non-overlapping 2-species mixtures[32]. The 24-species mixtures were included as an additional high diversity treatment, which contained an additional eight species not present in the other plots of the study site. Tree species composition differed between the two sites, with two separate species pools of 16 broadleaved species in each site and an additional 8 species shared between sites in the 24-species mixtures. All plots were weeded twice a year, with all upcoming vegetation between the planted trees being removed. Lack of or limited tree establishment (8 plots) and lack of arthropod sampling (10 plots, see below) limited the final set of plots to 46 (16 monocultures, 14 2-species mixtures, 8 4-species mixtures, 4 8-species mixtures, 2 16-species mixtures, and 2 24-species mixtures).

The Trait-Based Experiment (TBE), one of the experimental grassland experiments running in the framework of the Jena Experiment, is located close to Jena, Thuringia, Germany (50°55′N, 11°35′E; 130 m above sea level) and represents mesophilic temperate grasslands. The mean annual temperature at the study site is 9.9 °C, and mean annual precipitation is 610 mm (ref. [31]). The TBE was established in 2010 on a former arable land and comprises 138 study plots of 3.5×3.5 m^2. Sown plant species richness ranges from monocultures to mixtures of 2, 3, 4, and 8 species. The 20 plant species (grasses and non-legume herbs) sown in the experiment were selected from a set of 60 grassland species representing the whole species pool of the Jena Experiment, based on their degree of complementarity in 6 functional traits related to resource acquisition strategies[30]. Plant mixtures were assembled to represent varying degrees of plant functional diversity (four levels from low to high functional diversity based on the six selected plant traits) within species richness levels[30]. Plots were arranged in a randomized block design and are mown twice (according to the common management of extensively used hay meadows in the region) and weeded three times a year (to maintain the sown species composition). For our analyses, we used the 92 plots of the TBE (2 species pools of 8 species each, with full replication of the diversity gradient for each species pool) for which terrestrial laser-scanning data to determine vegetation structure were available.

Arthropod sampling and species richness. Arthropods were sampled in both experiments in 2014, using quantitative methods best suited for a representative assessment of their diversity in each ecosystem: branch beating, standardized assessments of trophobioses (mutualistic interactions between ants and hemipterans), and trap nests in the forest system; pitfall traps and suction sampling in the grassland system.

In the forest system, herbivorous and predatory arthropods were sampled from the trees by beating: arthropods were knocked down onto a white cloth sheet (ø 100 cm) by hitting the trees several times with a padded stick[22]. Sampling was conducted during two seasons of peak arthropod abundance (May and September 2014), using the first four rows of trees for a total of 40 planting positions in each plot. Arthropods were sorted in the laboratory, identified to family or genus level, and assigned to species or morphospecies. DNA barcoding of the cytochrome oxidase 1 was conducted following standard protocols[54] to verify our classification in potentially ambiguous cases (e.g., polymorphism, sexual dimorphism; see also ref. [55]). Data on ants and aphids were obtained from assessments of trophobiotic ant–aphid interactions conducted twice, in June/July and September/October 2014. For these assessments, trees in the core area of each plot were sampled[56]. Three branches per tree were randomly selected, and a total of 20 young leaves were visually inspected for the occurrence and the number of sap-sucking Hemiptera and honeydew-collecting ants[56,57]. Voucher specimens were collected and identified to the lowest possible taxonomic level. Parasitoid arthropods and their hymenopteran host species were sampled with standardized trap nests (polyvinyl chloride (PVC) tubes of 22 cm length and 12.5 cm diameter filled with reed internodes[58]). Trap nests fixed to wooden posts (1.5 m high) were exposed at two locations on each plot from September to December 2014. Internodes with nests of Hymenoptera were replaced monthly. Nests were brought to the laboratory and reared at ambient conditions until specimens hatched. Species were then identified to species or morphospecies. The following taxa were considered in the analysis of the forest plots: Araneae, Blattodea, Orthoptera, Mantodea, Psocoptera, Hemiptera, Coleoptera, Hymenoptera (including parasitoids), parasitic Diptera, and Lepidoptera. We assigned species to functional groups (herbivores, predators including omnivores, parasitoids, others) based on published literature[55] and expert classification (Supplementary Data 1). Pollinators were not considered as a functional group in our analyses because the sampling methods employed did not allow for a consistent assessment and reliable comparison between the experiments.

In the grassland system, epigeic arthropods were sampled with pitfall traps. Traps consisted of plastic cups with an opening diameter of 4.5 cm, were filled with a 3% formaldehyde solution, and covered by a small roof as a rain shelter[30]. In the center of each plot, one trap was installed and kept running from the end of April until the beginning of September 2014. The traps were emptied and refilled at 14-day intervals. Arthropods in the vegetation were sampled by means of suction sampling with a modified vacuum cleaner (Kärcher A2500, Winnenden, Germany). Suction sampling was conducted twice, in May and July 2014. Per plot and sampling date, two patches of $0.75 \times 0.75\ \mathrm{m}^2$ were sampled by putting a gauze cage over the vegetation (to prevent arthropods from escaping) and removing all arthropods from the cage with the suction sampler[19]. Adult individuals belonging to the following taxa were then identified, as far as possible, to species level: Isopoda, Myriapoda, Chilopoda, Araneae, Orthoptera, Hemiptera, Hymenoptera (including parasitoids), and Coleoptera (Supplementary Data 1). We note that the set of organism groups considered in the two experiments is not identical. This is due to differences in arthropod communities of the two different types of ecosystems considered (forest vs. grassland), which nevertheless reflect the general composition of the dominant groups of herbivores, predators, and parasitoids in each ecosystem.

Data on arthropod species richness were pooled per plot across sampling methods, i.e., adding together total species numbers for all sampling methods to obtain plot-level data on the overall species richness of all arthropods, and of herbivores, predators, and parasitoids, respectively. Species occurring with only one individual in the entire sample (singletons) were excluded, as were organism groups in the beating data that were not sampled representatively by beating (e.g., Hymenoptera and Diptera) and for which sampling with other methods, such as suction sampling and trap nests, was considered more adequate. We removed singletons to make the data set more robust, because species recorded with just one individual in the whole data set might be vagrants that are not really associated with the respective study systems or the specific plots they were recorded in. While singleton species accounted for 13–49% of the total number of species across all study plots (forest: 47%, 48%, 49%, and 20% of all, herbivorous, predatory, and parasitoid species, respectively; grassland: 31%, 30%, 28%, and 13% of all, herbivorous, predatory, and parasitoid species, respectively), singleton removal did not influence overall patterns among study plots of arthropod species richness and abundance, which were highly correlated in the data sets with and without singletons (Pearson correlation, $r > 0.97$, $P < 0.001$ in all cases and for all trophic levels). Because missing or dead trees of some species affected the number of trees present in the part of the plots sampled for arthropods in the forest system (independent of tree species richness[22]), we regressed arthropod species richness over the number of trees sampled by beating in each plot and used the residuals as a sample size-corrected metric of species richness. We used the number of individuals (and for trophobiotic ants and aphids the occurrence, i.e., the number of trophobioses per tree[56,57]) pooled over all sampling methods as measures of plot-level abundance.

Plant biomass. We estimated overall plant biomass as a predictor of arthropod species richness and species-specific biomass per plot for the calculation of trait-based functional plant diversity. For the forest system, we used estimates of wood volume as a proxy of leaf biomass per tree, calculated from data on basal area and tree height assessed in October 2014 (ref. [59]). Assessments were based on the central 6×6 trees per plot (out of the grid of 20×20 trees planted in each plot) in monocultures and 2-species mixtures and the central 12×12 trees in more diverse mixtures. Values were upscaled to represent the total plot biomass. In the grassland system, plant biomass was assessed twice in 2014, at peak standing biomass in May and August. In each plot, all vegetation was clipped 3 cm above ground in two randomly selected areas of $20 \times 50\ \mathrm{cm}^2$. Samples were sorted to species level and weighed after drying for 72 h at 70 °C. Data were averaged across the two replicates per plot at each sampling date and then pooled across dates for an overall value of biomass production across the growing season.

Plant functional traits and functional diversity. We used a range of plant functional traits that characterize the nutritional quality of leaves and that have generally been found to influence arthropod (in particular herbivore) abundances and species richness[34,39]. These traits comprised SLA, leaf dry matter content (LDMC), leaf nitrogen (N) concentration, leaf carbon (C) concentration, and leaf toughness. These traits have repeatedly been found to explain a large proportion of the variation in arthropod diversity, community structure, or functioning in the ecosystems studied here as well as in other ecosystems, for example, because they influence leaf palatability[22,33,34,39]. For the grassland experiment, we additionally considered leaf silicon concentration, because its presence particularly in grasses can significantly affect herbivores[60]. For both experiments, we used mean trait values per plant species as the average of trait measurements on individual plants, because plot-level data were not available for any of the traits in the forest experiment and for several of the traits measured in the grassland experiment.

Trait measurements followed standard protocols[61]. In the forest plots, traits were measured on sun-exposed leaves of a minimum of five individuals per tree species (ref. [62]). In the grasslands, bulk samples composed of 5–10 fully expanded leaves from a least three different individuals were collected in each plot, where the species occurred in the sown species combinations, for measurement of SLA, LDMC, N, and C in May and August 2012. We averaged trait values per species across the two measurement campaigns in the grassland experiment. Data on leaf toughness was not directly available from plants grown in the field but measured for five healthy and fully developed leaves on each of five replicate individual mesocosm plants (see ref. [63]), grown in PVC pipes (15 cm diameter, 60 cm length) filled with sieved field soil from the Jena Experiment mixed with 20% sand. Leaf toughness was measured as leaf penetration persistence at the center of the leaf blade in a stripe of 1 cm distance to the central vein using an electric penetrometer (force gauge FH50, Sauter GmbH, Germany, equipped with a 1.4 mm diameter metal needle). Silicon concentration was determined from species-specific biomass samples taken from 2005 to 2007 on the main experimental plots of the Jena Experiment[64]. We used a microwave digestion system (CEM Corporation, Matthews, NC, USA) for measurements. Ground plant material was digested at 180 °C using 3 ml HNO_3, 2 ml H_2O_2, 0.5 ml HF, and 5 ml H_3BO_3. Afterwards, silicon was determined by inductively coupled plasma optical emission spectroscopy (Optima 7000DV, Perkin Elmer) with ultraviolet detection and quantification at 251.6 nm (Si)[64].

Functional leaf trait diversity was calculated from multiple traits as Rao's quadratic entropy Q[65], which we used to quantify the mean pairwise dissimilarity among the plant species growing in a study plot based on the above traits. Trait values were weighted by the biomass data of each plant species in each plot (see above). For each trait, we further calculated CWM values (ref. [66]) as the biomass-weighted average of each trait per plot. While effects of CWM indicate mass-ratio effects of functional trait means (functional composition), Rao's Q quantifies the variation around this mean and therefore indicates effects of trait variability[35] (functional diversity). To reduce the dimensionality of the CWM data, we subjected the CWMs of the individual traits to a PCA. For both ecosystems, this yielded two principal components (PCs) that captured together 66 and 70%, respectively, of the overall variation in trait composition of the two experiments (Supplementary Tables 25 and 26). In both systems, increasing values of PC1 reflected increasing leaf toughness and decreasing leaf nitrogen concentrations, while PC2 reflected decreasing leaf carbon concentrations (Supplementary Tables 25 and 26).

Because analyzing selected traits might not necessarily capture the full variation in functional diversity, we additionally calculated plant phylogenetic diversity. Phylogenetic diversity might be used as a proxy of overall functional trait space if functional traits show a phylogenetic signal[44]. We used ultrametric phylogenetic trees available for both experiments[67,68] (Supplementary Fig. 2) and calculated phylogenetic diversity, analogous to functional diversity, as biomass-weighted Rao's Q. However, functional and phylogenetic diversity were highly correlated in both experiments (Pearson correlation, $r = 0.83$, DF = 44, $P < 0.001$ for the forest experiment, and $r = 0.86$, DF = 90, $P < 0.001$ for the grassland experiment, based on log-transformed values). The same applied to the relationship between phylogenetic diversity and plant species richness (Pearson correlation, $r = 0.82$, $P < 0.001$ in forest and $r = 0.76$, $P < 0.001$ in grassland, DF as above), whereas functional diversity was less strongly correlated with plant species richness (Pearson correlation, $r = 0.69$, $P < 0.001$ in both experiments, DF as above). To avoid overly complex models, we therefore did not include phylogenetic diversity in our analyses, as its variation was already well reflected by functional diversity and plant species richness.

Structural diversity. We derived two metrics of plant structural diversity at the plot level. The metrics indicate (i) the vertical stratification of plant height (and for trees: crown size) per plot and (ii) the horizontal variation of this stratification across each plot (Supplementary Fig. 3). These metrics were based on the spatial variability in plant height (and additionally for trees: crown size, quantified as crown projection area) as general indicators of structural diversity at the plot level. Plant height and crown size are related to the stratification of foliage[41]. Their spatial distribution (both vertically from the ground upward and horizontally in terms of spatial variation) influences important habitat features of arthropods, such as microclimate, availability of food, shelter, or habitat space (e.g., web-attachment points for web-building spiders[23,24]). Analyses on the spatial variability of these indicators within study plots may therefore provide information on the heterogeneity in the availability and spatial arrangement of habitats and resources.

Plant height and (for trees) crown projection area were measured in 2014. In the forest system, tree height and crown projection area were measured directly with measuring tapes in September and October 2014. Measurements were conducted on the central 6×6 (monocultures and 2-species mixtures) or 12×12 (more diverse mixtures) tree individuals in each plot. Tree height was quantified as the total length [cm] from stem base to apical meristem. Crown projection area was calculated as the area spanned by an ellipse connecting horizontal crown diameter measurements in two cardinal directions[69]. In the grassland system, measurements were conducted with the terrestrial laser scanner (TLS) Faro Focus 3D X330 (FARO Technologies Inc.). We scanned 92 plots before harvest in May 2014 at the peak of standing biomass. The TLS was mounted on a tripod in an upside-down position elevated 3.35 m above soil level. The scanner operates with a wavelength of 1550 nm and captures fully three-dimensional information of the plants allowing to extract accurate height measurements and spatial distributions at the mm level. Scans were performed with a scan resolution of 0.25 (corresponding to spatial resolution 3 mm at 3.35 m distance; see FARO Focus manual). For each plot, we extracted an area of 3.75 m^2 (1.5×2.5 m^2) below the scanner to reduce the effect of shadowing within scans. Individual scans of each plot were cleaned using standard stray filters and transformed from a point cloud into *XYZ* coordinates by using the proprietary software Scene (version 5.2.0, Faro Technologies, Inc., Lake Mary, Florida, USA). In addition, the point clouds were cleaned using a statistical outlier removal filter ($N = 6$, Sigma = 1.5) in the CloudCompare software (version 2.6). Plant height and variation of height were computed at a 5-cm grid interval. This corresponds to 50×30 grid cells on average in the observed area and is sufficient for capturing small-scale structural variability of individual grassland plants.

Vertical stratification of plant structure was quantified as the mean pairwise dissimilarity in plant height (and for trees: crown projection area) among all individual trees (forest) or 5 cm grid cells (grassland) per study plot, calculated as Rao's Q[65]. Horizontal variation of plant structure was calculated as the spatial variation in plant height (and for trees: crown projection area) within each study plot based on Moran's I[70]. Values of Moran's I close to 0 indicate a spatially random distribution of the variable of interest, while lower and higher values indicate spatial dispersion of dissimilar values and spatial clustering of similar values, respectively. We therefore interpreted increasing values of Moran's I as a trend toward increasing spatial aggregation of structurally similar plants within the study plots, which we considered as indicative of lower horizontal structural diversity at the plot level. We used inverse distance weighting for the computation of Morans' I, assuming reduced spatial dependence with increasing distances between individual plants. Dead trees and gaps without plants were assigned a height of 0 cm.

Because crown projection area increased with tree height (Pearson correlation, $r = 0.73$; $P < 0.001$), we subjected the metrics of Rao's Q and Moran's I for the forest system to a PCA. This yielded two orthogonal principal components (explaining 81% of the total variation in the data), the first one reflecting vertical stratification of plant structure, while the second one reflects the horizontal variation of plant structure as the aggregate of data on tree height and crown projection area (Supplementary Table 27). For the grassland system, we used Rao's Q and Moran's I (the latter multiplied by −1 to reflect increasing heterogeneity) of height distribution directly as metrics of vertical stratification and horizontal variation.

Path models. We used path analysis[71] to assess the direct (paths from plant diversity to arthropod richness) and indirect (paths via arthropod abundance) effects of taxonomic, functional, and structural diversity of the plant communities on arthropod species richness. As potential predictors, we considered plant species richness (planted or sown number of species per plot), plant functional diversity (Rao's Q of plant traits), plant trait composition (based on CWMs), vertical stratification and horizontal variation of plant structure (based on Rao's Q and Moran's I of plant height and, for the forest system, crown projection area), and plant biomass. We fitted individual models for overall arthropod species richness, as well as for the species richness of herbivores, predators, and parasitoids.

The initial models included the most relevant pathways derived from theoretical assumptions and correlations among the plant-based predictors (Supplementary Fig. 4). We assumed that plant species richness, as the experimental treatment variable, influences plant biomass[7], functional leaf trait diversity[72], and structural diversity[41]. Functional trait composition (PC2) was only marginally significantly related to plant species richness in the grassland experiment but not in the forest experiment. We therefore only considered this path in the grassland models. Moreover, we assumed that all plant-based predictors can directly influence arthropod abundance and species richness[16,22,25]. Finally, we expected arthropod abundance to influence arthropod species richness (e.g., more individuals hypothesis[37,73]). We additionally tested for significant residual covariances between the plant-based predictors (see Supplementary Fig. 4), as the different components of plant diversity might not be completely independent. We sequentially dropped non-informative pathways and covariances, if their removal resulted in a reduction of the AICc of the models[16,71]. The final models were those that minimized AICc values and included 0 in the 95% confidence interval of the root mean square error of approximation. We tested the robustness of the results by calculating bootstrapped P values based on 1000 bootstrap draws[71]. Arthropod data, plant biomass, plant species richness, and functional diversity were log-transformed for the analyses.

Based on this path modeling approach, we additionally tested two alternative path model variants. The first variant used the same initial models as described above, except for a residual covariance term between arthropod species richness and abundance rather than a directional pathway between the two. We simplified models as described above and compared the resulting AICc values to those of the final models of our initial approach. We considered the model variant with the lowest AICc as better supported when differences in AICc were >2, otherwise both model variants and their underlying hypotheses (directionality of abundance-richness relationships vs. abundance-richness covariance) were considered to be equally likely[74]. In a second variant, we based the path models on rarefied arthropod species richness (based on the minimum number of individuals per plot for each higher trophic level) to test how our interpretation of plant diversity effects on arthropod species richness changes after factoring out the potentially important influence of arthropod abundance (note: rarefaction was not possible for parasitoids in the forest experiment because the lowest number of individuals per plot was 1). Again, we used the same general model structure and simplification procedure as described above. However, because arthropod abundance was factored out by rarefaction, we did not include abundance and the corresponding pathways via abundance in these models.

All analyses were conducted in R 3.3.1 (www.r-project.org) with the packages vegan, FD, VoxR, and lavaan.

Reporting Summary. Further information on experimental design is available in the Nature Research Reporting Summary linked to this article.

Data availability

Data used in the analyses is available on the data repository of the German Centre of Integrative Biodiversity Research (iDiv) at https://doi.org/10.25829/idiv.295-17-1066. A reporting summary for this article is available as a Supplementary Information file. The source data underlying Figs. 1–3 and Supplementary Fig. 4 are provided as a Source Data file.

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Author contributions

N.E. conceived the idea for the manuscript; N.E. and H.B. coordinated the Jena and BEF-China experiment, respectively; A.S., N.E., M.K., A.E. and M.S. developed the study; A.S., A.E., M.S., N.B., W.H., A.-M.K., C.R., G.v.O., A.W., C.W., W.W., H.B. and N.E. designed research; A.S., A.E., M.K., M.S., C.G.-S., D.B., W.D., A.F., F.F., L.H., C.R., J.S. and J.Z. collected and/or contributed data; A.S. conducted the statistical analyses and wrote the manuscript, with input from all coauthors.

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Part II

Forest continuity and global change

Chapter 8

Effects of anthropogenic disturbances on soil microbial communities in oak forests persist for more than 100 years

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Effects of anthropogenic disturbances on soil microbial communities in oak forests persist for more than 100 years

A. Fichtner[1]*, G. von Oheimb[2], W. Härdtle[2], C. Wilken[1,2] & J.L.M. Gutknecht[3,4]

[1]*Institute for Natural Resource Conservation, University of Kiel, Olshausenstr. 75, 24118 Kiel, Germany;* [2]*Institute of Ecology, Leuphana University of Lüneburg, Scharnhorststr. 1, 21335 Lüneburg, Germany;* [3]*Helmholtz Centre for Environmental Research-UFZ, Department of Soil Ecology, Theodor-Lieser-Str. 4, 06120 Halle (Saale), Germany;* [4]*Department of Soil, Water, and Climate, University of Minnesota, 439 Borlaug Hall, 1991 Upper Buford Circle, St. Paul, MN 55108, USA.*

*Corresponding author: A. Fichtner, afichtner@ecology.uni-kiel.de

Abstract

Land-use change and land-use intensification are considered amongst the most influential disturbances affecting forest diversity, community structure, and forest dynamics. Legacy effects of land-use changes in ecosystem functioning and services may last several hundred years. Although numerous studies have reported the short-term legacy effects of past management, analyses of long-term responses (>100 years) are still lacking. Here, we demonstrate shifts in soil microbial community structure and enzymatic activity levels resulting from a long-term past disturbance intensity gradient in oak forests (former arable farming – former heathland farming – ancient forest). Differences in microbial community composition among sites with contrasting historic land-use were related to differences in soil chemical properties and abundances of arbuscular mycorrhizal fungi, saprotrophic and ectomycorrhizal fungi, and actinobacteria. Both microbial biomass and enzymatic activity levels were distinctly lower in ancient forests compared to historically cultivated sites (i.e. agriculture or heathland farming). We found evidence that past land-use has long-lasting impacts on the recovery of soil community development, much longer than commonly assumed. This in turn highlights the importance of ecological continuity for ecosystem functioning and services. Conservation management, focussing on the stability and diversity of forest ecosystems, therefore needs to consider past land-use legacies for evaluating ecosystem functions (such as soil ecological processes) and for evaluating effective strategies to adapt to environmental changes.

Keywords: bacteria, ecological continuity, ecosystem functioning, enzyme activity, forest succession, fungi, land-use legacy, microbial biomass, *Quercus petraea*

INTRODUCTION

Interactions between belowground and aboveground communities may strongly influence ecosystem functioning by regulating plant community dynamics and biogeochemical processes (Wardle et al., 2004a; Wurzburger and Hendrick, 2009; Mangan et al., 2010). Belowground, soil microbial communities decompose organic materials, mediate carbon and nitrogen cycling, and determine nutrient availability for plant growth (Sparling, 1997; Aubert et al., 2010). Aboveground plant communities significantly alter microbial community composition and functions through rooting patterns, rhizodeposition, water use, litter chemistry, canopy structure, and subsequent influences on soil properties and microclimate (Bauhus et al., 1998; Weintraub et al., 2007; Huang et al., 2008; Zhang et al., 2009; Aubert et al., 2010; Burton et al., 2010; Wu et al., 2012). An important caveat is that above–belowground relationships are mediated by local edaphic factors, and thus such factors should be taken into consideration when assessing these relationships (Boyle et al., 2008; Wu et al., 2012).

Land-use changes can significantly alter the soil characteristics and aboveground species dynamics from which above- and belowground interactions develop (Lauber et al., 2008). Such land-use driven changes have been recognized as a main factor altering ecosystem functions, including carbon (C) and nitrogen (N) cycling or plant species diversity and productivity (Koerner et al., 1997; Brunet and von Oheimb, 1998; Guo and Grifford, 2002; Wakeling et al., 2009; Baeten et al., 2010; Cusack et al., 2013). Numerous studies have reported impacts of land-use changes on soil microbial communities (Fraterrigo et al., 2006; Lauber et al., 2008; Burton et al., 2010; Jangid et al., 2011), and microbial successional changes are increasingly used as an indicator of ecosystem recovery after anthropogenic disturbances (Harris 2003; Banning et al., 2011). Land-use changes also influence microbial community structure and function and, consequently, nutrient cycling rates (e.g., Grayston et al., 2006; Potthast et al., 2012; Ramirez et al., 2012).

The persistence of these responses to land-use change is, however, still debated. Some chronosequence studies along successional gradients have shown that microbial communities tend to become more similar to those in native soils over time (Buckley and Schmidt, 2003; Jangid et al., 2010, 2011). However, there have been significant differences observed in microbial communities even after > 50 years of conversion from agricultural cultivation to forests (Fraterrigo et al., 2005, 2006). To our knowledge, no study has investigated land-use legacies on microbial communities > 100 years after afforestation. This is even though forest soils may continue to reflect their agricultural history for a far longer period, hypothetically through changes in soil chemical and structural properties (e.g. Verheyen et al., 1999; Compton and Boone, 2000; Jussy et al., 2002). Specifically, historical farming in temperate climates has resulted in higher soil phosphorous contents and lower soil carbon and nitrogen contents compared to sites with a long continuity of forest cover and soil development (Koerner et al., 1997; Dupouey et al., 2002; Fraterrigo et al. 2005; von Oheimb et al., 2008). Because microbial adaptation and recovery may play a significant role in ecosystem responses to human impacts (Mummey et al., 2002; Allison et al., 2010; Wallenstein and Hall, 2012), the long-term consequences of past land-use decisions on soil microbial communities are crucial for predicting changes in ecosystem functioning and services (Flinn and Vellend, 2005; Sun et al., 2011).

Here we examine the impact of land-use history on microbial community composition and functioning after more than 110 years of forest re-growth on former agricultural land. Very often, geographical past land-use patterns and environmental variation can be confounded (e.g. the fact that steeper slopes or poorer soils are more likely to be abandoned; Flinn and Vellend, 2005). To avoid this issue, we examined plots of sessile oak (*Quercus petraea*) dominated stands in the Lüneburg Heath region of Northwestern Germany that is characterized by homogeneous topography and soil conditions (Westphal, 2001). In addition, the land-use history in this region has been well documented over the last 240 years and detailed data on current site characteristics are available (Westphal, 2001; von Oheimb et al., 2008). Thus, we were able to select sites with very similar characteristics and tree species composition, but with different land-use histories. A previous study performed to determine past land-use effects on the edaphic properties of these forests (von Oheimb et al., 2008) showed that past agricultural practices resulted in long-term changes in essential soil characteristics, whereas differences between former heathlands and sites with a continuous forest history (ancient forest sites) were less pronounced.

Based on the previous research in these forests we hypothesized that different past land-uses would also have long-term impacts on microbial community composition and microbial extra-cellular enzyme activity. Specifically, we expected that long-term impacts on microbial communities would be strongest in former arable land compared to ancient forests, mirroring legacy effects of soil conditions related to past land-use intensity. Thus, our objective was to assess potential long-term effects of past land-use on (i) soil chemical properties, (ii) microbial biomass and community structure, and (iii) microbial extra-cellular enzyme activities. Furthermore we (iv) discuss the extent to which past land-use practices may have altered the recovery or trajectory of soil community development based on the results of our study. In order to measure microbial biomass and broad community structure simultaneously, we chose to use lipid analysis. Lipid analysis is a well-established method for quantitatively assessing microbial biomass and broad microbial groups including different fungal and bacterial communities (Vestal and White, 1989); it is also an effective measure of microbial responses to land-use and human impacts (for example: Mummey et al., 2002; Fraterrigo et al., 2006; Williams, 2007; Kulmatiski and Beard, 2011; Gutknecht et al., 2012). Microorganisms produce extra-cellular enzymes in order to degrade complex organic substrates into monomers for nutrient acquisition (Keeler et al., 2009). Extra-cellular enzyme activities can, therefore, represent microbial nutrient limitation and decomposition potential in response to changes in soil quality or land-use change (Sinsabaugh et al., 2002; Rinkes et al., 2011).

MATERIAL AND METHODS

Study area

This study was conducted in the Lüneburg Heath nature reserve (Lower Saxony, NW Germany; 53°15´N, 9°58´E, 70-150 m a.s.l), which comprises an area of 24,000 ha. The study area is characterized by a humid suboceanic climate with a mean annual precipitation of 811 mm and a mean annual temperature of 8.4 °C (Müller-Westermeier, 1996). The geological substrate is composed of fluvioglacial sandy deposits and drift sands from the Saale Ice Age. As a result of the high substrate acidity, the soils are mainly Podzols (Rode, 1999). The potential natural vegetation is acidophytic mixed beech–oak forest.

The landscape has changed markedly due to various human management practices over the past 240 years. While heathland was the predominant land-use type in the 18th century (80 %), a decline in historical farming activities, accompanied by afforestation measures during the last century, resulted in increased forest cover across the area (currently, app. 60%). At present the forests are dominated by coniferous species (68 % *Pinus sylvestris*, 14 % *Picea abies*, 5 % *Larix decidua*, 2% *Pseudotsuga menziesii*), while deciduous trees account for 11 % (5 % *Quercus petraea*, *Quercus robur*; 3 % *Fagus sylvatica*; 3 % *Betula pendula*; Westphal, 2001).

Study design and stand characteristics

The study was based on a past land-use intensity gradient, using data from 18 mature sessile oak stands (Table 1). We restricted the analysis to oak forests for several reasons. Because significant differences have been observed in the (chemical) properties of the upper soil layers under different tree species planted on former cultivated land (e.g. Bauhus et al., 1998; Graystone and Prescott, 2005; Wu et al. 2012), it is important to exclude this confounding factor by keeping the tree species composition constant. The vast majority of the ancient forest sites are near-natural mixed broadleaved forests with a high proportion of oak and beech. However, afforestation of former agricultural land with broadleaved tree species always involved oak, never beech. In total, about 20% of the area of the Lüneburg Heath nature reserve that was converted from arable land and heathland to forest during the period 1878 to 1998 is now dominated by oak trees (Ernst and Hanstein, 2001). Furthermore, within the framework of "close-to-nature forestry", most of the coniferous forests have been converted to mixed forests by planting oak trees over the last four decades.

Past land-use intensity was characterized on the basis of historical land-use systems: agriculture, heathland farming, and forestry. Information regarding past land-use was derived from historical maps of the "Kurhannoversche Landesaufnahme" from 1776 to 1786 and a forest management plan of 1887. The resulting gradient comprised (i) 'FA' oak stands established on former arable land, (ii) 'FH' oak stands established on former heathland and (iii) 'AF' oak stands on ancient forest sites. Agricultural practices in the 19th century included tillage and manure application. Fertilizer inputs were generally modest, with N-inputs mainly originating from organic sources. In contrast, sheep grazing was the main use of heathlands during this period. In addition, regular removal of litter, used for indoor sheep bedding, resulted in a decrease in the soil fertility in heathlands. Subsequently, manure-enriched litter was transferred to the arable fields, thus serving as an organic fertilizer (see Gimingham 1972 for a detailed description of historical heathland farming). Accordingly, the past land-use intensity decreases within the series FA – FH – AF. Forestry measures were restricted to selective logging (with no tillage). During 1981 and 1988, all study sites were ameliorated by liming (mean application: 3 t ha^{-1}).

Soil sampling and chemical analyses

In April 2011, we randomly collected five soil samples from the upper 5 cm mineral soil (A_{he}- horizon) for each study stand using a 100 cm^3 cylindrical metallic corer. The cores were taken a minimum distance of 5 m from each other and were immediately chilled. For subsequent analyses the five subsamples were thoroughly mixed to obtain one composite sample per stand. Total C, total N, total P, CEC and pH were determined from the homogenized soil samples. All samples were sieved (< 2 mm), ground and dried at 105 °C prior to soil chemical analyses.

Table 1 Land-use history ('FA' former arable land; 'FH' former heathland; 'AF' ancient forests) and the main stand characteristics of the investigated oak (*Quercus petraea*) forests. The shrub and herb layer (mean cover 30- 40%) was dominated by *Fagus sylvatica*, *Picea abies*, *Rubus fruticosus*, *R. idaeus*, *Vaccinium myrtillus*, *Dryopteris carthusiana* agg. and *Deschampsia flexuosa*.

	FA	FH	AW
Historical management activities	Ploughing, application of manure	Sheep grazing, sod-cutting	Firewood colection, litter ranking
Forest continuity (years)	app. 110	app. 120	> 235
Stand age (years) ^{A}	111 (11)	117 (16)	139 (18)
Stand volume (m^{3} ha^{-1}) ^{A}	295 (19)	257 (76)	346 (65)
Species composition (%) ^{B}			
Quercus petraea	86	80	67
Fagus sylvatica	2	-	25
Pinus sylvestris	6	15	4
Picea abies	6	3	4
Other tree species	-	1	-
n (plots)	6	6	6

^{A} mean (SD)

^{B} mean proportion of canopy tree basal area according to the forest management plan of 2011

Total C and N were determined with a C:N analyzer (Vario EL, Elementar, Hanau, Germany). For the determination of total P, samples were dissolved in an HNO_3–HCl–H_2O_2 solution (Wong et al., 1997) and digested using a microwave (MLS-ETHOS; MLS-GmbH, Leutkirch, Germany). Digested samples were analysed with an ICP-OES. Determination of CEC followed standard procedures as described by Steubing and Fangmeier (1992). Soil pH was measured in a 1:5 soil:water suspension.

Microbial lipid analysis

Lipid analysis was used to determine microbial biomass and microbial community structure. The applied procedure is a combination of phospholipid fatty acid analysis (PLFA, adapted from Bligh and Dyer, 1959) and fatty acid methyl ester analysis (FAME, modified from Gutknecht et al., 2012). From each composite soil sample, 2 g were extracted three times in a single phase citrate buffer (1.8 ml, 0.15 M), chloroform (2 ml), methanol (4 ml) mixture (0.9:1:2 volume ratio). After extraction, the volume ratio was changed to 0.9:1:1 to allow the phases to separate overnight at room temperature. The chloroform phase, containing the fatty acids, was retained and evaporated using a nitrogen evaporator. The procedure for FAME was then followed (Microbial ID Inc, Hayward CA); saponification followed by strong acid methanolysis and phase separation to extract the methyl-esterfied fatty acids. Methyl-esterfied fatty acids were run on a Gas chromatograph (Hewlett-Packard, HP 6890 Series GC-System) interfaced to a mass spectrometer (Agilent 5973) with an HP-5MS column (30 m, 0.25 m internal diameter, coated with a cross-linked 5% phenyl methyl rubber phase with a film thickness of 0.35 mm). Lipid peaks were determined manually using the associated Agilent FAME identification library, based on retention time, mass spectra, and comparison with standards. Peak areas were converted into nmol lipid g soil^{-1} using the internal standard C 19:0, and the efficiency of extraction was determined using a 13:0 surrogate standard added to each sample and blanks at the beginning of extractions.

The total nmol lipid g soil^{-1} (sum of all lipids present, 20 or less carbons in length) was used as an index of microbial biomass (Vestal and White, 1989). In addition, chemically similar lipid indicators were used to represent ecological groups of microorganisms. These included the following: Gram+ bacteria (sum of 13:0 iso, 13:0 anteiso, 14:0 iso, 15:0 iso, 15:0 anteiso, 16:0 iso, 17:0 iso, 17:0 anteiso, 18:0 iso and 18:0 anteiso), Gram- bacteria (sum of 10:0 2OH, 14:1, 14:0 2OH, 14:0 3OH, 16:1 ω9c, 16:1 ω7c, 16:1 ω7t, 17:1 11c or 9c, 17:1 7c or 8c, 16:0 2OH, 16:0 2OH, 16:1 OH, 18:1 ω12c, 18:1 ω9t, 18:1 ω7c, 18:1 ω5c, 18:1 2OH and 19:1), actinobacteria (sum of 16:0 10me, 16:0 me B, 16:0 11me, 17:0 me A, 18:1 me, 18:0 10me and 18:0 12me), anaerobic bacteria (17:0 cyclo and 19:0 cyclo), arbuscular mycorrhizal (AM) fungi (16:1 ω5c) as well as saprotrophic and ectomycorrhizal (S-EM) fungi (18:2 unknown, 18:2 ω6,9c and 18:1 ω9c; Balser et al., 2005). The ratios of fungal:bacterial lipids (f:b ratio) and Gram+ bacterial:Gram- bacterial lipids (G+:G- ratio) were also included in the data analysis.

Microbial extra-cellular enzyme activity

The activity of microbial extra-cellular enzymes was analyzed according to German et al. (2011). Soil sample suspensions were prepared by adding 1.0 g soil to 100 ml of 2.5 M TRIS buffer (pH 7) and homogenizing for 5 min. by low-level sonication. From the resulting suspensions, 200 µl were added to 96-well microplates containing 50 µl of fluorescent MUB (4-Methylumbelliferone) linked substrates to test the activity of three extra-cellular enzymes: phosphatase, β-glucosidase, and N-acetylglucosaminidase. The final concentrations of substrate solutions were 150 µM for phosphatase and β-glucosidase and 200 µM for N-acetylglucosaminidase. Substrate concentrations and incubation times were determined by preliminary analysis of representative soil samples from our study sites. Each 96-well plate also contained substrate controls (200 µl buffer and 50 µl of substrate), homogenate controls (200 µl of sample suspension and 50 µl of buffer), a dilution series to determine the sample quench coefficient (MUB and 200 µl sample suspension) and a dilution series to determine the emission coefficient (MUB and 200 µl TRIS buffer). The microplates were incubated at room temperature in the dark for one hour. To stop the reaction and for fluorescence measurements, 10 µl of 0.5 M NaOH was added after incubation to every well of each microplate. Fluorescence was measured using a Microplate Reader (Fluorescence Spectrophotometer VARIAN Cary Eclipse). Using the fluorescence of assay wells, controls, and the quench and emission coefficients, activities were calculated as nmol substrate cleaved g soil^{-1} h^{-1} as described by German et al. (2011).

Data analysis

Variation in microbial community assembly with land-use history was evaluated by analysis of dissimilarity (ADONIS, 1000 permutations) followed by a Bonferroni adjustment (Anderson, 2001). The analysis was performed on a matrix of Bray-Curtis dissimilarities based on the relative mole fractions of individual lipid markers (n = 36). Abundance data were square-root transformed and standardized (Wisconsin double standardization) prior to analysis. Only fatty acids > 0.5 mol percent were considered for the analysis. The same matrix was also used for non-metric multi-dimensional scaling (NMDS, using the *metaMDS* function of the *vegan* library in R, Oksanen et al., 2011) in order to reveal patterns in microbial composition among the past land-use types. To examine how microbial communities vary along the ordination axes, we calculated Pearson correlation coefficients between microbial groups and NMDS-axis scores. Similarly, Pearson correlation tests were applied to explore changes in the community structure with chemical soil properties. Finally, the microbial groups and soil parameters with significant Pearson axes correlations were included in the ordination plot using the function *envfit* in the *vegan* library in R. The length and direction of the vectors indicate the strength and direction of their correlation with NMDS-axis scores.

Differences between past land-use types and chemical soil properties, microbial abundance (untransformed data) and enzyme activities ($\log_{10}$-transformed data) were tested by ANOVA with a post hoc Tukey HSD test. To investigate the relationship between enzyme activities and microbial groups or total biomass we applied multiple linear regressions. The variable f:b ratio was omitted from the analysis because of its close correlation with the abundance of saprotrophic and ectomycorrhizal fungi (r = 0.85). The explanatory power of significant predictors was assessed by variance partitioning based on adjusted R^2 values (Zuur et al., 2007). All analyses were performed with R, version 2.14.2. (Team RDC, 2012).

RESULTS

Soil chemical properties

Chemical soil properties varied markedly between the three land-use types. Total C, N and P strongly decreased from FA / FH to AF, while C:N ratios were significantly higher (+ 37 %) at the AF sites compared to the FA sites (Table 2). Past land-use effects on pH and CEC were less distinct.

Table 2 Soil chemical characteristics (mean ± SE) of the study stands from the upper mineral soil (A_{he}- horizon). Different letters indicate statistically significant (Tukey HSD: $P_{adj.} < 0.05$) differences between the past land-use types. 'FA' former arable land; 'FH' former heathland; 'AF' ancient forests.

	FA	FH	AF
Total C (%)	2.54 (0.36) ^{a}	3.10 (1.00) ^{a}	1.41 (0.25) ^{a}
Total N (%)	0.13 (0.02) ^{a}	0.14 (0.05) ^{a}	0.05 (0.01) ^{b}
Total P (mg kg^{-1})	185.16 (17.34) ^{a}	135.50 (39.91)^{ab}	76.83 (11.27) ^{b}
C:N ratio	19.48 (1.19) ^{a}	23.57 (1.17)^{ab}	26.61 (1.74) ^{b}
C:P ratio	142.50 (20.43) ^{a}	220.50 (12.44) ^{b}	185.33 (17.25)^{a}
CEC (mval L^{-1})	4.78 (0.63) ^{a}	5.43 (1.30) ^{a}	3.58 (0.40) ^{a}
pH	4.05 (0.20) ^{a}	3.94 (0.14) ^{a}	3.98 (0.17) ^{a}

CEC: cation exchange capacity

Multivariate community composition

The NMDS ordination resulted in a two-dimensional solution with a final stress of 0.120. Microbial community development was strongly affected by past land-use intensity (ADONIS: $F = 2.47$, $P < 0.001$). Community composition in AF soils differed markedly from FA ($P_{adj.} < 0.01$), while a marginal difference ($P_{adj.} = 0.04$) was noted for AF and FH. Differences between FA and FH were not statistically significant ($P = 0.23$). PLFA profiles of the land-use types were clearly separated along the first NMDS axis ($P = 0.017$), while along axis 2 no past land-use effect was evident ($P = 0.44$; Fig. 1). Moreover, apart from one outstanding FA and FH sample, AF samples were the most scattered across the ordination diagram, indicating a trend towards higher structural heterogeneity between microbial communities (higher β-diversity) with decreasing past land-use intensity. Variation in microbial assemblages showed a strong response to chemical soil properties. Axis 1 corresponded significantly to a nutrient gradient of increasing C:N ratios ($r = 0.58$) and decreasing N, P, C and CEC contents (N: $r = -0.78$; P: $r = -0.77$; C : $r = -0.71$; CEC: $r = -0.73$; Table 3 and Fig. 1). Along this axis, assemblage composition was driven in large part by the abundance of S- EM fungi ($r = 0.68$) and actinobacteria ($r = -0.63$; Table 3).

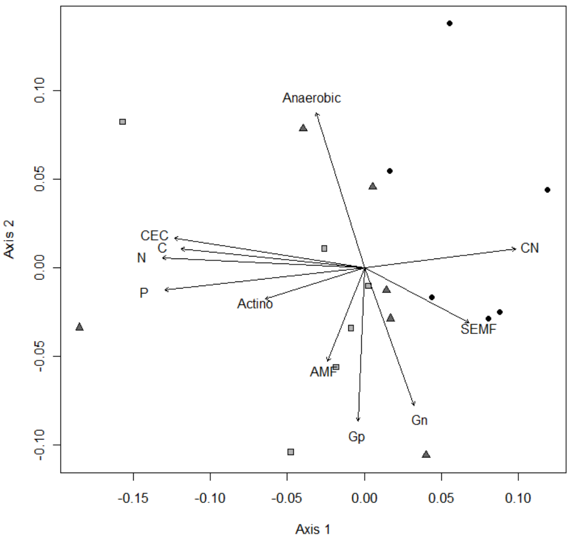

Fig. 1 Non-metric multi-dimensional scaling ordination of soil microbial communities in oak forests with different land-use histories: former arable land (light grey squares), former heathland (grey triangles) and ancient forests (black circles). Site scores ($n = 18$) represent microbial assemblages in the A-horizon. Arrows indicate significant ($P < 0.05$) joint axis correlations with microbial groups (AMF: arbuscular mycorrhizal fungi; SEMF: saprotrophic and ectomycorrhizal fungi; Actino: actinobacteria; Anaerobic: anaerobic bacteria, Gn: Gram- bacteria; Gp: Gram+ bacteria) and soil properties (C: total carbon content, N: total nitrogen content, P: total phosphorous content; CEC: cation exchange capacity; CN: C:N ratio).

Microbial biomass and broad groups

Historical farming had a marked impact on the distribution of microbial groups. In total, FH soils were associated with the highest microbial biomass, followed by FA (-23 %) and AF (-44 %; Fig. 2). However, differences were not statistically significant. This can be mainly attributed to the considerable variation within FH and FA plots. Values for the coefficient of variation accounted for 52.4 % (FH) and 30.3 % (FA) compared to 21.9 % (AF). On average, AF soils supported a 25% and 8% lower proportion of actinobacteria compared to FH and FA samples, respectively. AF soils, on average, also supported a 52% and 40% lower proportion of AM fungi compared to FH and FA samples. In addition, mean values of S-EM fungi and anaerobic bacteria tended to increase with decreasing past land-use intensity, but showed no significant differences among land-use types. The opposite trend was observed for Gram+ bacteria (Table 4).

Table 3 Correlation matrices of associations between NMDS axes scores, and microbial groups and chemical soil properties for 18 mature sessile oak (*Quercus petraea*) stands. Values indicate Pearson coefficients, significant correlations are in bold. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

	Axis 1	Axis 2
Microbial groups		
Gram+ bacteria	-0.047	**-0.841** **
Gram- bacteria	0.367	**-0.733** **
Anaerobic bacteria	-0.355	**0.832** ***
Actinobacteria	**-0.633** **	-0.145
AM fungi ^{A}	-0.268	**-0.494** *
S-EM fungi^{B}	**0.681** **	-0.259
G+:G- ratio	-0.398	0.962
Fungi:bacteria ratio	0.402	-0.254
Soil characteristics		
pH	-0.005	-0.264
Total C	**-0.707** **	0.054
Total N	**-0.777** ***	0.029
Total P	**-0.770** ***	-0.061
C:N ratio	**0.585** **	0.053
C:P ratio	-0.001	-0.026
CEC ^{C}	**-0.735** ***	0.084

^{A} AM arbuscular mycorrhiza

^{B} S-EM saprotrophic and ectomycorrhizal

^{C} cation exchange capacity

Microbial enzyme activities

Past land-use intensity significantly affected enzyme activity (N-acetylglucosaminidase: *F*: 12.29, $P < 0.001$; β-glucosidase: *F*: 6.11, $P < 0.05$; phosphatase: *F*: 3.58, $P < 0.01$) and was highest in FH, followed by FA and AF (Fig. 2). This pattern was consistent for all enzymes. Microbial activities in former arable land or heathland soils were, on average, up to five and nine times higher, respectively, than in ancient forest soils.

N-acetylglucosaminidase and β-glucosidase activities significantly increased with increasing total microbial biomass and abundance of AM fungi. Microbial biomass, however, was much more related to β-glucosidase than for N-acetylglucosaminidase activity. In contrast, phosphatase activity was positively related to actinobacterial abundance. No other microbial groups showed any significant ($P > 0.05$) relationships with enzyme activities (Table 5).

DISCUSSION

Effects of past land-use on soil microbial community structure and enzyme activities

We found strong support for the hypothesis that past land-use, even after a century of reforestation, still influences soil microbial community composition and microbial extra-cellular enzyme activities. However, contrary to our hypothesis, we found no evidence for distinct differences in soil microbial community composition or enzyme activity between historical farming practices (between agriculture and heathland grazing). Specifically, we observed considerably higher microbial biomass and enzyme activities on former heathlands and former arable lands compared to ancient oak forest sites, but not between the historically cultivated sites. This strongly suggests that legacy effects of past land-use can be a major driver of soil microbial community dynamics, but that the land use itself, and not necessarily the type of land use, may be important for these legacy effects.

Although very few studies have been able to assess persistent changes in soil conditions or soil communities resulting from land-use change after as long a time as were able to explore, our results contribute to a growing body of evidence that different land-use practices alter soil communities in the long term. This is in contrast to the common paradigm that microbial communities are infinitely plastic or can adapt to new conditions very rapidly (Schimel et al., 2007). Fraterrigo and colleagues (2006), for instance, found lower fungal abundance, higher bacterial abundance, and higher N-mineralization rates in forest stands 50 years after the stands had been reforested after agricultural cultivation. It has also been shown that bacterial communities continue to change over the course of 50–2000 years of rice cultivation, compared to non-cultivated soils (Bannert et al., 2011). In our study, we observed that arbuscular mycorrhizal fungi, actinobacteria, and enzyme activities were distinctly lower in ancient forest soils, the least fertile soils examined in our study, compared to recent forest

Table 4 Mean (± SE) site values (*n*= 6 per land-use type) for different microbial groups (mol %) in mature sessile oak (*Quercus petraea*) stands with contrasting past land-use intensities. Different letters indicate statistically significant (Tukey HSD: $P_{adj.} < 0.05$) differences between the past land-use types. 'FA' former arable land; 'FH' former heathland; 'AF' ancient forests.

	FA	FH	AF
Gram+ bacteria	8.36 (0.75) ^{a}	8.44 (0.54) ^{a}	7.13 (0.50) ^{a}
Gram- bacteria	26.82 (1.79) ^{a}	23.54 (3.20) ^{a}	24.82 (2.36) ^{a}
Anaerobic bacteria	21.63 (4.71) ^{a}	21.70 (2.61) ^{a}	24.10 (3.32) ^{a}
Actinobacteria	3.32 (0.14) ^{a}	4.10 (0.43) ^{a}	3.06 (0.19) ^{b}
AM fungi [A]	0.86 (0.11) ^{ab}	0.97 (0.11) ^{a}	0.52 (0.05) ^{b}
S-EM fungi [B]	5.92 (0.48) ^{a}	6.85 (0.42) ^{a}	7.13 (0.81) ^{a}
G+:G- ratio	0.31 (0.02) ^{a}	0.37 (0.04) ^{a}	0.30 (0.02) ^{a}
Fungi:bacteria ratio	0.12 (0.01) ^{a}	0.14 (0.01) ^{a}	0.13 (0.02) ^{a}

[A] AM arbuscular mycorrhiza

[B] S-EM saprotrophic and ectomycorrhizal

soils (FA, FH). The former arable lands and heathlands that we examined had persistently more fertile soils with approximately two-fold higher concentrations of N and P (Table 2). Thus, in this case, past land-use has actually led to soils with higher long-term nutrient concentrations (von Oheimb et al., 2008), and thus the potential to support more growth and enzyme activity of those microbial groups. Contrarily, our observed trend towards higher abundances of saprotrophic and ectomycorrhizal fungi in ancient forest soils can be explained by higher amounts and structural complexity of carbon sources (dead wood or litter) in forests with a long continuity of low anthropogenic disturbances compared to recent forests (von Oheimb et al., 2007), leading to more niche availability for larger fungal communities. Together these results suggest that changes in edaphic site properties alter microbial community composition and consequent microbial activities to a much greater extent than land-use per se (Lauber et al., 2008; Birkhofer et al., 2012).

A caveat to our study is that the trajectory of ecosystem development after long-term land-use can often be confounded by current modified 'original' plant communities (Kulmatiski and Beard, 2008). In our case, tree species composition distinctly varied between past land-use types with 19% (FH) and 28% (FA) higher abundance of *Q. petraea* compared to ancient forest sites (AF). In contrast, the proportion of *F. sylvatica*, which is the second most common species in ancient oak forests, was much lower in former arable lands and former heathlands, respectively (Table 1). Sites where there was agriculture or heathland farming in the past, of course, have greater oak dominance because they were deliberately reforested by planting oak seedlings. Although we should be aware of this caveat to our study, there is also evidence that past land-use is more influential for soil microbial communities than current plant community composition (Jangid et al., 2011). Thus, the observed differences in soil characteristics and the associated persistent changes in the soil microbial communities could be directly related to the effects of historic land-use and also to subsequent feedbacks from the altered tree species composition.

The process of conversion from former heathlands to forests may also explain our observed differences in microbial extra-cellular enzyme activities and actinobacterial abundances. Heathland soils are typically dominated by dwarf shrub species (of the Ericaceae, such as *Calluna vulgaris*) that are high in polyphenolic compounds. These polyphenolic compounds inhibit decomposition and thus, organic matter breaks down slowly in heathlands and they have a high potential for carbon storage (Nielsen et al., 1987). In addition, heathlands were traditionally used for grazing, and there may have been organic carbon inputs (originating from the sheep) that were stored in the soil because of the low decomposition rates. However, after afforestation with oak, ericaceous dwarf shrubs disappeared,

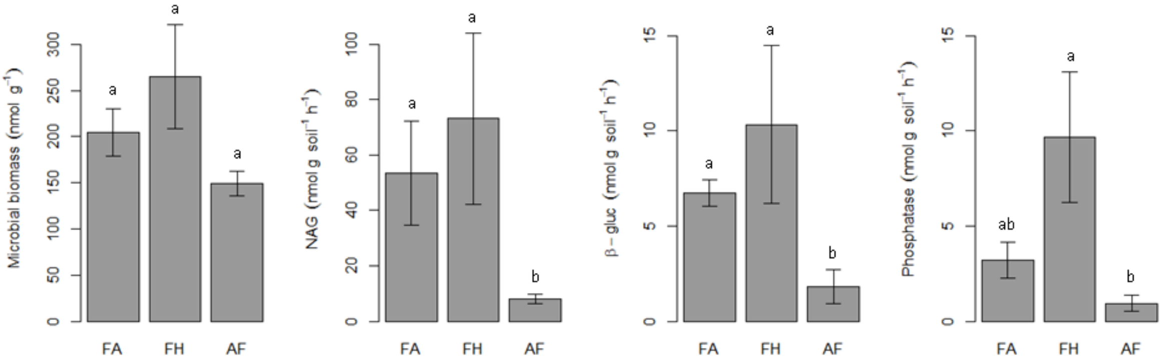

Fig. 2 Variation in mean (± SE) abundance of total microbial biomass (nmol lipid g soil^{-1}) and enzyme activities (nmol substrate cleaved g soil^{-1} h^{-1}) along a past land-use gradient. Different letters indicate statistically significant (Tukey HSD: $P_{adj.} < 0.05$) differences between the past land-use types. 'FA' former arable land; 'FH' former heathland; 'AF' ancient forests. NAG 'N-acetylglucosaminidase'; βgluc 'β-glucosidase'.

with a subsequent halt in the inputs of polyphenolic compounds. Over time (decades or centuries) this would lead to a greater capacity for decomposition, such as we observed with the increase in microbial biomass and extra-cellular enzyme activity. Another typical change in microbial communities after conversion of heathlands to forests is the shift in dominance from ericoid mycorrhizal fungi to ectomycorrhizal fungi. The ability of ericoid mycorrhizas to assimilate phenolic monomers and, by cleaving polyphenols, to secure the release of nutrients coprecipitated with these polymers is particularly relevant for the nutrition of ericaceous plants in heathlands (Read and Perez-Moreno, 2003). The conversion to oak forests and transition to an ectomycorrhizal based fungal community could explain the higher extra-cellular enzyme activities and actinobacterial abundance we observed. Ectomycorrhizal hyphae and associated mats are known to be associated with high levels of enzyme production (Pritsch et al., 2004; Kluber et al., 2010). This high level of enzyme production possibly comes directly from the fungi or from associated actinobacterial populations. The significant correlation we found between actinobacterial abundances and extra-cellular enzyme activities is thus logical given that actinobacteria are major producers of extra-cellular enzymes.

Effects of past land-use intensity on successional pathways of forest soil microbial communities

The magnitude and the direction of management effects may vary with ecosystem properties and past land-use intensity. There are two plausible, non-mutually exclusive, explanations for long-term past land-use effects on both soil microbial communities and nutrient cycling. First, depending on the precise initial site and soil conditions, as well as on subsequent management practices, recovery of forest ecosystems back to pristine or undisturbed conditions could take more than 200 years. Thus, the observed shifts in soil conditions, tree species composition and microbial community structure in our study sites are still out of a long-term equilibrium state and continue to recover from past land-use impacts. Given the relatively slow process of soil formation, slow recovery rate of soil microbial communities (Jangid et al., 2011) and the long-lived dominant plant species in forests, it seems plausible that successional pathways can be long-lasting. This is consistent with the findings of von Oheimb et al. (in prep.), who observed, for the same long-term chronosequence study sites, considerably higher variation in tree-ring width and higher mean growth rates of *Q. petraea* on former agricultural and heathland sites than on ancient woodland sites. Additionally von Oheimb et al. (in prep.) found significant correlations of tree-ring width with C:N ratio and P availability, which indicates that past land-use continues to

Table 5 Relationships between PLFA data (microbial groups and total biomass) and log-enzyme activity (nmol substrate cleaved g soil^{-1} h^{-1}) in 18 mature sessile oak (*Quercus petraea*) stands. The importance of the predictors is given by the partial R^2 derived from variance partitioning.

	Effect	*P*-value	partial R^2
N-acetylglucosaminidase			
Gram+ bacteria		n.s.	
Gram- bacteria		n.s.	
Anaerobic bacteria		n.s.	
Actinobacteria		n.s.	
AM fungi [A]	+	<0.001	0.344
S-EM fungi [B]		n.s.	
G+:G- ratio		n.s.	
Total microbial biomass	+	0.002	0.211
$R^2_{adj.}$		0.745	
β-glucosidase			
Gram+ bacteria		n.s.	
Gram- bacteria		n.s.	
Anaerobic bacteria		n.s.	
Actinobacteria		n.s.	
AM fungi [A]	+	0.013	0.134
S-EM fungi [B]		n.s.	
G+:G- ratio		n.s.	
Total microbial biomass	+	<0.001	0.386
$R^2_{adj.}$		0.687	
Phosphatase			
Gram+ bacteria		n.s.	
Gram- bacteria		n.s.	
Anaerobic bacteria		n.s.	
Actinobacteria	+	<0.001	
AM fungi [A]		n.s.	
S-EM fungi [B]		n.s.	
G+:G- ratio		n.s.	
Total microbial biomass		n.s.	
$R^2_{adj.}$		0.495	

[A] AM arbuscular mycorrhiza

[B] S-EM saprotrophic and ectomycorrhizal

affect forest soil conditions and tree growth patterns for more than a century. In other studies it has also been documented that ecosystem development shows a consistent pattern of increasing and then decreasing soil fertility, with the early developmental phases lasting 200 or more years (Dupouey et al., 2002; Wardle et al., 2004b; Peltzer et al., 2010). For example Cusack et al. (2013) reported long-term (> 200 years) effects of intensive cultivation on soil carbon pools and cycling. The recent forest communities (FA, FH) analyzed in our study are, therefore, probably still in this early developmental, high fertility phase. There are associated changes in microbial community structure along this sequence of recovery, although they are relatively unpredictable or poorly understood (Dickie et al., 2013). Our observations indicated higher abundances of actinobacterial and arbuscular mycorrhizal fungal lipid indicators as well as total lipid biomass in both former arable lands and former heathlands when compared to ancient forests (as discussed earlier).

The second possible explanation is that, instead of a progression toward recovery or equilibrium, past land-use has actually changed the long-term trajectory and adaptation of both forest and soil community development over time. Even though microbial communities may be adapted to natural disturbance regimes (Gutknecht et al., 2010, 2012), human induced land-use changes could represent disturbance events that are beyond the adaptive capacity, or that change the adaptive capacity, of the community in question (Scheffer et al., 2009; Leadley et al., 2010). This is due to the drastic alterations in historic site conditions (e.g. tillage, fertilization and altered tree species composition) created by those land-use changes. Our results indicate that past land-use has led to higher nutrient levels and altered vegetation composition. Consequently, these changes in ecosystem properties may have shifted the equilibrium state of the microbial community, and further research should address the question of whether this leads to long-term increases in decomposition and nutrient cycling in these forest ecosystems. Thresholds such as long-term land-use may, therefore, alter edaphic properties to an extent that induces positive feedbacks and thus are hard to change further or reverse (Lenton et al., 2008; Scheffer et al., 2009; Leadley et al., 2010). Accordingly, even ‘restored’ native forest or soil communities can never again represent historic forest conditions because of legacy effects of past management

CONCLUSIONS

In this study we found strong evidence that past land-use effects on forest soil microbial communities persist much longer than observed to date (e.g. Fraterrigo et al., 2005, 2006; Jangid et al., 2011). This in turn suggests that ecological continuity may be a major driver of ecosystem functioning and services. After more than one century of development during secondary succession, microbial community structure and enzyme activities were still significantly different between ancient and recent forest ecosystems. Thus, successional pathways of forest soil microbial communities probably depend on the intensity of past anthropogenic disturbance, since compositional shifts were less pronounced in former heathlands compared to former arable lands. This can be mainly attributed to differences in the initial soil conditions after anthropogenic disturbances.

Beyond the ability to generalize our results to other forest types, we conclude that a deeper understanding of various past-land-use legacies is crucial, because of their essential role for above- and belowground interactions. In this context, ancient forest sites are particularly important for the conservation of aboveground (e.g. Baeten et al., 2010) and belowground communities and thus, for the diversity and functioning of forest ecosystems.

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Chapter 9

Does forest continuity enhance the resilience of trees to environmental change?

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RESEARCH ARTICLE

Does Forest Continuity Enhance the Resilience of Trees to Environmental Change?

Goddert von Oheimb[1]*, Werner Härdtle[2], Dieter Eckstein[3], Hans-Hermann Engelke[4], Timo Hehnke[2], Bettina Wagner[5], Andreas Fichtner[2]

1. Institute of General Ecology and Environmental Protection, Technische Universität Dresden, Pienner Str. 7, 01737, Tharandt, Germany, **2.** Institute of Ecology, Leuphana University of Lüneburg, Scharnhorststr. 1, 21335, Lüneburg, Germany, **3.** Centre of Wood Sciences, University of Hamburg, Leuschnerstr. 91, 21031, Hamburg, Germany, **4.** Forestry Department Sellhorn, Niedersachsen State Forestry Department, Sellhorn 1, 29646, Bispingen, Germany, **5.** Albrecht-von-Haller Institute for Plant Sciences, University of Göttingen, Untere Karspüle 2, 37073, Göttingen, Germany

*Goddert_v_Oheimb@tu-dresden.de

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Abstract

There is ample evidence that continuously existing forests and afforestations on previously agricultural land differ with regard to ecosystem functions and services such as carbon sequestration, nutrient cycling and biodiversity. However, no studies have so far been conducted on possible long-term (>100 years) impacts on tree growth caused by differences in the ecological continuity of forest stands. In the present study we analysed the variation in tree-ring width of sessile oak (*Quercus petraea* (Matt.) Liebl.) trees (mean age 115–136 years) due to different land-use histories (continuously existing forests, afforestations both on arable land and on heathland). We also analysed the relation of growth patterns to soil nutrient stores and to climatic parameters (temperature, precipitation). Tree rings formed between 1896 and 2005 were widest in trees afforested on arable land. This can be attributed to higher nitrogen and phosphorous availability and indicates that former fertilisation may continue to affect the nutritional status of forest soils for more than one century after those activities have ceased. Moreover, these trees responded more strongly to environmental changes – as shown by a higher mean sensitivity of the tree-ring widths – than trees of continuously existing forests. However, the impact of climatic parameters on the variability in tree-ring width was generally small, but trees on former arable land showed the highest susceptibility to annually changing climatic conditions. We assume that incompletely developed humus horizons as well as differences in the edaphon are responsible for the more sensitive response of oak trees of recent forests (former arable land and former heathland) to variation in environmental conditions. We conclude that forests characterised by a long ecological continuity may be better adapted to global change than recent forest ecosystems.

Introduction

Forest ecosystems provide important ecological, social and economic services. They host much of the world's biodiversity and are key systems in stabilising biogeochemical cycles and climate conditions at regional and global scales [1]. However, changes in land use and deforestation have caused a worldwide and extensive decline of forest ecosystems [2]. In western Europe and North America, in particular, a range of actions were taken in the 19th and 20th centuries to prevent deforestation and to establish new forests, mainly on former agricultural or degraded land [3, 4]. In recent years, the moves to reduce atmospheric CO_2 levels have provided a strong impetus to expand the area covered by forests worldwide [5].

Despite the multiple positive effects of an increase in forest area, many questions regarding the evaluation of the overall ecological implications of such an afforestation policy remain open [6, 7]. There is ample evidence that the legacies of former land-use activities may continue to affect forest ecosystem functioning for decades or even centuries after those activities have ceased [8, 9]. Significant differences in plant species composition and diversity as well as in soil properties between areas continuously covered with forests for several centuries, i.e., sites with a long ecological continuity ([10]; also termed "ancient forests" [9]) and forests restored on former agricultural land have been extensively documented [11, 12, 13, 14, 15, 16, 17, 18, 19, 20]. In addition, numerous studies have reported impacts of land-use changes on soil microbial communities, microbial community function and, consequently, nutrient cycling rates [21, 22, 23, 24, 25]. Thus, over a long period of time, forests restored on former agricultural land may differ from continuously existing forests with regard to their ecosystem properties and desirable ecosystem services. Surprisingly, little information is available on the long-term consequences of land-use change on individual tree growth. To our knowledge, the present study is the first to use a dendroecological approach to compare long-term radial growth of sessile oak (*Quercus petraea* (Matt.) Liebl.) trees in continuously existing forests and afforestations on previously agricultural land.

Radial growth of trees is related to abiotic and biotic factors, tree age and forest management. Among the local abiotic site factors, soil fertility and soil water availability, most important for oak diameter growth [26, 27, 28], can be affected by past land-use. Past fertilisation can increase the soil pools of N and P in forests on former agricultural land [15, 29, 30, 31]. For example, Baeten et al. [32] showed that the growth performance of forest herbaceous species can be enhanced by increased P availability in post-agricultural forests. Cultivation procedures (tillage and fertilisation) reduce the thickness of the humus horizons or even cause them to disappear. After abandonment and reforestation, the forest floor redevelops, though at a slow rate. Von Oheimb et al. [15] predicted that a minimum of 250 years must pass before the forest floor C stores, typical for continuously existing oak forests, have accumulated on former arable land. Thinner and less developed humus horizons are accompanied by a deterioration of the water storage capacity of the soils [33]. High temperature and water stress caused by low precipitation during spring and summer as well as early and late frost events are the main influences on the climate-growth relationships of oak. However, under sub-oceanic and sub-continental conditions the sensitivity of sessile oak radial growth to climate was found to be generally low [34, 35, 36, 37, 38]. Furthermore, interactions between below-ground and above-ground communities may strongly affect tree growth, because soil microbial communities regulate key biogeochemical processes such as decomposition of organic materials, carbon and nitrogen cycling, and nutrient availability for plant growth [39, 40, 41]. There is a growing body of evidence that different land-use practices alter soil communities in the long term [21, 23, 25].

In this study we analysed the variability in growth of mature oak trees growing in continuously existing forests and in afforestations on former arable land and on former heathland. We expected tree-ring width of oak to be highest on former arable land, mirroring the after-effects of past fertilisation. We hypothesised that oak trees growing on continuously existing forest sites show a lower variability in their tree-ring width compared to those on afforested sites, indicating that they are less responsive to varying environmental conditions.

Materials and Methods

Study area

The study area is the nature reserve Lüneburg Heath (NW Germany, 53°15′N, 9°58′E, 60 m a.s.l.), comprising an area of 234 km^2 with soil and climate conditions representative of most parts of NW Central Europe. The climate is of a humid sub-oceanic type. Mean annual sum of precipitation is 811 mm and mean annual temperature is 8.4℃ [42]. Soils consist of deposits of the Saale Ice Age. The predominant soil types are Podzols.

In the study area both the land-use and forest history have been well-documented over the last 230 years [43]. In 1776, almost 80% of the area was covered by heathlands dominated by *Calluna vulgaris*, whilst agricultural fields and forests occupied about 10 and 5%, respectively. In the middle of the 19th century, farmers began to abandon heathlands and arable land and vast areas were afforested or underwent natural succession. Today, forests span about 60% and heathlands about 20% of the landscape.

Site selection

In the nature reserve, a total of 25 discrete sample sites dominated by *Quercus petraea* (1–4 ha in size and embedded in surrounding stands of *Pinus sylvestris*, *Picea abies*, or *Fagus sylvatica*) were chosen using recent forest maps and historical maps (including the so-called ''Kurhannoversche Landesaufnahme'' from 1776–1786). The historical maps indicate the type of land-use during the past 230 years and thus served to detect continuously existing forests (hereafter referred to as ''CEF''). It is assumed that these woodlands have never been deforested in the last 200 to 300 years, but used as woodland pastures [43]. Forest management plans from 1878 were used to detect oak stands in areas which had been arable land or heathland (hereafter referred to as ''FAL'' and ''FH'', respectively) prior to this date (Table 1). In addition, plans gave information about tree age and the silvicultural measures which were implemented from 1878 onwards. The age of the study trees was, on average, 124 years on FAL, 115 years on FH, and 136 years in the CEF. In recent decades, selective logging but no soil disturbance occurred on the sample sites.

Tree selection and sampling design

The research permission was provided by the Forestry Department Sellhorn, Niedersachsen State Forestry Department, Bispingen, Germany. No specific permissions were required for our activities. Our field studies did not involve any endangered species.

The dendroecological sampling was carried out from June to August 2006. For the selection of the study trees a grid was laid over each sample site. In this grid, 10 intersections were chosen randomly and the dominant oak tree nearest to an intersection was selected (=10 trees per sample site). A total of 250 trees were sampled. Radial growth was derived from two cores per tree taken at breast height (1.30 m) using an increment borer (Suunto 400, Vantaa, Finland; 40 cm in length and 0.5 cm in bit diameter).

Tree-ring analysis

The cores were air dried, fixed to a core-mounting, and their surface was smoothed with a core-microtome (WSL Birmensdorf, Switzerland). Subsequently, tree-ring widths (TRW) were measured using a measuring table with 0.01 mm resolution (Instrumenta Mechanik Labor IML, Wiesloch, Germany) combined with a binocular (Wild, Heerbrugg, Switzerland) and recorded using the IML software T-Tools pro. The data were analysed using the software TSAP-Win (Version 0.53, Rinntech, Heidelberg, Germany). First, the two TRW series per tree were cross-dated and averaged into a single tree-ring series. Then, an average series per sample site (site chronology) and finally per historical land-use type (land-use type chronology) were calculated. Due to differences in tree age within and between sites, the further analyses were confined to the common period from 1896–2005. The raw TRW data were used to visualize land-use type-specific

Table 1. Site land-use history and characteristics.

	Former arable land	Former heathland	Continously existing forest
Historical management activities	**Ploughing,**	**Sheep grazing,**	**Firewood colection,**
	application of manure	**sod-cutting**	**litter ranking**
No. sample sites	10	8	7
Stand age (years)	124	115	136
Stand volume ($m^3\ ha^{-1}$)	295	257	346
Species composition (%)^A			
Quercus petraea	86	80	67
Fagus sylvatica	2	-	25
Pinus sylvestris	6	15	4
Picea abies	6	3	4
Other tree species	-	1	-
Site index^B	3–4 (mesothrophic)	3–4 (mesothrophic)	3–4 (mesothrophic)
HG (r)	0.69^{ns}	0.67^{ns}	0.78^{ns}
TRW (mm)	1.8^{a}	1.7^{ab}	1.5^{b}
SD (mm)	0.61^{b}	0.41^{a}	0.37^{c}
AR-1	0.77^{ns}	0.56^{ns}	0.64^{ns}
MS	0.17^{a}	0.17^{a}	0.14^{b}

[A] Mean proportion of canopy tree basal area according to the forest management plan of 2011.

[B] The soil nutrient status of the sample sites was classified according to the German forest site mapping system. This index ranges from 1 (very low nutrient availability) to 6 (very high nutrient availability).

Structure and growth parameters (means) of sessile oak (*Quercus petraea*) stands in the nature reserve Lüneburg Heath (NW Germany) for the period from 1896 to 2005. Number of trees per sample site: 10. Abbreviations: HG=homogeneity of growth; TRW=tree-ring width; SD=standard deviation; AR-1=autocorrelation; MS=mean sensitivity. Different superscript letters indicate significant differences of tree ring series characteristics among the historical land-use types ($P_{adj.}<0.05$); ns=not significant.

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differences in radial increment (cf. Figs. 1 and 2; raw TRW data in Table S1). For the analysis of TRW-climate relationships, the raw TRW data have been detrended (see description below).

Soil and meteorological data

Soil data were taken from an accompanying study that analysed soil parameters appropriate for an assessment of the nutritional status of the sample sites (Table 2) [15]; there are significant differences between the soil parameters for the three historical land-use types. Furthermore, patterns differed for the respective soil horizons (i.e. organic layer and A-horizon). FAL showed significantly lower C and N contents in the organic layer. The C/N ratios (in the O- and A-horizon) were lowest on FAL and highest in the CEF. In addition, both plant-available P and total P contents were highest in the A-horizon of FAL, but were of a similar order of magnitude in FH and CEF. High P contents were reflected by low C/P ratios of this horizon on FAL.

Meteorological data (mean monthly precipitation and mean monthly temperature, available from 1862 onwards) were obtained from the German Weather Service (DWD, Hamburg, Germany) and from the Hamburger

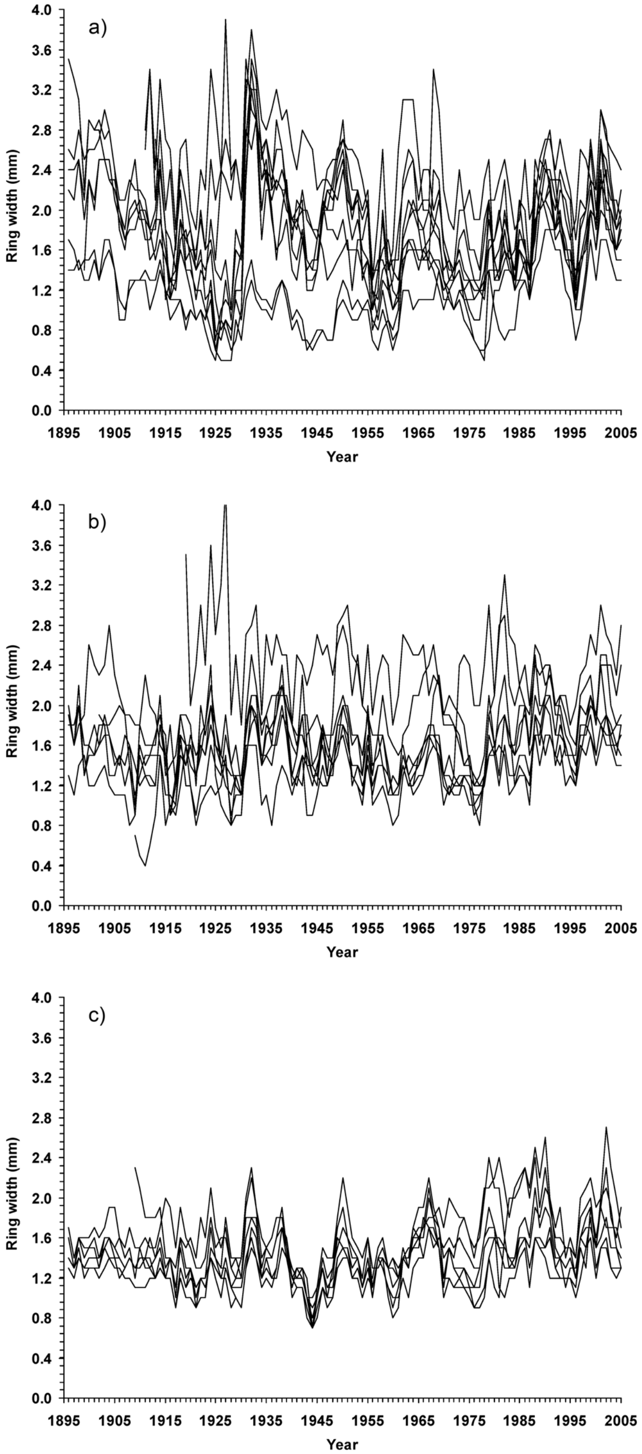

Figure 1. Variation of radial growth of sessile oak (*Quercus petraea*) among historical land-use types between 1896 and 2005. Data represent site chronologies based on 10 trees per sample site; a) former arable land (10 sites), (b) former heathland (8 sites), and (c) continuously existing forests (7 sites).

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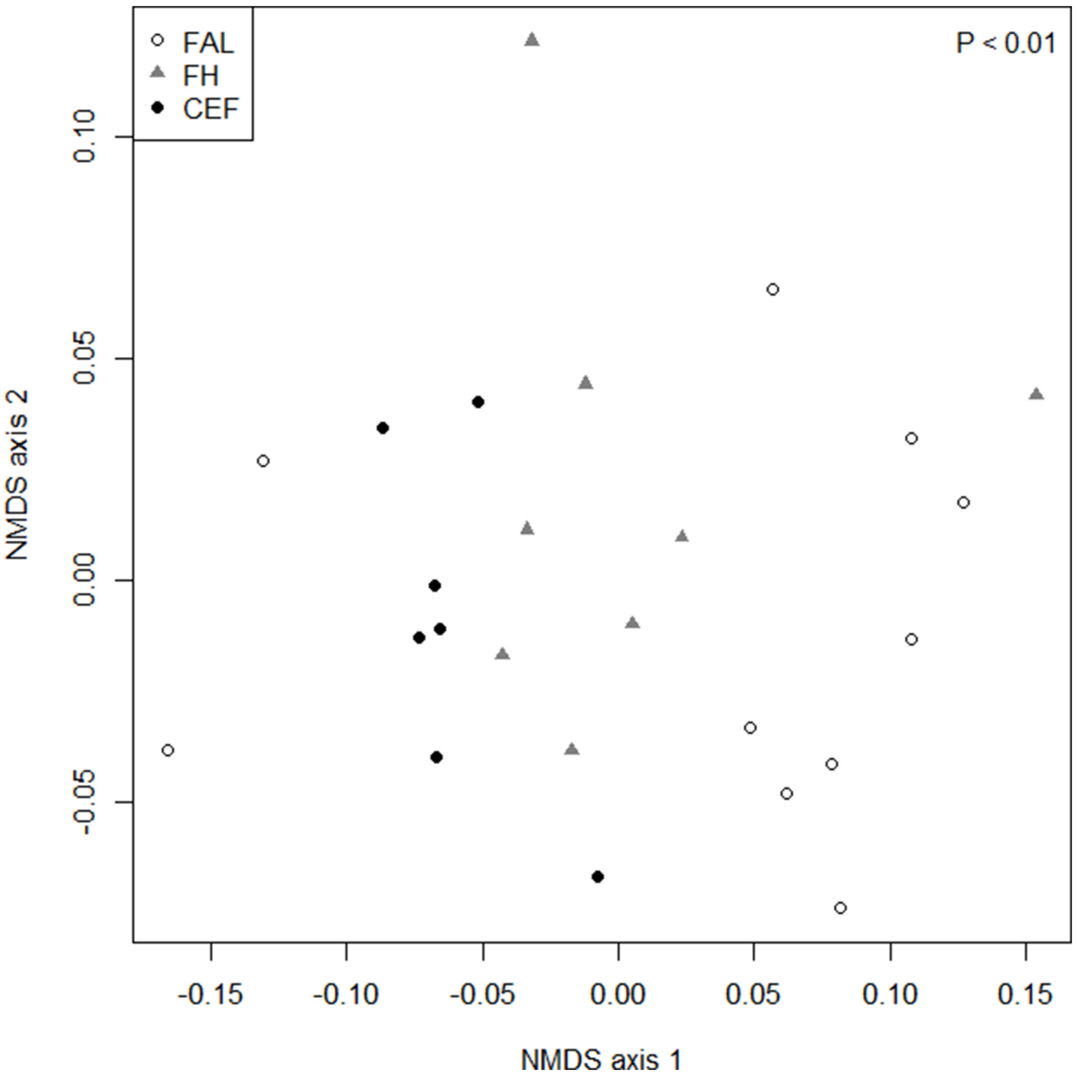

Figure 2. Similarity in temporal variation of growth rates in response to past land-use. Non-metric multi-dimensional scaling ordination (stress: 0.10) of site chronologies (period 1896–2005) of sessile oak (*Quercus petraea*) growing in oak forests with different land-use histories: Former arable land (FAL), former heathland (FH) and continuously existing forests (CEF). Site scores represent mean tree-ring width series derived from 10 trees per site.

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Bildungsserver (HBS, Hamburg, Germany) and are from the weather station at Wilsede (Lüneburg Heath), located within the study area. The meteorological data for the study period 1896–2005 are given in Tables S2 and S3.

Data analyses

The homogeneity of growth within each land-use type is expressed as the mean Pearson's correlation (r) among the respective TRW site chronologies. Descriptive statistics for TRW series (mean tree-ring width, standard deviation, first-order autocorrelation, and mean sensitivity) were calculated using TSAP-Win. The mean tree-ring width ± standard deviation allows a comparison of radial growth

Table 2. Soil ecological properties of the three historical land-use types (means and SD; n=10 sample sites per site type; all data from von Oheimb et al. [15]).

Soil parameters	Soil horizon	Former arable land		Former heathland		Continuously existing forests	
C-content (%)	O	9.27^b	(1.26)	19.17^a	(2.00)	18.80^a	(2.43)
	A	2.01	(0.20)	2.19	(0.68)	2.39	(0.57)
N-content (%)	O	0.47^b	(0.06)	0.88^a	(0.09)	0.80^a	(0.10)
	A	0.11	(0.01)	0.10	(0.03)	0.08	(0.02)
C/N-ratio	O	18.8^b	(0.3)	21.5^a	(0.8)	23.6^c	(0.6)
	A	20.2^b	(1.1)	26.8^a	(1.9)	31.2^a	(1.9)
P_{pa} (mg L^{-1})	O	6.9	(1.2)	6.5	(0.5)	8.9	(1.7)
	A	23.9^b	(3.8)	6.0^a	(1.6)	9.0^a	(3.3)
P_t (mg L^{-1})	O	61.5^b	(5.3)	102.8^a	(12.8)	104.5^{ab}	(17.2)
	A	261.9^b	(27.0)	143.5^a	(46.5)	140.7^a	(44.5)
C/P-ratio	O	218.9^b	(23.9)	286.3^a	(18.4)	287.1^a	(19.1)
	A	107.5^b	(14.9)	217.0^a	(18.7)	237.9^a	(19.8)
Base saturation (%)	O	35.2^a	(5.3)	35.5^a	(4.3)	24.7^b	(1.7)
	A	34.8	(7.1)	36.7	(6.1)	23.1	(5.3)
CEC (mval L^{-1})	O	21.4^b	(2.4)	30.3^a	(2.8)	39.6^c	(3.9)
	A	7.3	(0.9)	7.2	(1.7)	8.6	(2.0)
pH_{H2O}	O	4.2	(0.1)	4.1	(0.2)	4.0	(0.1)
	A	4.0	(0.1)	4.1	(0.1)	4.0	(0.1)

Soil parameter abbreviations: P_{pa}=plant available phosphorous; P_t=total P-content; CEC=cation exchange capacity; O=organic layer, A=A-horizon (i.e. upper mineral horizon). Different superscript letters indicate significant differences of a given parameter among the three historical land-use types ($P_{adj.}<0.05$).

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rates between the land-use types. The first order autocorrelation (AR-1) indicates the influence of the previous year's growth on the tree-ring width of the current year, and the mean sensitivity (ms) is a measure of the year-to-year variability in tree-ring width ranging from 0 to 1 [44, 45]. Differences in these statistical parameters (log-transformed) between the historical land-use types were tested for significance by a one-way analysis of variance (ANOVA) followed by a post-hoc performance (Tukey's HSD test).

The temporal variation in growth (period 1896–2005) depending on the land-use type was evaluated by an analysis of similarity (ANOSIM; [46]), performed on a matrix of Bray-Curtis dissimilarities based on the raw TRW site chronologies. To display differences in growth between and within land-use types, we used non-metric multi-dimensional scaling (NMDS, using the *metaMDS* function of the *vegan* library in R; [47]).

The relationship between TRW and soil chemistry was assessed by Pearson's correlation, using TRW site chronologies (from 1896–2005) and soil data. Due to a lack of soil data for four sample sites, the analysis was performed with 21 sample sites (data in Table S4). Climate impacts on TRW were analyzed by means of multiple linear regressions (following the approaches as described in Härdtle et al. [38, 48]). To this end, we detrended the raw TRW data of single trees using the residuals from five-year moving averages (TSAP-Win). This procedure removes long-term trends such as age effects but keeps the high-frequency (i.e. inter-annual) signals typical of a respective chronology [38, 48, 49, 50]. Then, the single tree-specific chronologies were averaged to site-specific chronologies. The subsequent regression analyses were based on these site chronologies. In the regression analyses, detrended TRW was considered as the dependent variable. Monthly precipitation and temperature from July of the previous year to August of the current year were used as the physiologically most meaningful predictors [37, 51]. In addition, we included precipitation totals of the previous and current growing season (April-October), mean annual temperature (previous and current year), and previous year's TRW as further predictors of radial increment. The climatic variables were detrended in the same way as the ring-width data. Model selection was based on the identification of significant ($P<0.05$) predictor variables. A correction for the degrees of freedom was applied considering autocorrelation (AR-1) between current and previous year's TRW (effective sampling size $N'=N\ (1-(AR\text{-}1))\ (1+(AR\text{-}1))^{-1}$ [52]. Regression analyses were carried out using the SPSS 20.0 package (SPSS Inc., Chicago/IL, US).

Results

There was a trend towards higher but more variable growth rates at afforested sites. The homogeneity of growth within each of the three historical land-use types was highest for CEF ($r=0.78$) followed by FAL (0.69) and FH (0.67) (Table 1; Fig. 1).

The mean TRW was significantly higher on FAL (1.8 mm) than in CEF (1.5 mm) (Table 1); on the FH an intermediate TRW was found (1.7 mm). Likewise, the mean standard deviation of the series declined significantly from FAL to FH to CEF. The first order-autocorrelation was high for all three land-use types but not statistically different between them. The mean sensitivity was significantly higher for trees of FAL and FH (both 0.17) than for trees of the CEF (0.14).

Tree-ring widths mirrored differences in soil chemistry, as increased TRW coincided with the higher nutrient levels found for the FAL (Table 3). Low C/N ratios (O-horizon and A-horizon), higher amounts of plant-available P and total P contents (A-horizon), and a higher base saturation (O-horizon) were significantly correlated with increased tree-ring widths. No relationship was found between tree-ring widths and soil pH values.

The first NMDS axis clearly separated the site chronologies (Fig. 2), indicating that the temporal variation in growth rates were driven by land-use legacies ($R=0.240$, $P<0.01$). TRW chronologies of CEF sites differed markedly from FAL ($R=0.\ 383$, $P<0.01$), while differences between CEF and FA were less distinct ($R=0.159$, $P<0.05$). A marginal difference was noted between FAL and FA ($R=0.164$, $P<0.05$). Moreover, within a land-use type the variability was lowest

Table 3. Pearson's correlations between mean tree-ring widths (of sample sites; n=21) and soil parameters.

Parameter	Soil horizon	r
C-content (%)	O	−0.46*
	A	ns
C/N-ratio		−1
	A	−0.56**
P_{pa} (mg L^{-1})	O	ns
	A	0.61**
P_t (mg L^{-1})	O	ns
	A	0.57**
C/P-ratio	O	ns
	A	−0.70**
Base saturation (%)	O	0.44*
	A	ns

Only significant correlations (*=$P<0.05$, **=$P<0.01$) with r>|0.5| are considered; ns=not significant; period of tree-ring analyses: 1896–2005. For abbreviations of soil parameters see Table 2.

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for CEF (highest similarity of site chronologies; Fig. 2), suggesting a trend towards a more balanced growth response with increasing forest continuity.

Trees on FAL showed the highest susceptibility to shifts in climatic conditions. However, the overall responses of TRW to climatic variability were low across land-use types (variance explained: FAL=20%, FH=7%, CEF=6%; Table 4). With the exception of FH, the previous year's TRW was a significant predictor for the current year's radial increment. On FAL, oak trees responded negatively to high spring (March, May) temperatures, but positively to mild conditions in February. Summer (June, July) precipitation was negatively correlated with the TRW of oak on FH and CEF.

Discussion

As hypothesized, the variability of TRW of oak trees tended to be higher in afforestations (FAL, FH) than in CEF. The low standard deviation and mean sensitivity of TRW in CEF suggest that these trees are less susceptible to shifts in environmental conditions than trees in afforestations. However, the underlying mechanisms that may explain this finding have not been studied so far. In principle, a number of different mechanisms are conceivable.

Relationships between growth variability and soil conditions

In CEF, humus horizons such as organic layers are well-developed and significantly thicker than in afforestations [15]. This is accompanied by an improved water storage capacity, which in turn can mitigate the effects of a severe drought during the growing season [33]. Thus, well developed humus horizons may also dampen adverse effects of increasing or more severe drought events

Table 4. Multiple linear regression analyses (stepwise forward selection) of effects of climatic variables on tree-ring width (TRW) of sessile oak trees (n of sample sites=25).

Dependent variable	TRW		
Predictors	**Former arable land**	**Former heathland**	**Continuously existing forests**
Previous year's TRW	0.24**		0.22*
Precipitation June		−0.21*	
Precipitation July			−0.19**
Temperature February	0.43**		
Temperature March	−0.65***		
Temperature May	−0.25**		
Temperature June	0.23**		
Temperature November$_{prev}$		−0.18*	
R	0.48	0.29	0.27
R_{adj}^2	0.20	0.07	0.06
P	<0.001	0.005	0.011
df_{Resid}	100	117	84

Values denote the partial correlation coefficient (beta) for each regression model. Significance of predictors: *=$P<0.05$, **=$P<0.01$, ***=$P<0.001$; "prev." as subscript character refers to climatic data of the previous year of tree-ring formation.

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related to climate change. Organic layers are also responsible for minimising fluctuations in soil temperature and of the moisture of the A-horizon [53]. In addition, the thickness of the humus horizons and the soil profile impact root distribution patterns of oak trees [54]. Increasing thickness of humus horizons increases the soil volume that can be exploited by roots and thus improves the potential availability of water and nutrient resources. This applies to acid sites in particular, as here the bulk of fine and coarse roots are concentrated in the humus horizons [55].

Tree growth is also related to soil properties such as soil nutrient cycles that are known to be affected by historical land-use practices in the long term [8]. Improved nutrient conditions were the main reason for significantly increased tree-ring widths of oak trees growing on FAL. This result can be attributed, in particular, to enhanced N availability as expressed by significantly lower C/N ratios. C/N ratios are an important indicator of litter decomposition and of N mineralisation rates, and high C/N ratios are related to a low soil biological activity [56]. Accordingly, tree-ring widths were strongly negatively correlated with C/N ratios (−0.64, $P<0.01$; Table 2). Generally, tree-ring width of oak trees responds positively to increasing N availability. This applies to acid sites in particular [28, 57], since N proved to be the most growth-limiting nutrient in acid soils [54]. Positive responses of tree-ring width to N supply have been observed in both young and old oak stands [58], and may explain the fact that radial growth on FAL was accelerated over the entire time span investigated, 1896–2005. However, it is likely that the continuous increase in tree-ring widths across sites which was evident from the 1970s onwards (see Fig. 1) can be attributed to the increasing rates of atmospheric N loads found in NW Europe [38, 59]. Besides N, P supply and base supply may be co-limiting factors for the growth of oak on strongly acid soils [58]. This may explain significant correlations between tree-ring widths and soil parameters which describe the availability of P and base cations.

Furthermore, there are distinct differences in soil microbial communities between afforestations (FAL, FH) and CEF. In the studied forests, Fichtner et al. [25] found a persistent (>100 years) and significant variation in microbial community structure and microbial extra-cellular enzyme activity based on land-use history. Arbuscular mycorrhizal fungi, actinobacteria, and enzyme activities were distinctly lower in soils of CEF compared to former agricultural land. In contrast, microbial communities in soils of CEF were associated with the highest abundance of saprotrophic and ectomycorrhizal fungi and the highest structural heterogeneity. Furthermore, a high abundance of gram-negative bacterial markers was observed in southern Appalachian (USA) forests established more than 50 years ago on formerly cultivated land, whereas CEF were characterised by high levels of fungal and gram-positive bacterial markers [21]. Consequently, a long forest continuity may lead to more diverse microbial assemblages and more complex mycorrhizal systems. This may help to buffer growth fluctuations in high growth and low growth years. Historical land-use activities may, thus, have long-term effects on soil properties of forest ecosystems that need to be taken into account (as "historical site factor") when analysing forest ecosystem processes [15, 25].

Relationships between growth variability and climatic conditions

Oak trees in our study displayed a low sensitivity of radial increment towards changes in climatic conditions across the different historical land-use types. This is reflected by the low proportion of variance in TRW explained by climatic variables (20, 7, and 6% for FAL, FH, and CEF, respectively). Our finding is in agreement with other studies, according to which climatic variables proved to be weak predictors for tree-ring widths of oak in central Europe [34, 36, 37, 38, 60]. Instead radial growth is largely controlled by non-climatic factors such as soil conditions and biotic stressors (e.g. insect infestation; [26, 35, 61]). However, at the northern or southern range margins of oak in Sweden or Slovenia, respectively, the climatic signal becomes stronger [62, 63]. Even extreme climatic events (such as the summer drought in 2003) are weakly mirrored in radial increment rates of *Quercus petraea* [64, 65], and climatic extremes may appear to cause oak decline only in combination with other stress factors (e.g. defoliation resulting from insect infestation, infection with pathogenic fungi; [61]).

However, the proportion of variance in TRW explained by climatic variables was highest for oak trees on formerly ploughed soils (20% on FAL sites), suggesting a higher climatic susceptibility of FAL trees in comparison to trees grown at the other sites. At FAL sites, high temperatures in spring (March, May) negatively affected TRW in particular, which is in agreement with Mérian et al. [37]. Moreover, the current year's increment rates do not only reflect the current year's growing conditions, but they also depict an integrative response to the environmental conditions a tree experienced in the course of the previous year (at least for trees on FAL and in CEF). This coincides with findings of Becker et al. [66], who identified current year's climatic variables as weak predictors for increment rates of *Quercus petraea*. Our results demonstrate that the overall growth response of sessile oak trees in relation to changes in climatic conditions is weak, but trees growing on CEF sites exhibit a particularly low susceptibility to climatic variability compared to trees that have been afforested on FAL.

Relationships between growth variability and stand structure

The interpretation of our results also needs to consider environmental parameters that have not been quantified in our study. As oak species are known to be light-demanding trees, more favourable light conditions may have promoted tree-ring widths at afforested sites [67]. However, we consider the effects of the light conditions to be circumstantial in our study, because tree-ring widths of trees on FH did not differ significantly from those of CEF, despite potentially higher insolation rates on the heathland sites. We also exclude logging as a potential factor responsible for the differences in tree-ring width, since all sample sites experienced similar management intensities from a long-term perspective (according to the forest management plans of the nature reserve). Moreover, variation in species composition can alter local neighbourhood interactions. A high proportion of allospecific neighbours is assumed to benefit the growth rates of individual trees due to niche complementarity [68, 69]. However, the temporal variation of growth rates are more distinct in mixed-species neighborhoods compared to monospecific stands [70]. Consequently, a higher dissimilarity in the growth pattern should be obvious for CEF (lowest proportion of conspecifics; Table 1). In contrast, tree-ring chronologies in CEF were associated with the highest growth synchronization (Fig. 1). We therefore conclude that differences in the mode of tree neighborhood effects (intra- versus interspecific competition) play a minor role in explaining the growth pattern observed. The same applies to factors such as insect or fungi infestation that might have caused short-term decreases in growth rates. Severe damage of trees from insect or fungi infestation resulting in high tree mortality has not been reported for the study area. As afforestations were carried out using seed or saplings from the same provenances, growth differences between trees were also unlikely to result from different genotypes [71].

Conclusions

Our study provides evidence that trees of recent forests tend to be more susceptible to shifting environmental conditions, as indicated by a higher mean sensitivity of tree-ring widths. ''Historical site factors'' are, thus, important for a deeper understanding of ecosystem functionality, since legacies resulting from historical land-use may still impact present-day patterns of tree growth. It is, therefore, likely that forests characterised by high ecological continuity are better adapted to global change than recent forest ecosystems.

These findings have important implications for the evaluation of current afforestation and nature conservation policies. Next to their outstanding role in preserving a high typical above- and belowground species diversity and functionality, sites with a long continuity (several hundred years) of forest cover may increasingly become more important in the context of ecosystem services (e.g. [31]). Consequently, at such sites of conservation priority, high-impact management measures like clear-cuts, tillage, fertilization or altering the natural vegetation by planting exotic tree species may negatively affect plant-soil interactions, and thereby reducing forest resilience with respect to environmental fluctuations. Implementing ecological continuity in forest management and conservation policies would potentially improve long-term ecosystem management approaches under changing environmental conditions.

Supporting Information

Table S1. Site chronologies of sessile oak (*Quercus petraea*) between 1896 and 2005 (tree-ring width in 1/10 mm).
doi:10.1371/journal.pone.0113507.s001 (PDF)

Table S2. Mean monthly precipitation and precipitation total of the growing season (April–October, rainvp) (in mm) at the weather station Wilsede (Lüneburg Heath, NW Germany) for the period 1896 to 2005.
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Table S3. Mean monthly temperature and mean annual temperature (mean temp) (in °C) at the weather station Wilsede (Lüneburg Heath, NW Germany) for the period 1896 to 2005.
doi:10.1371/journal.pone.0113507.s003 (PDF)

Table S4. Mean tree-ring width (TRW) of sessile oak (*Quercus petraea*) during the period 1896–2005 (in 1/10 mm) and soil parameters.
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Author Contributions

Conceived and designed the experiments: GVO WH. Performed the experiments: GVO TH BW. Analyzed the data: GVO DE AF TH BW WH. Contributed reagents/materials/analysis tools: DE AF. Contributed to the writing of the manuscript: GVO DE HHE AF BW WH.

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Chapter 10

Legacy effects of land-use modulate tree growth responses to climate extremes

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Legacy effects of land-use modulate tree growth responses to climate extremes

Katharina Mausolf[1*], Werner Härdtle[1], Kirstin Jansen[1], Benjamin M. Delory[1], Dietrich Hertel[2], Christoph Leuschner[2], Vicky M. Temperton[1], Goddert von Oheimb[3,4] and Andreas Fichtner[1]

[1]Katharina Mausolf: Leuphana University of Lüneburg, Institute of Ecology, Universitätsallee 1, 21335 Lüneburg, Germany; [1]Werner Härdtle: Leuphana University of Lüneburg, Institute of Ecology, Universitätsallee 1, 21335 Lüneburg, Germany; [1]Kirstin Jansen: Leuphana University of Lüneburg, Institute of Ecology, Universitätsallee 1, 21335 Lüneburg, Germany; [1]Benjamin M. Delory: Leuphana University of Lüneburg, Institute of Ecology, Universitätsallee 1, 21335 Lüneburg, Germany; [2]Dietrich Hertel: University of Goettingen, Albrecht von Haller Institute for Plant Sciences, Plant Ecology and Ecosystems Research, Untere Karspüle 2, 37073 Göttingen, Germany; [2]Christoph Leuschner: University of Goettingen, Albrecht von Haller Institute for Plant Sciences, Plant Ecology and Ecosystems Research, Untere Karspüle 2, 37073 Göttingen, Germany; [1]Vicky M. Temperton: Leuphana University of Lüneburg, Institute of Ecology, Universitätsallee 1, 21335 Lüneburg, Germany; [3,4]Goddert von Oheimb: [3]Technische Universität Dresden, Institute of General Ecology and Environmental Protection, Pienner Straße 7, 01737 Tharandt, Germany; [4]German Centre of Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5E, 04103 Leipzig, Germany; [1]Andreas Fichtner: Leuphana University of Lüneburg, Institute of Ecology, Universitätsallee 1, 21335 Lüneburg, Germany

*Correspondence: K. Mausolf, katharina.mausolf@leuphana.de

Abstract

Climate change can impact forest ecosystem processes via individual tree and community responses. While the importance of land-use legacies in modulating these processes have been increasingly recognised, evidence of former land-use mediated climate-growth relationships remain rare. We analysed how differences in former land-use (i.e. forest continuity) affect the growth response of European beech to climate extremes. Here, using dendrochronological and fine root data, we show that ancient forests (forests with a long forest continuity) and recent forests (forests afforested on former farmland) clearly differ with regard to climate-growth relationships. We found that sensitivity to climatic extremes was lower for trees growing in ancient forests, as reflected by significantly lower growth reductions during adverse climatic conditions. Fine root morphology also differed significantly between the former land-use types: on average, trees with high specific root length (SRL) and specific root area (SRA), and low root tissue density (RTD) were associated with recent forests, whereas the opposite traits were characteristic of ancient forests. Moreover, we found that trees of ancient forests hold a larger fine root system than trees of recent forests. Our results demonstrate that land-use legacy-mediated modifications in the size and morphology of the fine root system act as a mechanism in regulating drought resistance of beech, emphasising the need to consider the 'ecological memory' of forests when assessing or predicting the sensitivity of forest ecosystems to global environmental change.

Key words: Climate change, European beech, Fine roots, Forest continuity, Plant-climate interactions

INTRODUCTION

Forest ecosystems significantly contribute to global carbon sequestration (Bellassen and Luyssaert 2014), and tree species' above- and below-ground wood production is a major determinant for long-term carbon storage (Chambers et al. 2001). The future role of individual tree productivity in contributing to total net primary production (NPP) of forests, however, critically depends on how rates of tree carbon accumulation vary with ongoing global climate change (Reyer et al. 2014). Specifically, increased temperatures and water deficits during the growing season are expected to become more frequent worldwide (IPCC 2013), and these climatic changes are considered to have negative effects on tree growth and vitality in many regions of the world (Allen et al. 2010; Williams et al. 2013).

Beech forests represent the potential natural vegetation in large parts of Central Europe, and European beech (*Fagus sylvatica*) is considered an economically important tree species (Leuschner and Ellenberg 2017). Numerous studies have shown that *F. sylvatica* is sensitive to climatic extremes, e.g. reflected by significant growth declines after drought events or heat waves during the growing season (e.g. Di Filippo et al. 2007; Scharnweber et al. 2011; Härdtle et al. 2013; Zimmermann et al. 2015; Cavin and Jump 2016; Hacket-Pain et al. 2016). Moreover, increasing summer temperatures can trigger seed production of beech in the following year (Drobyshev et al. 2010; Müller-Haubold et al. 2015; Hacket-Pain et al. 2015), and thus impose an additional negative effect on radial growth and carbon storage in the trunk. Additionally to climate-induced tree radial growth reductions or shifts in above-ground allocation patterns due to more frequent masting events, plants also respond below-ground to climate variation via modifications of their fine root system (Bardgett et al. 2014; Fig. S1). For example, Hertel et al. (2013) found that mature beech trees exhibit a high allocational plasticity and are capable of increasing the size of the fine root system in response to water shortage.

More recently, global change research has focused on understanding not just single global change drivers (e.g. drought, carbon dioxide concentrations, nitrogen deposition) but also their interactions, since co-occurring drivers may not act additively (i.e. the summation of single effects), but have non-additive effects on ecosystem responses (i.e. show antagonistic or synergistic interactions; Zavaleta et al. 2003; Bradford et al. 2012; Meyer-Grünefeldt et al. 2015). For example, there is evidence that co-occurring effects of drought and nitrogen addition can amplify drought-induced growth reduction of young (Dziedek et al. 2016) and mature (Hess et al. 2018) beech trees. The response of forests to global environmental change might also depend on land-use changes in the past (Perring et al. 2016), which can have strong impacts on ecosystem functioning as well as above- and below-ground community composition (Foster et al. 2003; Flinn and Vellend 2005; Fraterrigo 2013; Fig. S1). Former land-use such as temporary crop cultivation has been shown to critically alter abiotic soil characteristics, resulting in e.g. lower phosphorus and higher carbon contents in the soil of ancient compared to recent forests (Compton and Boone 2000; von Oheimb et al. 2008; Leuschner et al. 2014). Such soil legacies in turn can alter carbon and nutrient cycling (Fraterrigo et al. 2006; Fichtner et al. 2014) due to changes in the soil microfauna (De la Peña et al. 2016) and microbial communities (e.g. Buckley and Schmidt 2001). Although these legacy effects can persist for centuries in forest soils (Fichtner et al. 2014), possible long-lasting impact on tree growth has only rarely been studied (but see von Oheimb et al. 2014). For example, legacies of former fertilization may impose long-lasting impacts on trees' current fine root system, which in turn may modulate its capacity to respond to adverse climatic conditions (see Fig. S1). There is an increasing awareness of the importance of land-use legacies in the context of global environmental change (Perring et al. 2016), but how such legacy effects influence the responsiveness of tree species to climate extremes remains unclear. This knowledge, however, is a key for improving our ability to develop adaptive management strategies in response to multiple, interacting drivers of global change (Johnstone et al. 2016).

Here, we use individual tree-ring chronologies (i.e. the tree-ring series of single trees) from temperate European beech forests to examine how land-use history determines the radial growth of *F. sylvatica* during fluctuating climatic conditions. We used individual tree rather than site chronologies (i.e. pooled tree-ring chronologies of a given site) to account for the variability in individual growth responses, which has been shown to be fundamental when assessing the response of forest ecosystems to climate change (e.g. Zang et al. 2014). We hypothesise that changes in biotic and abiotic soil conditions resulting from former land-use play an important role in determining drought sensitivity of beech via modifications of the fine root system. Thus, beech trees growing in ancient forests (i.e. sites associated with long forest continuity) are less sensitive to adverse climatic conditions than those growing on sites afforested on former farmland (grassland or arable land). To test these hypotheses, we quantified changes in soil chemical properties, above- (i.e. radial growth rates) and below-ground responses (i.e. fine root biomass and root morphological traits) allowing us to explore processes underlying climate-growth relationships.

MATERIAL AND METHODS

Study sites and study design

The study was conducted in mature beech forests (*Galio-Fagetum* community) of Northern Germany (state of Schleswig-Holstein, 54°19' N, 10°7' E). The area is characterised by a sub-oceanic climate with a mean annual precipitation of 777 mm and a mean annual temperature of 8.5°C (DWD Climate Data Center 2017). Elevation ranges from 32 to 81 m a.s.l., and the predominant soil types are (pseudogleyic) Luvisols. The management regime (i.e. individual-tree selection cutting) was consistently similar over the past 100 years.

To examine the effect of former land-use on growth response of *F. sylvatica* to varying climatic conditions, we identified eight forests that differed in former land-use and forest continuity (i.e. the temporal extent of the biotic and abiotic development of a focal forest without land-use change): ancient forests (n = 4), which are characterised by a continuity in forest cover of at least 230 years (note that the forests are not defined by the stand or tree age, but that the area must have been a forest habitat for over 230 years), and recent forests (n = 4), which were afforested between 1870 and 1930 on former farmland (grassland: n = 3, arable land: n = 1). Information on land-use history was derived from historical maps of the "Vahrendorfsche Landesaufnahme" (1789-1796) and "Preußische Landesaufnahme" (1879). All stands were dominated by beech trees (>90% of stems) of 85-130 years in age and had similar structure (Table S1). Within each forest, we randomly selected 2-5 study plots (40 m x 40 m), resulting in a total of 28 plots (recent forests: 13, ancient forests: 15). To account for edge effects, the minimum radial distance of the study plots to forest edges was 70 m. All trees with a diameter at breast height (DBH; at 1.30 m) >7 cm were measured within a plot. For each measured tree, DBH and species identity were recorded. To avoid confounding effects between land-use history and stand or site characteristics (Fraterrigo 2013), we restricted the analyses to stands that were similar in tree species composition, stand structure, management, soil type and topography, but differed in their former land-use (i.e. forest continuity; Table S1).

Dendrochronological data

For each plot, we randomly selected ten dominant beech trees of the upper canopy resulting in a total of 280 target trees. To determine radial growth rates, we cored target trees at 1.30 m above-ground and extracted two bark to pith increment cores (using a 0.5 cm diameter and 40 cm length increment borer, Suunto 400, Vantaa, Finland) at right-angled positions from the southern and eastern side of the tree. Wood cores were fixed with pushpins and air dried on core-mountings, before core surfaces were cut off (using a core-microtome; WSL, Birmensdorf, Switzerland). Annual tree-ring width (TRW) was measured from bark to pith with a measuring table (resolution of 0.01 mm; Instrumenta Mechanik Labor GmbH, Wiesloch, Germany) combined with a microscope (Wild, Heerbrugg, Switzerland). To minimise measurement errors, we cross-dated and averaged each of the paired samples to one composite growth series per tree (Holmes 1983). Crossdating was done visually and statistically based on the cross-dating index (CDI) given by TSAP-Win (Version 4.69k, Rinntech, Heidelberg, Germany). The CDI combines both, the values of *Gleichlaeufigkeit* and *t-values*, which describe the similarity between tree-ring series (see Dulamsuren et al. 2017). According to Müller (2007) a CDI of ≥20 was used as threshold value. As a result, we omitted 37 trees (13%) for subsequent analyses which did not meet this criterion. To minimise the effect of tree age on annual growth rates, TRW data of individual tree chronologies were standardized. Standardization was performed in TSAP-Win by first calculating the five-year moving average trend of each chronology. In a second step measured tree-ring series were divided through the five-year moving average trends, resulting in a dimension-less index of tree-ring width (TRI) (for more information see Dulamsuren et al. 2017). Radial growth measurements were performed using IML software T-Tools Pro (Version 1.4, Instrumenta Mechanik Labor GmbH, Wiesloch, Germany). Descriptive dendrochronological statistics were based on individual tree chronologies and calculated using TSAP-Win (Table S2). Plot chronologies are shown in Figure S2.

Soil data

To characterise soil chemical properties at each of the 28 plots, we randomly selected five soil samples from two soil depths (0–10 cm and 10–30 cm) of the mineral horizon by using a "Pürckhauer" driller. The cores were taken in spring 2015 and were immediately kept cool at 4 °C. For subsequent analyses the five subsamples were thoroughly mixed to obtain one composite sample per plot and soil depth. Total carbon (C), nitrogen (N) and phosphorus (P) concentrations, plant available nitrogen (N_{pa}; i.e. the total amount of salt extractable NH_4^+ and NO_3^-), base saturation (BS), cation exchange capacity (CEC) and pH-value (measured in H_2O and $CaCl_2$) were determined from the homogenised soil samples. All samples were sieved (<2 mm), ground and dried (with exception of samples destined for N_{pa} measurements) prior to soil chemical analyses. Total C and N concentrations were determined with a gas chromatographic analyser (Vario EL, Elementar, Hanau, Germany). For the determination of total P concentration, we used microwave assisted digestion (MARS Xpress, CEM GmbH, Kamp-Lintfort, Germany) with HNO_3 as described by Ozbay et al. (2016) and measured total P content after digestion with an ICP-OES (Optima 3300 RL, Perkin Elmer Inc., Waltham, USA). Concentrations of N_{pa}-fractions were analysed by spectrophotometry after $CaCl_2$ extraction according to Hoffmann (1997). Determination of CEC and pH-values followed standard procedures as described by Steubing and Fangmeier (1992).

Fine root data

To characterise beech fine root traits at each of the 28 plots, we randomly selected six sampling locations per plot and took soil samples from two soil depths (0–10 cm and 10–30 cm) of the mineral horizon by using a corer (3.5 cm in diameter) per sample location. The cores were taken in October 2015 and then stored in plastic bags at 4 °C in the laboratory. Prior to analysis, roots were cleaned from soil residues with running water over a sieve (mesh size: 0.5 mm) and fine roots (>10 mm in length, <2 mm in diameter) were separated from larger diameter rootlets using a pair of tweezers. Fine roots were further divided in living and dead roots under the stereo-microscope and species identity (beech vs. other species) was determined. Selection criteria (i.e. colour, root elasticity and cohesion of the cortex, periderm and stele) following Hertel et al. (2013). Only living fine roots of beech trees were used for subsequent analyses. Morphological traits were analysed by using a scanner (Flatbed Scanner EPSON Perfection V800/V850 1.9; resolution: 200 dpi). Scanned roots were processed by using the software WinRhizo (Régent Instruments Inc., Quebec, Canada) to determine root surface area, total root length and mean root diameter. After scanning, roots were dried at 70 °C and fine root biomass was determined for each soil depth. On this basis, we determined total biomass and five root traits for each soil depth separately: mean root diameter (MRD, mm), specific root area (SRA, $cm^2\ g^{-1}$), specific root length (SRL, $m\ g^{-1}$), root tissue density (RTD, $g\ cm^{-3}$) and root area index (RAI, $m^2\ m^{-2}$). SRA and SRL were calculated from root area and root length divided by dry root biomass, while RAI was calculated from specific root area multiplied by dry root biomass. RTD was obtained from dry root biomass divided by root volume. For subsequent analyses we used the median values across sampling locations to characterise the biomass and fine root traits of each plot.

Climate data

To characterise climatic conditions, we obtained regional temperature and precipitation data from a weather station in Kiel (Kiel-Holtenau, DWD Climate Data Center 2017, Germany), which is most representative for the study sites. We selected three seasons that have been shown to have strong impact on tree growth: current spring and summer, as well as previous summer (Hacket-Pain et al. 2016). On this basis, we calculated seasonal (spring: March, April, May; summer: June, July, August) means for the period 1993 to 2013 by aggregating monthly mean temperatures and precipitation sums. To simplify selection of bioclimatic variables, we applied the De Martonne humidity-aridity index (DMI; De Martonne 1926;) based on seasonal means (see Zang et al. 2014 for a related approach). We selected the DMI as climate index for the following reasons: First, it allows to obtain climate data based on regional measurements. Second, Buyan et al. (2017) showed that DMI is an appropriate climate index to investigate the effects of short-term and intermediate climate events on radial growth rates of beech. DMI was calculated as seasonal precipitation sums (in cm) divided by mean seasonal temperature (in °C + 10). This resulted in climate indices for current spring (DMI-spring) and summer (DMI-summer), as well as for previous summer (DMI-$summer_p$) conditions. Lower DMI-values indicate warm-dry and larger values cool-wet conditions.

Data analysis

We used linear mixed-effects models to test whether climate-growth relationships vary with former land-use (i.e. forest continuity). TRI was used as response variable, and climate indices (DMI-spring, DMI-summer, DMI-$summer_p$), tree age and former land-use type (ancient vs. recent forests) were used as explanatory variables. To test for a possible land-use history dependency of climate effects, we additionally considered all possible two-way interaction terms between former land-use type and climate indices. To account for spatial dependency, study plot was used as a random effect. Moreover, we used a first-order autoregressive covariance structure (AR-1) to account for temporal autocorrelation in observations among years (tree nested within plot; Zuur et al. 2009). Different competing models were evaluated by sequential comparison (backward selection) based on the Akaike Information Criterion (AIC) and maximum likelihood (ML) estimation, using the *stepAIC* function in R. We further simplified the model with the lowest AIC value by removing all terms that were not significant according to likelihood ratio tests. Parameter estimates of the final model were fitted using the restricted maximum likelihood (REML) method (Zuur et al. 2009). All continuous predictors were standardized (mean = 0; SD = 1) before analysis.

To explore the link between land-use legacies and climate sensitivity of beech, we used data for the recent (1994-2013) climate regime. We limited the time span of our analysis for several reasons: First, trees in recent forests were younger compared to those growing in ancient forests (Table S1). Thus, age-related differences in masting frequencies may cause spurious correlations between climate-related changes in TRI and forest type. To avoid such bias, beech trees must be older than 40 years old, thus ensuring equivalent potential seed production (Wagner et al. 2010). Second, climatic changes were strongest during recent decades (IPCC 2013). Thus, effects of land-use legacies on climate-growth relationships should be most relevant for this period. Moreover, to separate the effects of seed production from the interrelation between land-use legacies and climate-growth relationships, we derived information on masting events of *F. sylvatica* for our study region for the last two decades (Dammann et al. 2016). Masting frequency was high during the period 1994-2013, which matches the observed frequency increase of mast events in Central Europe (Övergaard et al. 2007). Although local information on masting events was not available for our study stands, we assume that the regional masting patterns also hold for our local study stands, because beech is a wind-pollinated, self-incompatible species (i.e. self-pollination produces mainly empty nuts), and therefore masting events generally occur synchronously over larger spatial scales (Packham et al. 2012). According to Dammann et al. (2016), we defined years where less than 10% of the trees exhibited a strong fruit production as non-mast years. Models were fitted for all years (1994-2013; n = 20) and non-mast years (non- mast; n = 10) within this period separately.

Changes in overall fine root trait composition in response to former land-use were evaluated by multivariate permutational analysis of variation (PERMANOVA; Anderson 2001) using 1000 permutations. The analysis was performed on a matrix of Bray-Curtis dissimilarities based on square-root transformed and standardized (Wisconsin double standardisation) fine root trait data (biomass, MRD, SRA, SRL, RTD, RAI). To visualise differences between former land-use types, we performed non-metric multidimensional scaling (NMDS) ordinations based on the same Bray-Curtis dissimilarity matrix. To examine how changes in fine root trait composition were associated with chemical soil properties, we calculated Pearson correlation coefficients between soil variables and NMDS-axis scores. The multivariate analyses were performed for each soil depth separately. The effect of former land-use on total fine root biomass (log-transformed) and specific morphological traits was analysed using analysis of variance (ANOVA).

At plot level, we built structural equation models (SEMs) to evaluate the linkage of soil nutrient availability and fine root traits (biomass and morphology) and their impact on drought resistance of *F. sylvatica*. For each target tree, we calculated drought resistance (see Supplementary Methods) and used the median values of drought resistance across all target trees within a given plot to characterise climate sensitivity at plot level. For each soil depth, we first selected those soil chemical properties that were most strongly related to drought resistance and yielded stable models as indicators for soil nutrient availability. Second, we chose RTD as an indicator for root morphology, because it is associated with plant species' resource use strategy (Kramer-Walter et al. 2016). Given the close correlation between RTD and SRL and SRA, respectively (Table S3), plots with higher RTD were assumed to be those with lower SRA and SRL. We hypothesise that a higher soil nutrient availability would result in a lower fine root biomass and lower RTD (and higher SRL and SRA, respectively), leading to a lower drought resistance. Additionally, we hypothesise that variation in fine root biomass has an indirect effect on drought resistance via altering fine root morphology. SEMs were fitted for each soil depth separately (0–10 cm, 10–30 cm). Drought resistance, biomass and RTD were log-transformed to improve their linearity with other variables in the model (Grace et al. 2010). Model fit statistics were evaluated following Kline (2014): chi-square test with associated *P* value (*P* >0.05 indicates that sample and observed covariance matrices are not statistically different), root mean square error (RMSEA), standardized root mean square residual (SRMR) and comparative fit index (CFI). Low values of RMSEA (≤0.05; note that the generality of RMSEA thresholds is a matter of debate; see Kline 2014) and SRMR (<0.10) and high values of CFI (≥0.90) indicate a good model fit.

Prior to analyses, data exploration was performed following Zuur et al. (2010) and model assumptions were visually checked and confirmed according to Zuur et al. (2009). All analyses were conducted in R (version 3.3.1) using the packages MASS (Venables and Ripley 2002), lavaan (Rosseel 2012), nmle (Pinheiro et al. 2016) and vegan (Oksanen et al. 2016).

RESULTS

Legacy effects of land-use on soil properties

Overall, former land-use had a long-lasting impact on soil chemical properties. On average, total P concentration of recent forest soils was 29% (0–10 cm: *P* = 0.099) and 53% (10–30 cm: *P* = 0.036) higher than of ancient forest soils. Similarly, C:P ratio was 30% (0–10 cm: *P* = 0.011) and 32% (10–30 cm: *P* = 0.111) lower in recent than in ancient forests. C:N ratio was lower in recent forest soils and differed significantly between former land-use types in 10–30 cm soil depth (*P* = 0.012). Former land-use effects on plant available N, total N and C concentrations or soil pH, CEC and BS were less distinct (Table S1).

Legacy effects of land-use on trees' above-ground response

On average, standardized annual basal area increment of beech was 38% higher (*P* = 0.013) and more variable (*coefficient of variation* recent forests: 44.7%, ancient forests: 35.0%) in recent than in ancient forests during the last two decades (1994-2013; Table S2). The importance of land-use legacies as a driver of climate-growth relationships during the last two decades was highlighted by the significant interaction between former land-use type and current and previous summer climatic conditions, respectively, for all years (DMI-summer: *P* <0.001, DMI-summer$_p$: *P* = 0.009) and for non-mast years (DMI- summer: *P* <0.001, DMI-summer$_p$: *P* <0.001; Table S4). Growth reduction due to elevated summer temperatures and drought (i.e. reduced DMI-summer values) was significantly higher in recent than in ancient forests, while the positive effect of higher summer precipitation and lower summer temperatures (i.e. elevated DMI-summer values) on growth rates was significantly stronger in recent than in ancient forests (Fig. 1a). This pattern became even stronger when excluding masting events, meaning that beech trees growing in ancient forests exhibited smaller changes in growth rates during extreme climate events and were not negatively affected by adverse climatic conditions (i.e. positive values of TRI along the DMI-gradient). In contrast, growth rates of trees from recent forest sites declined under adverse climatic summer conditions (Fig. 2b). Differences between former land-use types were less distinct for the effect of previous year summer conditions, although the sensitivity to changes in DMI-summer$_p$ was stronger for ancient than recent forests (Fig. 1). Moreover, high precipitation and low temperature during spring (i.e. elevated DMI-spring values) increased the growth rates of beech trees, regardless of former land-use (*P* <0.001). This effect became stronger when excluding masting events, as indicated by the higher effect size (i.e. estimates for the standardized regression coefficients; Table S4).

Legacy effects of land-use on trees' below-ground response

The spectrum of fine root traits characterising the two forest types differed significantly between recent and ancient forests (0–10 cm: *P* = 0.002, 10–30 cm: *P* = 0.013), and this effect was most evident for the upper 10 cm of the mineral soil (Fig. 2). Former land-use types were clearly separated along the first NMDS axis, while the land-use effect was less evident along axis 2 (Table S5). The main functional traits driving the differences between former land-use types were specific root length (SRL), specific root area (SRA) and root tissue density (RTD). On average, beech trees growing in recent forests had 46 (0–10 cm: *P* <0.001) to 50% (10–30 cm: *P* = 0.005) higher SRL, 33 (10–30 cm: *P* = 0.007) to 37% (0–10 cm: *P* = 0.003) higher SRA and 22 (10–30 cm: *P* = 0.038) to 27%

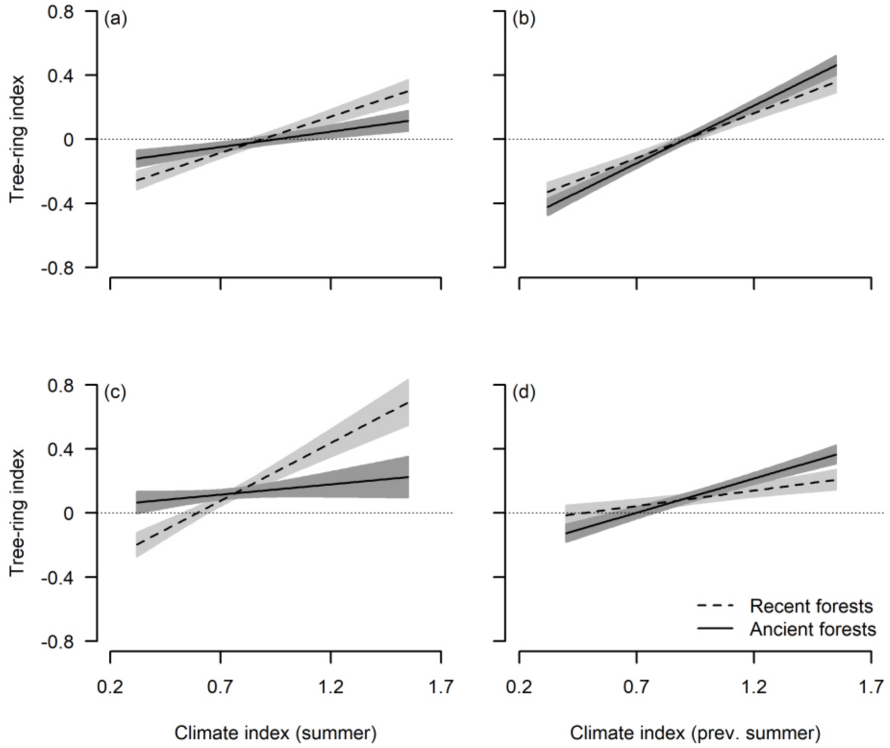

Figure 1 Effect of former land-use type (ancient versus recent forests) on the growth (tree-ring width index, TRI) responsiveness of European beech (*Fagus sylvatica* L.) to interannual fluctuations in climate during the last two decades (1994–2013) considering (a, b) all years (n=20) and (c, d) years without masting events (n=10). The climatic gradient is characterised by the De Martonne aridity-humidity index (DMI) based on current and previous summer climatic conditions (temperature and precipitation). The climate index ranges from warm-dry (low values of DMI) to cool-wet (high values of DMI) climatic conditions. Lines correspond to the predicted response based on mixed-effects models and shaded areas indicate the 95% confidence interval. DMI-spring parameter estimate was fixed at its mean value.

(0– 10 cm: P = 0.034) lower RTD than trees in ancient forests. Differences in mean root diameter and root area index between former land-use types were less distinct (both P >0.05). In addition, mean fine root biomass was 26 (10– 30 cm, P = 0.168) to 55% (0–10 cm, P = 0.006) higher in ancient than in recent forests (Table 1).

Variation in fine root traits showed a strong response to soil chemical properties. For 0–10 cm soil depth, axis 1 scores corresponded significantly to a nutrient availability gradient characterized by decreasing P concentration (r = -0.66, P <0.001) and increasing C:P ratio (r = 0.56, P = 0.002), thus reflecting the lower nutrient availability generally found in ancient forest soils (Table S1). Likewise, axis 1 scores for 10–30 cm soil depth were significantly related to C:N ratio (r = -0.60, P = 0.001), C:P ratio (r = - 0.43, P = 0.027) and C concentration (r = -0.43, P = 0.026; Table S6). Note that NMDS axis 1 score configuration differed between the two soil depths (Fig. 2).

Linking above- and below-ground responses

Forest continuity increased the resistance of individual radial growth rate to drought. On average, drought resistance was significantly higher for trees growing in ancient forests (P = 0.010; Fig. S3).

The SEM for 0–10 cm soil depth provided a good fit to the data (χ^2 = 0.17, df = 1, P = 0.681; RMSEA = 0.000; CFI = 1.000; SRMR = 0.013), and explained 41% of the variation in drought resistance (Fig. 3a). Total P concentration had a strong effect on fine root biomass (P <0.001), but not on fine root morphology (RTD; P = 0.790). Moreover, fine root biomass was positively related to drought resistance (P <0.001) and RTD (P = 0.023). Thus, drought resistance was promoted by an increase in fine root biomass,

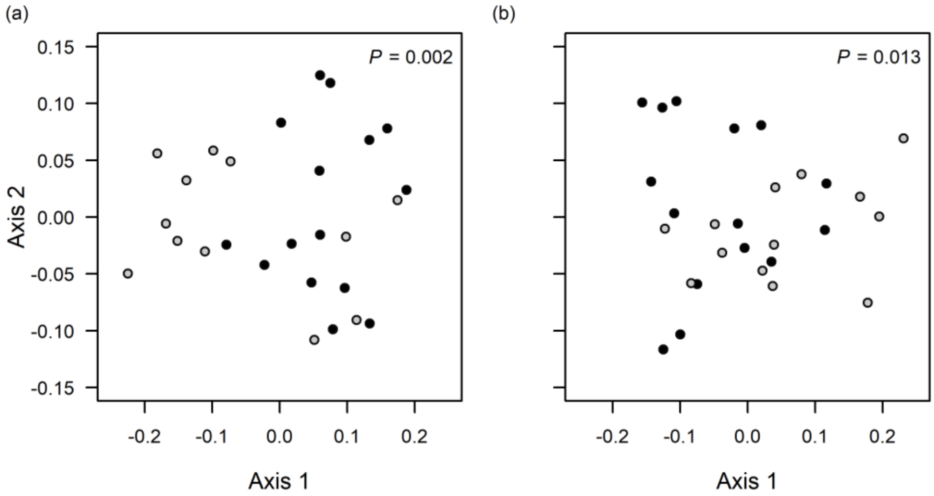

Figure 2 Non-metric multidimensional scaling (NMDS) ordination of fine root traits of *Fagus sylvatica* in (a) 0–10 cm and (b) 10–30 cm soil depth. The NMDS ordination was based on Bray-Curtis dissimilarities and used two dimensions (stress: 0.04 for 0–10 cm and 0.05 for 10–30 cm). The linear fit between ordination distances and root data ($R^2 = 0.99$, for both soil depths) indicated an appropriate representation of the variation in fine root trait composition between former land-use types (black dots: ancient forests, grey dots: recent forests); *P*-values indicate the statistical significance of compositional differences between former land-use types.

which in turn was largely the result of lower P availability. Alternative models, using C:P ratio or specific root length gave similar results (Fig. S4), indicating that fine root biomass acts as a mechanism for the negative effect of soil fertility on drought resistance in the upper soil layer.

The SEM for 10–30 cm soil depth provided a good fit to the data ($\chi^2 = 0.21$, df = 1, $P = 0.147$; RMSEA = 0.199; CFI = 0.958; SRMR = 0.059), and explained 25% of the variation in drought resistance (Fig. 3b). Contrary to the model in 0–10 cm, C:P ratio was positively related to fine root biomass ($P = 0.063$) and RTD $P = 0.001$), but drought resistance increased via increasing RTD ($P = 0.003$) and not via increasing fine root biomass ($P = 0.150$). An alternative model, using specific root length as an indicator for morphology gave similar results (Fig. S5a). Note that using total P concentration, which had the strongest effect on drought resistance, resulted in an unstable model (Fig S5b). However, C:P ratio was closely related to total P concentration ($r = -0.73$, $P < 0.001$), providing equivalent support for the importance of soil fertility for regulating fine root morphology.

Table 1 Differences in fine root biomass , fine root morphological traits (MRD, SRA, SRL, RTD) and root area index (RAI) of European beech growing in stands with different forest continuity (ancient versus recent forests) in 0–10 cm and 10–30 cm soil depth.

	Recent forests	Ancient forests
Biomass (g m^{-2})		
0–10 cm	**106.38 (21.94)**	**164.99 (14.88)**
10–30 cm	45.25 (5.63)	56.92 (6.52)
MRD (mm)		
0–10 cm	0.41 (0.01)	0.43 (0.01)
10–30 cm	0.45 (0.02)	0.48 (0.01)
SRA (cm^2 g^{-1})		
0–10 cm	**219.26 (14.53)**	**159.95 (10.92)**
10–30 cm	**184.37 (12.89)**	**139.03 (9.15)**
SRL (m g^{-1})		
0–10 cm	**16.94 (1.13)**	**11.64 (0.62)**
10–30 cm	**13.88 (1.31)**	**9.26 (0.81)**
RTD (g cm^{-3})		
0–10 cm	**0.48 (0.05)**	**0.66 (0.06)**
10–30 cm	**0.53 (0.03)**	**0.68 (0.06)**
RAI (m^2 m^{-2})		
0–10 cm	2.13 (0.36)	2.68 (0.26)
10–30 cm	0.70 (0.07)	0.75 (0.09)
n (plots)	13	15

Values are means and their standard error (in brackets). Significant ($P < 0.05$) differences between former land-use types are highlighted in bold. MRD: mean root diameter, SRA: specific root area, SRL: specific root length, RTD: root tissue density.

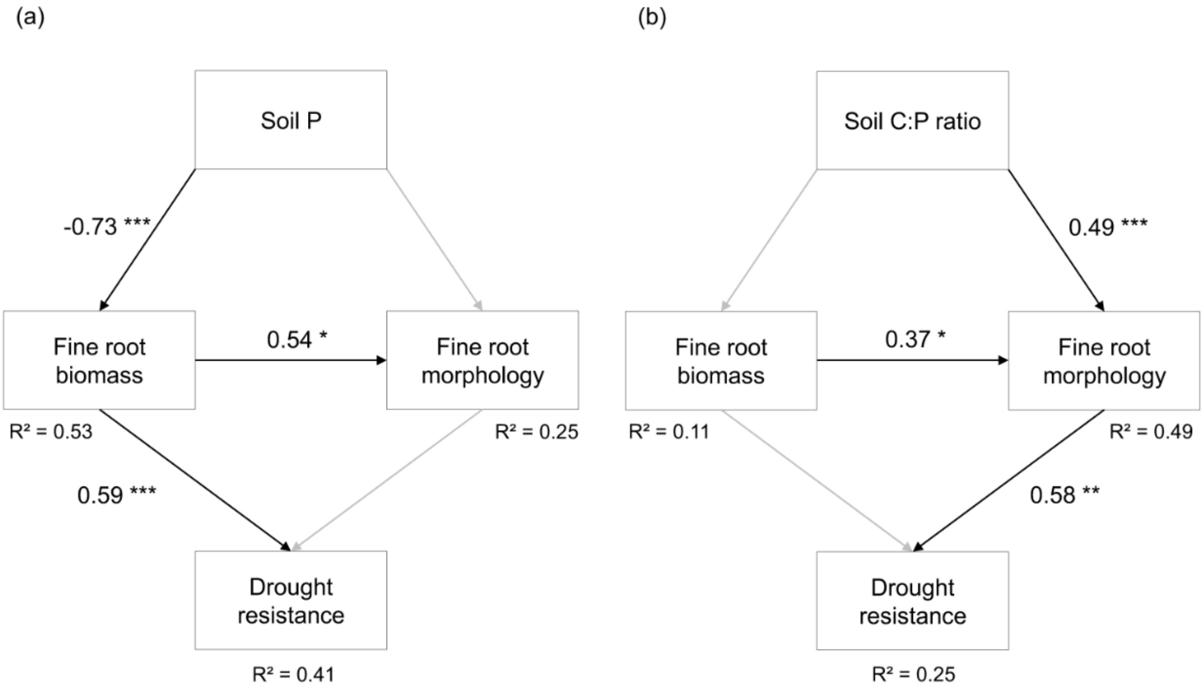

Figure 3 Structural equation models linking drought resistance, soil nutrient availability and fine root traits (biomass and morphology) in (a) 0–10 cm and (b) 10–30 cm soil depth. Fine root tissue density was selected as an indicator for morphology. Black lines denote significant and grey lines non-significant pathways. Numbers at arrows are standardized regression coefficients, thus the magnitude of the coefficients is proportional to their effect size. Asterisks denote a significant pathway in the model (*$P < 0.05$, ** $P < 0.01$, *** $P < 0.001$). R^2 values for each endogenous variable are given below the boxes. C: total carbon concentration, P: total phosphorus concentration.

DISCUSSION

Our results provide evidence that legacy effects of land-use play an important role in determining radial stem growth rates in response to climate variation. As hypothesised, growth reduction in hot and dry summers was substantially lower in trees growing in ancient compared to trees in recent forests. We further obtained evidence that land-use legacies may influence the standing fine root biomass of beech as well as fine root morphological properties. Consistent with these findings, we found that legacies of former fertilization (particularly increased level of soil phosphorus) are a key driver for variation in drought resistance via regulating the size and morphology of the fine root system. These data suggest that the differential climate response of the two forest types may depend on fine root properties, which in turn result – at least in part – from soil legacies of the former land-use. Our results point to the importance of considering interactions between historical land-use and drivers of global change when evaluating or predicting the trajectory of forest ecosystem change.

Overall, radial growth rates of *F. sylvatica* were negatively affected by increasing temperatures and higher drought intensity during summer and spring. This is in agreement with earlier studies on *F. sylvatica* reporting high growing season temperatures and low growing season precipitation as the driving climate factors for growth reductions across Europe (Zimmermann et al. 2015; Cavin and Jump 2016; Hacket-Pain et al. 2016; Knutzen et al. 2017). Growth reduction in hot and dry summers may result from partial stomatal closure and reduced carbon assimilation, leaf area reduction, turgor loss in the stem cambial cells or increased carbohydrate allocation to root and fruit production (Aranda et al. 2012). Climate events of the previous year can also lead to growth reductions in the following year through masting events, which are triggered by high temperatures in the previous summer, or other carry-over effects related to carbohydrate depletion in the previous summer (Drobyshev et al. 2010; Hacket-Pain et al. 2015; Müller-Haubold et al. 2015). In this context, we found that land-use legacies modulated growth response to changing climatic conditions during the current and previous summer. The climate sensitivity to the current summer conditions was significantly higher for trees growing in recent compared to ancient forests. This positive effect of forest continuity on climate sensitivity of *F. sylvatica* became even stronger after accounting for masting effects. While growth reductions (i.e. negative TRI values) still occurred for recent forests during low summer precipitation and high summer temperature of the current year, growth rates of ancient forests were not negatively affected (i.e. positive TRI values) by climate variations, suggesting that forest continuity is a key determinant of the sensitivity of beech trees to adverse climatic conditions. This is consistent with the results of a previous study, in which oak trees growing in ancient forests in northern Germany were found to be less sensitive to climate variation than those growing at afforested sites (von Oheimb et al. 2014). In contrast, differences in climate sensitivity between former land-use types were less distinct for the effects of previous summer conditions, with trees in ancient forests showing stronger responses than trees in recent forests. This may be attributable to differences in tree age, as seed production is positively related to tree age (Genet et al. 2010) and the sampled trees in ancient forests were on average 25 years older than trees in recent forests.

In general, the negative effects of previous summer temperature and precipitation extremes were stronger than those of the current year, indicating that patterns of carbohydrate and nutrient allocation to above- and below-ground sinks and related to mast fruiting are fundamental for identifying mechanisms underlying climate-growth relationships in beech. Indeed, when taking masting events into account we found that growth responses of trees in recent forests to previous summer conditions were largely driven by seed production (as indicated by positive TRI values during adverse climatic conditions in non-mast years), while the trees' responses in ancient forests were driven by both masting events and the carry-over of carbohydrate depletion in the previous summer (as indicated by negative TRI values during adverse climatic conditions in non-mast years). This aligns with ecophysiological studies on N remobilisation within trees in relation to elevated atmospheric carbon dioxide availability, that show that the previous year's uptake of N affects current year growth significantly (Temperton et al. 2003; Millard and Grelet 2010).

Climate-growth relationships for *F. sylvatica* have been shown to vary with elevation (Di Filippo et al. 2007; Dulamsuren et al. 2017), social status of the trees (Lebourgeois et al. 2014) and tree neighbourhood (Mölder and Leuschner 2014; Metz et al. 2016). Given that all target trees were similar in social status and the studied stands were comparable with respect to structure, species composition, soil type and topographic conditions (Table S1), these effects probably do not contribute significantly to explaining the differences between ancient and recent forests. Instead, our fine root data suggest that contrasting climate-growth relationships between ancient and recent forests may in part result from land-use legacy-mediated modifications of the fine root system. We found that the fine root trait spectrum significantly differed between the two former land-use types. These differences might be caused by differences in soil P concentration, C:P and C:N ratio, that have been shown to be higher (P) and lower (C:P ratio, C:N ratio), respectively, in recent forests soils in the study region (von Oheimb et al. 2008; see Table S1). Moreover, microbial enzyme activities in recent forest soils with former arable cultivation were found to be considerably higher than in ancient forest soils (Fichtner et al. 2014), leading to higher decomposition rates, and thus nutrient availability. Higher availability of P in recent forest soils likely is promoting radial stem growth (von Oheimb et al. 2014; see Table S1 and S3), while it might negatively affect the amount of carbon allocated to roots which could reduce the trees' drought resistance in the recent forests. This is in line with the prediction of optimal resource partitioning theory, according to which plants allocate less carbon to roots with increasing nutrient availability, decreasing root-shoot ratio (Thornley 1972). As root-shoot ratio is considered a key trait that strongly determines a tree's susceptibility to drought (Aranda et al. 2012; Dziedek et al. 2017), our results suggest that the observed higher drought sensitivity of the trees in recent forests may be linked to the 32% lower fine root biomass in the topsoil (0–30 cm) of these stands. Indeed, we found that drought resistance of beech decreased in stands with high soil P availability indirectly via decreasing the size of the fine root system in the uppermost 10 cm of the mineral soil. This coincides with findings where trees exhibited lower fine root biomass in response to higher soil P availability (Yuan & Chen 2010). Clearly, deep roots may be more decisive for maintaining tree water uptake in periods of drought (Meier et al. 2018), but surface roots with higher N and P uptake capacity may be important as well, since drought can expose trees to nutrient shortage during dry spells.

Fine roots represent a small but functionally highly active part of tree biomass, which supply water and nutrients to the tree, contribute considerable amounts of organic C and nutrients to carbon and nutrient cycling in forest soils, and are critically linked to the drought susceptibility of trees (Brunner et al. 2015). Studies across latitudes have shown that both temperature and N availability are the main determinants of root trait variation in temperate and boreal tree species (Ostonen et al. 2011; Freschet et al. 2017). Our study demonstrates that land-use legacies can also have a strong impact on fine root trait variation of a single tree species at a local scale. While most studies agree on the existence of a unidimensional resource economics spectrum above-ground (i.e. trait syndromes associated with resource acquisition or conservation; see Reich 2014), the existence of a root economics spectrum is still a matter of debate, mainly because of a lack of consistency among and within studies (Mommer and Weemstra 2012; Weemstra et al. 2016). Evidence for a root economics spectrum was found in herbaceous and shrub species (Roumet et al. 2016), but not in trees (Weemstra et al. 2016). In trees, there is growing evidence that fine root traits are multidimensional (Kramer-Walter et al. 2016). Some traits, such as RTD, seem to be negatively correlated with relative growth rate, while others like fine root diameter and SRL may not be related to the plant economics spectrum. Thus, trees seem to be less constrained when building fine roots in comparison with leaves, because high root tissue density can be related to either a high or low SRL (Kramer-Walter et al. 2016). Our finding that the fine root trait spectrum of beech is related to former land-use suggests that land-use legacy indirectly impacts the belowground resource acquisition strategy of trees via its effects on soil properties, thus affecting the susceptibility of trees to climate events. The higher soil fertility (largely due to higher P concentration) of the recent forests was associated with a significantly higher SRL, SRA and a lower RTD in comparison to ancient forests. These results are in line with previous studies showing that (1) fast and productive tree species often exhibit low RTD, and (2) low RTD is often associated with greater soil nutrient availability (Kramer-Walter et al. 2016; Freschet et al. 2017).The much higher specific root surface area and substantially lower root tissue density in recent forest stands may well have increased the trees' sensitivity to summer droughts, as fine root mortality typically is higher in fine roots with lower density (Eissenstat and Yanai 1997). This coincides with or finding that drought resistance of beech strongly depended on RTD in 10–30 cm soil depth. That is, trees growing in more fertile soils (recent forests) exhibited thinner, less dense fine roots (low RTD), which in turn resulted in a lower resistance to drought. The lower SRL observed in ancient forests, however, likely is associated with a greater root lifespan and an enhanced colonization of fine roots by ectomycorrhizae (Comas et al. 2014; Weemstra et al. 2016).

Although we found significant differences in climate sensitivity and fine root characteristics (biomass and morphology) between the former land-use types, an important caveat is related to the temporal resolution of our data as data on fine root dynamics were not available in this study. The likelihood that seasonal variation of fine root traits, however, has a strong effect on results obtained from a single inventory is relatively small: First, both beech's fine root biomass and morphology was found to be less variable over time, even during drought events (Leuschner et al. 2001; Hertel et al. 2013). Second, morphological traits are generally considered as a function of root age and diameter, resulting in a higher turnover of young and thin roots (i.e. fine roots) compared to older and larger rootlets (Eissenstat et al. 2000; McCormack et al. 2012). Thus, fine roots should be those with lowest morphological response to interannual variation in climate due to their comparable low longevity.

Enhanced mycorrhizal associations in ancient forest soils as reported by Fraterrigo et al. (2006) could also explain the lower susceptibility of beech trees to drought through enhanced water transport capacity under situations where water availability is low (Brunner et al. 2015). On the other hand, several studies have shown that root tips of European beech did not show differences in the degree of ectomycorrhizal symbiosis between contrasting soil water or nutrient conditions (Leuschner et al. 2004; Hertel et al. 2013).

Our results indicate that climate-growth relationships of *F. sylvatica* in northern Germany depend critically on former land-use, suggesting that ancient beech forests are less susceptible to climate extremes. In ancient beech forests, annual radial growth rates were less affected by adverse climatic conditions such as hot and dry summers, which highlights the importance of forest continuity for forest stability and the maintenance of productivity and carbon sequestration in the face of rapid climatic change. Preserving ancient forests could thus benefit both biodiversity conservation and the mitigation of climate warming. This has important policy implications, as global biodiversity loss and climate change are amongst the most important ecological challenges for humanity in the 21st century. A legacy-based perspective on forest ecosystems can therefore enhance our mechanistic understanding of climate-growth relationships in the face of global environmental change, and this new understanding will have important implications for land use and conservation or restoration practice.

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Chapter 11

Phenotypic plasticity explains response patterns of European beech (*Fagus sylvatica* L.) saplings to nitrogen fertilization and drought events

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Article

Phenotypic Plasticity Explains Response Patterns of European Beech (*Fagus sylvatica* L.) Saplings to Nitrogen Fertilization and Drought Events

Christoph Dziedek [1], Andreas Fichtner [1,*], Leonor Calvo [2], Elena Marcos [2], Kirstin Jansen [1], Matthias Kunz [3], David Walmsley [1], Goddert von Oheimb [3] and Werner Härdtle [1]

[1] Institute of Ecology, Leuphana University of Lüneburg, 21335 Lüneburg, Germany; dziedek@uni-lueneburg.de (C.D.); kjansen@uni-lueneburg.de (K.J.); walmsley@uni-lueneburg.de (D.W.); haerdtle@uni-lueneburg.de (W.H.)

[2] Faculty of Biological and Environmental Sciences, Ecology, University of León, 24071 León, Spain; leonor.calvo@unileon.es (L.C.); elena.marcos@unileon.es (E.M.)

[3] Institute of General Ecology and Environmental Protection, Technische Universität Dresden, 01735 Tharandt, Germany; matthias.kunz@tu-dresden.de (M.K.); goddert.von_oheimb@tu-dresden.de (G.V.O.)

* Correspondence: fichtner@uni-lueneburg.de; Tel.: +49-4131-6772-823; Fax: +49-4131-6772-808

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Abstract: Climate and atmospheric changes affect forest ecosystems worldwide, but little is known about the interactive effects of global change drivers on tree growth. In the present study, we analyzed single and combined effects of nitrogen (N) fertilization and drought events (D) on the growth of European beech (*Fagus sylvatica* L.) saplings in a greenhouse experiment. We quantified morphological and physiological responses to treatments for one- and two-year-old plants. N fertilization increased the saplings' aboveground biomass investments, making them more susceptible to D treatments. This was reflected by the highest tissue dieback in combined N and D treatments and a significant N × D interaction for leaf δ^{13}C signatures. Thus, atmospheric N deposition can strengthen the drought sensitivity of beech saplings. One-year-old plants reacted more sensitively to D treatments than two-year-old plants (indicated by D-induced shifts in leaf δ^{13}C signatures of one-year-old and two-year-old plants by +0.5‰ and −0.2‰, respectively), attributable to their higher shoot:root-ratios (1.8 and 1.2, respectively). In summary, the saplings' treatment responses were determined by their phenotypic plasticity (shifts in shoot:root-ratios), which in turn was a function of both the saplings' age (effects of allometric growth trajectories = apparent plasticity) and environmental impacts (effects of N fertilization = plastic allometry).

Keywords: allometric growth; apparent plasticity; δ^{13}C; global change; plastic allometry; shoot:root ratio

1. Introduction

Many ecosystems are currently subject to unprecedented shifts in environmental conditions on both regional and global scales [1]. This is true of forest ecosystems in particular, since trees are characterized by long life-cycles, and growth processes are mediated by the environment over centuries [2]. Among the currently active drivers of global change, climate and atmospheric changes (such as altered precipitation regimes and the deposition of reactive forms of nitrogen) have been shown to be amongst the major drivers of biodiversity loss and shifts in ecosystem functions [3]. Current climate projections assume rising mean annual temperatures, changing precipitation patterns, and shifts in the frequency and magnitude of extreme weather events (including more severe summer drought events [4]). In forest ecosystems, this may affect ecosystem functions such as primary production and carbon sequestration or the diversity and functional composition of tree species [5–7]. Atmospheric nitrogen (N) deposition has tripled in the past century, with an upward trend expected for the coming decades [8,9]. Airborne N loads are considered to be responsible for enhanced radial increment of trees, but also for adverse effects on the biodiversity of forests [10,11]. While critically high loads of airborne N have affected ecosystem processes over the past decades, the impact of climate change is expected to increase in importance over the course of this century. This means that ecosystems which already have altered nitrogen levels are now subject to climate change, and both factors will continue to act upon ecosystems in the coming decades [12].

Although an increasing body of research has addressed ecosystem responses to environmental shifts by means of single-factor approaches, little is known about the interactive effects of co-occurring global change drivers and how these may affect ecosystem processes and services in the future [13,14]. It is, for example, conceivable that tree growth responses to climate change could be strengthened by the deposition of reactive forms of N, probably due to fertilization effects on morphological traits such as shoot:root ratios ("plastic allometry" [15]). Thus, the extent to which climate shifts may alter tree growth patterns over time will depend on how N deposition will interact with climate warming or drought events [16]. Recent experiments have demonstrated that the combination of summer drought and N fertilization resulted in non-additive effects on plant growth and vitality [17–19]. As a consequence, N-fertilized plants may exhibit higher drought sensitivity as compared to non-fertilized ones.

A further but—with regard to many tree species—not adequately considered factor influencing a plant species' response to environmental shifts is plant age. Many trees follow allometric growth trajectories that are characterized by age-related shifts in biomass allocation patterns ("partitioning"; [15,20,21]). This is reflected by traits such as shoot:root ratios, which are expected to decrease with increasing sapling age. As a consequence, a sapling's drought sensitivity may decrease with an age-related increase of belowground investments ("apparent plasticity" [15]). Thus, a tree's phenotypic plasticity (in terms of both plastic allometry and apparent plasticity) may influence its growth responses to environmental change [22].

In the present study, we analyzed growth responses of tree saplings to combined effects of N fertilization and drought events, taking *Fagus sylvatica* L. as an example. We focused on this tree species because *Fagus sylvatica* is the most abundant and dominating broad-leaved tree species in many parts of Western and Central Europe, and, therefore, is of particular importance from an ecological and economic point of view [23]. Although several studies have investigated the drought sensitivity of beech provenances along precipitation gradients in Central Europe and the Mediterranean region (for an overview see [24]), little is known about the drought sensitivity of beech populations of the south-western range margin (i.e., the Iberian Peninsula), an area that is considered one of the glacial refugia of *Fagus sylvatica* [25]). Since the genotypic plasticity and allelic richness of beech trees in this region are expected to be particularly high [25,26], these populations may play an important role in the context of diversity conservation and the selection of proper genotypes for forestry under the prospect of a drier and warmer climate [24,27–29]. However, it remains unclear how sensitive these beech populations are in responding to co-occurring drivers of global change such as drought events and N deposition.

In the present study, we performed a two-year greenhouse experiment in which we altered the temporal combinations of N fertilization and summer drought, taking beech saplings originating from populations of the Cantabrian Mountain as an example. Specifically, we asked to what extent growth responses of tree saplings to single and combined effects of these drivers of global change were influenced by the saplings age (i.e., we compared the growth responses of one-year-old and two-year-old plants). Beech saplings were subjected to N fertilization in the first and second year of the experiment, but some of the N-fertilized saplings were also exposed to drought events in the second year (i.e., drought took effect on already fertilized plants). Growth responses of saplings were measured in terms of morphological response variables (increment of height, stem diameter, and leaf biomass, total dry weight of aboveground and belowground biomass, tissue die-back) and physiological response variables (leaf C and N concentrations, leaf C:N ratios, and leaf $\delta^{13}C$ signatures as a proxy for the plants' intrinsic water use efficiency [30]). To test for age-related responses, we compared growth responses of one- and two-year-old plants. We hypothesized that (i) N-fertilized plants would exhibit higher drought sensitivity than non-fertilized plants; and (ii) one-year-old plants would be more sensitive to drought treatments than two-year-old plants.

2. Materials and Methods

2.1. Seed Collection

Fagus sylvatica seeds were collected across seven forest sites on north-facing slopes in the Cantabrian Mountains (NW Spain; Figure 1) in autumn 2009 (distances between sampling sites were 3–50 km; for forest site characteristics see Table S1 and Dziedek et al. [31]).

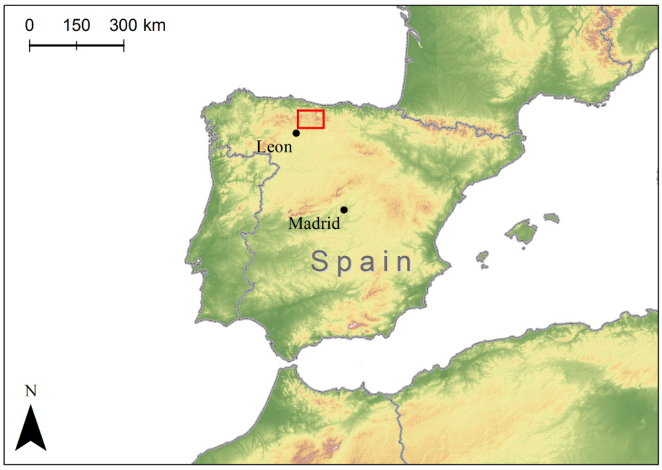

Figure 1. Location of the forest area in the Cantabrian Mountains (North Spain), in which seeds of beech trees were sampled (rectangle).

2.2. Sapling Cultivation And Treatments

The experiment was performed in a greenhouse at the Thünen-Institute (Hamburg, Germany) from spring 2010 to autumn 2011. After stratification in winter 2009/2010, seeds were raised in small pots (so-called "Jiffy Strips", Meyer KG, Rellingen, Germany) and seedlings were transplanted into circular plastic pots in May 2010 (one seedling per pot with 1 L of volume; cultivation substrate: TKS 2, Floragard, Oldenburg, Germany). In the second year of the experiment (2011), saplings were transplanted into circular 3 L plastic pots (one sapling per pot) to account for an increasing belowground biomass (cf. cultivation methods described by [24,31]).

In 2010, a total of 336 pots were randomly assigned to the two treatments applied in the first year: control and nitrogen treatment (i.e., 168 pots per treatment). In 2011, the pots from the 2010 control treatment were randomly assigned to a control and a drought treatment (n = 84 pots in each new treatment). Similarly, the 168 pots from the 2010 nitrogen treatment were randomly assigned to a nitrogen treatment and a combined nitrogen-drought treatment performed in 2011. Thus, 84 pots, respectively, were subjected to four different treatments in 2011: control, nitrogen treatment, drought treatment, and a combined nitrogen-drought treatment (henceforth referred to as control, D, N, and ND treatment, respectively). Pots in the control and N treatment (applied in 2010 and 2011) were well watered during the experiment to avoid drought effects (ca. 40% soil water content). Plants in the D and ND treatments were subjected to two drought periods (applied in 2011), during which no watering took place and the soil water content was reduced to ca. 10%. Both drought periods lasted for about two weeks in June and August 2011 (the duration depended on the development of the pots' soil moisture, quantified by daily weighing during the D treatment). After D treatments, plants were again regularly watered (i.e., 40% soil water content). In the N and ND treatments, N was applied (as NH_4NO_3) in both study years in a quantity equivalent to 50 kg·N·ha^{-1}·year^{-1} (as solution in deionized water; corresponding to current maximum N deposition rates at the natural sites). Nutrient solutions were applied every two weeks from 15th July to 15th September (in 2010 and 2011, except for the two-week drought periods in the ND treatment in 2011). Controls and D treatments received the same amount of deionized water. The mean temperature in the greenhouse was 17.5 °C and 19.0 °C, and the mean relative humidity was 77% and 71% in the first year and second year of the experiment, respectively (means from July to October in 2010 and May to September in 2011). All pots were randomly relocated every four weeks to avoid position effects.

2.3. Measurement of Response Variables

In 2010, the following response variables were measured at the end of the growing season (October): stem diameter (measured 5 cm above the root collar in N-S and E-W direction), plant height (measured from the root collar to the shoot apex), and total leaf biomass (inferred from the number of leaves per tree individual and the mean biomass of a single leaf, determined after leaf harvest at the end of the experiment). In September 2011, all saplings were harvested and the following variables were measured: stem diameter, plant height, number of dead branches, and number of necrotic leaves (more than two-third of the leaf area with necrotic tissue). The root biomass was sampled by carefully wet sieving roots until soil residues were removed as far as possible. As this cleaning procedure was very laborious, belowground biomass was quantified for a subset of randomly selected saplings only (n = 28 per treatment). All biomass samples (shoots, leaves, and roots) were dried to a constant weight at 40 °C, and the following variables were determined: leaf biomass (dry weight = DW of all leaves), aboveground biomass (DW of shoots and leaves), root biomass DW, and shoot:root ratios (aboveground biomass:belowground biomass ratio; n = 28 per treatment). Using both years' data, we also calculated the annual stem, height, and total leaf biomass increment.

Analyses of morphological responses were complemented by the analyses of physiological responses (i.e., leaf C and N concentrations, leaf C:N rations, leaf δ^{13}C signatures; cf. [24,31]). To this end, leaf samples (one sample comprised all leaves of a tree individual) were ground in a centrifugal mill (ZM 200, Retsch, Haan, Germany) and re-dried at 40 °C for 3 days. C and N concentrations and δ^{13}C signatures were measured using a continuous flow elemental analyzer-isotope mass spectrometer (vario EL cube, Elementar, Hanau, Germany), coupled to an Isoprime Isotope-ratio mass spectrometer (IRMS, Isoprime Ltd., Cheadle Hulme, UK). Isotope signatures were presented in the delta (δ) notation (in per mil; ‰) as a relative deviation from an international standard (PeeDee Belemnite). The relative precision of repeated analyses of an International Atomic Energy Agency-standard (IAEA-CH-3) was ±0.1‰.

To assess the effect of sapling age on shoot:root ratios and leaf δ^{13}C signatures, we compared data from the present study with measurements from Dziedek et al. ([31]; one-year-old plants).

2.4. Statistical Analyses

We applied linear mixed-effects models (LMMs) to analyze the effects of treatment (control, D, N, ND) on morphological and physiological responses. To account for variability between forest sites, we used forest site as a random effect. We used the same mixed-model approach to analyze age-related effects (one-year old vs. two-year-old plants) of N and D treatments and their interactions on shoot:root ratio and leaf δ^{13}C signatures. As some response variables were count data (i.e., number of dead branches and necrotic leaves), we fitted generalized linear mixed-effects models (GLMMs) assuming a Poisson error distribution with a logit link function. We found no indication for overdispersion. The response variables "belowground biomass" and "shoot:root ratio" were log-transformed to meet model assumptions [32]. Model selection (determination of the best-fitting and most parsimonious model) was based on the Akaike information criterion (AIC) using maximum likelihood (ML) estimations and the model with the smallest AIC was chosen as the best-fitting model [33]. Parameter estimates of the best-fitting models were based on the restricted maximum likelihood (REML) method. All statistical analyses were conducted with R 3.1.2 (R Project for Statistical Computing; http://www.R-project.org) with the packages lme4 [34] and lmerTest [35].

3. Results

3.1. Effects of N, D, and ND Treatments on Two-Year-Old Saplings

N and ND treatments caused a significant increase in the aboveground biomass production (in terms of stem increment, leaf biomass increment, and total aboveground biomass), but had no significant effect on the belowground biomass (Table 1 and Table S2). Moreover, the plants' height increment increased in the ND treatment in comparison to the controls. The relative increase in the aboveground biomass allocation resulted in significantly higher shoot:root ratios in the N and ND treatments (Table S2). Branch dieback was significant only in the ND treatment ($p = 0.006$), whereas N fertilization reduced the number of necrotic leaves (negative estimate; Table 1). N fertilization caused a distinct increase in N concentrations, which in turn resulted in decreasing C:N ratios (Tables 1 and S2). Leaf δ^{13}C signatures were not significantly affected by N fertilization. D treatments had no effect on morphological responses, but caused decreasing values for C concentrations, N concentrations, and leaf δ^{13}C signatures (Tables 1 and S2).

3.2. Effects of Sapling-Age

On average, one-year-old plants showed significantly higher shoot:root ratios than two-year-old plants (Table 2; $p < 0.001$). In the controls, shoot:root ratios decreased from 1.78 in the first year to 1.20 in the second year (Figure 2a). The effects of the N treatments on shoot:root ratios were not affected by plant age (i.e., no significant N × Age interaction; Table 2). This indicates that N fertilization caused an increase in shoot:root ratios irrespective of the plants age.

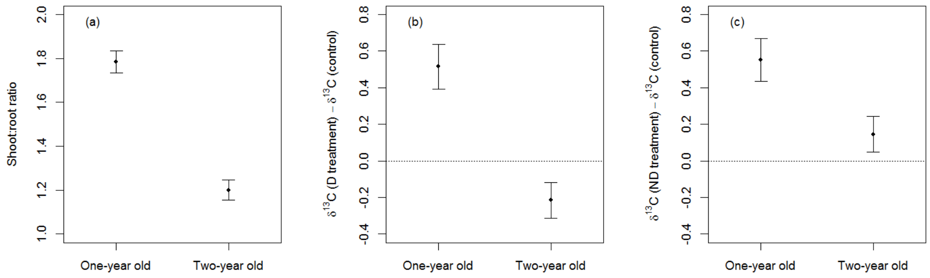

Figure 2. (**a**) Shoot:root ratios (mean ± 1SE) of one-year-old and two-year-old *Fagus sylvatica* plants in the control treatment. Age-related differences are significant at $\alpha = 0.001$. Differences in tissue δ^{13}C signatures (mean ± 1SE) between (**b**) drought treatments (D) and the control ($p < 0.001$) and (**c**) combined nitrogen and drought treatments (ND) and the control ($p = 0.008$) of one-year-old and two-year-old *Fagus sylvatica* plants.

In addition, we found age-related responses of leaf δ^{13}C signatures to D and ND treatments, indicated by a significant D × Age interaction for leaf δ^{13}C signatures (Table 2). Whereas D treatments caused an increase in leaf δ^{13}C values of one-year-old plants by about 0.53‰ (from −29.36‰ to −28.83‰), leaf δ^{13}C values of two-year-old plants decreased by about 0.19‰ (from −29.05‰ to −29.24‰; Figure 2b). In the ND treatment, we found a significant increase in leaf δ^{13}C values by about 0.57‰ for one-year-old plants (from −29.36‰ to −28.79‰), whereas shifts in δ^{13}C values were non-significant for two-year-old plants (increase by about 0.09‰ from −29.05‰ to −28.96‰; Figure 2c). Importantly, N treatments strengthened an increase in leaf δ^{13}C signatures following D treatments, indicated by significant D × N interaction (and a positive estimate) for both one-year-old and two-year-old plants ($p = 0.042$).

Table 1. Results of mixed-effects models (LMM and GLMM) for treatment effects in response to morphological and physiological variables. Abbreviations of treatments: D = drought treatment, N = nitrogen treatment, ND = combined nitrogen and drought treatment; significant effects ($p < 0.05$) are indicated in bold.

Morphological Variables	**Stem Increment**			**Height Increment**			**Leaf Biomass Increment**			**Aboveground Biomass**		
	Estimate	*t*-value	*p*-value	Estimate	*t*-value	*p*-value	Estimate	*t*-value	*p*-value	Estimate	*t*-value	*p*-value
Intercept	1.867	16.828	**<0.001**	3.837	3.617	**0.004**	2.546	9.986	**<0.001**	18.121	19.998	**<0.001**
D	0.026	0.260	0.793	0.048	0.054	0.957	0.158	1.158	0.248	0.609	0.709	0.479
N	0.566	5.649	**<0.001**	2.021	2.292	0.023	0.397	2.932	**0.004**	2.712	3.170	**0.002**
ND	0.567	5.675	**<0.001**	2.599	2.956	**0.003**	0.461	3.413	**<0.001**	3.593	4.211	**<0.001**
Morphological Variables	**Belowground Biomass**			**Shoot:Root Ratio**			**No. of Necrotic Leaves**			**No. of Dead Branches**		
	Estimate	*t*-value	*p*-value	Estimate	*t*-value	*p*-value	Estimate	χ^2	*p*-value	Estimate	χ^2	*p*-value
Intercept	2.669	41.668	**<0.001**	0.073	3.690	**0.002**	0.550	2.363	**0.018**	0.072	−0.270	0.787
D	0.047	0.599	0.550	0.008	−0.375	0.709	0.464	1.675	0.094	0.079	−0.386	0.700
N	0.068	0.866	0.389	0.059	2.857	**0.005**	−0.620	−2.130	**0.033**	0.216	1.101	0.270
ND	0.109	0.079	0.169	0.043	2.061	**0.041**	−0.330	−1.163	0.245	0.512	2.724	**0.006**
Physiological Variables	**C Concentration Leaves**			**N Concentration Leaves**			**C:N Ratio**			**Leaf δ^{13}C Signature**		
	Estimate	*t*-value	*p*-value	Estimate	*t*-value	*p*-value	Estimate	*t*-value	*p*-value	Estimate	*t*-value	*p*-value
Intercept	463.205	1.987	**<0.001**	15.413	27.799	**<0.001**	30.777	29.853	**<0.001**	29.049	−167.820	**<0.001**
D	−3.738	2.931	**0.004**	−1.354	−4.296	**<0.001**	2.420	4.634	**<0.001**	−0.197	−2.175	**0.030**
N	−2.466	1.934	0.054	3.138	9.954	**<0.001**	−5.380	10.302	**<0.001**	−0.094	−0.134	0.302
ND	−2.482	1.945	0.053	2.557	8.107	**<0.001**	−4.718	−9.031	**<0.001**	0.083	0.920	0.358

Table 2. Best-fitting mixed-effects models for (a) shoot:root ratio and (b) leaf $\delta^{13}C$ signatures of *Fagus sylvatica* saplings. Shoot:root ratios and leaf $\delta^{13}C$ signatures were modelled as a function of the saplings' age (one-year old vs. two-year-old plants), drought treatments (D, ND), nitrogen treatments (N, ND), and their interactions. The best-fitting model was selected using the Akaike information criterion (AIC).

Fixed Effects	**Estimate**	***t*-Value**	***p*-Value**
(a) Shoot:root ratio			
Intercept	1.747	22.185	<0.001
D	0.023	4.649	<0.001
N	0.089	2.078	0.038
Age (1 year vs. 2 years)	−0.456	−4.392	<0.001
D × Age	−0.258	−2.621	0.009
(b) Leaf $\delta^{13}C$ signature			
Intercept	−29.688	−159.014	<0.001
D	0.442	5.431	<0.001
N	−0.034	−0.516	0.606
Age (1 year vs. 2 years)	1.058	8.188	<0.001
D × N	0.191	2.035	0.042
D × Age	−0.546	−5.804	<0.001

4. Discussion and Conclusions

4.1. Treatment (N, D, ND) Effects on Sapling Growth

Beech saplings significantly increased their aboveground investments in N and ND treatments and hence followed the "resource optimization hypothesis" [36], according to which plants increase their aboveground biomass allocation as a result of improved nutrient supply. This observation is in agreement with other studies [17,18,37,38], and was also mirrored by increased shoot:root ratios in the N and ND treatments. However, only plants from the ND treatment showed a significant biomass dieback. This finding supports our first hypothesis ("N-fertilized plants exhibit higher drought sensitivity") and suggests that combined effects of N fertilization and drought may adversely affect the vitality of beech saplings. This interpretation is supported by the finding that N treatments strengthened the effect of drought on leaf $\delta^{13}C$ signatures (D × N interaction; Table 2). This might be explained with the observed shifts in biomass allocation patterns (i.e., increasing shoot:root ratios), as has also been documented by other studies. [39,40]. An indication of drought stress based on the plants' leaf $\delta^{13}C$ signatures in the ND treatment was particularly pronounced for one-year-old plants (see paragraph on "effects of sapling age"). We cannot rule out the possibility that other factors, such as nutrient imbalances or a failure of photoassimilate transport, may have also contributed to the dieback of branches of two-year-old plants, because these factors are impaired by N fertilization [41].

4.2. Effects of Sapling Age

Comparisons of leaf $\delta^{13}C$ signatures showed that plant responses to treatments were strongly influenced by sapling age. This supports our second hypothesis that one-year-old plants would react more sensitively to treatments than two-year-old plants, particularly with regard to drought events. We hypothesize that differences in drought sensitivity were mainly related to the plants' shoot:root ratios [22], which significantly differed for one-year-old and two-year-old beech saplings (i.e., two-year-old plants showed relatively higher belowground investments than one-year-old plants). As a consequence of these age-related shifts in biomass allocation patterns (i.e., apparent plasticity; according to Weiner [15]), two-year-old plants may be less drought sensitive and may experience less constraints in their water supply, particularly in periods of drought [42,43]. This interpretation is supported by the finding that leaf $\delta^{13}C$ signatures of one-year-old plants increased by 0.53‰ and 0.57‰

in the D and ND treatment, respectively, whereas two-year-old plants showed no significant shifts or even decreasing values in leaf $\delta^{13}C$ signatures in response to the ND and D treatments, respectively.

Given that the biomass allocation patterns of many plant species follow allometric trajectories and are therefore a function of plant age [15], our findings on age-related responses might have general implications for predictions of plant responses to environmental stressors such as climate or atmospheric changes. In forest ecosystems, for example, biomass allocation patterns strongly depend on tree age [44], but relationships between the trees' life-stages and their sensitivity to climate and atmospheric changes have not been well investigated or are even unknown [45]. Ettinger and HilleRisLambers [46] found that climate change-related tree mortality in forest ecosystems was strongly affected by stand development processes, and effects of decreasing precipitation or increasing temperatures on tree growth significantly decreased with stand age. A study by Luo and Chen [45] confirmed that climate change-associated increases in tree mortality were significantly higher in young compared to old forests due to the higher sensitivity of young trees to regional warming and drought. Thus, observations from mature forest stands might underestimate climate change effects on tree mortality. Luo and Chen [45] concluded that life-stage related analyses of tree growth are crucial to better understand and predict forest responses to climate change. This might also apply to an assessment of interaction effects of drought and N deposition on tree growth: given that one-year-old seedlings have the highest shoot:root ratios (according to age-related allometric trajectories; [15]) and that N fertilization further increases shoot:root ratios (according to the resource optimization hypothesis), then N-fertilized one-year-old seedlings should exhibit the highest sensitivity to drought events (also suggested by the significant D × N interaction for leaf δ^{13} signatures). This conclusion is supported by the experiments of Dziedek et al. [31], which showed that a combination of N fertilization and drought negatively affected the total biomass production and strongly increased the formation of necrotic leaf tissue.

In conclusion, our experiments provided evidence that nitrogen fertilization has the potential to increase the drought sensitivity of beech saplings due to its impact on biomass partitioning, with consequences for the plants' shoot:root ratios (i.e., plastic allometry of tree saplings). However, this increase in drought sensitivity is confounded with sapling age, because sapling development seems to follow allometric growth trajectories in which partitioning patterns are also life-stage dependent (i.e., apparent plasticity of tree saplings). As a consequence, predictions of tree growth responses to atmospheric and climate changes should consider the effects related to both the plastic allometry and apparent plasticity of a tree species' development. We are aware that greenhouse experiments are limited with regard to a generalization of findings, and our study does not allow us to directly infer growth response of naturally regenerated trees to global change effects. However, allometric growth trajectories should also apply to naturally regenerated tree saplings. This would indicate that assessments of tree growth responses to global change should include life-stage related shifts in a tree's sensitivity to co-occurring global change drivers.

Supplementary Materials: The following are available online at http://www.mdpi.com/1999-4907/8/3/91/s1, Table S1: Site characteristics (from Dziedek et al. [31]), Table S2: Summary of treatment effects on the response variables measured, Table S3: Data for two-year-old trees, Table S4: Data for one-year-old and two-year-old trees (comparisons of shoot:root ratios and leaf δ^{13} signatures). References [47,48] are cited in the supplementary materials").

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Chapter 12

Nitrogen addition enhances drought sensitivity of young deciduous tree species

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Nitrogen Addition Enhances Drought Sensitivity of Young Deciduous Tree Species

*Christoph Dziedek[1], Werner Härdtle[1], Goddert von Oheimb[2] and Andreas Fichtner[1]**

[1] Institute of Ecology, Leuphana University of Lüneburg, Lüneburg, Germany, [2] Institute of General Ecology and Environmental Protection, Dresden University of Technology, Tharandt, Germany

Understanding how trees respond to global change drivers is central to predict changes in forest structure and functions. Although there is evidence on the mode of nitrogen (N) and drought (D) effects on tree growth, our understanding of the interplay of these factors is still limited. Simultaneously, as mixtures are expected to be less sensitive to global change as compared to monocultures, we aimed to investigate the combined effects of N addition and D on the productivity of three tree species (*Fagus sylvatica*, *Quercus petraea*, *Pseudotsuga menziesii*) in relation to functional diverse species mixtures using data from a 4-year field experiment in Northwest Germany. Here we show that species mixing can mitigate the negative effects of combined N fertilization and D events, but the community response is mainly driven by the combination of certain traits rather than the tree species richness of a community. For beech, we found that negative effects of D on growth rates were amplified by N fertilization (i.e., combined treatment effects were non-additive), while for oak and fir, the simultaneous effects of N and D were additive. Beech and oak were identified as most sensitive to combined N+D effects with a strong size-dependency observed for beech, suggesting that the negative impact of N+D becomes stronger with time as beech grows larger. As a consequence, the net biodiversity effect declined at the community level, which can be mainly assigned to a distinct loss of complementarity in beech-oak mixtures. This pattern, however, was not evident in the other species-mixtures, indicating that neighborhood composition (i.e., trait combination), but not tree species richness mediated the relationship between tree diversity and treatment effects on tree growth. Our findings point to the importance of the qualitative role (‘trait portfolio’) that biodiversity play in determining resistance of diverse tree communities to environmental changes. As such, they provide further understanding for adaptive management strategies in the context of global change.

Keywords: climate change, complementarity, ecosystem functioning, insurance hypothesis, nitrogen deposition, plant–climate interactions, temperate forest, tree growth

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Sebastian Leuzinger,
Auckland University of Technology,
New Zealand

Reviewed by:
Rebekka Bögelein,
University of Trier, Germany
Rodica Pena,
University of Göttingen, Germany

***Correspondence:**
Andreas Fichtner
fichtner@leuphana.de

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INTRODUCTION

Forest ecosystems are currently facing unprecedented shifts in environmental conditions, with implications for biodiversity patterns, ecosystem functions and services (Anderson-Teixeira et al., 2015). Important drivers of environmental shifts are, among others, climate change and atmospheric changes, for example the deposition of reactive forms of nitrogen (Vitousek et al., 1997; Sala et al., 2000). Climate change, accompanied by increasing temperatures and more frequent drought events (IPCC, 2013), is expected to severely affect carbon and water cycles of forest ecosystems (Grossiord et al., 2014). Moreover, drought events and increasing summer temperatures may impose constraints on growth and competitiveness of trees species that are considered sensitive to water shortage (Geßler et al., 2007; Grossiord et al., 2014). On the other hand, atmospheric deposition of nitrogen (N) has tripled since 1860 and is expected to further increase in coming decades (Galloway et al., 2004). In forest ecosystems, N deposition is considered responsible for accelerated biomass increment in recent decades, because tree growth is often limited by the availability of N (Rennenberg et al., 1998; Nadelhoffer, 2000; Pretzsch et al., 2014). Long-term N loading has also been shown to alter soil nutrient cycling and promote soil acidification, leaching of nitrate and soil cations (Magill et al., 1997; Aber et al., 1998; Rennenberg et al., 1998). Consequently, both an increase in nitrogen deposition and drought events may have severe consequences for forest community dynamics, and thus for ecosystem functioning and services.

Due to the global importance of forest ecosystems, there is a bulk of research that addressed the effects of global change drivers on various ecosystem functions (for a global overview see Allen et al., 2010; Bobbink et al., 2010). Many studies, however, have focused on single-factor approaches, whereas analyses on interaction effects are scarce (Zavaleta et al., 2003; Yang et al., 2013), particularly for combined N and D effects (Nilsen, 1995; Meyer-Grünefeldt et al., 2015b,a). It is conceivable, for example, that co-occurring drivers of global change do not act additively (i.e., the summation of single effects), but have non-additive effects on ecosystem responses (i.e., show antagonistic or synergistic interactions; Meyer-Grünefeldt et al., 2015b). This implies that ecosystem responses to multiple environmental shifts cannot be inferred from single-factor studies alone, and emphasizes the need for concomitant multi-factor approaches (Lindenmayer et al., 2010; Ochoa-Hueso et al., 2014; Hautier et al., 2014).

Next to the physiological response of individual trees, the structure and composition of forest ecosystems is central for allowing forest to adapt to global environmental changes (Coomes et al., 2014; De Frenne et al., 2015). In this context, species diversity is assumed to mitigate climate change effects on forest productivity, because diverse forests are expected to react less sensitively to environmental shifts as compared to monocultures (Filotas et al., 2014). Overall, there is increasing evidence that biodiversity promotes various ecosystem functions and services (e.g., Cardinale et al., 2012), and three main mechanisms have been proved to drive diversity-functioning relationships: complementarity (i.e., resource partitioning and facilitation), selection (or sampling) effects (i.e., the higher likelihood that mixtures contain highly productive species) and ecological insurance (Loreau and Hector, 2001; Scherer-Lorenzen, 2014). Many recent biodiversity-ecosystem functioning experiments provided evidence that increasing diversity can reduce the variability of ecosystem properties, and thus increase the temporal stability (e.g., in terms of resistance or resilience) at the ecosystem level (Tilman et al., 2006; Hector et al., 2010; Proulx et al., 2010; Isbell et al., 2015). For instance, observational and simulational studies have shown a positive relationship between tree species richness and the stability of wood production (Jucker et al., 2014; Morin et al., 2014). This beneficial stabilizing effect of biodiversity, also termed as ‘insurance hypothesis’ (Yachi and Loreau, 1999), can arise from overyielding (i.e., the productivity of mixtures is higher than the average of the monocultures or most productive monoculture), the spatial (i.e., niche partitioning), or temporal (i.e., species asynchrony) complementarity between species or facilitative plant-interactions (Loreau, 2010; Hector et al., 2010; McIntire and Fajardo, 2014). Thus, biodiversity related ‘insurance effects’ imply that diverse forests are composed of tree species that (i) differ with regard to intrinsic responses to environmental change, (ii) differ with regard to the speed with which they respond to environmental disturbances, or (iii) show a reduction in the strength of competition (Loreau and de Mazancourt, 2013).

We evaluated how N addition and drought interactively affect tree growth in monocultures and mixtures. In a 4-year field experiment with juvenile trees, in which we altered species combinations and species richness levels, we exposed monocultures and mixtures to full-factorial combinations of summer drought and N fertilization. Experiments were conducted with three different tree species: European beech (*Fagus sylvatica*), Sessile oak (*Quercus petraea*), and Douglas fir (*Pseudotsuga menziesii*), henceforth referred to as beech, oak, and fir, respectively. These species differ in key functional traits that are linked to productivity and shade tolerance (e.g., specific leaf area, leaf longevity, and wood density) and are considered to be ecologically and/or economically important from a European perspective (Valladares and Niinemets, 2008; Ellenberg and Leuschner, 2010; Lasky et al., 2014). Specifically, we asked, how sole and combined effects of N fertilization and drought mediate (i) tree-level growth in relation to species identity (of the target and neighboring trees), (ii) stand-level growth in relation to species combination and richness, and (iii) complementarity and selection effects and thus net biodiversity effects of tree communities.

MATERIALS AND METHODS

Study Area

All experimental sites were established in near-natural broad-leaved forest ecosystems typical of the lowlands of NW Germany (Lower Saxony, 53° 8′ 7.827′′ N 10° 22′ 20.96′′). Soils of the study area developed from sediments of the penultimate glacial period, and prevailing soil types are acidic Cambisols or Luvisols (according to the WRB system, 2006). Mean pH_{H2O}-values in the upper mineral (A−) horizon ranged between 3.9 and 4.7. The natural forest communities at these sites are acidic beech forests that belong to the Galio odorati-Fagetum (Ellenberg and Leuschner, 2010). The climate is of a sub-oceanic type. Mean precipitation is 718 mm yr^{-1}, and the annual mean temperature is 9.2°C.

Experimental Design and Plant Material

In April 2010 we established a 4-year field experiment using a randomized block design (with seven replicate blocks). Blocks were established under larger canopy gaps (0.25–0.50 ha in size) to simulate a quasi-natural regeneration situation under an opened canopy. All blocks were fenced during the experiment to exclude grazing effects. Each block consisted of six plots with different species combinations, where three target species (beech, oak, and fir) were grown, either in monoculture, 2-species or 3-species mixtures (for species combinations see **Table 1**). Each plot was divided into four subplots (1 m × 1 m) with 0.5 m wide buffer strips, and each subplot was randomly assigned to one of the following treatments: control, nitrogen (N) fertilization, drought treatment, and a combination of N fertilization and drought treatment (henceforth referred to as control, N treatment, D treatment, and N+D treatment, respectively). The experiment thus comprised six species combinations and four treatment levels, resulting in a total of 24 experimental combinations (each 7 × replicated).

In April 2010, each subplot was planted with 25 3-year-old tree saplings (planting distance: 20 cm), which originated from a local forest nursery. In mixed-species subplots, trees were planted in a systematic species alteration pattern (e.g., beech-oak-fir-beech-oak-fir etc.). To account for edge effects, only the central nine individuals were considered as target trees for subsequent analyses. All treatments started in the year 2012, i.e., 2 years after sapling planting. This delayed start was chosen to avoid confounding effects between experimental treatments and planting.

In the N treatments (i.e., N and N+D), N was applied (as NH_4NO_3) in a quantity equivalent to 50 kg N ha^{-1} yr^{-1} (as solution in deionized water). This treatment strength was chosen to simulate the effects of atmospheric N deposition which some forest ecosystems currently receive in NW Europe (with 50 kg N ha^{-1} yr^{-1} representing the upper range limit of current deposition rates; Galloway et al., 2004; Bobbink et al., 2010).

TABLE 1 | Design of the experiment.

Species	Diversity level	Species combination	No. trees
Fagus sylvatica (beech)	mono	–	252
Quercus petraea (oak)	mono	–	252
Pseudotsuga menziesii (fir)	mono	–	252
Fagus sylvatica	mix2	beech-oak	140
Fagus sylvatica	mix2	beech-fir	140
Quercus petraea	mix2	beech-oak	112
Pseudotsuga menziesii	mix2	beech-fir	112
Fagus sylvatica	mix3	beech-oak-fir	84
Quercus petraea	mix3	beech-oak-fir	84
Pseudotsuga menziesii	mix3	beech-oak-fir	84
Total			1512

Number of planted target trees of each diversity level and species combination. Mono, monoculture; mix2, 2-species mixture; mix3, 3-species mixture.

To simulate summer drought events (D treatments; i.e., D and N+D) we installed rain-out shelters (2–3 m aboveground) with UV transparent foil (UV-B Window, folitec GmbH, Westerburg, Germany) in the respective subplots to exclude any precipitation. The rain-out shelters were installed from July 9th to July 31st and August 13th to September 7th in 2012, and from July 5th to September 5th in 2013. Effects of D treatments on soil water contents were determined by means of volumetric soil water content sensors (based on Time Domain Reflectometry; Decagon Devices, Pullman, WA, USA) that were installed in four representative blocks in 2012 and 2013 in the upper mineral soil (0–5 cm). Measurements of volumetric soil water contents indicated that D treatments reduced the soil water content by about 20% (volumetric losses compared to field capacity, achieved during the last week of the D treatments), which corresponds to a moderate-severe drought event in the study region (Rose et al., 2009).

Tree Measurements

For all trees, height and biomass were determined. Tree height (measured from the root collar to the top) was recorded at the beginning of the treatment application (April 2012) and at the end of the experiment in September 2013, which corresponded to a 2-year growing period. For each tree we calculated relative growth rate (RGR) of tree height as $RGR = (\ln H_2 - \ln H_1)/(t_2 - t_1)$, where H_1 and H_2 are the tree heights at the beginning (t_1) and end (t_2) of the experiment. We used RGR instead of absolute growth rates as a response variable to model individual tree growth, because RGR is less sensitive toward differences in initial size (Mencuccini et al., 2005). After tree harvest (September 2013), we additionally measured the stem biomass (including branches) and the biomass of leaves or needles for all tree individuals. Biomass samples were dried at 40°C for 3 days (until weight constancy) and

TABLE 2 | Target tree characteristics of the three study species.

	Mean (*SD*)	Range
Fagus sylvatica		
Initial tree height (cm)	89.4 (16.5)	52.0–141.0
AGB (g)	51.5 (41.4)	4.5–305.1
AGR (cm $year^{-1}$)	16.7 (11.4)	0.0–55.5
RGR (cm cm^{-1} $year^{-1}$)	0.15 (0.08)	0.0–0.37
Quercus petraea		
Initial tree height (cm)	101.0 (25.2)	38.0–178.0
AGB (g)	53.0 (48.3)	0.1–323.8
AGR (cm $year^{-1}$)	17.2 (12.3)	0.0–59.0
RGR (cm cm^{-1} $year^{-1}$)	0.13 (0.08)	0.0–0.36
Pseudotsuga menziesii		
Initial tree height (cm)	118.6 (25.9)	62.0–202.0
AGB (g)	150.3 (107.7)	16.2–683.2
AGR (cm $year^{-1}$)	28.6 (13.7)	0.0–87.0
RGR (cm cm^{-1} $year^{-1}$)	0.19 (0.07)	0.0–0.37

Absolute (AGR) and relative growth rate (RGR) of tree height refer to a 2-year census interval; AGB, aboveground biomass at the end of the census interval.

subsequently weighted. Target tree characteristics are provided in **Table 2**.

Data Analysis

Individual tree growth analyses was focused on 1291 target trees in total (beech: 558, oak: 320, fir: 413). Due to mortality, 12% of the original 1512 target trees were not available to be measured at the end of the experiment. Oak showed highest mortality, followed by fir and beech, but we found no statistically significant treatment effect across species (beech: $P = 0.10$; oak: $P = 0.91$; fir: $P = 0.83$; Supplementary Figure S1). Moreover, observations with negative growth rates (3% of the surviving trees) were assumed to be damage-related (e.g., due to planting failures or falling large-sized branches) or to have measurement error, and therefore omitted in the subsequent height growth analysis to avoid biased estimates. However, trees with zero increments were retained.

To examine the tree size, treatment, and species diversity (measured as species richness) dependence of RGR of the three target species, we applied linear mixed models using block, plot and treatment as nested random factors. We fitted several alternative models for each target species separately including initial height, treatment, species combination, and their interactions as fixed effects. To address the skewed response and heteroscedasticity of the beech and oak growth data, the residual error was modeled using a variance function based on the power of the fitted values (Pinheiro and Bates, 2004). Models were selected based on the Akaike Information Criterion (AIC) and maximum likelihood (ML) estimations. Moreover, we ranked the models based on Akaike weights (w_i), which are the relative likelihood of each model to be the best-fitting model, given the complete set of candidate models (Burnham and Anderson, 2002). Only models with an AIC difference (ΔAIC) ≤ 2 (compared with the best-fitting model) were considered as models with substantial support (Burnham and Anderson, 2002), and for each species the model with the highest Akaike weights was chosen as the most parsimonious model. Parameter estimates of the best-fitting models were based on the restricted maximum likelihood (REML) method.

The strength of each treatment effect on RGR rates was determined by the magnitude of treatment effect (MTE). MTE was calculated as $\mathrm{MTE} = (X_T - X_C)/(X_T + X_C)$, where X_T is the predicted response of target tree *i* in the global change driver treatments (N, D, N+D) and X_C the predicted response in the control (C) treatment. This index ranges from –1 (negative global change driver influence) to +1 (positive global change driver influence) for each species, thus facilitating between-species comparisons. Differences in MTE among species were evaluated by analysis of variance (ANOVA) with a *post hoc* performance (Tukey HSD test).

Total aboveground biomass (all woody compartments and leaves; AGB) was used as a response for tree vigor. For trees that died during the experiment we used the average species-specific AGB of each treatment and species combination. We applied the additive partitioning method according to Loreau and Hector (2001) to quantify the net biodiversity effect (NE) on AGB of species mixtures, which we further partitioned into the complementarity (CE), and selection effect (SE). NE, CE, and SE were calculated using the following equations:

$$\mathrm{NE} = \Sigma \mathrm{Y} - \overline{\mathrm{M}}$$

$$\mathrm{CE} = \mathrm{N} \times \overline{\mathrm{M}} \times \overline{\Delta \mathrm{RY}}$$

$$\mathrm{SE} = \mathrm{N} \times \mathrm{cov}(\mathrm{M}, \Delta \mathrm{RY})$$

where Y is the observed AGB for each species in mixture and M is the yield of a species growing in monoculture. N is the number of species and ΔRY the deviation from the expected relative yield of a species in mixture ($\Delta \mathrm{RY} = (\mathrm{Y/M}) - (1/\mathrm{N})$).

To account for size differences of the species-mixtures, and thus allow for inter-site comparisons, diversity components were standardized dividing NE, CE, and SE by the expected AGB based on monocultures (see Morin et al., 2011). For the subsequent analysis these values were square-root transformed to meet the model assumptions while preserving the original positive and negative signs (Loreau and Hector, 2001). For each species combination we fitted a linear-mixed effects model using treatment as fixed effect and block as random factor to account for potential differences in site conditions. All statistical analyses were performed in R (version 3.1.0[1]) using the packages *nlme* and *MuMIn*.

RESULTS

Effects of Nitrogen Fertilization and Drought on Tree-Level Height Growth

For all species the minimum adequate models according to the AIC included tree size, treatment and species composition effects (**Table 3**). For beech, the treatment effects significantly depended on tree size ($P < 0.01$; **Table 4**), with treatment effects becoming more pronounced with increasing height. For oak and fir, the RGR-treatment relationships were consistent across the observed height range. Compared to control plots, RGR of oak was significantly lower in the N+D treatment ($P < 0.05$), and marginally significant lower in the N treatment ($P \leq 0.1$), while a significant decline in RGR of fir was induced by drought ($P < 0.05$). Moreover, a significant species composition effect on the shape of the size response was observed for beech ($P < 0.001$) and oak ($P < 0.01$), while for fir, the species composition effect ($P < 0.01$) was independent of tree size (**Table 4**). There was no support for a statistically significant three-way interaction effect on RGR, showing that for each species the size-treatment relationship did not shift with species composition (**Table 3**). Graphical validation plots indicated unbiased estimates. The best-supported models explained between 41% (beech), 44% (oak), and 51% (fir) of the variation in RGR of height.

The positive RGR-size relationship was most pronounced for beech with a greater increase in growth rates when growing in mixture with fir (**Figure 1**). Similarly, RGR of oak trees in monoculture increased with size. In contrast, the influence of

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[1] http://www.R-project.org

TABLE 3 | Model selection statistics (Akaike Information Criterion ΔAIC and Akaike weights w_i) for various candidate models describing the RGR of tree height as a function of initial tree height (H), treatment (T), and species composition (C) effects of European beech (*Fagus sylvatica*), Sessile oak (*Quercus petraea*), and Douglas fir (*Pseudotsuga menziesii*).

Model	Fixed effects							*Fagus sylvatica*		*Quercus petraea*		*Pseudotsuga menziesii*	
	H	T	C	H × T	H × C	T × C	H × T × C	ΔAIC	w_i	ΔAIC	w_i	ΔAIC	w_i
1	×	×						23.99	0.00	4.47	0.08	11.57	0.00
2	×		×					15.72	0.00	7.94	0.01	2.38	0.09
3		×	×					73.76	0.00	9.46	0.01	7.21	0.01
4	×	×	×					19.45	0.00	7.25	0.02	**0.01**	**0.30**
5	×	×	×	×				13.67	0.00	10.08	0.00	0.00	0.30
6	×	×	×		×			10.82	0.00	**0.13**	**0.50**	1.20	0.16
7	×	×	×			×		25.29	0.00	8.32	0.01	7.38	0.01
8	×	×	×	×	×			**0.00**	**0.91**	3.51	0.07	1.75	0.12
9	×	×	×	×		×		19.64	0.00	8.55	0.00	7.81	0.01
10	×	×	×		×	×		14.00	0.00	0.00	0.26	8.42	0.00
11	×	×	×	×	×	x		4.74	0.08	2.55	0.05	9.46	0.00
12	×	×	×	×	×	×	x	15.61	0.00	5.20	0.00	15.21	0.00

The best-supported models with the highest Akaike weights are highlighted in bold. For Douglas fir the more parsimonious model that included a marginal significant height-treatment interaction ($P = 0.09$) was rejected, since the main effects-only model fit the data equally well (ΔAIC = 0.01, w_i for both models = 30%).

size was less evident for oak growing in 2- or 3-species mixtures and fir growing either in monoculture or mixture. The mode of growth response to treatment effects, however, was significantly different among species and tree sizes (**Figure 2**). Oak and fir showed an additive response (summation of the single effects) to simultaneous N addition and drought, whereas the response of beech was non-additive (i.e., an antagonistic response of smaller and a synergistic response of larger individuals). This trend was consistent along the investigated diversity gradient, since we did not observe interacting effects of treatment and species composition (**Table 3**).

Compared to the control, RGR of small trees in the N treatment was lower for beech and oak, but higher for fir (**Figure 2**). In contrast to oak, growth rates of large beech and fir trees were enhanced by nitrogen enrichment ($P_{\text{adj.}} < 0.01$). In contrast, drought reduced height growth of all species and sizes with effects being strongest for large-sized beech trees ($P_{\text{adj.}} < 0.001$). The combination of N addition and drought was negative for all species, but size-dependency was strongest for beech. The sensitivity of oak and fir to N+D was equally high for small and large trees, with effects being much stronger for oak. Large beech trees, however, suffered most from N+D, resulting in a sevenfold decline in growth rates compared to small individuals. Thus, growth reductions induced by combined N and D effects of large individuals significantly increased within the series fir < oak < beech (all comparisons: $P_{\text{adj.}} < 0.05$; **Figure 2**).

TABLE 4 | Best-fitting mixed-effects models for RGR of tree height of (a) European beech (*Fagus sylvatica*), (b) Sessile oak (*Quercus petraea*) and (c) Douglas fir (*Pseudotsuga menziesii*).

Fixed effects	d.f.	*L*-ratio	*P*-value
(a) *Fagus sylvatica*			
Initial tree height (H)	1	56.3	<0.001
Treatment (T)	3	2.3	0.517
Species composition (C)	3	10.5	0.014
H × T	3	15.3	0.002
H × C	3	20.9	<0.001
(b) *Quercus petraea*			
Initial tree height (H)	1	4.2	0.040
Treatment (T)	3	6.7	0.082
Species composition (C)	2	1.2	0.543
H × C	2	10.0	0.007
(c) *Pseudotsuga menziesii*			
Initial tree height (H)	1	15.6	<0.001
Treatment (T)	3	8.4	0.039
Species composition (C)	2	9.2	0.002

P-values were derived from likelihood-ratio tests based on maximum likelihood (ML) estimations.

AGB was closely related to RGR, and the strength of the relationship did not significantly differ among species (Supplementary Figure S2).

Effects of Nitrogen Fertilization and Drought on Stand-Level Biomass Production

In the absence of D or N treatments the mixture effect on overall stand productivity was positive for all species mixtures (**Figure 3**). Overyielding was evident in 81% of the control plots and in 69% of the sites (blocks) across treatments (Supplementary Table S1), but we observed a large variation across sites (Supplementary Table S2).

The impact of global change drivers (D, N, or N+D) on the net biodiversity effect was driven by species identity rather than species diversity. Regardless of treatment, the average net diversity effects of beech-fir and beech-oak-fir stands remained positive and did not statistically differ from the control (**Figure 3**). In contrast, for beech-oak mixtures the magnitude and direction of diversity effects differed between treatments. N addition reduced the positive effect of species mixture to become

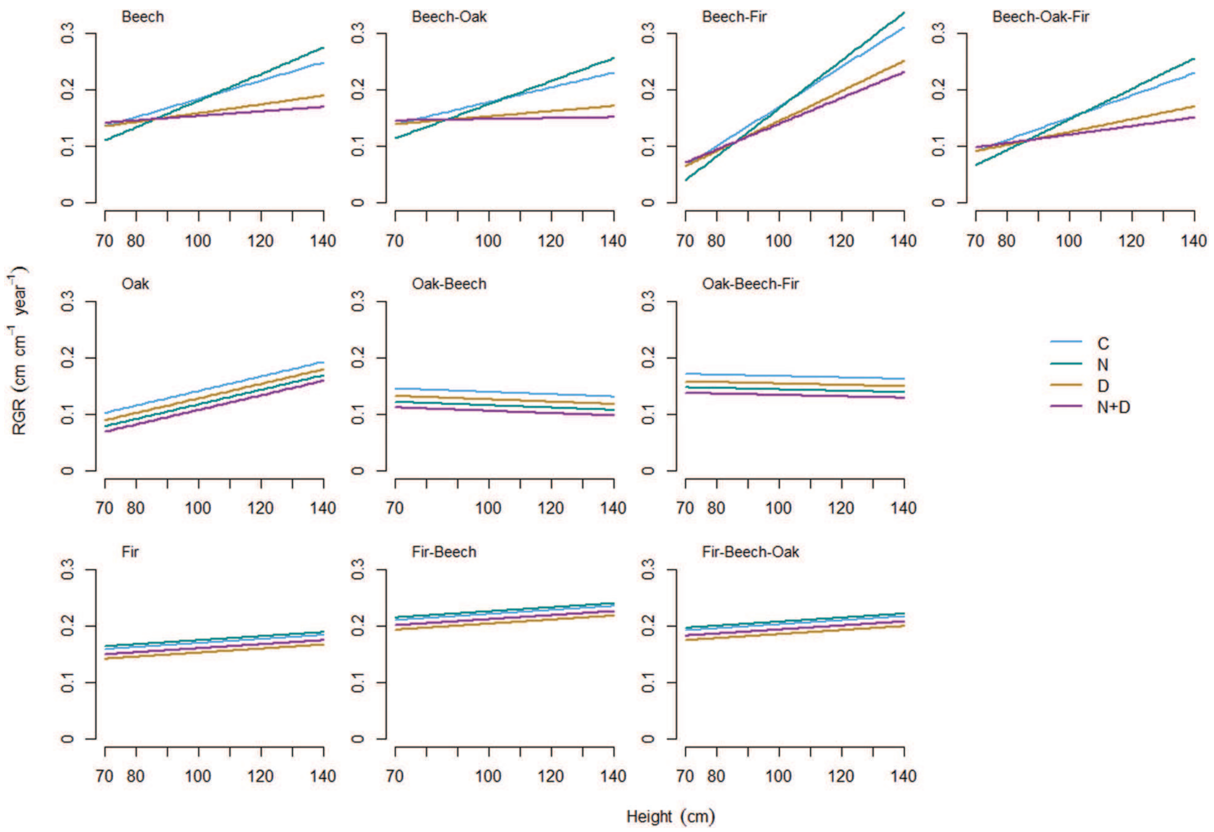

FIGURE 1 | Relationship between tree size (initial height), global change effects (C, control; N, nitrogen addition; D, drought; N+D: nitrogen addition plus drought), species diversity (monoculture; 2-species mixture, and 3-species mixture) and relative growth rate (RGR) of tree height for European beech (*Fagus sylvatica;* upper row), Sessile oak (*Quercus petraea;* middle row) and Douglas fir (*Pseudotsuga menziesii*; lower row). Regression lines are based on the predictions of the best-fitted models in **Table 4**.

neutral ($P = 0.1$), whereas the combined effects of N addition and drought caused a significant loss of biodiversity effects and underyielding, respectively ($P < 0.05$; **Figure 3**). This pattern can be primarily attributed to the loss of complementarity effects with regard to the N+D treatment ($P < 0.05$) and selection effects in relation to the N treatment ($P < 0.1$). Similarly, different underlying complementarity and selection effects were obvious for beech-fir and beech-oak-fir mixtures. In 61% of the beech-fir sites the selection effect was greater than the complementarity effect, particularly in the D treatment. Thus, high stand biomass productivities can be mainly ascribed to fir. In the 3-species mixture the selection effect became negative in the N+D treatment ($P = 0.1$) and neutral in the N treatment, but CE were always greater than SE (**Figure 3**).

DISCUSSION

Species-Specific Growth Response to Combined Effects of Nitrogen Addition and Drought

Our results show that tree growth response to treatments was mainly driven by species identity rather than species diversity, and the combined effects of N and D treatments proved to be both additive and non-additive. In the first case, the combined effects of N+D on RGR of tree height corresponded with the sum of the single effects (oak and fir), but in the latter case the combination of both factors caused negative growth responses, with mutually amplifying effects (for large beech trees, despite the positive single effect of N fertilization). This finding suggests that – at least in the case of beech – growth responses to environmental shifts are difficult to infer from species responses to single factors (Zavaleta et al., 2003). Several mechanisms may account for the non-additive effects of N+D treatments. First, N fertilization often results in a shift in biomass allocation patterns (in favor of aboveground biomass), resulting in a concomitant increase of biomass shoot-root ratios (Thomas and Hilker, 2000; Meyer-Grünefeldt et al., 2015b). For example, leave biomass investments of coniferous tree species increased with N fertilization (Högberg et al., 1993), and can thus increase the water consumption and probability of water stress (Nilsen, 1995). The responses described above are in agreement with the ‘resource optimization hypothesis’, according to which plants show (relatively) higher aboveground investments (and hence higher shoot-root ratios) with increasing nutrient availability

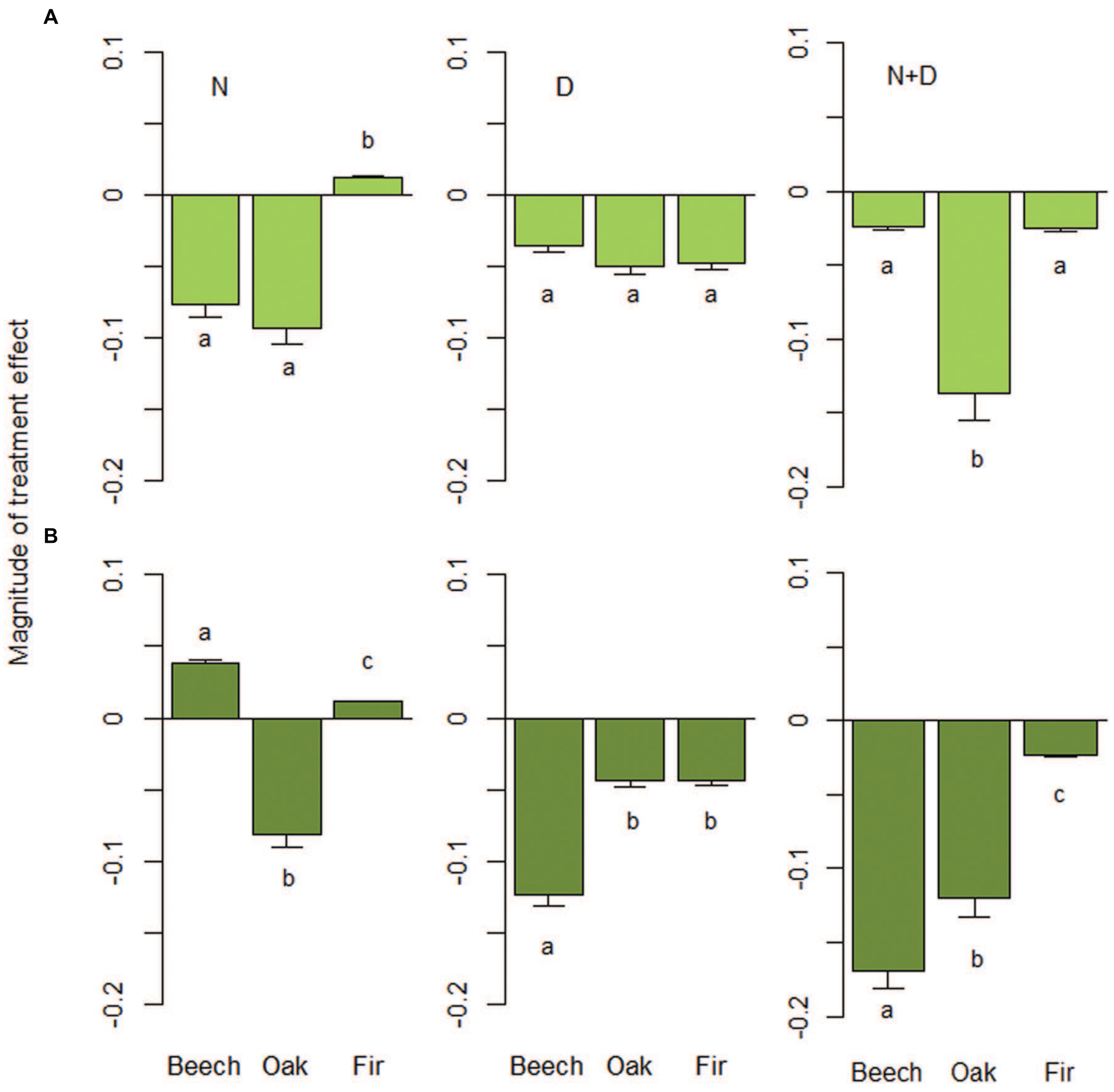

FIGURE 2 | Magnitude of treatment effect (MTE) for nitrogen addition (N), drought (D) and their combination (N+D). For each species (European beech: *Fagus sylvatica*, Sessile oak: *Quercus petraea,* and Douglas fir: *Pseudotsuga menziesii*), MTEs were predicted for **(A)** small-sized (initial height of 80 cm) and **(B)** large-sized trees (initial height of 130 cm) based on our best-fitting models (see **Table 4**). Error bars show standard errors based on across-species combination response. Different letters indicate significant differences (Tukey-test: $P < 0.05$) among species.

(McConnaughay and Coleman, 1999; Ågren and Franklin, 2003). High shoot-root ratios, in turn, can lead to increasing evaporative demands and thus a higher sensitivity to drought events (Meyer-Grünefeldt et al., 2015b). Second, N fertilization can increase fine- and coarse-root mortality and decrease the mycorrhiza colonization, both of which can impair supply and therefore increase their drought sensitivity (Hendricks et al., 2000; Nadelhoffer, 2000; Teste et al., 2012). Third, as trees can optimize the fine root and branch hydraulic system in water-limited environments (Hertel et al., 2013; Schuldt et al., 2016), an increasing N availability might prevent such adaptation mechanisms and therefore increase the suspectibility to drougth.

Tree species also responded differently to N fertilization, with a facilitation of (large) beech and fir trees, but adverse effects on oak. Deleterious effects of N fertilization on juvenile oak trees have also been reported in the study of BassiriRad et al. (2015), without a clear indication of the underlying mechanisms. In our study, species-specific responses are likely related to their traits and competitive hierarchy. Oak trees are light-demanding and may suffer from an unfavorable light environment when overgrown from larger neighbors, particularly at N-fertilized sites (Ellenberg and Leuschner, 2010). In this context, the strong size-asymmetry of treatment effects for beech suggests that our findings are related to size-asymmetric competition, because larger individuals mostly obtain a disproportionate share of

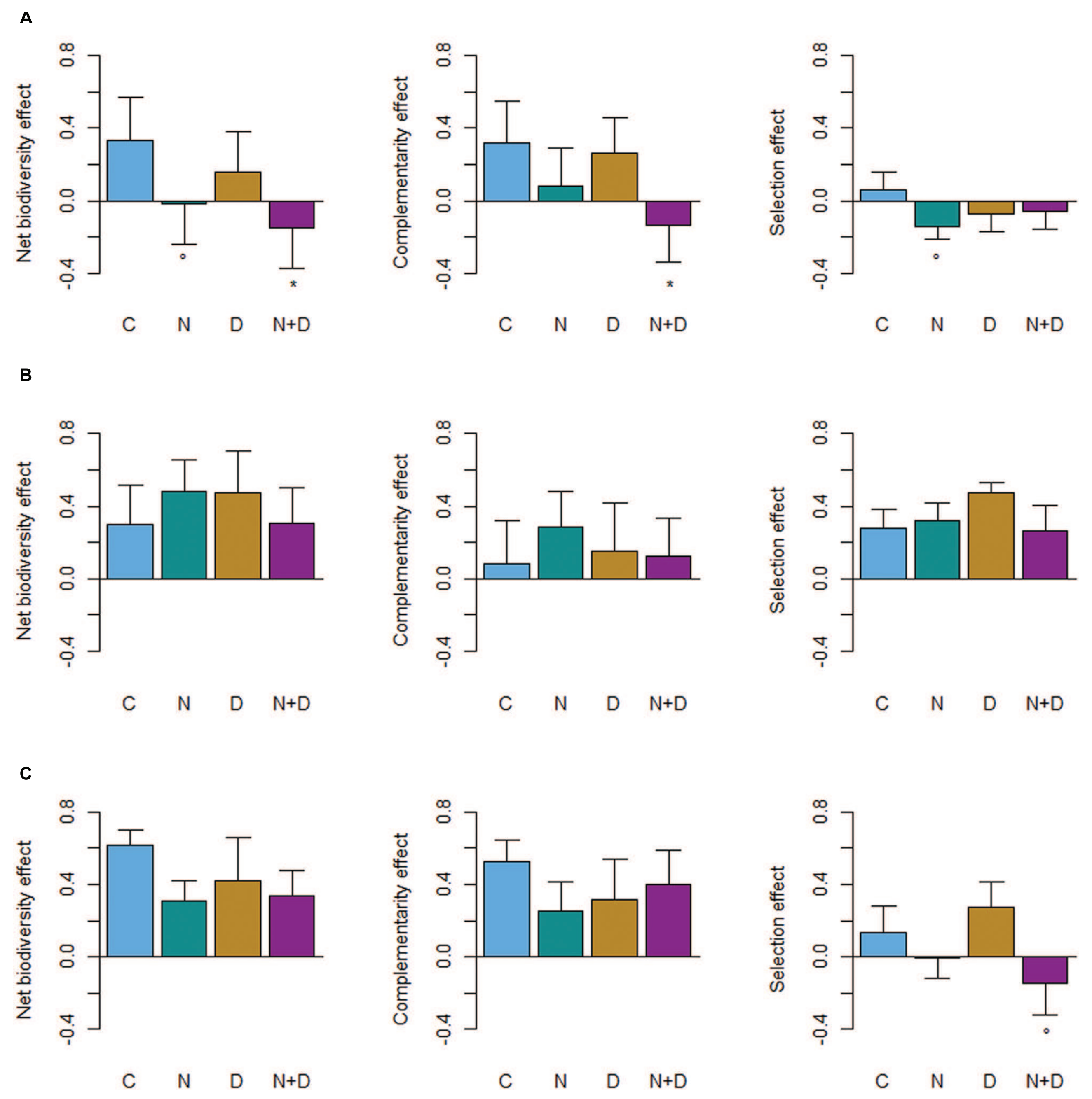

FIGURE 3 | Changes in net biodiversity, complementarity and selection effects with global change drivers (C, control; N, nitrogen addition; D, drought; N+D: nitrogen addition and drought) for (A) beech-oak stands (*Fagus sylvatica–Quercus petraea*), (B) beech-fir stands (*Fagus sylvatica–Pseudotsuga menziesii*), and (C) beech-oak- fir stands (*Fagus sylvatica–Quercus petraea–Pseudotsuga menziesii*). Values are square-root transformed to meet model assumptions while preserving the original positive and negative signs. Asterisks indicate significant differences ($P < 0.05$) and open circles marginal significant differences ($P \leq 0.1$) between the control (C) plots and global change driver (N, D, N+D) treatments.

resources and thus suppress the growth of smaller individuals (Potvin and Dutilleul, 2009). As a consequence, larger trees have a competitive advantage in resource acquisition over smaller individuals, and thus benefit most from additional nutrients, explaining the N-induced height growth decline of smaller oak and beech trees.

Species differences in the sensitivity to drought, as shown for larger individuals in our study, coincides with the well-known ecophysiology of these species (see for example Thomas, 2000; Geßler et al., 2007; Meier and Leuschner, 2008; Friedrichs et al., 2009; Härdtle et al., 2014). In a study of five temperate adult tree species, Zimmermann et al. (2015) found that beech is most susceptible to drought, which is in line with our observed increasing drought sensitivity as beech trees grew larger. Thus, species-specific differences in drought sensitivity might result in shifts in the competitive hierarchy in mixed-species tree communities. Our study, however, provided no evidence for changes of treatment effects depending on community composition. This suggests that treatment effects at the scale of individual trees were highly species-specific, and growth responses of juvenile trees to treatments were strongly mediated by the species' trait characteristics (also see discussion below) and local neigborhood conditions (Lübbe et al., 2015, 2016). An additional explanation to the statistically non-significant three-way interaction (H × T × C) and two-way interaction (T × C) is that diversity effects may need time to fully evolve in long-living plant communities such as forests, and therefore may become more pronounced as trees become larger.

We found that tree size-related changes in RGR were context-specific (neighborhood composition) and varied with species identity. Species interactions leading to a spatial complementarity in resource use due to differences in leaf habit (e.g., Coomes et al., 2009) are likely to be important in beech-fir mixtures. As a result, species mixing can mitigate drought susceptibility of mature beech trees by reducing intra-specific competition (Metz et al., 2016). In contrast, oak trees (as the most light-demanding species) proved to be week competitors (at least under the given experimental settings), and benefitted most from growing with conspecific neighbors. Thus, positive mixture effects in our study may be primarily the result of trait induced competitive hierarchies (Kunstler et al., 2012) and the species' trait characteristics also accounted for the observed interacting effects of tree size and species composition.

Functional Composition of Forests Modulate the Effects of Nitrogen Addition and Drought on Stand Productivity

Overyielding was evident for almost all plots across treatments, which is in agreement with many previous studies reporting a positive effect of tree diversity on forest productivity (e.g., Paquette and Messier, 2011; Vilà et al., 2013; Forrester and Bauhus, 2016). However, in our experiment the NE on stand-level productivity strongly depended on both the species composition and the species-specific responses to treatments. In the beech-oak mixture, we found a significant underyielding in the N+D treatment, attributable to negative N+D effects on CE. We hypothesize that the negative NE was brought about by the negative responses of beech and oak to N+D treatments already observed at the tree-level. This, in turn, would indicate that stand-level, and tree-level responses to 'environmental shifts' are closely related, or, more specifically, may depend on the trait characteristics of the species included in a mixture (Lübbe et al., 2015). This interpretation is supported by the result that we found no NE and a negative SE for beech-oak mixtures in the N treatment, likely brought about by the strong negative response of oak trees to N fertilization. We conclude that the resistance of a species mixture to environmental shifts may be more determined by the traits typical of the species included in a mixture than by the mere complementarity of the traits (or the functional dissimilarity) of these species (as given in the case of beech and oak). Biodiversity thus would not serve *per se* as an 'insurance' for the mitigation of global change effects on ecosystem functions (Lübbe et al., 2015), but would act in terms of a 'trait portfolio' that preserves a broad spectrum of functional traits enabling a species' resistance to environmental stressor (comparable to a lock-and-key model, according to which only particular traits ensure higher resistance of plant communities to environmental shifts; Polley et al., 2013). This perspective emphasizes the importance of both the quantity and quality of biodiversity for ecosystem resistance to environmental change (Mouillot et al., 2013).

The hypothesis provided above also supports the interpretation of treatment responses of those mixtures in which fir was included (i.e., beech-fir and beech-oak-fir mixtures). In these mixtures we found positive NE across treatments, suggesting that fir acted as a kind of 'buffer' mitigating the (partly negative) effects of N fertilization and drought. In the beech-fir mixture, positive NE were mainly attributable to SE, particularly in the D treatment. Obviously, the low sensitivity of fir to D and N+D treatments (of small and small + large trees, respectively; see Bansal et al., 2015) was conveyed to the stand-level, resulting in the observed positive NE across treatments. In the 3-species mixture, fir obviously mitigated the adverse effects of N and N+D observed for the beech-oak mixture, resulting in positive CE (substantially contributing to the NE). We hypothesize that trait-characteristics of fir mainly concurred to the observed response pattern (e.g., its low drought sensitivity; Bansal et al., 2015), resulting in an increased stand-level resistance of the tree-mixture. In summary, stand-level responses to treatments (and corresponding NE) were strongly mediated by species composition and the species' functional trait characteristics included in a mixture. This finding is in line with our observation on the individual tree level and matches observations in other tree diversity experiments, according to which species identity often proved to be as influential as species richness effects on productivity patterns (Jacob et al., 2010; Lang et al., 2012; Grossiord et al., 2013; Ratcliffe et al., 2015).

CONCLUSION

Our results highlight the importance of assessing interacting effects of nitrogen addition and drought to evaluate forest productivity in response to global environmental change. We are aware of the limitation to generalize results from juvenile tree field-experiments to adult tree communities, but manipulations of N and D treatments are hardly achievable in later forest development stages due to the longevity of trees. Hence, our experimental framework provides a unique opportunity to enhance our mechanistic understanding of tree growth in the context of global change by disentangling the effects of various global change drivers and their interactions unequivocally.

We found evidence that the magnitude and direction of combined global change driver effects depend on species identity and neighborhood composition (i.e., trait combination) rather than the level of tree species richness. Thus, species diversity might not mitigate *per se* the impact of drought and increasing N deposition in long-living plant communities. Instead, the occurrence of certain trait combinations ('trait portfolio') in diverse communities might act as an 'insurance' for the mitigation of global change effects on ecosystem functions. This suggests that the quality of trait composition ('lock-and-key principle') is a main component of the ecological insurance hypothesis.

AUTHOR CONTRIBUTIONS

WH and GvO conceived the study. CD performed the field and laboratory work, and AF analyzed the data. AF, CD, WH, and GvO wrote the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: http://journal.frontiersin.org/article/10.3389/fpls.2016.01100

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Chapter 13

Impacts of multiple environmental change drivers on growth of European beech (*Fagus sylvatica*): forest history matters

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Impacts of multiple environmental change drivers on growth of European beech (*Fagus sylvatica*): forest history matters

Katharina Mausolf[a*], Werner Härdtle[a], Dietrich Hertel[b], Christoph Leuschner[b] and Andreas Fichtner[a]

[a]Katharina Mausolf: Leuphana University of Lüneburg, Institute of Ecology, Universitätsallee 1, 21335 Lüneburg, Germany; [a]Werner Härdtle: Leuphana University of Lüneburg, Institute of Ecology, Universitätsallee 1, 21335 Lüneburg, Germany; [b]Dietrich Hertel: University of Goettingen, Albrecht von Haller Institute for Plant Sciences, Plant Ecology and Ecosystems Research, Untere Karspüle 2, 37073 Göttingen, Germany; [b]Christoph Leuschner: University of Goettingen, Albrecht von Haller Institute for Plant Sciences, Plant Ecology and Ecosystems Research, Untere Karspüle 2, 37073 Göttingen, Germany; [a]Andreas Fichtner: Leuphana University of Lüneburg, Institute of Ecology, Universitätsallee 1, 21335 Lüneburg, Germany

* Correspondence: K. Mausolf: katharina.mausolf@leuphana.de

Abstract

Revealing the interactive effects of multiple environmental change drivers (water deficits, nitrogen (N) deposition, land-use change) is crucial for evaluating actual and possible future changes in forest ecosystem functioning. Here, we analyse whether and to what extent combined effects of spring and summer water deficits and variable amounts of N deposition affect radial growth of beech trees growing on forest sites with a different forest history. Dendrochronological data showed that trees growing on ancient forest sites (forest continuity > 200 years) exhibit a higher negative growth response under high N deposition and simultaneous spring water deficits than trees growing on recent (post-agricultural) forest sites. Based on additional analyses of the fine root system and masting behaviour, we propose two different mechanisms to explain differing influences of N deposition and water deficits on negative radial growth responses in recent and ancient forests: (1) for both forest history types, growth reductions during summer water deficits result from the antagonistic effects of elevated N deposition according to the 'resource optimization hypothesis'. The tendency towards higher negative growth responses in recent forests seem to be caused by a higher fine root mortality and lower standing fine root biomass compared to ancient forests; (2) higher growth reductions in ancient forests during spring water deficits are likely the result of mass fructification, which is enhanced by N deposition. We conclude that nutrient cycling may differ between forests with contrasting forest history, which can modulate the growth trajectories of forests in response to multiple, co-occurring environmental changes.

Keywords: ancient forests, climate change, European beech, mast event, nutrient cycling, phosphorus legacy effect, recent forests, reproduction-growth trade-off

INTRODUCTION

Both, climate change and increasing levels of atmospheric nitrogen (N) deposition are considered important drivers of environmental change that alter key processes in forest ecosystems (Lindner and others 2010; Greaver and others 2016) and impose threats to forest biodiversity (Sala and others 2000). Although there is increasing evidence of the (single) effects of climate shifts and N deposition on tree growth, our understanding of conceivable interaction effects of these drivers of environmental change is still limited. Furthermore, many forest ecosystems of old cultural landscapes, for example in Central Europe, are characterised by a long history of land-use changes, which in turn might affect their response to present changes in environmental conditions (Perring and others 2016). It is therefore key to understand the interactive effects of land-use legacies and multiple drivers of global change to predict future forest responses in terms of important functions such as biomass production and carbon (C) sequestration. In particular, little is known about the interactive effects of forest history and drivers of environmental change on tree growth, such as simultaneous water deficits in the growing season and atmospheric N deposition.

In large parts of Central Europe, beech forest ecosystems represent the potential natural vegetation, and European beech (*Fagus sylvatica* L.) is considered to be one of the most economically and ecologically important tree species (Leuschner and Ellenberg 2017). Beech is competitively superior to other tree species in many areas of Central Europe, even though it is acknowledged that beech is highly sensitive to drought (Leuschner and Meier 2018), meaning that beech shows higher climate warming-related growth declines compared to other European tree species (Zimmermann and others 2015). The climate-growth response of beech was observed to vary with factors such as precipitation (Müller-Haubold and others 2013), elevation (Di Filippo and others 2007; Dulamsuren and others 2017), forest management history (Mausolf and others 2018a), and tree species composition of the stand (Metz and others 2016).

There is evidence that N deposition (as a single driver of environmental change) has several effects on forest ecosystem functioning. According to Michel and others (2018), atmospheric deposition of reactive N compounds in forest ecosystems enhance the risk of soil acidification, or have profound consequences for forest productivity and plant species composition. N deposition has been found to reduce the diversity and alter the species composition of the forest ground vegetation and of epiphytic lichens in temperate forests (Bobbink and others 1998). On the tree level, N deposition can increase both foliar N content and stand leaf area, thereby promoting C gain and C sequestration (De Vries and others 2014; Schulte-Uebbing and De Vries 2018). Correspondingly, a stimulating effect of moderate N deposition on stem growth increment was found for temperate beech forests (Gentilesca and others 2018).

Fore beech, experimental (Dziedek and others 2016, 2017) and observational (Hess and others 2018) studies demonstrated that the combined effects of multiple environmental change drivers are non-additive, where N deposition enhance a trees' climate sensitivity. This response was mainly related to an increase in the shoot-to-root ratio. According to the 'resource optimization hypothesis', which predicts plants to allocate less C to roots and to increase shoot-to-root ratio with increasing nutrient availability (Ågren and Franklin 2003), an increase in drought sensitivity of fertilized plants can be attributed to both; changes in the fine root system (Dziedek and others 2017; Hess and others 2018) and a higher evaporative demands aboveground (Meyer-Grünefeldt and others 2013). Thus, we can assume a direct non-additive effect on radial growth, when two environmental change drivers (water deficits and N deposition) act together.

Beside this direct effect of environmental change drivers on the radial stem growth of beech, the increased frequency of mast years (e.g. years with a high fruit production) in European beech stands has been identified as a cause of periodic growth declines (Hacket-Pain and others 2015). Instead of investing resources such as C and N into radial growth, they are consumed to produce large seed crops, which reduces radial growth in mast years ('reproduction-growth trade-off'; Hacket-Pain and others 2015). Evidence exists that high temperatures or high solar radiation in the previous summer function as triggers of high seed production (Müller-Haubold and others 2015), suggesting a second pathway, through which future climate extremes could influence the radial growth of beech (Hacket-Pain and others 2018). However, the impact of N deposition on seed production is still debated (Müller-Haubold and others 2015; Braun and others 2017). It is conceivable that N deposition exerts an indirect, mast-mediated effect on the radial growth of beech as well and, thus, (non-additively) interacts with climate extremes.

In regions with a long forest use history, the currently acting drivers of environmental change and their effect on forest productivity and stress response may further depend on possible legacies of former land use, which likely act through altered soil nutrient and/or water availability (Bürgi and others 2017; Maes and others 2018). For example, former land use such as past agricultural activity has been found to cause long-lasting shifts in soil chemical properties (Fraterrigo and others 2005; von Oheimb and others 2008; Kopecký and Vojta 2009; Blondeel and others 2018) and soil microbiomes (Fichtner and others 2014; De la Peña and others 2016) in recent forest ecosystems. Altered edaphic conditions due to land-use legacies, in turn, were shown to indirectly affect the susceptibility of tree growth to adverse climatic conditions (von Oheimb and others 2014), mediated by changes in fine root biomass and morphology (Mausolf and others 2018b).

Based on this knowledge we used dendroecological data of beech trees growing in stands differing in forest history. Additionally we used climate variables, N deposition data, and records of mast intensity to disentangle possible (non-additive) effects on the growth of adult beech trees in a fully factorial approach. We hypothesized that (i) forest history, and therefore legacies of former land use, alter the response of adult beech trees to the simultaneous acting of water deficits and high N deposition, and (ii) mast intensity plays a crucial role in mediating the growth response of beech to water deficits and N deposition.

MATERIAL AND METHODS

Study sites and study design

The study was conducted in beech forests (Galio-Fagetum community) near the city of Kiel in northern Germany (Schleswig-Holstein, 54°19' N, 10°7' E). The area is characterized by a sub-oceanic climate with a mean annual precipitation of 777 mm and a mean annual temperature of 8.5°C (DWD Climate Data Center 2017). Elevation ranges from 32 to 81 m a.s.l. Soils originated from deposits of the last (Weichselian) glaciation and consist of till (clay/sandy loam) with varying carbonate content in deeper soil layers. The predominant soil types are (pseudogleyic) Luvisols.

To assess the effect of former land use on the growth response of beech to varying environmental conditions, we identified eight forests dominated by beech (canopy cover of beech >90 %) that differed in former land-use history: Ancient forests (*n* = 4), characterized by a continuity in forest cover of at least 230 years (indicated in historical maps); and recent forests (*n* = 4), established between 1870 and 1930 on former agricultural land (grassland: *n* = 3, arable land: *n* = 1). To avoid confounding effects between land-use history and stand or site characteristics (Fraterrigo 2013), we restricted the analyses to stands that were similar in stand structure (i.e. mature, even-aged stands) on sites with similar topography (level terrain) and edaphic conditions (i.e. (very) good nutrient and water supply). All investigated beech stands have been managed for at least 100 years (see Table 1 for further stand and target tree attributes). Within each stand, we randomly established 2-5 study plots (40 × 40 m), resulting in a total of 28 plots. All trees within a plot with diameter at breast height (DBH; at 1.30 m) >7 cm were measured in 2014. For each measured tree, DBH and species identity were recorded.

Tree-ring analyses

In each plot, we randomly selected ten dominant beech trees of the upper canopy, resulting in a total of 280 target trees. To determine radial growth rates, we cored target trees at 1.30 m height above ground and extracted two bark-to-pith increment cores perpendicular to each other from the southern and eastern side of the trees using a borer of 0.5 cm diameter and 40 cm length (Suunto 400, Vantaa, Finland) in 2014. The preparation and measurement of the wood cores followed the protocol of Mausolf and others (2018b) using a core-microtome of WSL (Birmensdorf, Switzerland) for surface preparation and measuring annual tree-ring width (TRW) from bark to pith with a measuring table (resolution of 0.01 mm; IML GmbH, Wiesloch, Germany) and the IML software T-Tools Pro (version 1.4, IML GmbH, Wiesloch, Germany). Subsequently, single TRW series per tree were cross-dated. We used the cross-dating index provided by TSAP-Win (Version 4.69k, Rinntech, Heidelberg, Germany) to evaluate matches between the two cores of a tree. A CDI > 20 was used as a threshold. Accordingly, the cores of 37 of the 280 trees (13 %) were omitted due to inconsistent matching between the two cores of a tree. Afterwards, the averaged TRW series per tree were standardized for size- and age-related differences between trees. We used the moving-average standardization procedure provided by the software TSAP-Win to retain as much as possible of the interannual climate signal within the chronologies. First, we calculated the five-year moving average trend of each chronology. In a second step, tree-ring series were divided by the five-year moving average trends, resulting in a dimensionless index of tree-ring width (TRI) (Dulamsuren and others 2017). Descriptive dendrochronological statistics were based on individual tree chronologies and calculated using TSAP-Win (Table 1).

Climate, nitrogen deposition, and mast intensity data

We used the standardized precipitation-evapotranspiration index (SPEI) to quantify temporal changes in climatic conditions. The SPEI represents a climatic water balance index that comprises both precipitation and potential evapotranspiration (Vincente-Serrano and others 2010) and allows best to analyse the effects of

Table 1 Summary statistics of structural stand characteristics of the 28 study plots in 2014 and target tree characteristics of the 243 target trees for the period investigated (2000-2013).

	Ancient forests Mean (SE)	Recent forests Mean (SE)
Stand characteristics		
Forest continuity (years)	>230	100-140
Stand density (stems ha^{-1})	177.94 (18.60)	198.08 (14.25)
Stand basal area (m^2 ha^{-1})	34.49 (1.74)	34.41 (2.06)
Species composition (%)		
beech	95.84	91.70
others	4.16	8.30
n (plots)	15	13
Target tree characteristics		
Age (years)[a]	**126.89 (1.48)**	**101.31 (2.30)**
Mean diameter at breast height (cm)	**58.23 (0.56)**	**54.07 (0.70)**
$TRW_{2000\text{-}2013}$ (mm)	2.17 (0.07)	2.51 (0.09)
Maximum $TRW_{2000\text{-}2013}$ (mm)	3.49 (0.09)	3.95 (0.12)
Minimum $TRW_{2000\text{-}2013}$ (mm)	**0.88 (0.04)**	**1.25 (0.07)**
SD ($TRW_{2000\text{-}2013}$)	0.77 (0.02)	0.78 (0.02)
AC ($TRW_{2000\text{-}2013}$)	**0.21 (0.02)**	**0.30 (0.02)**
n (trees)	134	109

[a] values are related to cambial age at coring height. TRW: Tree-ring width index; SD: standard deviation; AC: first-order autocorrelation. Values are means and standard errors (SE, in brackets). Significant differences (p <0.05) between the two forest history types are highlighted in bold. *P*-values for target tree characteristics were obtained from mixed-effects models using study plot as random effect; all stand characteristics data from Mausolf and others (2018b).

climate change in beech tree-ring chronologies for variable time scales (Bhuyan and others 2017). SPEI data were extracted from the Global SPEI database (http://spei.csic.es/database.html, accessed 14.09.2017) for the nearest 0.5 grid cell (54°45' N, 10°25' E). We selected climate indices for spring and summer conditions, as beech has been shown to be most sensitive to climatic variations during these periods (Lebourgeois and others 2014; Hacket-Pain and others 2015; Bosela and others 2016). For each season, we used aggregated SPEI values based on a three-month period (i.e. $SPEI_{spring}$ for March, April, May; $SPEI_{summer}$ for June, July, August; Figure S1).

Nitrogen deposition data (N_{dep}) for the years 2000-2013 were provided by the German Environment Agency (UBA, Dessau, Germany) and based on monthly deposition measurements within a grid of gauging stations across Germany (UBA 2014). Measurements were conducted with wet-only-samplers (type ARS 721, according to the VDI standard 3870) (LLUR 2010; UBA 2014). N_{dep} sampling was conducted near the city of Bornhöved in the framework of the Level II permanent monitoring plot network which is part of the International Co-operative Program on the Assessment of Air Pollution Effects on Forests, established to perform ecosystem-related studies on cause-effect relationships (Michel and others 2018). Distance between the N_{dep} sampling site and the investigated forest sites is 35 km at maximum, we therefore assume that the Bornhöved data describe the deposition climate at our sites well. N_{dep}-values were calculated as the sum of the amount of N deposited in the form of ammonium (NH_4^+-N in kg ha^{-1} a^{-1}) and nitrate (NO_3^--N in kg ha^{-1} a^{-1}). To reduce the number of explanatory variables in our models, we used Pearson correlations to evaluate the linkage between different N_{dep}-values and annual TRI values of single trees. We tested for correlation between the seasonal (spring and summer) totals of deposited N in the year of ring formation and in the year previous to tree-ring formation, as well as for the totals of deposited N during the entire growing season (April to October) and annual deposition data. The tightest correlation between TRI and N_{dep}-values was found for values of the current growing season and N_{dep} for the current summer (r = -0.37; p <0.001; r = -0.38; p <0.001; Pearson correlation between TRI and deposited N during growing season and summer, respectively). As N_{dep} in the growing season (N_{depGS}) and N_{dep} in summer show a high collinearity, we only used N_{depGS} as explanatory variable (Figure S1).

Information about the frequency of beech masting was derived from Dammann and others (2016), who give masting intensity as the percentage of beech trees showing high seed production in a given year in the federal state Schleswig-Holstein. Since masting events in beech generally occur synchronously over larger spatial scales (Packham and others 2012), data from Dammann and others (2016) were considered applicable for our study sites (see Hacket-Pain and others 2018 for a similar approach).

Fine root data and soil chemical properties

To characterise beech fine root mass at each of the 28 plots, we randomly selected six sampling locations per plot for the fine root inventory in October 2015. Sampling was conducted by using a soil borer (3.5 cm diameter) to a depth of 30 cm of the mineral horizon. The soil cores were divided in two fractions, 0-10 cm depth and 10-30 cm depth. To determine the fine root biomass and necromass root samples were cleaned from soil residuals above a sieve (mesh size. 0.5 mm). Afterwards fine root fractions (rootlets >10 mm in length, <2 mm in diameter) were divided by species identity (beech vs. other species) and living and dead rootlets under a stereo-microscope. Selection criteria (i.e. colour, root elasticity and cohesion of the cortex, periderm and stele) following Hertel and others (2013). Sorted fine roots were dried at 70° C for 24h, afterwards dry matter of living and dead beech fine roots were determined for each soil depth separately. As the highest proportion of the fine root system is located in the uppermost soil layers here we only use the values for 0-10 cm depth.

In addition, soil chemical properties of the 28 plots were analysed in 2015 and published by Mausolf and others 2018b (for a description of the methods see Mausolf and others 2018b). The chemical characterisation of the soils showed differences between the stands which are likely caused by former land-use. Soils of recent forests were associated with significantly lower carbon to phosphorus (C/P) ratios and a tendency towards a higher base saturation (BS). Soil chemical properties of the uppermost 10 cm of the mineral soil are shown in Table S1.

Data analysis

The time series of available N_{dep} data restricted our analyses to the period 2000-2013. In this interval, we found six years with positive and eight years with negative $SPEI_{spring}$-values, whereas eight years were characterised by positive and six with negative $SPEI_{summer}$-values. Nitrogen deposition during the growing season (N_{depGS}) ranged between 5.3 and 10.2 kg N ha^{-1} a^{-1} (Figure S1). We applied linear mixed effects models to test whether N_{depGS}, shifts in the climatic water balance during spring ($SPEI_{spring}$) and summer ($SPEI_{summer}$), and former land use (forest history) exert interacting effects on TRI. To account for spatial dependency, 'study plot' was used as a random effect. We used a compound symmetry correlation structure to account for temporal autocorrelation among years ('tree' nested in 'plot'; Zuur and others 2009). Competing models were evaluated by sequential comparison (backward selection) based on the Akaike Information Criterion (AIC) and maximum likelihood. Furthermore, we simplified the model with the lowest AIC value by removing non-significant terms. Parameter estimates of the final model were fitted using the restricted maximum likelihood (REML) method (Zuur and others 2009). We fitted a global model containing climatic conditions during spring and summer to account for both effects simultaneously. All continuous predictors were standardized (mean = 0, SD = 1) before analysis.

To evaluate the linkage of N deposition during the growing season and radial tree growth, we performed confirmatory path analysis by using structural equation model (SEM) techniques (Grace and others 2012, Lefcheck 2016). As the radial growth of beech is greatly influenced by masting which is triggered by high temperatures during the previous summer, we included information on masting intensity and the mean maximum temperature during previous June and July (Max_{JJ-1}) derived from the CRU TS gridded dataset (v 4.01, Harris and others 2014) to our models (see Hacket-Pain and others 2018 for a related approach). We hypothesised that the effect of N deposition on radial growth consists not only of a fertilizer effect, i.e. a direct positive influence on tree growth, but there is also an indirect pathway of N deposition on tree growth mediated through masting intensity. Confirmatory path analysis were performed for each forest history type (ancient forests vs. recent forests) separately, using pooled values of TRI per year and forest history type to reduce all variables to single annual values. To account for temporal correlation among subsequent years, we used generalized least square models with a first-order autoregressive correlation structure. Model fits were evaluated by using the model fit statistics *Fisher's C* and *p-values*. Models were checked for missing paths by using the *dSep*-function of *piecewiseSEM*.

Prior to analyses, data exploration was performed following Zuur and others (2010) and model assumptions were visually checked and confirmed according to Zuur and others (2009). All analyses were conducted in R (version 3.5.1) using the packages *MASS* (Venables and Ripley 2002), *nmle* (Pinheiro and others 2016), *piecewiseSEM* (Lefcheck 2018) and *vegan* (Oksanen and others 2016).

RESULTS

On average, TRW tended to be higher in recent than in ancient forests (2.51 mm vs. 2.17 mm, respectively), but this difference was not significant (Table 1). However, ancient forests showed a significantly lower mean minimum TRW than recent forests (0.88 mm vs. 1.25 mm, p <0.05, Table 1). The best-fitting growth model revealed positive effects of SPEI and negative effects of N_{depGS}, with the effect of N_{depGS} on TRI being stronger than that of SPEI (Table 2).

The best-fitting growth model showed a three-way interaction between N_{depGS}, $SPEI_{spring}$ and forest history type (Fig 1; Table 2; p =0.006). Under low N_{depGS}, radial growth in both forest history types was only little influenced by negative climatic water balances during spring; a negative response in radial growth, i.e. negative TRI values, due to water deficits was predicted to occur only in the trees of the ancient forests (Fig 1a). In contrast, radial growth of trees growing in recent forests did not show a strong response to water deficits in spring and responded only slightly with increased radial growth rates to a more positive climatic water balance. In the ancient forests, radial growth was significantly promoted by a more positive climatic water balance (Fig 1a). Moreover, the increase in radial growth rates was steeper in ancient forests than in recent forests under slightly negative $SPEI_{spring}$- values. While deterioration of the climatic water balance did not have a marked negative effect on TRI under low N_{depGS}-rates, high N_{depGS} caused a strong negative response of radial growth rates in both forest history types even under ample water supply (Fig 1b). The negative response in radial growth rates under negative $SPEI_{spring}$- values was stronger for the trees of ancient than recent forests.

The best-fitting growth model indicated that high N_{depGS} and negative $SPEI_{summer}$-values have a negative interactive effect on TRI (Fig S2; p <0.001), and this effect was consistent across forest history types. Furthermore, radial tree growth responses tended to be more sensitive to water deficits during summer in recent forests, as indicated by the marginal significant interaction between $SPEI_{summer}$ and forest history type (p < 0.0572). Due to the marginal significance this interaction term was removed from the best-fitting growth model.

Table 2 Regression coefficients of the best-fitting mixed-effects model for tree-ring width index (TRI) of European beech for spring and summer.

	Estimate (SE)	*p*-value
Intercept	-0.095 (0.01)	<0.001
$SPEI_{spring}$	0.387 (0.02)	<0.001
$SPEI_{summer}$	0.423 (0.02)	<0.001
N_{depGS}	-0.457 (0.02)	<0.001
Forest history type (RF)	-0.013 (0.01)	0.234
$SPEI_{spring}$ × N_{depGS}	0.168 (0.02)	<0.001
$SPEI_{summer}$ × $N_{dep\ GS}$	0.305 (0.02)	<0.001
N_{depGS} × RF	0.076 (0.02)	0.001
$SPEI_{spring}$ × RF	-0.092 (0.03)	<0.001
$SPEI_{spring}$ × N_{depGS} × RF	0.047 (0.02)	0.006

Predictor estimates were standardized, hence their magnitude is proportional to the effect size. Note that the intercept refers to the response of ancient forests, while 'RF' indicates recent forests. $SPEI_{spring}$: standardized precipitation-evapotranspiration index aggregated for March, April and May; $SPEI_{summer}$: standardized precipitation-evapotranspiration index aggregated for June, July and August; N_{depGS}: total of deposited nitrogen (N) during the growing season (April-October; kg N ha^{-1} a^{-1}); SE: standard error.

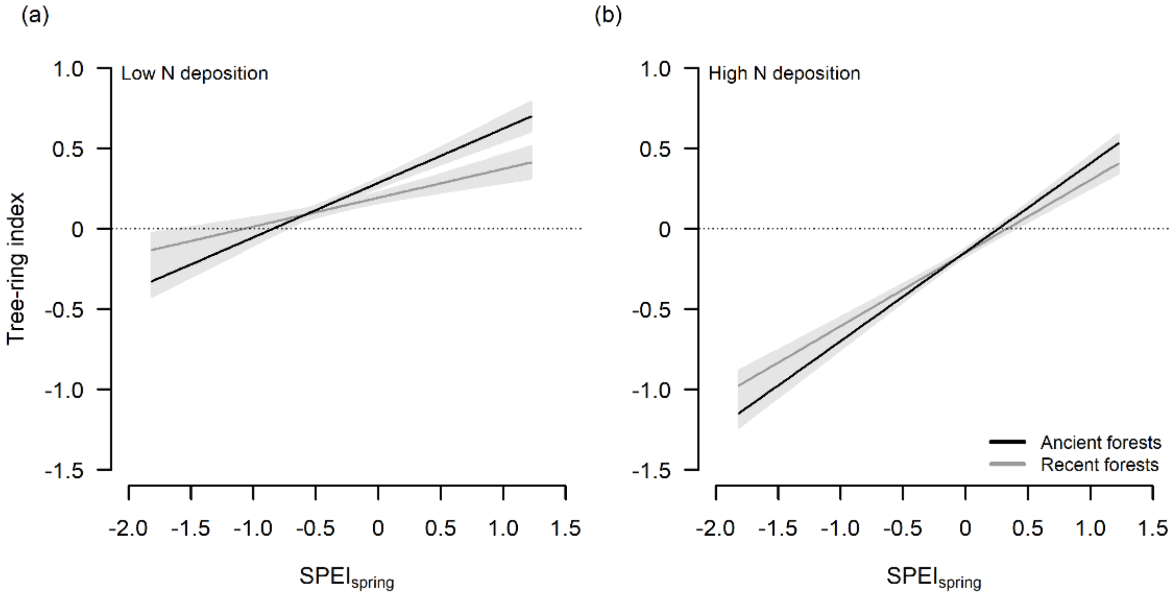

Figure 1 Effect of forest history type (ancient vs. recent forests) on the growth (tree-ring width index, TRI) response of European beech to interannual fluctuations in the climatic conditions during spring (2000–2013) considering **(a)** years with low nitrogen (N) deposition (30% quantile) and **(b)** years with high N deposition (70% quantile). The climatic gradient is characterised by the standardised precipitation-evapotranspiration index (SPEI) aggregated for the months March to May. Negative SPEI values display conditions with a tendency of water deficits (negative climatic water balance), positive values display conditions with ample water supply (positive climatic water balance). Lines correspond to the predicted response based on mixed-effects models and shaded areas indicate the 95% confidence interval.

In contrast to the effects of SPEI$_{spring}$, we found no significant three-way interaction between N$_{depGS}$, SPEI$_{summer}$ and forest history type.

For each forest history type, the confirmatory path analyses provided a good fit to the data (Fisher's C = 1.787, $p = 0.409$, df = 2 for ancient forests; Fisher's C = 1.219, $p = 0.544$, df = 2 for recent forests). Directed separation analysis confirmed no missing paths within the models. The path analyses confirmed a significant indirect effect of N$_{depGS}$ on radial tree growth through masting intensity. N$_{depGS}$ was positively related to masting intensity (with 31% of the variation of masting intensity explained), which in turn negatively affected TRI. This effect was only significant for the trees of the ancient forests (Fig. 2). A direct effect of N$_{depGS}$ on TRI was not significant for both forest history types, and it tended to be negative. The explained variation in TRI was slightly higher for ancient forests (R^2 = 0.36 and R^2 = 0.45 for recent and ancient forests, respectively).

DISCUSSION

Our findings confirm our first hypothesis that forest history, and therefore legacies of former land use, alters the response of adult beech trees to the simultaneous effects of water deficits and high N deposition. The separate analysis of data from spring (March to May) and summer (June to August) produced different results with respect to the role of forest history in modulating the radial growth response to multiple environmental change drivers. On the one hand, high N deposition combined with summer water deficits led to a negative trend in radial increment in both forest history types. On the other hand, sensitivity to high N deposition and water deficits in spring was higher in trees from the ancient forests, as indicated by the three-way interaction between spring climate conditions, N deposition during the growing season, and forest history type.

Direct effects of N deposition and water deficits on radial growth

In general, our results are in line with other studies on the effects of high N deposition, which found antagonistic effects of high N loads and

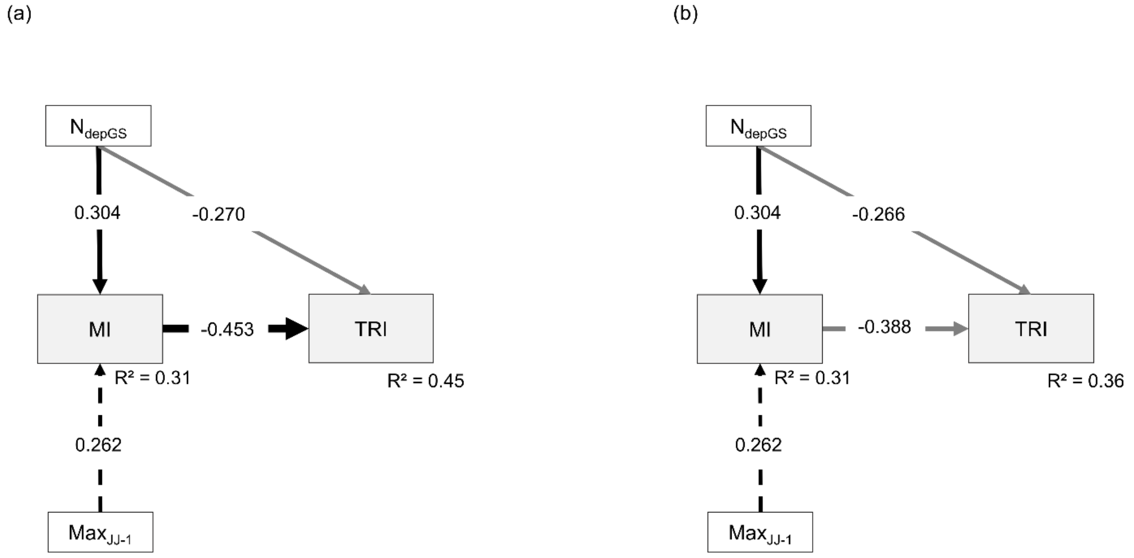

Figure 2 Confirmatory path analyses linking nitrogen (N) deposition and climate conditions, mast intensity and tree growth in **(a)** ancient forests and **(b)** recent forests across the years 2000-2013. Black solid, grey solid, and dashed lines indicate significant ($p < 0.05$), non-significant ($p > 0.1$) and marginal significant ($p < 0.1$) relationships, respectively. Positive and negative numbers at arrows are standardized regression coefficients; thus, the magnitude of the coefficients is proportional to their effect size. R^2-values for each endogenous variable are given below the boxes. Abbreviations: MI: Mast intensity (% of trees showing a high seed production), TRI: Tree-ring width index, N_{depGS}: Cumulative amount of N deposited during the growing season (April-October, kg N ha^{-1} a^{-1}), Max_{JJ-1}: Mean maximum temperature during June and July of the previous year.

high growing season temperatures on the radial growth of adult beech (i.e. Braun and others 2017; Hess and others 2018). Hess and others (2018) suggested that N fertilization triggers an aboveground shift in plant-internal resource allocation which is in line with the predictions of the resource optimization hypothesis (Ågren and Franklin 2003) and assumed a possible decline in root productivity. A reduced fine root biomass in N-rich soils as the consequence of high N deposition could explain a lower radial growth rate in the face of water deficits, as the trees might be more susceptible to summer water deficits in both forest history types.

Radial growth of trees tended to be more sensitive to water deficits during summer than radial growth of trees in ancient forest stands (interaction $SPEI_{summer}$ × forest history type; $p = 0.0572$). This might be the result of differences in the fine root biomass of the investigated stands, which in turn are related to by changes in soil chemical properties through former land-use activities (Mausolf and others 2018b, Table S1). Physiologically even more relevant could be the observation that the fine root necromass:biomass ratio was about two times higher in the recent than the ancient forests, pointing at a higher root mortality in the former (Fig. S3). While it is unclear, whether the lower fine root biomass and higher root necromass:biomass ratio in the recent forests is a consequence of the higher P and N availability or is caused by other edaphic factors, it is likely that a reduced fine root biomass:aboveground biomass ratio increases the trees' susceptibility to water deficits.

N deposition effects on growth mediated through mast fruiting and possible interaction with water deficits

Interactive effects of water deficits in spring and elevated N deposition increased the sensitivity of radial growth of trees growing in ancient forests. Confirmatory path analyses clearly suggest that mast intensity plays a crucial role in mediating growth responses of beech trees to water deficits and N deposition, thus confirming our second hypothesis. Beech as a masting tree species produces a large number of nuts every three to six years, which alternate with non-seed years (Packham 2012). As high seed production comes at a high cost in terms of resource consumption, vegetative growth (i.e. radial stem growth) in mast years, and sometimes in subsequent years as well, is lower than in non-mast years (Mund and others 2010; Hacket-Pain and others 2015; Müller-Haubold and others 2015). During recent decades, the frequency of mast events as well as the seed crop itself has increased in many beech stands across Central Europe (Övergaard and others 2007; Paar and others 2011; Müller-Haubold and others 2015), suggesting that climatic or edaphic drivers of fruit production have changed. The mechanisms triggering the synchronous investment of a large amount of resources into reproduction in beech are still a matter of debate. High temperatures, and also high radiation intensities during the period of bud formation in previous-year summer were found to be a key driver for the switch from vegetative growth to the investment of resources into reproduction (Övergaard and others 2007; Müller-Haubold and others 2015; Hacket-Pain and others 2018; Lebourgeois and others 2018). Additionally, pollination success during spring is a strong driver for the production of large amounts of seed crop (Pearse and others 2016; Lebourgeois and others 2018; Nussbaumer and others 2018), as beech is a self-incompatible, wind-pollinated species (Packham 2012). Since beech nuts are relatively rich in N, nitrogen availability in particular is discussed as a key driver of masting (Smaill and others 2011; Bogdziewicz and others 2017). In a study about the resource consumption with seed crop production in *Fagus crenata*, Abe and others (2016) found that inner seed maturation highly depends on N availability. Furthermore, Miyazaki and others (2014) showed that N is a key regulator for the expression of various genes responsible for flowering in *Fagus crenata*, indicating that high N availability promotes flowering and fruit ripening. Hence, the physiological basis for an N deposition effect on the reproduction dynamics of *Fagus* is quite well understood. The path analyses confirmed a positive effect of N deposition on masting intensity in the *Fagus sylvatica* trees of our study, which is in agreement with these findings. We are aware of the limitation to generalize results from short-term N deposition time series (i.e. N deposition data were only available from 2000 to 2013 in this study). However, our results suggest that simultaneously occurring environmental change drivers may not only affect radial growth responses of beech trees, but may also change their reproductive behaviour.

An interesting finding is that a significant negative effect of masting intensity on TRI was only found for trees growing in ancient forests, but not for those of the recent forests. The shift in resource investment (C and N) from vegetative growth (i.e. radial stem growth) to reproductive growth (i.e. seed production) thus seems to be stronger in trees growing in ancient forests. We hypothesize that the apparently more pronounced reproduction-growth trade-off in ancient forests is caused by a higher sensitivity of these less disturbed systems to the mast-triggering effect of increased availability of reactive N compounds, which would be in line with the resource matching hypothesis according to which a plant's resource investment varies with resource availability (Abe and others 2016; Kelly 1994). Given that more research is needed to evaluate the mechanisms underlying the observed differences in radial growth response between forest history types, our findings suggest that recent and ancient forests may be associated with different modes of nutrient acquisition and recycling, which in turn can influence many other ecosystem properties (Lang and others 2016). Consistently lower C/P- and C/N-ratios in the soils of the recent forests might therefore indicate that these forest history types are characterised by more open (acquiring) nutrient cycles. In contrast, ancient forests (associated with lower P availability in the uppermost mineral soil layer and lower N availability in deeper mineral soil layers) likely are characterised by tighter (recycling) nutrient cycles (Lang and others 2016), which should be more responsive in growth to reproduction-mediated effects of additional N input.

CONCLUSIONS

Overall, we assume that the different growth responsiveness of beech in ancient and recent forests to N deposition and water deficits is likely a consequence of differences in nutrient cycling and availability, caused by partial interruption of biogeochemical cycles and land-use influences in the past. Water deficits in spring in combination with elevated N deposition have therefore the potential to promote a reproduction-growth trade-off of beech trees primarily growing in ancient forests. Our results indicate that the 'ecological memory' of a forest is a crucial component for assessing ecosystem reactions to simultaneously acting environmental change drivers. It should be noted that our data does not allow for exploring forest history-mediated effects of simultaneous long-term N deposition and water deficits on radial tree growth and reproduction behaviour.

Thus, it would be valuable in future research to assess the role of forest history in modulating complex relationships between co-occurring shifts in environmental conditions based on long-term observations and larger spatial scales.

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Part III

Forest management and global change

Chapter 14

Higher drought sensitivity of radial growth of European beech in managed than in unmanaged forests

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Higher drought sensitivity of radial growth of European beech in managed than in unmanaged forests

Katharina Mausolf[a*], Paul Wilm[a], Werner Härdtle[a], Kirstin Jansen[a], Bernhard Schuldt[b], Knut Sturm[c], Goddert von Oheimb[d], Dietrich Hertel[b], Christoph Leuschner[b] and Andreas Fichtner[a]

[a]*Leuphana University of Lüneburg, Institute of Ecology, Universitätsallee 1, 21335 Lüneburg, Germany;* [b]*University of Goettingen, Albrecht von Haller Institute for Plant Sciences, Plant Ecology and Ecosystems Research, Untere Karspüle 2, 37073 Göttingen, Germany;* [c]*Community Forest Lübeck, Alt Lauerhof 1, 23568 Lübeck, Germany;* [d]*Technische Universität Dresden, Institute of General Ecology and Environmental Protection, Pienner Straße 7, 01737 Tharandt, Germany*

[*]Correspondence author: K. Mausolf, mausolf@leuphana.de

Abstract

Climate extremes are predicted to become more frequent and intense in future. Thus, understanding how trees respond to adverse climatic conditions is crucial for evaluating possible future changes in forest ecosystem functioning. Although much information about climate effects on the growth of temperate trees has been collected in recent decades, our understanding of the influence of forest management legacies on climate-growth relationships is still limited. We used individual tree-ring chronologies from managed and unmanaged European beech forests, located in the same growth district (i.e. with almost identical climatic and soil conditions), to examine how forest management legacies (recently managed with selection cutting, >20 years unmanaged, >50 years unmanaged) influence the radial growth of *Fagus sylvatica* during fluctuating climatic conditions. On average, trees in managed stands had a 50% higher radial growth rate than trees in unmanaged stands during the last two decades. However, the beech trees in the unmanaged stands were less sensitive to drought than those in the managed stands. This effect was most pronounced in the forest with longest management abandonment (>50 years), indicating that the drought sensitivity of mature beech trees is in these forests the lower, the longer the period since forest management cessation is. Management-mediated modifications in crown size and thus water demand are one likely cause of the observed higher climate sensitivity of beech in the managed stands. Our results indicate a possible trade-off between radial growth rate and drought tolerance of beech. This suggests that reducing stem density for maximizing the radial growth of target trees, as is common practice in managed forests, can increase the trees' drought sensitivity. In the prospect of climate change, more information on the impact of forest management practices on the climate-growth relationships of trees is urgently needed.

Keywords: Canopy release, climate change, drought sensitivity, forest thinning, management legacy, radial growth

INTRODUCTION

Forests dominated by European beech (*Fagus sylvatica;* hereafter: beech) represent the natural vegetation of large parts of Central Europe (due to its oceanic to sub-oceanic climate; Leuschner & Ellenberg 2017) and they play an important role for Europes' forestry sector. The increasing variability of climate and the more frequent occurrence of climatic extremes such as heat waves and severe droughts (IPCC 2013), however, will impact tree growth in future (Easterling et al. 2000; Anderegg et al. 2015). Specifically, there is increasing evidence that beech is more sensitive to climatic extremes than most other Central European broadleaf tree species (Köcher et al. 2009; Zang et al. 2014; Zimmermann et al. 2015; Kunz et al. 2018), and the species shows a recent growth decline at sites even in the core of its distribution range, which was attributed to climate warming (Cavin & Jump 2017; Knutzen et al. 2017). In this context, various forest management practices have been proposed to reduce the climate change impact on temperate forests, e.g. reducing stand density, promoting structural diversity and tree species richness or introducing drought-tolerant tree species or genotypes (Keenan 2015; Ammer

2017). For example, numerous studies have shown that thinning can mitigate the impact of drought on tree growth due to a reduced water demand at the stand level (e.g. D'Amato et al. 2013; Bosela et al. 2016; Sohn et al. 2016). Other studies, however, indicate that the short-term benefits of thinning may in the longer term enhance the trees' susceptibility to drought due to altered tree architecture and physiological constitution (e.g. leaf area/sapwood area ratio) (McDowell et al. 2013; Clark et al. 2016; Jump et al. 2017). Given that trees are long-lived organisms which may have an 'ecological memory' (Johnstone et al. 2016), legacy effects of land-use and silvicultural treatments should have an important influence on the trees' climate sensitivity (Perring et al. 2016). Recent research has provided evidence that the drought sensitivity of beech depends partly on the type of former land-use (i.e. farmland vs. forest) and forest continuity (Mausolf et al. 2018). However, studies investigating legacy effects of forest management in paired managed and unmanaged forests remain rare. Although Bosela et al. (2018) found recently in a cross-European study that the climate sensitivity of beech seems not to depend on forest management, as the long-term response of the trees to adverse climatic conditions was similar in unmanaged and managed forests, our understanding of legacy effects of forest management on climate-growth relationships at the local neighbourhood level remains rudimentary.

Here, we use individual tree-ring chronologies (i.e. the tree-ring series of individual trees) from managed and long-term (>50 years) and short-term (>20 years) unmanaged European beech forests to explore, how forest management history affects the radial growth of *F. sylvatica* during fluctuating climatic conditions. To examine the link between forest management and climate sensitivity, we applied a local neighbourhood approach to model climate-growth relationships of target trees in response to neighbour removal. Specifically, we asked the following questions: (i) Are there legacy effects of forest management which modulate the growth of individual trees in response to climate extremes? (ii) Is drought sensitivity mediated by the length of abandonment of forest management? and (iii) What are the underlying mechanisms driving possible differences in climate-growth relationships in managed and unmanaged forests?

MATERIALS AND METHODS

Study design and stand characteristics

The study was conducted in Baltic beech forests (Galio-Fagetum community) of the forest district Stadtwald Lübeck (53°47' N, 10°37' E; total forest area: 4657 ha), which is located in the moraine landscapes of south-eastern Schleswig-Holstein, Northwest Germany (Fig. S1). Elevation ranges from 0 to 90 m asl. The study area is characterised by a sub-oceanic climate with a mean annual precipitation of 789 mm and a mean annual temperature of 8.3 °C (DWD 2017a). Edaphic conditions of the beech forests investigated are characterised by moderately moist to moist moraine soils originating from the last (Weichselian) glaciation. Soil texture consists of till (clay/sandy loam) with varying carbonate content in the deeper layers of the mineral soil, providing an optimal nutrient and water supply for tree growth.

We selected four stands in European beech forests located at four different study sites (Fig. S1). The study stands reflect a gradient of forest management history that ranged from long-term (>50 years; U50-SZ) and short-term (>20 years; U20-HEV) unmanaged (U) to managed (M; M-BKS, M-RIZ; abbreviations of localities see Table 1) beech forests. M-BKS and M-RIZ are managed according to a low-impact approach (e.g. single-tree harvest with minimal thinning interventions and the development of high growing stocks) based on the protection of natural disturbance regimes within managed stands (for more detailed information see Sturm 1993). Since differences in the forest continuity of a site can modulate tree growth responses to climate extremes (Mausolf et al. 2018), we chose study sites that had a forest continuity for at least 200 years according to Glaser & Hauke (2004) to allow a meaningful comparison between managed and unmanaged stands. Moreover, to avoid confounding effects between forest management history and stand or site characteristics, we restricted the analyses to stands that were similar in tree species composition, stand age, topography and soil type, but differed in their management history. All stands were dominated by *F. sylvatica* (>95%), were located in level terrain and had (pseudogleyic) Luvisols as the predominant soil

Table 1 Summary statistics of structural and edaphic properties of the study stands. Values are means and their standard error (in brackets). Different superscript letters indicate significant ($P_{adj.}$ <0.05) differences between study sites. DBH: diameter at breast height, H/D-ratio: height/diameter-ratio, C: carbon, N: nitrogen, P_{resin}: resin extractable phosphorus, CEC: cation exchange capacity, BS: base saturation. Average harvested timber volume since 1994: M-BKS 30.73 m^3 ha^{-1}; M-RIZ 55.07 m^3 ha^{-1}).

	Schattiner Zuschlag (U50-SZ)	Hevenbruch (U20-HEV)	Berkenstrücken (M-BKS)	Ritzerau (M-RIZ)
Stand characteristics				
Management history	unmanaged >50 years	unmanaged >20 years	managed	managed
Tree species composition				
Beech (%)	100	100	100	96
Oak (%)	0	0	0	4
Stand volume (m^3 ha^{-1})^1	903	690	652	613
Stand basal area (m^2 ha^{-1})	58.83	33.97	39.40	28.48
Stem density (n ha^{-1})	368.75	193.75	187.50	156.25
DBH (cm)	43.96 (1.31) $^{n.s.}$	44.50 (2.90) $^{n.s.}$	46.51 (4.20) $^{n.s.}$	45.05 (3.48) $^{n.s.}$
Tree height (m)^2	40.94 (0.14) ^{a}	36.33 (0.29) ^{b}	39.29 (0.23) ^{c}	36.72 (0.28) ^{b}
H/D-ratio^2	0.77 (0.01) ^{a}	0.64 (0.01) ^{b}	0.61 (0.01) ^{b}	0.63 (0.01) ^{b}
Soil properties				
Soil type	(pseudogleyic) Luvisol	(pseudogleyic) Luvisol	(pseudogleyic) Luvisol	(pseudogleyic) Luvisol
pH (H_2O)	4.10 (0.07) ^{a}	3.71 (0.08) ^{b}	4.42 (0.21) ^{a}	3.57 (0.03) ^{b}
C_{total} (%)	4.35 (0.47) ^{ab}	8.60 (1.44) ^{a}	3.69 (0.42) ^{b}	6.86 (1.53) ^{ab}
N_{total} (%)	0.28 (0.03) ^{ab}	0.49 (0.07) ^{a}	0.26 (0.02) ^{b}	0.38 (0.07) ^{ab}
C:N	15.87 (0.34) ^{ab}	17.57 (0.32) ^{a}	14.31 (0.58) ^{b}	17.81 (0.69) ^{a}
P_{resin} (mg g d.m.$^{-1}$)	0.10 (0.02) $^{n.s.}$	0.13 (0.03) $^{n.s.}$	0.08 (0.03) $^{n.s.}$	0.16 (0.03) $^{n.s.}$
C:P_{resin}	453.26 (63.65) $^{n.s.}$	689.19 (82.68) $^{n.s.}$	513.90 (118.98) $^{n.s.}$	471.87 (98.26) $^{n.s.}$
CEC (µmol$_c$ g d.m.$^{-1}$)	97.41 (10.08) ^{ab}	123.36 (7.93) ^{b}	77.51 (11.45) ^{a}	82.16 (11.76) ^{ab}
BS%	23.72 (3.93) $^{n.s.}$	11.75 (2.47) $^{n.s.}$	30.91 (7.52) $^{n.s.}$	16.74 (3.42) $^{n.s.}$

^{1} values refer to the data obtained from the permanent sample plot inventory in 2013

^{2} values refer to ten randomly selected canopy trees

type (Table 1). Tree age of the canopy trees ranged between 105 and 120 years (Table 2).

To characterise stand structure, we selected a representative 40 x 40 m plot within each stand. All trees with a diameter at breast height (DBH; at 1.30 m) larger than 7.5 cm were measured, and for each measured tree, species identity and DBH were recorded. Tree height was measured for ten randomly selected trees of the upper canopy. Structurally, the studied stands are multi-layered and uneven-aged and developed from natural regeneration (Fig. S2). Mean stem density amounted to 281 trees ha^{-1} in the unmanaged stands, and to 172 trees ha^{-1} in the managed stands, reflecting the harvest of target trees. Correspondingly, mean stand basal area was 37% larger in unmanaged compared to managed stands (U: 46.4 m^2 ha^{-1}, M: 33.9 m^2 ha^{-1}). Soil chemical properties were analysed based on four randomly selected soil samples of the upper mineral soil horizon (A-horizon). Within each stand, soil samples were taken using a metallic corer (volume: 100 cm^3). Analyses were performed following the detailed protocol described by Leuschner et al. (2014). Total carbon (C), nitrogen (N) and resin-extractable phosphorus (P_{resin}), base saturation (BS), cation exchange capacity (CEC) and pH-values (measured in H_2O) were determined from sieved and homogenised soil samples. Soil carbonate content was estimated through the evolution of CO_2 after adding HCl, showing that all topsoil samples were free of carbonate. Therefore, all measured soil carbon was assumed to represent soil organic carbon (SOC). Stand characteristics and soil properties are summarized in Table 1. Soil chemical properties did not significantly vary between managed and unmanaged stands

Table 2 Differences in target tree characteristics and tree-ring statistics of European beech growing in stands with different forest history. Values are means and their standard error (in brackets). Different superscript letters indicate significant ($P_{adj.}$ <0.05) differences between study sites. DBH: diameter at breast height; BAI: Basal area increment; TRW: Tree-ring width; AC (TRW): AC: first-order autocorrelation, expressing the interannual TRW persistence.

	Schattiner Zuschlag (U50-SZ)	Hevenbruch (U20-HEV)	Berkenstrücken (M-BKS)	Ritzerau (M-RIZ)
Target tree characteristics[1]				
Management history	unmanaged >50 years	unmanaged >20 years	managed	managed
Tree age (years)[2]	107.77 (1.86) ^{a}	119.97 (1.82) ^{b}	103.59 (2.03) ^{a}	104.93 (1.52) ^{a}
Diameter at 1.30 m (cm)	57.45 (0.65) ^{a}	59.60 (0.67) ^{ab}	61.81 (0.71) ^{b}	61.23 (0.68) ^{b}
Basal area (cm^2)	2602.18 (59.99) ^{a}	2799.81 (64.27) ^{ab}	3011.41 (68.95) ^{b}	2954.67 (64.95) ^{b}
Tree height (m)	41.74 (0.10) ^{a}	36.39 (0.36) ^{b}	37.28 (0.40) ^{b}	34.97 (0.45) ^{c}
Crown projection area (m^2)	75.01 (3.78) ^{a}	91.21 (4.05) ^{b}	117.11 (4.34) ^{c}	127.21 (4.72) ^{c}
Aboveground biomass (MgC)	1.87 (0.05) $^{n.s.}$	1.74 (0.05) $^{n.s.}$	1.92 (0.05) $^{n.s.}$	1.77 (0.06) $^{n.s.}$
Tree-ring statistics[3]				
BAI (cm^2 $year^{-1}$)	20.86 (0.73) ^{a}	21.77 (0.89) ^{a}	27.93 (1.21) ^{b}	28.28 (1.24) ^{b}
TRW (mm)	2.48 (0.05) ^{a}	2.40 (0.06) ^{a}	2.92 (0.07) ^{b}	2.92 (0.08) ^{b}
Maximum TRW (mm)	5.12 (0.15) ^{a}	5.09 (0.17) ^{a}	5.44 (0.14) ^{ab}	5.70 (0.17) ^{b}
Minimum TRW (mm)	0.39 (0.03) ^{a}	0.48 (0.03) ^{ab}	0.74 (0.07) ^{c}	0.58 (0.04) ^{bc}
AC (TRW)	0.70 (0.02) ^{a}	0.66 (0.02) ^{ab}	0.65 (0.02) ^{ab}	0.60 (0.02) ^{b}
Number of target trees	30	29	29	30

[1] values refer to the date of sampling (2016)

[2] tree age is related to cambial age at coring height

[3] values refer to tree chronologies (mean across the entire lifespan of each tree), note that 'Hevenbruch' was managed until 1994

(PERMANOVA: F = 1.28, P = 0.292; Fig. S3). However, there was a trend towards slightly higher soil fertility at the U50-SZ and M-BKS sites than at U20-HEV and M-RIZ (Table 1).

Tree data

Within each study stand, we randomly selected 30 beech trees from the upper canopy with similar DBH (57-62 cm; Table 2) resulting in a total of 120 target trees. For each target tree, DBH, tree height and crown projection area (CPA) were determined in spring 2016. CPA was calculated as the area of a disc derived from averaging over four crown diameter measurements. Wood volume was calculated based on DBH and tree height measurements using the allometric function for European beech of Bergel et al. (1973). Tree volume was then converted in aboveground biomass (AGB, in MgC) by applying the wood density value of beech for monocultures (665.43 kg m^{-3}; Zeller et al. 2017) and the standard conversion of 0.5 gC per gram of biomass.

To assess the impact of forest management on climate-growth relationships, all selected target trees in the managed stands were located north to a management-induced gap created by single tree harvesting, and defined by the closest cut stump (target stump) of a crop tree. Mean estimated target stump diameter was 72 cm, and mean distance between target tree and cut target stump amounted to 7 m. Mean number of cut stumps within the local neighbourhood (i.e. closest neighbours) of a target tree amounted to 2.8. All stumps were associated with later decay stages, meaning that the estimated stump age was greater than 10 years. To ensure meaningful comparisons between managed and unmanaged stands, selected target trees growing in unmanaged stands were surrounded by neighbours to avoid effects of natural gaps.

Wood coring and tree ring analysis

For each target tree, we collected one bark-to-pith increment core at 1 m height above the ground in spring 2016. Cores were taken from the cardinal points west to east using an increment borer (Suunto 400, Vantaa, Finland, 0.5 cm diameter and 40 cm length). Each core was air-dried in the laboratory and annual tree-ring width (TRW) was measured from bark to pith with 0.01 mm resolution (see Mausolf et al. 2018 for more detailed information). To minimise measurement errors, cross-dating of single tree chronologies was performed by using site chronologies from former studies conducted in the same study region as a reference (Mausolf et al. 2018). Cross-dating was done following Mausolf et al. (2018). Due to incomplete and broken wood cores, we omitted two trees from subsequent analyses. To minimise the effect of tree age on annual growth rates, TRW data of individual tree chronologies were standardized. Standardization was performed in TSAP-Win by first calculating the five-year moving average trend of each chronology. In a second step, measured tree-ring series were divided through the five-year moving average trends, resulting in a dimension-less index of tree-ring width (TRI) (for more information see Dulamsuren et al. 2017). As TRI is centred around zero, negative values indicate growth decline, whereas positive values indicate growth stimulation. Radial growth measurements were performed using IML software T-Tools Pro (Version 1.4, Instrumenta Mechanik Labor GmbH, Wiesloch, Germany). Descriptive dendrochronological statistics were based on individual tree chronologies and calculated using TSAP-Win (Table 2). For further analyses we used individual tree rather than site chronologies (i.e. pooled tree-ring chronologies of a given site) to account for the variability in individual growth responses, which has been shown to be crucial, when assessing the response of forest ecosystems to climate change (Carrer 2011; Zang et al. 2014).

Climate data

To quantify changes in climatic conditions, we used the standardized precipitation-evapotranspiration index (SPEI), which is a climatic water balance index that considers precipitation and potential evapotranspiration (Vicente-Serrano et al. 2010) and allows to study the effects of climate change for varying time scales (Bhuyan et al. 2017). Following Buyan et al. (2017) describing the SPEI of different timescales to show best explanatory power in climate-growth analyses of beech we decided to use SPEI for further analyses. SPEI data were extracted from the Global SPEI database (http://spei.csic.es/database.html, accessed 14.09.2017) for the nearest 0.5 grid cell (54°45’ N, 10°45’ E), meteorological data were achieved from the nearest weather station (DWD 2017b). We selected climate indices for spring, summer and previous summer conditions, as beech has been shown to be most sensitive to climatic variations during these periods (Lebourgeois et al. 2014; Hacket-Pain et al. 2015). We calculated SPEIs for different time scales (ranging from one to six months), and selected those periods that showed the strongest correlation (Pearson correlation) with TRIs (across all target trees and study stands) during the analysed timespan (1995-2014). The following SPEIs, based on a three-month time scale, were used in the climate-response analysis: seasonal values for current spring (March, April, May; SPEI-spring; $r = 0.33$; $P < 0.001$), summer (June, July, August; SPEI-summer, $r = 0.22$; $P < 0.001$) and previous summer (June, July, August; SPEI-previous summer, $r = 0.15$; $P < 0.001$), based on a three-month period.

Data analysis

We used linear mixed-effects models to test whether climate-growth relationships vary with forest management history. We limited our analysis to the recent (1995-2014) climate regime for several reasons: First, the study site ‘Hevenbruch’ (U20-HEV), our short-term unmanaged stand, was managed until 1994. Second, detailed information on management history was only available for this period. Third, climatic fluctuations were strongest during recent decades (IPCC 2013). Thus, effects of management history are assumed to be most relevant during this period. TRI was used as response variable, and climate indices (SPEI-spring, SPEI-summer, SPEI-previous summer), tree size (using basal area) and management type (managed vs. unmanaged forest) were used as explanatory variables. To test for a potential dependence of climate effects on forest management history, we additionally considered all possible two-way interaction terms between management type and climate indices. To account for differences in abiotic site conditions, the studied stand was used as a random effect. Moreover, we used a first-order autoregressive covariance structure (AR-1) to account for temporal autocorrelation in observations among years (tree nested within stand; Zuur et al. 2009). Different competing models were evaluated by sequential comparison (backward selection) based on the Akaike Information Criterion (AIC) and maximum likelihood (ML) estimation, using the *stepAIC* function in R. We further simplified the model with the lowest AIC value by removing all terms that were not significant according to likelihood ratio tests. Parameter estimates of the final model were fitted using the restricted maximum likelihood (REML) method (Zuur et al. 2009). All continuous predictors were standardized (mean = 0; SD = 1) before analysis.

We used Hedges'*d* effect size as a standardized measure to quantify the mean difference of the effects of forest management legacies on TRI during climate extremes (Hedges & Olkin 1985). We defined extreme climate events (extremely dry or extremely wet) as those periods with the lowest and highest SPEI during the last two decades (1995-2014), respectively (Table S1). Note that negative values of SPEI indicate periods with water deficit, and vice versa. Hedges' *d* effect size was calculated based on observed TRI values. Positive values of Hedges' *d* indicate stronger responses, meaning growth stimulation (positive TRI values) or growth reduction (negative TRI values), of beech growing in managed compared to unmanaged beech forests, and vice versa. Hedges' *d* values of 0.2, 0.5 and 0.8 indicate a small, moderate and large effect, respectively (Koricheva et al. 2013).

Differences in stand, soil and target tree characteristics among the study stands were analysed using analysis of variance (ANOVA) followed by a post-hoc test (Tukey-HSD). Data exploration was performed prior to all analyses, following Zuur et al. (2010). Furthermore, model assumptions were visually checked and confirmed according to Zuur et al. (2009). All analyses were performed in R (version 3.3.1.) using the packages MASS (Venables & Ripley 2002), nmle (Pinheiro et al. 2016) and vegan (Oksanen et al. 2016).

RESULTS

On average, radial growth rates were 27% to 83% higher in managed (BKS: 43.41 ± 2.42 cm^2 year^{-1}, RIZ: 42.26 ± 2.36 cm^2 year^{-1}) than in unmanaged stands (HEV: 33.33 ± 2.32 cm^2 year^{-1}, SZ: 23.61 ± 1.46 cm^2 year^{-1}) during the last two decades ($P_{\text{adj.}}$ <0.05; Fig. S3). The best-fitting growth model included positive effects of tree basal area and SPEI (i.e. climatic conditions in spring, summer and previous summer), with climatic effects on TRI being strongest for variation in spring (Table 3). For SPEI-summer, the climate-growth relationship was consistent across managed and unmanaged stands. The sensitivity of beech growth to climatic conditions in spring and previous summer, however, depended on forest management history, as indicated by the significant interaction between management type and SPEI-spring and SPEI-previous summer, respectively (both: *P* <0.01; Table 3). Results based on SPEI were qualitatively the same compared to those using precipitation and temperature data separately, meaning that TRI of trees in managed stands was more strongly related to changes in current year spring precipitation as well as previous year summer temperature than those growing in unmanaged stands (Table S2).

Table 3 Regression coefficients from the best-fitting mixed-effects model for tree-ring width index (TRI) of European beech (*Fagus sylvatica*). Predictor estimates were standardized, hence their magnitude is proportional to the effect size. Note that the intercept refers to the response of unmanaged stands, while 'M' indicates managed stands. BA: basal area, SPEI: standardized precipitation-evapotranspiration index, SE: standard error.

Fixed effects	Estimate	SE	*P*-value
Intercept	-0.064	0.022	0.005
BA	0.054	0.016	<0.001
SPEI-spring	0.320	0.022	<0.001
SPEI-summer	0.260	0.015	<0.001
SPEI-previous summer	0.226	0.022	<0.001
Managed stands (M)	-0.060	0.032	0.207
SPEI-spring * M	0.129	0.031	<0.001
SPEI - prev. summer * M	0.082	0.031	0.008

Growth stimulation (i.e. positive TRI-values) was higher in managed stands during years with ample water supply (i.e. positive SPEI-values; Fig. 1), but the benefit of trees growing in managed stands during climate extremes (extremely wet) was not significant (Hedges' *d*: 0.29; Fig. 2a). In contrast, trees in unmanaged stands showed considerably lower growth reduction (i.e. negative TRI-values) during years with a water deficit (i.e. negative SPEI-values) compared to those growing in managed stands, with effects

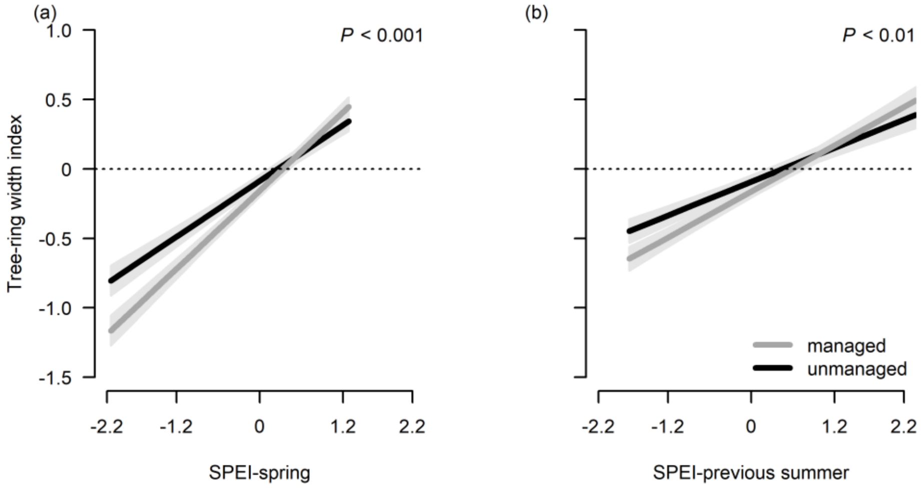

Figure 1 Effect of management history (managed versus unmanaged forests) on the growth (tree-ring width index, TRI) responsiveness of European beech (*Fagus sylvatica* L.) to interannual fluctuations in climate during the last two decades (1995–2014) considering (a) the response to the climatic water balance during spring and (b) the response to the climatic balance during the previous summer. Periodic water surplus or deficits are estimated by the standardized precipitation-evapotranspiration index (SPEI) in a seasonal (three month) resolution. Negative values of SPEI indicate a water deficit, positive values a positive climatic water balance. Lines correspond to the predicted response based on mixed-effects models and shaded areas indicate the 95% confidence interval. The basal area and SPEI-summer parameter estimate were fixed at their mean values.

being stronger for drought events in spring (Fig. 1a) than in previous summer (Fig. 1b). Particularly, during severe drought, trees in unmanaged stands exhibited significantly lower growth decline compared to those in managed stands (Hedges' *d*: 0.94; *P* <0.05; Fig. 2b). Such effects of forest management history became even stronger when considering the length of forest management abandonment. Values of Hedges' *d* increased from 0.46 (short-term unmanaged vs. managed stands; *P* <0.05) to 1.42 (long-term unmanaged vs. managed stands; *P* <0.05). Moreover, growth reduction during extreme drought in spring was positively related

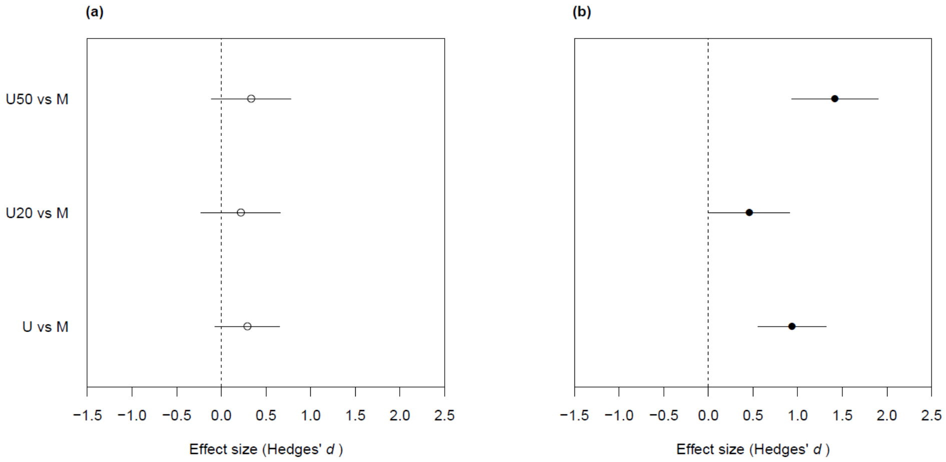

Figure 2 Effects of forest management history on (a) growth stimulation (i.e. positive tree-ring width indices) and (b) growth reduction (i.e. negative tree-ring width indices) of European beech (*Fagus sylvatica*) during climate extremes in spring (extremely dry or extremely wet events). Error bars denote the 95% confidence intervals. Closed circles indicate significant (*P* <0.05) and open circles indicate non-significant (*P* >0.05) effect sizes. Positive values indicate stronger responses (growth stimulation or reduction) of beech growing in managed compared to unmanaged beech forests, and vice versa. M: managed, U50: unmanaged >50 years, U20: unmanaged >20 years; U: U50 + U20.

to crown projection area (P <0.01; Fig. 3), meaning that trees with large-sized crowns were prone to drought events in particular (highest negative values of TRI). Due to lower stem density, average crown size was greater in the managed stands (means of 117 and 127 m^2) than in the unmanaged ones (75 and 91 m^2, Table 2), and growth decline was greater in the former.

DISCUSSION

We found that legacy effects of forest management modulate the response of beech to climate extremes. Specifically, trees growing in managed stands showed a larger growth decline during severe drought in spring than trees in unmanaged beech forests. This finding contrasts the common belief that thinning and thus canopy release improves the water status of remaining broad-leaved trees (Breda et al. 1995; Sohn et al. 2016; Diaconu et al. 2017).

Beech has been identified as being relatively sensitive to summer drought and elevated summer temperatures (Geßler et al. 2007; Köcher et al. 2009; Packham 2012), which may relate to its large shade crown and comparably high water consumption (Leuschner & Ellenberg 2017), and a relatively high vulnerability to cavitation due to a less negative P_{50} value than in other broadleaf trees (Choat et al. 2012). In accordance, high temperatures and low precipitation during current and previous year growing seasons, particularly during May to July, were identified as main factors driving the observed recent growth decline in various regions of Europe (Zimmermann et al. 2015; Hacket-Pain et al. 2016; Knutzen et al. 2017). This is consistent with our finding of overall decreasing radial growth rates of beech in northern Germany under elevated climatic water deficits in spring and current and previous years' summer. In contrast to other studies on beech growth decline (e.g. Knutzen et al. 2017), we found that early-season drought (March to May) was decisive and not summer (June to August) water shortage. Our results match with those of Bosela et al. (2016) and Mausolf et al. (2018), where early-season water shortage was also found to be the main driver of declining radial growth rates in beech. Importantly, our results also show that drought sensitivity of beech strongly depends on management history with trees growing in unmanaged forests being less sensitive to drought events during spring and previous summer. The influence of current and previous year water deficits on radial growth is explained by the phenology of cambial activity. A large part (~75%) of annual tree-ring formation in beech is completed until the end of June (Packham 2012). Thus, carbohydrates assimilated during previous summer and current spring likely contribute most to the current-year tree-ring, whereas the C gain of the current summer should play a minor role. This is in line with the fact that early growing season conditions and remobilization processes rather than current summer conditions significantly influence tree-ring width in beech when assessing the whole tree-ring (Hentschel et al. 2016). Moreover, up to 20% of a tree-ring of European beech in spring can be built from remobilized storage compounds (Skomarkova et al. 2006). Furthermore, water deficits are often associated with high summer temperatures, which may negatively affect the radial growth of beech in the next year through a stimulation of mass fruiting. Full masting can consume more than 50% of annual C gain (Hacket-Pain et al. 2015, Müller-Haubold et al. 2015), thereby reducing radial growth in the subsequent year.

Crown size is considered a key tree trait controlling the radial growth of trees due to its relation to leaf area and thus photosynthetic carbon gain and transpirative water loss (Niinemets 2010). Crown size may also reflect

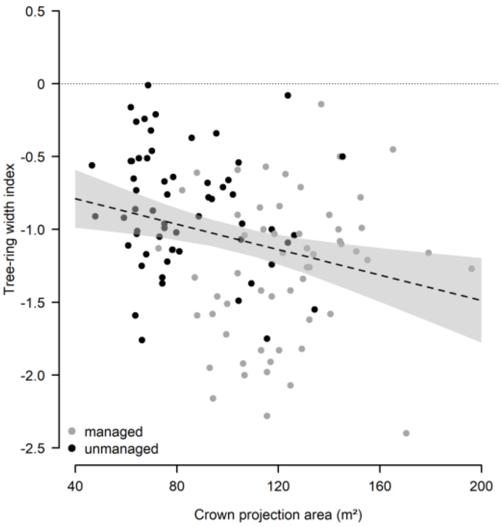

Figure 3 Relationship between tree-ring width index (TRI) and crown projection area (CPA) of European beech (*Fagus sylvatica*). Negative values of TRI indicate growth decline. The black line is a linear model fit (P = 0.003) and the shaded area indicates the 95% confidence interval. Points represent observed values of TRI for extreme climate events (extremely dry) in spring (2011) and crown projection area (2016) for trees growing in managed (grey) and unmanaged (black) beech forests.

the tree's past competitive strength (Fichtner et al. 2013). The removal of competitive neighbours in thinning operations typically leads to enhanced growth of the remaining trees through rapid crown expansion, which is a characteristic response of *F. sylvatica* (Lebourgeois et al. 2014). In the managed stands, the beech trees had on average an about 50% larger crown size than in the denser unmanaged stands, which must have increased carbon gain after having cut the neighbours, but sap flux density in the stem xylem should also have increased due to growing canopy water loss. Trees will adapt their hydraulic architecture to an expanding crown and growing water consumption, but the critical question is, whether the increase in hydraulic efficiency with radial sapwood expansion through the formation of new tree rings keeps pace with the growing evaporative demand on the leaf side. Noyer et al. (2017) showed that trees released from intense competition in managed stands increase their vessel diameter, which will increase hydraulic conductance, but larger vessels in turn can lead to a higher risk of hydraulic failure and embolism during drought. Thus, it is likely that the higher water demand of trees with light-exposed and expanding crowns in the direct neighbourhood of tree cutting-gaps will increase the trees' susceptibility to severe drought, at least for several years until hydraulic adaptation is completed. Although the branch hydraulic architecture of beech acclimates sufficiently fast after canopy opening to avoid hydraulic dysfunction (Lemoine et al. 2002), this acclimation potential at the canopy level seems insufficient. A related phenomenon was recently described by Jump et al. (2017) as structural overshoot, meaning that the promotion of tree growth by favourable environmental conditions (via management) can enhance the risk of a temporal mismatch between water demand and water supply in times of drought. Structural overshoot may explain our finding of increasing drought-induced growth decline with increasing crown size, when the hydraulic system and/or the root system are not able to meet the water demand of the expanding crown.

Other factors which could be responsible for the higher drought sensitivity of beeches in the managed stands are differences in stand microclimate and in the soil biological activity and mycorrhizal net. In the absence of selective cutting, stem density and canopy closure were higher in the unmanaged forests, which must have resulted in reduced light transmission to the ground and a higher air humidity level in the stands (Rambo & North 2009; Latif & Blackburn 2010). High-resolution radial increment measurements on beech stems have shown that the cambial activity of this species is in the peak growing phase less dependent on high rainfall amounts than on high air humidity (Köcher et al. 2012). This highlights the importance of a closed canopy for the vitality of late-successional beech, which likely is more sensitive to abrupt changes in the microclimate and air humidity, as resulting from forest management activities (Aussenac 2000), than other temperate broadleaf trees. Moreover, it might be conceivable that absorbing roots of trees in densely-stocked unmanaged stands had migrated to deeper soil layers to avoid belowground competition for water (Schenk 2005). Therefore, sensitivity to drought stress during climate extremes should be lower, because water uptake can occur from deeper soil layers. In contrast, trees growing in managed stands might develop fine roots primarily in upper soil layers due to reduced belowground competition for water uptake after thinning. Given that upper soil layers are prone to soil drying, trees in managed stands could exhibit higher sensitivity to extreme drought. In addition, management-induced compaction of forest soils has been found to result in long-lasting impact on the soil microbial community (Hartmann et al. 2014), which could influence the drought susceptibility of the trees.

CONCLUSION

Our findings highlight the relevance of understanding how legacy effects interact with drivers of global environmental change. We found a strong effect of forest management legacies on the climate sensitivity of beech and could show that drought-induced growth declines during spring are less severe in the unmanaged stands. Overall, our results suggest that management practices conducted to promote the growth of target trees, such as neighbour removal, can result in increased drought sensitivity of the remaining trees. The different responsiveness of stands with 20 years or 50 years of management abandonment suggests that the length of the period since management cessation plays a crucial role in determining the trees' susceptibility to drought. Among the factors that could explain the variable responsiveness of beech trees in managed and unmanaged stands, we discuss differences in canopy size which could affect the water status of the trees, microclimate alteration, and putative management-induced effects on the soil. We obtained evidence of a trade-off between high radial growth rates and high drought tolerance in beech, which deserves further study. The results of our study may be of high relevance for the management of beech forests in a warming climate, but it has to be kept in mind, that local site conditions such as soil moisture regime and soil fertility likely are influencing the climate-growth relationship. Managed and unmanaged beech stands growing under deviating environmental conditions and management regimes could thus behave differently. Further research is needed to improve our understanding of the interactive effects between management legacies and drivers of global environmental change.

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Chapter 15

Crown size-growth relationships of European beech (*Fagus sylvatica* L.) are driven by the interplay of disturbance intensity and inter-specific competition

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Crown size-growth relationships of European beech (*Fagus sylvatica* L.) are driven by the interplay of disturbance intensity and inter-specific competition

A. Fichtner[1]*, K. Sturm[2], C. Rickert[1], G. von Oheimb[3], W. Härdtle[3]

[1]*Institute for Natural Resource Conservation, University of Kiel, Olshausenstr. 75, 24118 Kiel, Germany;* [2]*Community Forest Lübeck, Kronsforder Hauptstraße 80, 23560 Lübeck, Germany;* [3]*Institute of Ecology, Leuphana University of Lüneburg, Scharnhorststr. 1, 21335 Lüneburg, Germany*

*Corresponding author: A. Fichtner, afichtner@ecology.uni-kiel.de

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Abstract

Crown size is considered one of the most important traits that affect radial tree growth, but it remains unclear how (anthropogenic) disturbance intensity affects crown size-radial growth relationships. This knowledge, however, is crucial for a better comprehension and prediction of community dynamics, and thus to support management decisions. We analyzed changes in stem and crown characteristics of dominant canopy European beech (*Fagus sylvatica*) trees along an anthropogenic disturbance gradient based on the duration of non-forestry use. We further investigated the dependency of basal area increment on crown surface area and linked this relationship to growth efficiency. Crown efficiency (basal area growth per unit crown surface area) was used as an indicator for the effectiveness of tree growth. Further stand attributes included stand density and tree species composition. Changes in crown efficiency with tree and stand attributes were assessed using generalized additive models (GAMs). Tree morphology sensitively responded to disturbance intensity. However, the indicative value of crown surface area for basal area increment decreased with increasing duration of non-forestry use and stand density. We found that the interplay between disturbance intensity and species composition modulates crown efficiency of dominant beech trees. Inter-specific competition enhanced crown efficiency in unmanaged stands, whereas managed stands showed an opposite trend. Consequently, crown efficiency significantly increased with decreasing disturbance intensity and intra-specific competition. Thus the widely accepted close correlation between crown size and radial increment needs reconsideration for trees growing under (near-) natural conditions. We hypothesize that carbon allocation in densely stocked stands can be adapted to an efficient trunk-crown relation, which in turn weakens crown size-radial growth relationships as known from managed stands. The importance of continuity in tree-tree interactions therefore imposes significant constraints on the generality of crown traits as radial growth determinants in beech forests. Our findings indicate that a higher structural complexity and stand productivity might be achieved in managed stands by a wider variety of crown size classes and tree species assemblages. Hence, stand dynamics can benefit from lowering anthropogenic disturbances and favouring self-regulation, which would be a further step towards near-natural forest management.

Keywords: basal area increment, crown efficiency, disturbance, niche differentiation, plant interactions, tree architecture

INTRODUCTION

Crown size is positively related to the light interception of a tree, and thus to tree's carbon budget (Sterck et al., 2001; Hemery et al., 2005). Therefore, it is regarded as an important indicator for individual tree growth assessments, and individual-based growth models that include crown traits are commonly applied in forestry (Hasenauer, 2006; Pretzsch, 2009).

Crown traits respond sensitive to changes of crowding conditions, hence reflecting tree's cumulative competition status within a stand (Davi et al., 2008; Lintunen and Kaitaniemi, 2010; Thorpe et al., 2010). Increasing competition alters the resource acquisition capacity of a tree by reducing crown length and diameter (Short and Burkhart, 1992; Brown et al., 2007; Lang et al., 2010), which in turn results in a lower biomass production (on the tree individual level). For this reason, growing space extensions by thinning are frequently used in forestry to promote lateral crown growth of residual trees and thereby favour radial increment (Hasenauer and Monserud, 1996; Drobyshev et al., 2007). Various studies, however, have demonstrated that intensive biomass removal in forest ecosystems (e.g. by thinning) contradict climate and biodiversity objectives (e.g. Bauhus et al., 2009; Brunet et al., 2010; Verkerk et al., 2011; Schulze et al., 2012). Furthermore, size-asymmetric competition response of European beech (*Fagus sylvatica* L.) alters the effectiveness of thinning effects, particularly on fertile sites (Fichtner et al., 2012). Consequently, an understanding of the mechanisms underlying density-dependent tree growth pattern (e.g. competition for canopy space) is crucial for a better comprehension and prediction of community dynamics, and thus to support management decisions (Purves et al., 2007; Davi et al., 2008).

Crown size is considered one of the most important traits that affect radial tree growth and crown efficiency is commonly used as a proxy to assess tree vigor (Assmann, 1970). There is evidence that thinning positively affects crown efficiency of deciduous (e.g. *Fagus sylvatica*: Pouderoux et al., 2000) and coniferous trees (e.g. *Pinus ponderosa*: Mainwaring and Maguire, 2004). Numerous studies from thinning experiments showed that crown efficiency increases with crown dominance (Hamilton, 1969; Roberts and Long, 1992; O'Hara 1996), whereas within a given crown class, trees with smaller crowns tended to be more efficient (Assmann, 1970; O'Hara, 1988; Sterba and Amateis, 1998). Contrarily, Reid et al. (2004) found an opposite pattern, suggesting suppressed coniferous trees to be more efficient than dominant ones. Thus, stand level productivity is linked to a complex vertical crown size distribution (O'Hara, 1989). However, the vast majority of thinning experiments have been conducted in rather small-sized plots and mono-species stands or uneven-aged coniferous stands (O'Hara, 1996; Maguire et al., 1998). In contrast, studies on the relationship between crown size and radial increment for deciduous trees in multi-layered, uneven-aged natural tree communities are scarce (Norton et al., 2005). The specific objectives of this study therefore are (i) to assess shifts in crown morphology of *F. sylvatica* with various levels of natural stand development and stand densities, (ii) to re-evaluate the indicative value of crown size for radial tree growth under (near-) natural growing conditions, and (iii) to evaluate crown efficiency (basal area growth per unit of crown surface area) in response to anthropogenic disturbance. We used non-manipulative data from mature managed and unmanaged lowland beech forests, which represent an important beech forest ecosystem type within the European range of beech (Bohn et al., 2002/2003).

METHODS

Study area

The study was conducted in meso- to eutrophic beech forests (*Galio-Fagetum*; EU habitat code: 9130) of the forest district Stadtwald Lübeck (53°47' N, 10°37' E), which is located in the moraine landscapes of Schleswig-Holstein, Northwest Germany. The forest area is dominated by deciduous trees (72 %) and comprises 4297 ha. The dominant tree species is *F. sylvatica*, and the predominant phytocoenoses are affiliated to the *Fagion sylvaticae* alliance. Elevation ranges from 0 to 90 m asl. The study area is characterized by a sub-oceanic climate with a mean annual precipitation between 580 and 871 mm and a mean annual temperature of 8.3 °C (Gauer and Aldinger, 2005). Edaphic conditions of the forests investigated are characterized by moderately moist to moist recent moraine soils originating from the Weichselian glaciation. Soil texture consists of till (clay/sandy loam) with varying carbonate content, providing an optimal nutrient and water supply for tree growth. The predominant soil types are (pseudogleyic) Luvisols and Cambisols.

Disturbance levels and field data

The study was based on an anthropogenic disturbance gradient across 42 mature beech stands with various proportions of other trees, such as pedunculate oak (*Quercus robur*), European hornbeam (*Carpinus betulus*), European ash (*Fraxinus excelsior*), sycamore maple (*Acer pseudoplatanus*), wild cherry (*Prunus avium*) and silver birch (*Betula pendula*). The gradient included stands managed according to a low-impact approach based on the protection of natural disturbance regimes (e.g. Sturm, 1993) and unmanaged stands from two large and coherent forest nature reserves (48 ha and 184 ha). Structurally, the investigated stands are multi-layered and uneven-aged and developed from natural regeneration (Fichtner, 2009).

Disturbance intensity (DI) was derived from the duration of non-forestry use, ranging from 'currently managed' to long-term (>50 years) abandonment. We defined three levels of disturbance: (i) 'M' managed stands, (ii) 'U12' short-term (12 years) unmanaged stands, and (iii) 'U50' long-term (>50 years) unmanaged stands.

We randomly selected 60 dominant beech trees (hereafter target trees) of the upper layer (canopy trees; classes 1–2 according to Kraft, 1884) from 500 m^2 plots. The plots were established in 1992 and 2004, and are part of a systematic sample plot inventory network (180 x 230 m grid). For each target tree diameter at breast height (DBH at 1.30 m), tree height, crown radius, crown length and crown position were measured in 2007. Crown length was defined as the vertical distance from the lowest leaf to the top leaf and crown position as the height of the lowest crown leaf. Crown radius was determined as the average value of radii measurements in six different directions (N, E, S, W, maximum and minimum crown radius). Additionally, we calculated the following architectural traits: Stem slenderness (tree height–tree diameter ratio), crown ratio (crown length–tree height ratio), crown projection area (using the formula for an ellipse) and crown surface area (hereafter crown area). Crown area (CA) was calculated as (Kramer, 1988):

$$CA = \pi\, CR / 6\, CL^2\, [(4\, CL^2 + CR^2)^{3/2} - CR^3)] \quad \text{eqn1}$$

where CR is crown radius and CL is crown length. Crown area as defined here (i.e., including crown length) is a more accurate representation of the potential light interception experienced by a target tree than crown projection area, particularly when comparing tree growth in managed and unmanaged stands (Courbaud, 2000).

We further determined stand density and species composition of each study plot by: (i) summing the basal area of all living trees (DBH >7 cm) within a plot, and (ii) calculating the proportion of beech trees (PBT) within a plot as the percentage of basal area composed of beech individuals.

Data analysis

Variation in tree morphology with disturbance intensity was evaluated by analysis of dissimilarity (ADONIS, 1000 permutations) followed by a Bonferroni adjustment (Anderson, 2001). The analysis was performed on a matrix of Bray-Curtis dissimilarities based on standardized (Wisconsin double standardization) architectural traits: crown radius, crown length, crown position, crown ratio and stem slenderness. Differences in architectural traits and stand characteristics among disturbance levels were tested by analysis of variance (ANOVA) with a post-hoc performance (Tukey HSD test).

A basic parametric growth function was selected to analyze the dependency of annual basal area growth (BAI) on crown area:

$$\log(BAI_{ij}) = \alpha + \beta \log(CA_{ij}) + \varepsilon_{ij} \quad \text{eqn 2}$$

where α describes the mean annual basal area growth of tree i in plot j, β the crown area effect on growth and ε is the residual error. 15-year basal area growth was calculated as the difference between the tree basal area (cm^2) of 2007 and 1992 divided by the number of vegetation periods. Basal area values of 1992 were derived from inventory data for the corresponding trees. Separate models were fitted for the three disturbance levels.

To understand disturbance intensity related changes in tree growth pattern, we used crown efficiency (CE) as an indicator for the effectiveness of tree growth (Reid et al., 2004). Crown efficiency was calculated as the basal area increment per unit crown area. To investigate the effect of species composition (inter- vs. intra-specific competition) on crown efficiency, we used an index of inter-specific competition (CI) computed as CI = 1 - (PBT / 100). The index ranges from 0 (no inter-specific competition) to 1 (maximum inter-specific competition).

We estimated crown efficiency using generalized additive models (GAMs, Hastie and Tibshirani, 1990) with a Gaussian distribution and identity link based on a function of crown area (log-transformed), inter-specific competition index and disturbance intensity. We additionally considered two interaction terms (CA x DI and CI x DI), which allowed us to test for shifts in community compositional-specific and crown area-specific growth response with different disturbance intensities (Zuur et al., 2009). The basis dimension was set to $k = 3$ to allow some complexity in the growth function, while

Table 1 Variation in stand and tree characteristics across the anthropogenic disturbance gradient. Values refer to dominant beech (*Fagus sylvatica*) trees growing in mature lowland beech forests (*Galio-Fagetum*). Superscript letters indicate significant differences between means (at the α = 0.05 level; Tukey's HSD post-hoc test). M: managed stands; U12: short-term (12 years) unmanaged stands; U50: long-term (>50 years) unmanaged stands; CV: coefficient of variation.

	M		**U12**		**U50**	
	mean (SE)	CV	mean (SE)	CV	mean (SE)	CV
Stand attributes						
Stand volume (m^3 ha^{-1})	467.56^{a} (31.96)	30.57	544.19^{a} (32.55)	26.74	714.18^{b} (47.03)	29.44
Stand density (m^2 ha^{-1})	31.65^{a} (2.23)	31.53	34.95^{a} (1.42)	18.15	44.01^{b} (1.95)	19.83
Proportion beech trees (%)	81.33 (4.66)	26.61	76.98 (5.11)	32.00	80.45 (5.33)	29.64
Target tree attributes						
Tree age (years)	115.85^{a} (1.13)	4.36	130.95^{b} (2.27)	7.75	125.60^{b} (2.40)	8.54
Diameter at 1.30 m (cm)	51.44 (3.14)	27.32	48.51 (2.85)	26.35	46.36 (2.95)	28.52
Height (m)	33.09^{ab} (1.36)	18.32	32.46^{b} (0.93)	12.76	35.98^{a} (1.18)	14.70
Stem slenderness	0.67^{a} (0.03)	19.72	0.71^{ab} (0.04)	23.48	0.82^{b} (0.04)	23.83
Crown radius (m)	6.21^{a} (0.37)	26.97	5.65^{a} (0.34)	27.01	4.29^{b} (0.40)	41.61
Crown length (m)	17.22^{a} (1.39)	36.14	13.48^{b} (0.54)	18.11	13.94^{b} (0.85)	27.37
Crown position (m)	17.87^{a} (0.71)	17.71	18.95^{a} (0.64)	15.06	22.04^{b} (0.93)	18.95
Crown ratio	0.53^{a} (0.04)	37.23	0.42^{b} (0.01)	12.15	0.39^{b} (0.02)	21.52
Crown surface area (m^2)	491.10^{a} (56.98)	51.89	350.48^{ab} (31.49)	40.18	274.04^{b} (37.18)	60.68
Crown projection area (m^2)	121.70^{a} (14.50)	53.28	104.85^{ab} (11.74)	50.08	65.46^{b} (14.07)	96.14
Basal area growth (cm^2 year^{-1})	33.76^{a} (3.83)	50.72	33.16^{ab} (4.11)	55.44	22.63^{b} (3.32)	65.59
Crown efficiency (cm^2 m^{-2} year^{-1})	0.075 (0.01)	34.90	0.094 (0.01)	41.14	0.093 (0.02)	52.65
N° (plots)		18		14		10
N° (trees)		20		20		20

avoiding over-fitting the data (Wood, 2006). The general model structure is:

$$\mathrm{CE}_{ij} = \alpha + f_1 \log(\mathrm{CA}_{ij}) + f_2(\mathrm{CI}_j) + \beta\, \mathrm{DI}_j + \varepsilon_{ij} \quad \text{eqn 3}$$

where α denotes the mean crown efficiency, $f_{1,2}$ are nonlinear smoothers estimated as thin plate regression splines describing the crown area and inter-specific competition effects on crown efficiency of tree i in plot j, β is a parametric coefficient for the effect of disturbance intensity, and ε is the residual error. Different competing models were evaluated by sequential comparison (backward selection) based on the Akaike Information Criterion (AIC). Only models with an AIC difference (ΔAIC) <2.00 (compared with the best fit model) were considered as models with substantial support (Buhrnham and Anderson, 2002). We additionally tested a model with a random plot effect, but the likelihood ratio test indicated no substantial between-plot variation ($L = 0.44$, $p = 0.51$).

To quantify the interplay between disturbance intensity and inter-specific competition index on the effectiveness of tree growth, we further predicted crown efficiency for each target tree based on our best-fitted model. We used mean values of crown area along the disturbance gradient, while varying inter-specific competition indices. Differences between disturbance intensities were tested by ANOVA followed by a post-hoc performance (Tukey HSD test).

All statistical analyses were performed using R (R Development Core Team, 2012, Version 2.14.2).

RESULTS

Stand characteristics

Stand density varied among disturbance levels with significantly higher values in U50 (44 m^2 ha^{-1}) compared to M (32 m^2 ha^{-1}) and U12 (35 m^2 ha^{-1}; Table 1). Differences in species

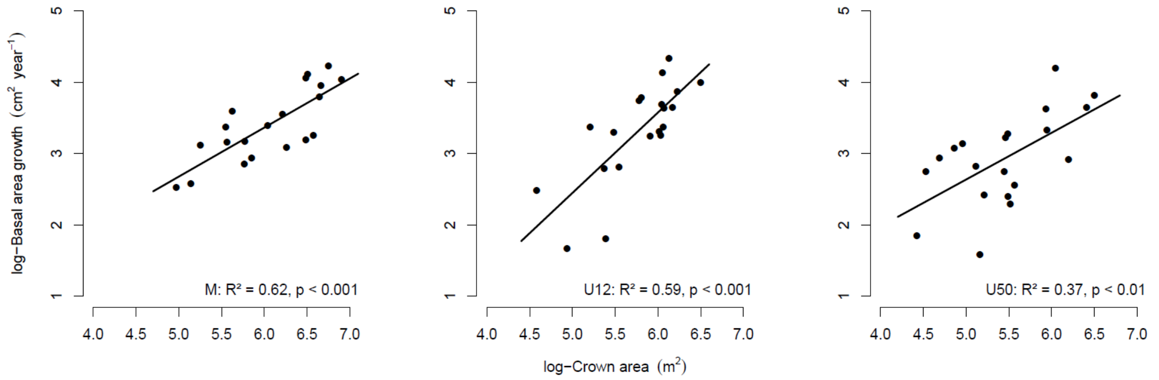

Figure 1 Shifts in crown area-basal area growth relationship with anthropogenic disturbance intensity in mature beech forests. M: managed stands; U12: short-term (12 years) unmanaged stands; U50: long-term (>50 years) unmanaged stands.

composition, however, were not significant. Mean proportions of beech trees ranging from 80 % (U12, U50) to 81 % (M; Table 1). *Quercus robur* was the most dominant accompanying species in both, managed and unmanaged stands, followed by *Carpinus betulus* and *Fraxinus excelsior*. The high proportion of oak can be primarily attributed to human facilitation in the past.

Tree morphology

ADONIS indicated that disturbance intensity was a strong predictor for the variation in tree morphology of *F. sylvatica* (*F*: 6.64, $p < 0.001$). Trees growing in M and U12 had significantly different architectural traits than those in U50 (M vs. U50: $p_{adj.} < 0.001$; U12 vs. U50: $p_{adj.} < 0.05$). Growth performance in M and U12 was similar (M vs. U12: $p_{adj.} = 0.13$). On average, tree morphology of individuals in U50 was characterized by small, shallow and high positioned crowns and slender stems, respectively, whereas the opposite was found for trees in M (Table 1). A significantly lower crown radius and higher crown position only occurred after long-term abandonment of forest management. In contrast, crown length and crown ratio were most sensitive to disturbance intensity with significantly lower values in unmanaged stands, even after short-term abandonment of forest management. Stem slenderness increased with decreasing disturbance intensity.

Crown size effects on radial growth

On average, crown area significantly declined with decreasing disturbance intensity (Table 1). Mean values of trees growing in unmanaged stands were 29 % (U12) to 44 % (U50) lower than in managed stands. Basal area increment also decreased in unmanaged stands compared to M (by 2 % in U12 and 33 % in U50). However, there was weak statistical support for differences in mean basal area growth not only between M and U12 ($p_{adj.} = 0.99$), but also between M and U50 ($p_{adj.} = 0.10$). This can be primarily attributed to the increasing individual variability in growth rates in unmanaged stands (coefficients of variation: M = 51 %, U12 = 55 %, U50 = 66 %; Table 1).

Basal area growth was positively related to crown area for each disturbance level (Fig. 1). However, the importance of crown area as growth predictor distinctly declined with decreasing disturbance intensity. The proportion of explained variance was 40% lower in U50 compared to M. U50-trees with large-sized crowns corresponded to high growth rates, whereas U50-trees with small- or medium-sized crowns showed a highly variable and thus tree-specific growth pattern.

Crown efficiency

The model that best explained variation in crown efficiency included a linear crown area effect and nonlinear inter-specific competition effects varying with different levels of disturbance (Table 2). The interaction between CI and DI was the strongest predictor, with an asymptotic (U50) or exponential (U12) increase of crown efficiency in response to decreasing intra-specific competition in unmanaged stands (Fig. 2). An opposite trend with a weak linearly decreasing pattern was obvious for M. The effect of log-crown area was comparatively small ($\beta = -0.02$, $p < 0.05$). Accordingly, crown efficiency in mixed stands differed significantly among disturbance intensities (F: 83.14, $p < 0.001$). Average values increased with decreasing disturbance intensities and ranged from 0.07 (M) to 0.11 (U50). In contrast, disturbance intensity had no significant effect on crown efficiency in pure stands (F: 1.64, p = 0.23, Fig. 3). Overall, trees in unmanaged forests showed a considerably more effective tree growth (in terms of radial increment) than those in managed stands (U12: +36 %, U50: +54 %).

Table 2 Model selection statistics for different candidate models describing crown efficiency as a function of disturbance intensity (DI), inter-specific competition index (CI) and crown area (CA). The Akaike's Information Criterion (AIC), difference in AIC relative to the best-fitted model (ΔAIC) and degree of freedom (d.f.) are presented. Parameter estimates for the best-fitted model are given at the bottom of the table.

Model terms	AIC	ΔAIC	d.f.
DI + CI	-217.41	9.36	5.00
DI + log-CA	-217.98	8.79	5.00
DI + log-CA + CI	-221.26	5.51	6.45
DI + log-CA + CI + log-CA * D	-222.84	3.93	9.51
DI + log-CA + CI + CI * DI	**-226.77**	**0.00**	9.12

	Estimate / edf	*t* / *F*	*P*
Parametric terms			
Intercept	0.138	3.81	0.0004
U12	0.024	1.66	0.1028
U50	0.054	5.10	< 0.001
log-CA	-0.021	-2.33	0.0238
Smooth terms			
f (DI * M)	1.886	4.52	0.0148
f (DI * U12)	2.071	9.76	0.0001
f (DI * U50)	2.154	9.61	0.0001

DISCUSSION

Efficient resource utilization of *F. sylvatica* in response to disturbance intensity

The importance of crown size as growth determinant was found to be inconsistent among managed and unmanaged forests. Given the close correlation between crown area and basal area growth in managed stands, trees with larger crowns are assumed to be those with higher growth rates (e.g. Assmann, 1970; O'Hara, 1988; Drobyshev et al., 2007). In contrast, our results demonstrate that crown size becomes less important in undisturbed tree communities.

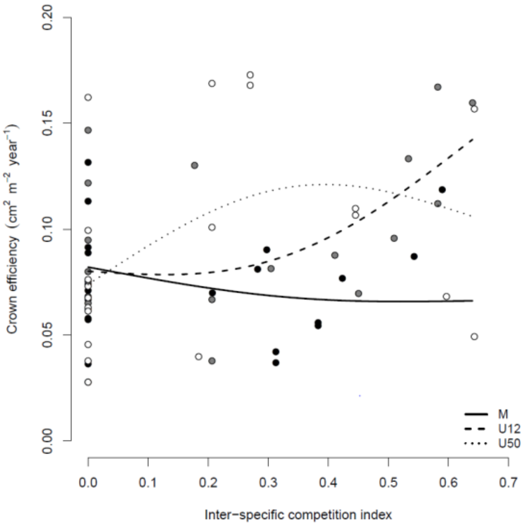

Figure 2 Disturbance-related variation in crown efficiency with different levels of inter-specific competition. The competition index ranges from 0 (no inter-specific competition) to 1 (maximum inter-specific competition). Crown area was kept constant at the corresponding means. Smooth curves were obtained by fitting a generalized additive model. M: managed stands (black circles); U12: short-term (12 years, grey circles) unmanaged stands; U50: long-term (>50 years, open circles) unmanaged stands.

Tree morphology of shade-tolerant species is optimized for light capture (Aiba and Nakashizuka, 2009), and morphological traits such as crown size are mainly determined by the competition for light and space (Grams and Andersen, 2007). Consequently, tree growth largely depends on light interception (e.g. King et al., 2005; Kunstler et al., 2005). We found evidence, however, that basal area growth of trees in long-term unmanaged, crowded stands was much less affected by crown area than that of trees growing in managed and regularly disturbed stands. We hypothesize that this discrepancy results mainly from contrasting crown efficiencies (e.g. tree vigor), rather than differences in photosynthetic capacities. Particularly in uneven-aged stands effectiveness of tree growth is strongly determined by light conditions (O'Hara 1996; Maguire et al., 1998). Constant disturbances such as the removal of trees with small and medium-sized crowns prevent morphological adjustments and thereby diminish individual differences in growth potentials. Yet, morphological adjustments enable trees to reduce competitive pressure from neighbors, and thus improve their carbon acquisition, particularly in mixed-species forests

(Lang et al., 2010, 2012; Seidel et al., 2011; Dieler and Pretzsch, 2013). Significant morphological differences in our study indicate that trees in unmanaged stands are able to modify their architecture, and thus alter growth strategies to optimize their growth pattern. Accordingly, competition for canopy space may become less important in long-term unmanaged, dense stands.

Natural stand dynamics are strongly altered by silvicultural practices, since thinning interventions aim to promote the growth and quality of residual trees by reducing competitors (Oliver and Larson, 1996). As a result, basal area growth in managed stands was strongly related to crown area, because after growing space extension target trees allocate assimilates primarily to lateral crown growth (Hemery et al., 2005). In contrast, the variation in growth rates of trees in unmanaged stands increased with decreasing crown area. This suggests that assimilate acquisition depends more strongly on individual-specific morphological adjustments than on potential light availability. Vieilledent et al. (2010) demonstrated for (half-) shade tolerant coniferous species that individual variability in tree allometry (e.g. crown traits) is a major driver that explains differences in light resource exploitation. Moreover, the high importance of individual-specific growth traits in unmanaged forests can be partly explained by the high morphological plasticity of *F. sylvatica* (Schröter et al., 2012). In their study of an old-growth, long-term unmanaged beech forest, the authors conclude that this high plasticity allows beech's light resource utilization to become highly effective by reducing intra-specific competition, which in turn provides the maintenance of high stand productivity, even in densely stocked stands. Neglecting natural individual variability in tree growth strategies thus restricts conclusions on tree-tree interactions in forest communities.

We could not observe distinct disturbance-related variations in crown efficiency for trees experiencing a high level of intra-specific competition (cf. Fig. 3). Moreover, it seems that the interplay between disturbance intensity and species composition modulates crown efficiency of dominant canopy trees. Accordingly, long-term species coexistence in unmanaged forests may shift carbon allocation pattern towards a more pronounced trunk-storage, and thus may compensate for lower light interception. Recently, Zhang et al. (2012) showed that species trait variation (e.g. shade tolerance) is a key factor determining forest productivity. Hence, the pattern observed here is likely to be attributed to increased heterogeneity of niche differences induced by the duration and intensity of inter-specific competition. This, in turn, allows tree species to become more efficient with regard to

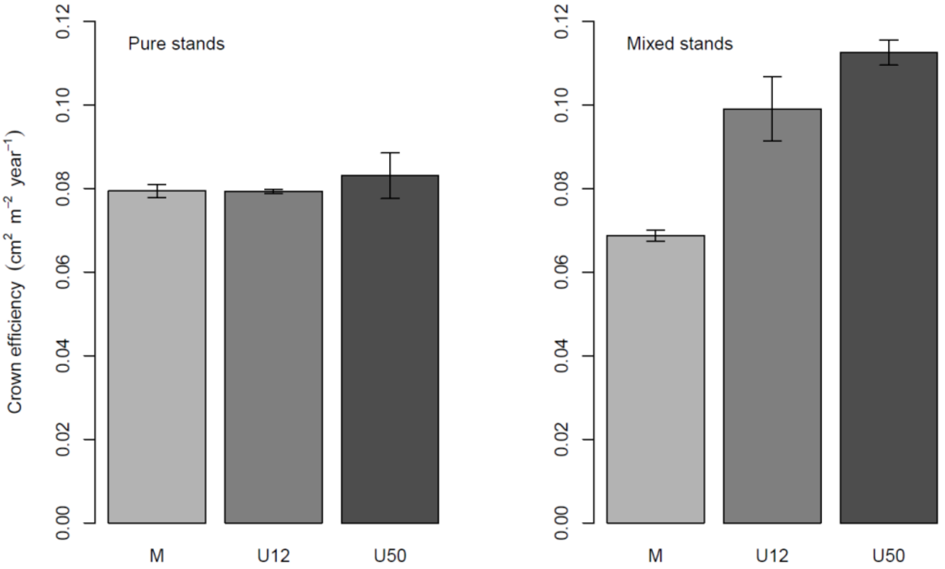

Figure 3 Changes in mean crown efficiency in pure and mixed stands across different disturbance levels. Predictions were derived from the growth pattern presented in Fig. 2. Error bars represent 95% confidence intervals. Non-overlapping confidence intervals indicate significant differences ($p_{adj.} < 0.001$) among disturbance levels. M: managed stands; U12: short-term (12 years) unmanaged stands; U50: long-term (>50 years) unmanaged stands. Pure stands were defined as CI ranging between 0 and 0.1.

light resource allocation (Aiba and Nakashizuka, 2009; Coomes et al., 2009), because increasing growth efficiency might be related to increasing crown efficiency. Moreover, niche differentiation alters crown space occupancy patterns and crown competition, which in turn are related to radial tree growth (Pretzsch and Schütze, 2005).

Implications for forest community structure

Understanding the impacts of anthropogenic disturbances on tree growth patterns is crucial for forest ecology, because growth is directly related to forest structure and biomass, which in turn affects ecosystem functionality. Our study showed that *F. sylvatica* in unmanaged forests is able to achieve similar growth rates by smaller crown sizes compared to beech trees in managed stands. This indicates that carbon allocation in densely stocked stands can be adapted to an efficient trunk-crown relation, and thus meets management and conservation objectives. Consequently, a higher structural complexity in managed stands can be achieved by a wider variety of crown size classes and tree species assemblages, which in turn would benefit primary productivity in temperate forests (Morin et al., 2012) as well as biodiversity patterns (Brunet et al., 2010). A high variation in crown characteristics leads to a high heterogeneity of light conditions over time, which is particularly important in densely stocked stands (Vieilledent et al., 2010). Additionally, an increasing variability in crown structures might ensure a higher resilience towards stochastic natural disturbances (Seidl et al., 2011) and an improved adaptation to crowding (Pretzsch and Dieler, 2012). Both, management and conservation strategies with a focus on natural stand attributes could therefore benefit from lowering anthropogenic disturbance intensity (e.g. crown thinning) in beech forests.

CONCLUSIONS

We hypothesized that radial growth is strongly related to crown size. Instead, no consistent pattern was obvious for dominant canopy trees along an anthropogenic disturbance gradient. The increasing effectiveness in tree growth with increasing duration of natural stand dynamics suggests that this interrelation is largely induced by management, and needs reconsideration for trees growing under (near-) natural conditions. Hence, there is no universally applicable crown area-growth relationship. Instead, the application of crown size as an indicator for tree growth largely depends on the continuity in tree-tree interactions (e.g. niche differentiation), and thus does not universally reflect the growth potential of dominant canopy trees in beech forest ecosystems. This is particularly important, because changes in tree allometry potentially affect forest structure and allow species coexistence along vertical and horizontal light gradients over time (Aiba and Nakashizuka, 2009). Therefore, our understanding of tree-tree interactions might be refined by the consideration of the continuity of ecological processes. We are aware that our analyses might be limited by the relative small sample size. However, the observed growth patterns should motivate further studies to link growth mechanisms and species traits to disturbance gradients.

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Chapter 16

Competition response of European beech *Fagus sylvatica* L. varies with tree size and abiotic stress: minimizing anthropogenic disturbances in forests

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Competition response of European beech *Fagus sylvatica* L. varies with tree size and abiotic stress: minimizing anthropogenic disturbances in forests

A. Fichtner[1]*, K. Sturm[2], C. Rickert[1], W. Härdtle[3] and J. Schrautzer[4]

[1]Institute for the Conservation of Natural Resources, University of Kiel, Olshausenstr. 75, 24118, Kiel, Germany; [2]Community Forest Lübeck, Kronsforder Hauptstraße 80, 23560, Lübeck, Germany; [3]Institute of Ecology, University of Lüneburg, Scharnhorststr. 1, 21335, Lüneburg, Germany; and [4]Institute for Ecosystem Research, University of Kiel, Olshausenstr. 75, 24118, Kiel, Germany

Summary

1. New forest management approaches aim to ensure high biodiversity and climatic adaptability. Silvicultural practices can alter tree–tree interactions and thus influence forest structure and composition. However, knowledge of the interacting effects of competitive and abiotic stress in tree communities is still limited.

2. We assessed growth dynamics of European beech *Fagus sylvatica* in oligo- to eutrophic lowland beech forests by quantifying variation in the importance and intensity of competitive interactions among adult trees along a productivity gradient defined by nutrient availability and hydrological characteristics. We further predicted changes in competition indices with various levels of crowding for different forest types. Basal area growth of 1819 canopy trees was analysed using forest inventory data.

3. Competition response of adult trees was inconsistent among forest types. For small timber trees, the intensity (absolute effect) and importance (effect relative to abiotic constraints) of competition decreased with increasing abiotic stress. Growth responses of medium and large timber trees, however, revealed an opposite trend. Thus, in tree communities, competition effects did not follow a general pattern, because tree maturation altered the responsiveness of trees to environmental stress.

4. Resource dependency of competition effects was most pronounced for large timber trees, with lowest sensitivity to changes in crowding conditions occurring on fertile sites. For small and medium timber trees, however, competition effects were strongest in dense stands, with lowest sensitivity to changes in crowding conditions on resource-limited sites.

5. *Synthesis and applications*. Tree–tree interactions in beech forests showed a clear pattern which depended on tree maturation and resource supply. This highlights the importance of considering tree size-related changes along environmental gradients in regional growth models. Our findings indicate that management practices could facilitate both timber production and nature conservation demands by adapting thinning approaches to age- and resource-related tree growth patterns. We propose a distinct reduction in thinning intensity, particularly for larger beech trees growing on sites with optimum below-ground resources. This would increase the permanent stand volumes and promote natural stand dynamics, which in turn would benefit biodiversity typical of old-growth beech forest ecosystems.

Key-words: basal area increment, competition, plant interaction, size asymmetry, stress gradient hypothesis, sustainable forest management, thinning

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*Corresponding author. E-mail: afichtner@ecology.uni-kiel.de

Introduction

Competition among trees is one of the main drivers determining the structure and composition of tree communities (Oliver & Larson 1996). Thus, it is important to understand the mechanisms mediating inter- and intraspecific competition of trees from both an ecological and economical point of view (Nord-Larsen *et al.* 2003). The interpretation of competition effects, however, largely depends on the way competition is assessed (Freckleton & Watkinson 1999).

Adult tree growth is strongly affected by crown competition and competition for resources. Although all trees compete for nutrients, competition for light is particularly important for smaller trees (Coomes & Allen 2007). Furthermore, competitive effects are assumed to be altered by changing levels of abiotic stress (Bertness & Callaway 1994). Resource supply has a stronger influence on light competition on fertile sites than on nutrient-poor sites (Pretzsch & Biber 2010). However, the interactions between tree size and resource availability have rarely been analysed (Schwinning & Weiner 1998). Although the underlying stress gradient hypothesis (SGH) is debated (Maestre *et al.* 2009; Smit, Rietkerk & Wassen 2009), numerous experimental studies on herbaceous plants or juvenile trees have shown that competition among individuals becomes less severe with increasing abiotic stress (e.g. Callaway *et al.* 2002; Lortie & Callaway 2006) and shifts from below-ground to above-ground competition with increasing resource supply (see Tilman 1982 for the underlying theoretical model). In this context, the distinction between the absolute impact of competition (competition intensity) and the impact of competition in relation to other processes along an abiotic gradient (competition importance) plays a crucial role in assessing plant interactions (Welden & Slauson 1986; Brooker & Kikvidze 2008). A refined version of the SGH additionally suggests that the plant responsiveness along abiotic stress gradients should be related to the stress type (resource vs. non-resource) and the stress tolerance of the interacting species (Maestre *et al.* 2009). Apart from studies on herbaceous plants or juvenile trees, little quantitative non-manipulative information is available on plant–plant interactions along environmental gradients (Callaway 1998; Coomes & Allen 2007; Baribault & Kobe 2011), and studies assessing the competition's relative impact are scarce (Kunstler *et al.* 2011).

Thinning is an important silvicultural method to promote the growth and quality of residual trees by reducing competitors although growth acceleration patterns largely depend on site quality and stand age (Assmann 1970). Moreover, thinning intensity is negatively related to forest integrity (e.g. carbon storage, structural complexity and species diversity; Mund & Schulze 2006; Brunet, Fritz & Richnau 2010). In this context, a better understanding of tree responsiveness to varying levels of competitive and abiotic stress becomes crucial to support management decisions with regard to changing environmental conditions. Competition response of trees in uneven-aged mixed stands, however, is largely unknown, because most competition analyses are based on data from long-term thinning experiments in even-aged stands. These data can help to evaluate growth responses to varying levels of competition reduction under defined growing conditions in typically even-aged and mono-species stands on smaller scales (e.g. European beech, Utschig & Küsters 2003; Pretzsch 2005), but might not hold for more complex tree–tree interactions in uneven-aged, mixed tree communities on larger spatial scales (e.g. growth districts and areas). In contrast, data derived from non-manipulative sample plot inventories provide an alternative dynamic approach. Such data allow the development of flexible growth models which can gradually replace the commonly used yield tables in forestry and will reflect tree growth under changing environmental conditions more accurately (Hasenauer 2006; Pretzsch 2009).

To assess competition effects on tree growth, we used inventory data from lowland beech forest communities. We focused on the following hypothesis: (i) Competition intensity and importance is highest at sites with low levels of abiotic stress. (ii) Competition effects remain unaltered during tree maturation. Furthermore, we evaluated (iii) the implications of the SGH for near-natural management approaches.

Materials and methods

STUDY SITES AND DESIGN

For this study, a total of 597 plots were selected in European beech *Fagus sylvatica* forests of the forest districts Stadtwald Lübeck (53°47′ N, 10°37′ E) and Stadtwald Mölln (53°38′ N, 10°42′ E), which are located in the moraine landscapes of Schleswig-Holstein, Northwest Germany. The forest areas are dominated by deciduous trees (Lübeck: 72%; Mölln: 41%) with total area of 4297 ha (Lübeck) and 1150 ha (Mölln). Elevation ranges from 0 to 90 m asl. The study area is characterized by a suboceanic climate with a mean annual precipitation between 580 and 871 mm and a mean annual temperature of 8·3 °C (Gauer & Aldinger 2005).

Forests are managed according to a low-impact approach based on the protection of natural disturbance regimes within managed stands (Sturm 1993; Westpahl *et al.* 2004) and are certified according to the Forest Stewardship Council (FSC). We included unmanaged, crowded stands in the modelling data set as regional reference areas to ensure that a comprehensive gradient of stand density was used. Structurally, the investigated stands are multi-layered and uneven-aged (see Fig. S1, Supporting Information).

To test large-scale (regional) edaphic effects on tree growth, we stratified the plots according to their geological substrate. The resulting three beech forest types were characterized by a productivity gradient based on nutrient and water availability: (i) 'GF-till' meso- to eutrophic beech forests (*Galio-Fagetum*; EU habitat code: 9130) on moderately moist to moist recent moraine soils originating from the Weichselian glaciation. Soil texture consists of till (clay/sandy loam) with varying carbonate content, providing an optimal nutrient and water supply. The predominant soil types are (pseudogleyic) Luvisols and Cambisols. (ii) 'GF-clay' mesotrophic beech forests (*Galio-Fagetum*; EU habitat code: 9130) on hydromorphic recent moraine soils. The strong stagnant water influence is induced by basin clay deposits which are covered with silt or sand of varying thickness. These soils have a deficit in aeration during periods of excess water, which in turn increases the abiotic stress for tree growth. The prevailing soil types are strongly pseudogleyic Cambisols and Planosols. (iii) 'DF' oligotrophic beech forests (*Deschampsio-Fagetum*; EU habitat code: 9110) on recent moraine soils which consist of glacial sand deposits of the Weichselian glaciation. A low retention capacity for nutrients and water is caused by a high sand content, which increases the risk of trees suffering drought during summer. The soils are rather acidic (pH 3·5–5·0) compared to the recent moraine. The predominant soil types are podsolic Cambisols.

Optimal growing conditions (lowest level of abiotic stress) are associated with GF-till sites, whereas suboptimal situations are characterized by low top soil aeration during wet periods (GF-clay) or additive effects of summer drought and low nutrient availability (DF). The gradient of decreasing productivity is expressed by the significant decline in site index values, which is a proxy for the growth potential at a given site (Table 1). Thus, the abiotic stress level increases within the series GF-till – GF-clay – DF.

INVENTORY DATA

We used tree and stand data from sample plot inventories, conducted in 1992 and 2003 (Lübeck) as well as in 1999 and 2009 (Mölln). Measurements were taken in a regular spatial resolution of 180 × 130 m (Lübeck) and 100 × 200 m (Mölln), respectively. Within circular plots (Mölln, plot size: 250 m^2) or concentric circular plots (Lübeck, total plot size: 500 m^2), all living trees > 7 cm diameter at breast height (*DBH*) were considered. For each tree, the species, social status and *DBH* were determined. *DBH* values represent the average tree size derived from 2 cross-measurements at 1·3 m. Tree height was measured for a subset of 2–4 trees of each species and layer. Annual basal area growth (*BAI*) was calculated as the difference between the tree basal areas (cm^2) at the end and beginning of the sample period divided by the number of vegetation periods.

For the growth analyses, we randomly selected 1819 beech trees (target trees) from 250-m^2 (Lübeck) and 125-m^2 (Mölln) circular subplots, placed at the centre of the sample plots to account for edge effects. Only dominant and co-dominant target trees of the upper layer (canopy trees) were considered (classes 1–3 according to Kraft 1884).

Table 1. Mean (±SD) tree and stand characteristics of the investigated forest types and the associated stress gradient. 'GF-till' meso- to eutrophic beech forests (*Galio-Fagetum*) on moderately moist to moist recent moraine soils; 'GF-clay' mesotrophic beech forests (*Galio-Fagetum*) on hydromorphic recent moraine soils; 'DF' oligotrophic, acidophytic beech forests (*Deschampsio-Fagetum*) on sandy recent moraine soils. Data represent initial inventory values of the modelling data set. The soil nutrient status of the study plots was classified according to the German forest site mapping system (Arbeitskreis Standortskartierung 1996). This index ranges from 1 (very low nutrient availability) to 6 (very high nutrient availability)

	GF-till	GF-clay	DF
Abiotic stressor			
Nutrient-based	–	–	Nutrient deficiency
Water-based	–	Temporal water excess	Temporal water deficiency
Soil nutrient class (*n* plots)			
Eutrophic sites (index 5-6)	173	27	–
Mesotrophic sites (index 3–4)	139	151	–
Oligotrophic sites (index 1–2)	–	–	107
Site index* (m)	33·3^{a} ± 4·4	31·2^{b} ± 3·9	29·6^{c} ± 4·0
Tree age (year)	71·1 ± 36·7	74·9 ± 40·2	94·0 ± 46·7
Tree diameter (cm) at 1·30 m	28·6 ± 15·0	29·6 ± 17·0	31·7 ± 16·3
Tree height (m)	22·7 ± 8·1	21·9 ± 7·6	23·6 ± 7·4
Basal area growth (cm^2 $year^{-1}$)	22·4 ± 15·8	20·7 ± 16·8	25·8 ± 19·9
Relative radial growth rate† (%)	6·08 ± 8·2	4·61 ± 5·5	4·42 ± 4·1
Basal area all trees (m^2 ha^{-1})	27·6 ± 11·8	28·2 ± 10·1	27·3 ± 11·8
Basal area larger trees (m^2 ha^{-1})	15·8 ± 10·3	18·7 ± 10·3	12·2 ± 9·9
Proportion beech trees (%)	76·6 ± 24·8	64·2 ± 28·6	73·8 ± 28·5
n (forests)	17	10	1
n (plots)	312	178	107
n (trees)	1046	553	220

*Mean height of the 100 largest beech trees, different letters indicate significant differences among forest types (Tukey's HSD test: GF-till vs GF-clay: $P = 0{\cdot}001$; GF-till vs DF: $P < 0{\cdot}001$; GF-clay vs DF: $P < 0{\cdot}05$).

†Basal area growth-basal area ratio.

DATA ANALYSIS

Preliminary analyses indicated nonlinear *BAI-DBH* and *BAI-BAL* relationships. We therefore applied generalized additive mixed models (GAMMs) with a log link function and gamma distribution to assess growth patterns along the productivity gradient (Wood 2006). Study site and plot were used as random factors, accounting for the intraclass correlation at the site and plot level. To address the skewed response and heteroscedasticity of the *BAI* data, a gamma probability distribution was preferred, because it retains the structure of the data while accounting for a heteroscedastic error structure and avoiding biased inferences associated with logarithmic transformations (see Gea-Izquierdo & Cañellas 2009).

Basal area increment was modelled as a basic function of tree size (*DBH*) and tree's competitive status. Basal area of larger trees (*BAL*) was used as a distance-independent measure of crowding (Wykoff, Crookston & Stage 1982) and calculated as the total basal area of trees larger than the subject tree within a plot. To account for variation in the effect of species composition (inter- versus intraspecific competition), we calculated the proportion of beech trees within a plot (*PBT*) as the percentage of basal area composed of beech tree individuals. The resulting GAMM is:

$$BAI_{ijk} = \exp(\alpha + f_1(DBH_{ijk}) + f_2(BAL_{ijk}) + \beta(PB_{ij}) + b_i + b_{ij} + \varepsilon_{ijk}) \qquad \text{eqn 1}$$

where BAI_{ijk} is the mean basal area growth, α is the intercept, $f_{1,2}$ are smoothing functions (thin plate regression splines) of tree size and crowding effects and β is a parametric coefficient of the beech proportion effect. $b_i + b_{ij}$ denote the random effects of forest site$_i$ and plot$_j$ and ε is the residual error of the k-th tree. The optimal amount of smoothing was determined by cross-validation (Wood 2006). To test for size dependency of crowding effects, we additionally considered a two-way interaction term f (DBH, BAL). All models were fitted for each beech forest type separately. Additionally, we compared our semi-parametric model with a log-transformed parametric growth function and normal probability distribution, but the GAMM resulted in a better statistical fit (see Appendix S1, Supporting Information).

Different competing models were evaluated by sequential comparison (backward selection) based on the Akaike Information Criterion (AIC). Only models with an AIC difference (ΔAIC) < 4·00 (compared with the best fit model) were considered as models with substantial support (Buhrnham & Anderson 2002). The optimal random effects structure was based on restricted maximum likelihood (REML) estimation, the optimal fixed effects structure was identified by maximum likelihood (ML) method. Parameter estimates of the final model were fitted using the restricted maximum likelihood (REML) method (Zuur *et al.* 2009). Model accuracy was judged according to the adjusted coefficient of determination ($R^2_{adj.}$) and mean error. The relative influence of the predictors was determined by calculating the percentage change in $R^2_{adj.}$ owing to the inclusion of the subject predictor in the model.

To evaluate competition effects, we used two different competition measures: Competition intensity (C_{int}) and competition importance (C_{imp}). For each beech forest type, we predicted the radial growth (G) of a focal tree based on our best-fitted models, either in the presence (+) or in the absence (−) of larger competitors. We used the average value of beech proportion along the productivity gradient, while varying tree size and crowding conditions.

C_{int} was quantified as the response ratio between the growth of a target tree in a low- and a high-density stand (Brooker *et al.* 2005):

$$C_{int} = (G_- - G_+)/max(G_-, G_+) \qquad \text{eqn 2}$$

where G_- and G_+ are the basal area growth of a target tree experiencing a low level of crowding (BAL was set at 0 m^2 ha^{-1}) and a high level of crowding (BAL was set at 30 m^2 ha^{-1}). Accordingly, higher indices were taken to be those with greater absolute competition impact. As we were interested particularly in management implications, we further analysed changes in C_{int} with various levels of crowding (BAL varied between 1 and 30 m^2 ha^{-1}) by predicting the proportion of growth decline because of crowding. The crowding response (CR) was calculated as:

$$CR = 1 - ((G_- - G_{+,i})/max(G_-, G_+)) \quad \text{with } i = 1, \ldots, 30 \text{ m}^2\text{ha}^{-1} \qquad \text{eqn 3}$$

To determine significant changes in C_{int} with tree size and stand density, we applied a recursive partitioning approach using the function *ctree* implemented in the R library *party* (Hothorn, Hornik & Zeileis 2006). The resulting splits (threshold values) indicate a significant shift in growth reduction in relation to competition intensity. We used the threshold as a management-related indicator for the effectiveness of thinning, because it reflects the balance between maximum growth acceleration and growing stock capacity. The 95% confidence intervals for the thresholds were calculated based on 1000 bootstrap samples.

C_{imp} can be described as the impact of competition in relation to the total environment (competition and abiotic constraint, Brooker *et al.* 2005):

$$C_{imp} = (G_- - G_+)/(MaxG_- - min(G_-, G_+)) \qquad \text{eqn 4}$$

where $Max\ G_-$ is the maximum value of G_- along the investigated gradient. Accordingly, higher indices were taken to be those with greater competition impact incorporating the role of other processes. Similarly to C_{int}, we predicted the crowding response (CR) to analyse the density dependence effects on competition importance using eqn 4.

To test tree size-related effects at low and high crowding levels, trees were stratified into three timber tree size classes and competition indices were calculated for each size class separately: (i) small timber trees: DBH 20–35 cm, (ii) medium timber trees: DBH 36–50 cm and (iii) large timber trees: DBH 51–70 cm. Differences in competition indices between forest types were tested by analysis of variance (ANOVA) followed by a post hoc performance (Tukey's HSD test).

Finally, we calculated for each forest type the relationship between the basal area of all trees (BA) and the basal area larger trees (BAL) to facilitate practical management implications.

All statistical analyses were performed using R (R Development Core Team 2009, version 2.10.1). The nonlinear models were fitted using the *gamm* function from the *mgcv* library.

Results

GROWTH PATTERN

Tree size, crowding condition and level of intraspecific competition explained between 43% (GF-till, GF-clay) and 47% (DF) of the variation in log-basal area growth. At GF-till sites, the effect of canopy tree crowding on radial growth depended on tree size, while the crowding–diameter relationship was consistent across the observed diameter range of GF-clay and DF (Table 2). DBH was a much stronger predictor than BAL or PBT. Canopy tree crowding accounted for 4–18%, which underlines the high importance of tree size as an indicator for the tree's past competition status in uneven-aged stands (Prévosto & Curt 2004). For all forest types, increasing intensity of intraspecific competition was negatively related to tree growth. An increase in beech proportion by 10% resulted in an average growth reduction of 5% (GF-till −4·1%; GF-clay −4·7%; DF −4·2%). Graphical model validation plots indicated no trends in the residuals (Fig. S2, Supporting Information), and parameter estimates of the final models are summarized in Table S1 (Supporting Information).

Table 2. Results of the model selection for the basal area growth of canopy trees (*Fagus sylvatica*) using Akaike's information criterion (AIC). Models were fitted by generalized additive mixed models (GAMMs) for each forest type separately. Tree size at 1·30 m (*DBH*), basal area larger trees (*BAL*) and proportion of beech trees (*PBT*) were included as fixed effects, forest site and study plot as random factors. The best-fitted model structure is highlighted in bold, and the corresponding adjusted coefficient of determination (R²) and mean error are given. The relative influence of the predictors was calculated as the percentage change in $R^2_{adj.}$ when the subject predictor was included in the model. 'GF-till' meso- to eutrophic beech forests on moderately moist to moist soils; 'GF-clay' mesotrophic beech forests on hydromorphic soils; 'DF' oligotrophic, acidophytic beech forests

Predictor variables	GF-till	GF-clay	DF
DBH + BAL + PBT	1774·0	**1134·1**	**392·0**
DBH + BAL	1785·1	1142·2	395·8
DBH + PBT	1828·1	1146·9	404·0
BAL + PBT	2002·8	1317·3	454·8
DBH + BAL + PBT + DBH * BAL	**1767·0**	1138·0	414·5
$R^2_{adj.}$ best model	0·434	0·426	0·469
Relative influence DBH (%)	75	83	88
Relative influence BAL (%)	18	4	9
Relative influence PBT (%)	7	13	3
Mean error (cm^{-2} $year^{-1}$) best model	0·8	1·9	1·8

COMPETITION INTENSITY

Tree growth was negatively affected by increasing competition. However, the intensity strongly varied between forest types (Fig. 1). In GF-till, the effects of density reduction were most influential for smaller trees (20–40 cm), while the sensitivity to local crowding of large timber trees (>50 cm) was negligible. Absolute differences between tree sizes were largest in medium- and high-crowded stands (*BAL,* 15–30 m^2 ha^{-1}; *BA,* 26–38 m^2 ha^{-1}, Fig. S3, Supporting Information). Crowding response of GF-clay and DF was negatively related to stand density, with absolute differences between tree sizes being comparably small.

The amplitude of mean C_{int} values significantly differed along the productivity gradient across all diameter classes (Fig. 2). The response of small timber trees (20–35 cm) to competition reduction was significantly higher in GF-till than in GF-clay and DF ($P_{adj.} < 0{\cdot}001$). An opposite trend was obvious for medium (36–50 cm) and large (>50 cm) timber trees, with highest values in GF-clay and DF ($P_{adj.} < 0{\cdot}01$). Large trees in GF-till showed a fourfold weaker effect than those in GF-clay or DF. Moreover, the threshold analysis for thinning efficiency indicated that C_{int} significantly declined at *DBH* 42 cm in GF-till ($P < 0{\cdot}001$, 95% CI: 37–51 cm; Fig. S4, Supporting Information), at *DBH* 27 cm in GF-clay ($P < 0{\cdot}001$, 95% CI: 24–39 cm; Fig. S5, Supporting Information) and at *DBH* 45 cm in DF ($P < 0{\cdot}001$, 95% CI: 38–50 cm; Fig. S6, Supporting Information). However, it should be noted that thresholds for GF-clay and DF represent marginal changes (see Fig. 2). There was no distinct effect of crowding intensities on the thresholds (Table S2, Supporting Information).

COMPETITION IMPORTANCE

On average, competition response was much stronger in GF-clay and DF than in GF-till (Fig. 3). Tree size effects on C_{imp} were inversely related to C_{int}, with effects being strongest for largest trees and weakest for smallest trees. Differences in the magnitude of tree size effects, however, increased with increasing abiotic stress. Regardless of

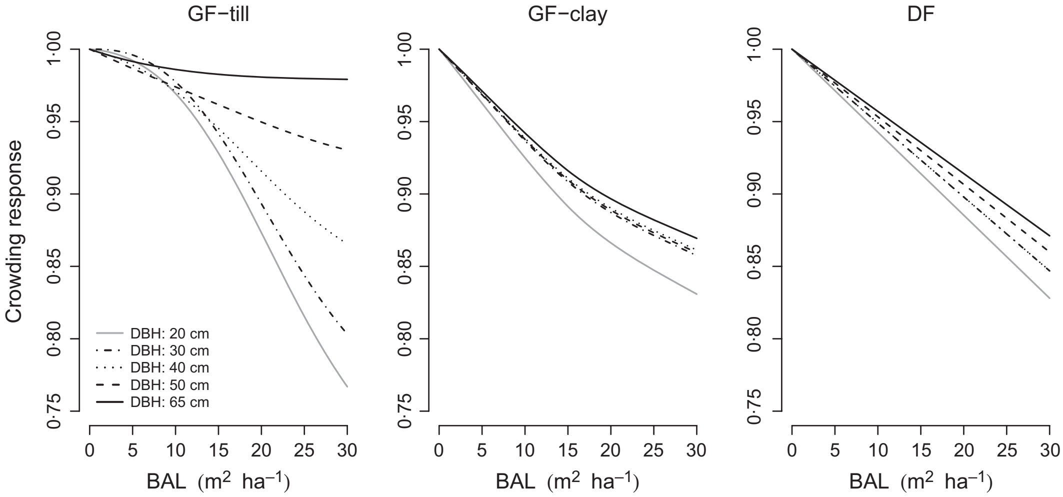

Fig. 1. Effect of tree size (*DBH*) on the competition intensity–crowding relationship. The response index ranges from 0 (maximal response) to 1 (no response) and indicates the percentage change in growth reduction because of crowding. Crowding condition (*BAL*) is described as the basal area of larger canopy trees within a study plot. Regression lines represent the predicted response pattern of *Fagus sylvatica* obtained by generalized additive mixed models. 'GF-till' meso- to eutrophic beech forests on moderately moist to moist soils; 'GF-clay' mesotrophic beech forests on hydromorphic soils; 'DF' oligotrophic, acidophytic beech forests.

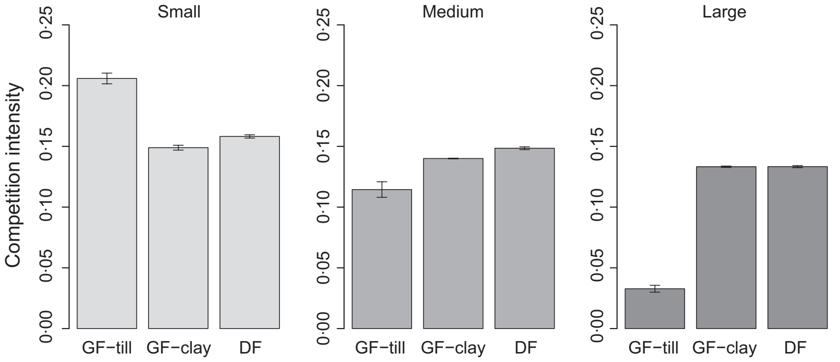

Fig. 2. Change in competition intensity during tree maturation for three timber tree size classes (small '*DBH* 20–35 cm'; medium '*DBH* 36–50 cm' and large '*DBH* 51–70 cm'). The competitive interaction index ranges from 0 (no competition) to 1 (maximal effect of competition) and indicates the impact of competition on the radial growth of *Fagus sylvatica* in a specific abiotic environment (forest type). Error bars represent 95% confidence intervals. Non-overlapping confidence intervals indicate significant differences ($P_{adj.} < 0{\cdot}01$) among forest types. 'GF-till' meso- to eutrophic beech forests on moderately moist to moist soils; 'GF-clay' mesotrophic beech forests on hydromorphic soils; 'DF' oligotrophic, acidophytic beech forests.

resource availability, density-dependent growth reductions in small and medium timber trees were generally stronger in dense stands, whereas especially for mature trees (>65 cm), C_{imp} was high almost over the entire investigated density range (*BAL,* 10–30 m^2 ha^{-1}; *BA*, 20–39 m^2 ha^{-1}).

Changes in the mean C_{imp} values along the productivity gradient were similar to C_{int} (Fig. 4).

Discussion

THE ROLE OF COMPETITION IMPORTANCE AND INTENSITY IN LOWLAND BEECH FOREST COMMUNITIES

We hypothesized that competition becomes less important with increasing abiotic stress (Bertness & Callaway 1994), which is supported by the declining relative influence of *BAL* (see Table 2). Likely, this trend was linked to the decreasing competitiveness of beech with increasing water (e.g. waterlogging, severe drought) or nutrient stress (Peters 1997; Härdtle, von Oheimb & Westphal 2003). When considering variations in tree size, however, for adult trees along a productivity gradient, no consistent pattern was obvious. Contrary to our expectations, the stress gradient hypothesis (SGH) seemed to hold for small timber trees, while competition effects on medium and large timber trees were strongest in resource-limited environments, thus contradicting the SGH predictions. This might be in accordance with the increasing adaptation capacity of *F. sylvatica* during tree maturation and thus reduced resource restrictions. The higher adaptation

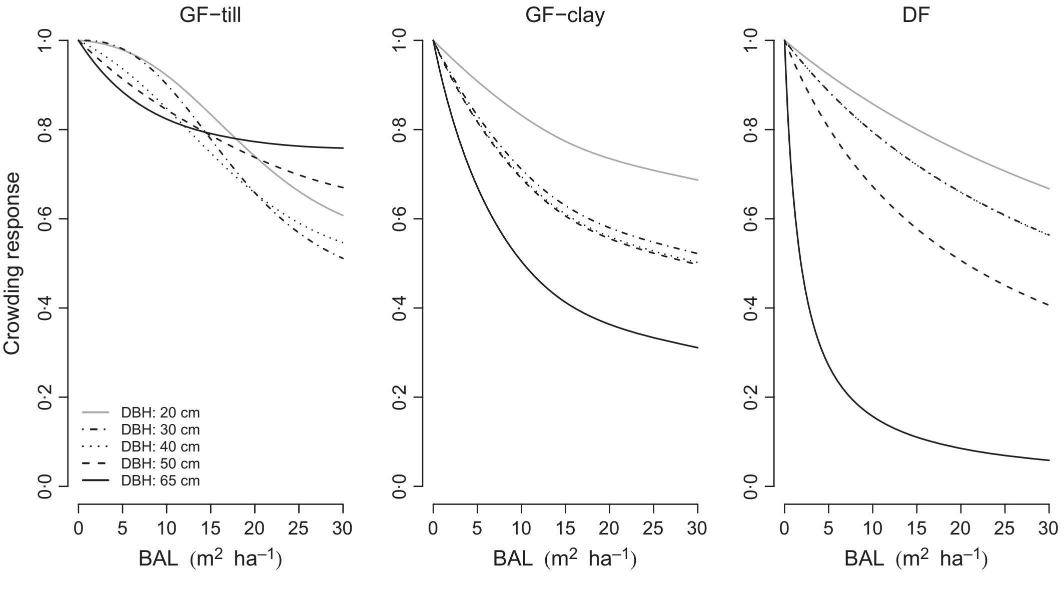

Fig. 3. Effect of tree size (*DBH*) on the competition importance–crowding relationship. Crowding condition (*BAL*) is described as the basal area of larger canopy trees within a study plot (see Fig. 1 for more details). 'GF-till' meso- to eutrophic beech forests on moderately moist to moist soils; 'GF-clay' mesotrophic beech forests on hydromorphic soils; 'DF' oligotrophic, acidophytic beech forests.

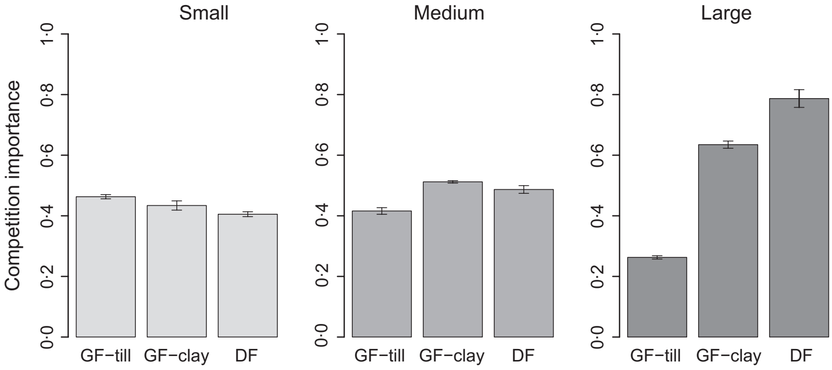

Fig. 4. Change in competition importance during tree maturation for three timber tree size classes (small '*DBH* 20–35 cm'; medium '*DBH* 36–50 cm' and large '*DBH* 51–70 cm'). The competitive interaction index ranges from 0 (no competition) to 1 (maximal effect of competition) and indicates the impact of competition in relation to the total environment (competition and abiotic constraint). Error bars represent 95% confidence intervals. Non-overlapping confidence intervals indicate significant differences ($P_{adj.} < 0{\cdot}01$) among forest types. 'GF-till' meso- to eutrophic beech forests on moderately moist to moist soils; 'GF-clay' mesotrophic beech forests on hydromorphic soils; 'DF' oligotrophic, acidophytic beech forests.

capacity of larger individuals in resource-limited environments is probably linked to a deeper root system and thus to an improved water and nutrient access (Dawson 1996). Furthermore, larger trees might be able to pre-empt growth resources and become more competitive (Schwinning & Weiner 1998) or develop root densities in favourable zones and thus compensate the high sensitivity of *F. sylvatica* to hydromorphic soils (Diekmann *et al.* 1999). Consequently, tree size-related growth patterns seemed to gain relevance in uneven-aged tree communities, and the SGH might not be universally applicable for tree growth under near-natural growing conditions.

Moreover, we found evidence that competitive interactions were affected by different crowding intensities. For large trees, competition was equally important in dense and less crowded stands, with effects being more pronounced on sites with moderate and low resource availability. In contrast, competition was most important for small- and medium-sized trees in dense stands, with highest sensitivity for changes in crowding conditions on fertile sites (GF-till). Thus, the resource dependency of competition effects appeared to be variable during tree maturation. This contradicts findings from Pretzsch & Biber (2010), who could not observe resource- and tree size-related competition effects for *F. sylvatica* along a fertility gradient. Our results demonstrate that competitive interactions shift in importance during tree maturation, most likely due to tree size-specific allocation pattern and temporal variations in the strength and duration of competition (Niinemets 2010).

The effect of increasing intraspecific competition on tree growth was generally negative. As *F. sylvatica* represents the most competitive tree species in forest ecosystems of Europe, a reduction in beech proportion can be assigned to an overall decreasing competitive stress within the stand. Accordingly, the niche theory predicts that competition becomes less important as niche differences increase (Chesson 2000). Thus, different ecological strategies alter crown space occupancy patterns and crown competition, which in turn favour radial tree growth (Assmann 1970; Pretzsch & Schütze 2005).

In a recent study, Kunstler *et al.* (2011) found evidence that competition importance in tree–tree interactions supports the assumptions of the SGH. Adult trees (e.g. of *F. sylvatica*) responded with increasing C_{imp} to increasing values of bioclimatic growth determinants. However, the authors did not observe significant changes along climatic gradients regarding C_{int}. This is partly consistent with our findings, whereas the discrepancy between the study of Kunstler *et al.* (2011) and ours may be explained by altitude differences (mountain vs. lowland forests) and the investigated diameter range, because the average diameter generally declines with altitude. Mean diameter of *F. sylvatica* trees in mountain forests was 22 cm (maximum *DBH*: 56 cm), while mean diameters of trees in the present study were 29 cm (GF-till, maximum *DBH*: 80 cm), 30 cm (GF-clay, maximum *DBH*: 92 cm) and 32 cm (DF, maximum *DBH*: 83 cm), respectively. Thus, Kunstler *et al.* (2011) could hardly predict the response of mature beech trees (>50 cm) in relation to density-dependent effects. However, our results suggest additionally that both C_{imp} and C_{int} vary notably with tree maturation. The distinct decline of C_{int} with tree maturation in environments without abiotic constraints might be a result of differences in biotic stress tolerance (Liancourt, Callaway & Michalet 2005), because we observed the highest tolerance towards competition for large and vigorous trees on fertile sites. Furthermore, growth efficiency of dominant trees is likely to increase in crowded stands on edaphically optimal sites (Utschig & Küsters 2003). We emphasize that our results do not hold for tree growth pattern in sparsely stocked stands (<20 m^2 ha^{-1}), because under such growing conditions even large-sized trees respond with high radial growth acceleration to growing space expansions (Wilhelm, Letter & Eder 1999).

In this context, it is worth mentioning the indirect assessment of the underlying abiotic stress gradient in our study, because we could not directly relate our results to measured or modelled soil parameters over longer periods. However, the trophic–hydrologic gradient investigated in our study corresponds with the most important lowland beech forest ecosystems in Europe (Leuschner, Meier & Hertel 2006). Our results suggest that tree–tree interactions along abiotic gradients do not follow a simple pattern (Maestre, Valladares & Reynolds 2006; Maestre *et al.* 2009), because the magnitudes of C_{imp} and C_{int} vary during tree (i.e. size) and stand (i.e. crowding level) development. Thus, for tree communities, the SGH might be refined by consideration of maturation aspects.

IMPLICATIONS FOR NEAR-NATURAL FOREST MANAGEMENT

Both C_{int} and C_{imp} could be considered as criteria for near-natural management strategies, which in turn would allow more flexible adjustments to varying growing conditions in the future. C_{int} indicates growth reduction because of competition at a specific level of resource availability, and thus the growth acceleration potential, whereas C_{imp} indicates how environmental stress alters growth patterns along abiotic gradients. For example, our results suggest that tree size-dependent competition effects might become more important with regard to changing environmental stress, rather than differences in crowding intensities. This is particularly important, because trees with low competition tolerance are predisposed to additional temporary abiotic stress (Linares, Camarero & Carreira 2010).

To our knowledge, this is the first study to quantify tree size-dependent effects on tree–tree interactions along abiotic stress gradients. The identified thresholds for thinning efficiency indicate that growth acceleration decreased during tree maturation, with strongest impacts for tree growth under optimum growing conditions (from an edaphic point of view). Thinning effects declined within the series GF-till$_{20\text{-}40\ \mathrm{cm}}$ – GF-clay/DF$_{20\text{-}50\ \mathrm{cm}}$ – GF-clay/DF$_{>50\ \mathrm{cm}}$ – GF-till$_{>40\ \mathrm{cm}}$. A crucial result was that radial growth of canopy trees with a $DBH > 40$ cm seemed to be hardly affected by competition (absolute impact) in GF-till. As a consequence, competitor removal in such diameter dimensions would result in a strong reduction in timber volume in relation to timber increment and in a higher probability of cutting damages. Because natural stand dynamics in beech forests are characterized by small-scale variation in forest development stages (Piovesan *et al.* 2005), it seems feasible for uneven-aged stands to apply thinning strategies to specific diameter classes and forest development stages. Reduced thinning intensities shift diameter distribution towards more complex stand structures with higher permanent growing stocks, which in turn represent a key factor for realising sustainability on stand level.

Our findings are of considerable relevance, because they directly relate to practical aspects of forest biodiversity and management strategies. Forest management guidelines require simple but ecologically effective key values (Moning & Müller 2009), among which stem diameter range and stand volume are considered appropriate surrogates that can easily be integrated in management schemes. Linking competition responses with thinning intensity and growing stocks, we propose the following low-impact management strategies for lowland beech forests:

1. Thinning interventions should be exclusively performed in a diameter range of 20–40 cm, particularly on sites with optimum nutrient and water supply (GF-till). Interventions in later developmental stages should be restricted to harvest cuts. On sites with restricted below-ground resources (GF-clay, DF), thinning strength could be increased by *c.* 25%, because absolute thinning effects are lower compared with fertile sites. This contrasts commonly applied thinning strategies in beech stands, which include continuous treatments throughout the development stages until the harvest cut (e.g. Nagel & Spellmann 2008).

2. For GF-till, we suggest permanent stand volumes of 600 $\mathrm{m}^3\ \mathrm{ha}^{-1}$, which represents 80% of the growing stock of mature stands in unmanaged reference areas (Fichtner 2009). For GF-clay and DF, permanent stand volumes should be adjusted to the natural growth potential and can amount to 450 $\mathrm{m}^3\ \mathrm{ha}^{-1}$. These values exceed by far recommended permanent stand volumes for uneven-aged beech forests (e.g. plenter forests, Schütz 2006).

The management strategies proposed above will facilitate both timber production and nature conservation demands. There is evidence that intensive logging, particularly in old stands, reduces species diversity at stand and landscape scale, mainly due to homogenization of forest structures and loss of microhabitats (Paillet *et al.* 2009). Particularly, affected forest species are characterized by low dispersal abilities (Brunet & von Oheimb 1998), or are stenotopic and require microhabitats related to old-growth stands (e.g. old or large trees, snags, coarse woody debris; Brunet, Fritz & Richnau 2010). Decreasing management intensity in combination with a prolonged rotation age will favour natural stand dynamics (e.g. lesser soil disturbance, accumulation of biomass, extension of senescent processes, formation of dead wood), and thus biodiversity patterns characteristic for old-growth stands. This was recently demonstrated for several forest-dwelling species across different taxonomic groups (Moning & Müller 2009; Paillet *et al.* 2009). As a consequence, stands subjected to low-impact management practices may not only host more forest-dwelling species, but may also serve as source biotopes for other stands (Moning & Müller 2009).

In conclusion, our results provide important additional insight into competitive interactions in tree communities along environmental gradients. Although our 10-year study may be limited with respect to long-term growth dynamics, the bias of the present regional individual-tree growth models is much smaller compared with those derived from long-term thinning experiments (e.g. yield table models, Pretzsch 2009). Future research based on long-term non-manipulative inventory data would help to generalize our observations to other forest communities. Nevertheless, it seems that the identified growth response to competition might hold for other shade-tolerant tree species (Kunstler *et al.* 2011), even if the authors did not test tree size effects. We found strong divergence in tree growth response to competition among the investigated beech forest types. Therefore, management practices should be adjusted to the specific growth dynamics and potentials. Implementing ecological theory into management strategies, and thus increasing the benefit of natural productivity and self-regulation would be a further step towards near-natural forest management. A dynamic, low-impact management approach that favours high permanent stand volumes and stand age, respectively, seems to be a possibility to link ecological (e.g. biodiversity, carbon storage) and economical (e.g. quality timber production) concerns in forest management.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. Diameter distribution of the study stands.

Fig. S2. Residual plots of the final generalized additive mixed models.

Fig. S3. GAM predicted relationship between basal area all trees and basal area larger trees.

Fig. S4. Conditional inference tree for the GF-till data.

Fig. S5. Conditional inference tree for the GF-clay data.

Fig. S6. Conditional inference tree for the DF data.

Table S1. Parameter estimates of the final generalized additive mixed models.

Table S2. Variation in threshold values with varying crowding intensities.

Appendix S1. Comparison of different growth functions.

Chapter 17

Facilitative-competitive interactions in an old-growth forest: the importance of large-diameter trees as benefactors and stimulators for forest community assembly

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RESEARCH ARTICLE

Facilitative-Competitive Interactions in an Old-Growth Forest: The Importance of Large-Diameter Trees as Benefactors and Stimulators for Forest Community Assembly

Andreas Fichtner[1] *, **David I. Forrester**[2], **Werner Härdtle**[1], **Knut Sturm**[3], **Goddert von Oheimb**[4]

1 Institute of Ecology, Leuphana University of Lüneburg, Lüneburg, Germany, **2** Chair of Silviculture, University of Freiburg, Freiburg, Germany, **3** Community Forest Lübeck, Lübeck, Germany, **4** Institute of General Ecology and Environmental Protection, Technische Universität Dresden, Tharandt, Germany

* fichtner@leuphana.de

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Abstract

The role of competition in tree communities is increasingly well understood, while little is known about the patterns and mechanisms of the interplay between above- and belowground competition in tree communities. This knowledge, however, is crucial for a better understanding of community dynamics and developing adaptive near-natural management strategies. We assessed neighbourhood interactions in an unmanaged old-growth European beech (*Fagus sylvatica*) forest by quantifying variation in the intensity of above- (shading) and belowground competition (crowding) among dominant and co-dominant canopy beech trees during tree maturation. Shading had on average a much larger impact on radial growth than crowding and the sensitivity to changes in competitive conditions was lowest for crowding effects. We found that each mode of competition reduced the effect of the other. Increasing crowding reduced the negative effect of shading, and at high levels of shading, crowding actually had a facilitative effect and increased growth. Our study demonstrates that complementarity in above- and belowground processes enable *F*. *sylvatica* to alter resource acquisition strategies, thus optimising tree radial growth. As a result, competition seemed to become less important in stands with a high growing stock and tree communities with a long continuity of anthropogenic undisturbed population dynamics. We suggest that growth rates do not exclusively depend on the density of potential competitors at the intraspecific level, but on the conspecific aggregation of large-diameter trees and their functional role for regulating biotic filtering processes. This finding highlights the potential importance of the rarely examined relationship between the spatial aggregation pattern of large-diameter trees and the outcome of neighbourhood interactions, which may be central to community dynamics and the related forest ecosystem services.

Introduction

Tree–tree interactions are important structuring mechanisms for forest community dynamics, and the outcome of these biotic interactions has already been identified to vary across environmental gradients and tree growth stages (e.g., [1–7]). These interactions can be competitive or facilitative and complementary and the direction of biotic interactions may shift with different environmental conditions [7,8,9,10]. Generally, interactions shift towards facilitation as stress increases [11]. For example, if the availability of a given soil resource declines along a spatial or temporal gradient, then facilitation or complementarity could increase if the plants interact in ways that improve the availability or uptake of that resource [7]. Or, as productivity and leaf area increases, competition for light is also likely to become more intense and complementarity can increase if the plants interact in ways that improve light absorption [12]. Moreover, competitive interactions often become less severe in mixed-species communities (e.g., [5,13]), and the negative effects of competition on adult tree growth are on average greater for shading than for crowding [14,15]. In monospecific stands, neighbourhood interactions affecting growth dynamics are determined by factors other than species identity. It has been suggested that the spatial arrangement of trees plays a key role in regulating the intensity of inter–tree competition within structurally diverse old-growth forests [16].

The competitive ability of plants is strongly related to their size, and competitive interactions among trees can be size-asymmetric or size-symmetric [17]. There is more or less consensus that competition for light among terrestrial plants is strongly size-asymmetric [18,19], particularly in later successional stages [20]. In contrast, competition for belowground resources (e.g. water and nutrients) can be size-asymmetric or size-symmetric [19,21–26]. In addition to the importance of differentiating between the modes of competition (e.g. above- vs. belowground and symmetric vs. asymmetric), the potential interactions between above- and belowground competition have received increasing attention in plant ecology, such as whether these effects are additive (e.g. the summation of single effects) or non-additive (e.g. antagonistic or synergistic interaction) [27]. Next to competition many studies increasingly stress facilitation or complementarity as an important driver for community dynamics (e.g., [11,28,29,30]). Most of these findings, however, refer to mixed-species communities or tree seedlings [7,11,31], but mechanisms of facilitative or complementarity interactions between adult trees in monospecific stands are poorly understood.

In this study, we aim to determine how interactions between adult trees are related to above- and belowground processes at the intraspecific level. To answer this question, we used growth data from a long-term (> 50 years) unmanaged old-growth European beech (*Fagus sylvatica*) forest, encompassing a large range of tree sizes (diameter at breast height, DBH 7–116 cm) and age classes (35–240 years). More specifically, we asked (i) whether above- or belowground competition has a stronger effect on tree radial-growth, (ii) whether competitive interactions vary with tree size, and (iii) whether the effects of above- and belowground competition are additive (i.e. the summation of shading and crowding effects) or non-additive (i.e. antagonistic or synergistic interaction).

Materials and Methods

Study area

This study was conducted in an 8 ha (200 m × 400 m) permanent plot of an old-growth forest ('Serrahn') located in the core zone of the Müritz National Park (Mecklenburg-Western Pomerania, NE Germany, 53° 20' N, 13° 12' E). The predominant forest communities in the national park can be assigned to oligotrophic beech forests (*Luzulo-Fagetum*) on dystric cambisols and podzoluvisol soils, and to mesotrophic beech forests (*Milio-Fagetum*) on luvisols. Soils are developed on a parent material of loamy sand and the main humus type is moder. 268 ha of the Serrahn forest are part of the UNESCO World Natural Heritage Site "Primeval beech forests of the Carpathians and the ancient beech forest of Germany" and represent a prime example of natural beech forest dynamics. The climate is suboceanic-subcontinental with annual means for precipitation of 593 mm and for temperature of 7.8°C [32]. Elevation is approximately 100 m a.s.l.

Forest history and structure

The Serrahn forest is characterised by a long (>450 years) continuity of forest cover [33]. From the beginning of the 19th century the Serrahn forest was used as a game park with low intensity silvicultural interventions. In 1960, it was declared a forest nature reserve and management ceased. During the last 40 years, stand structure became more heterogeneous over small spatial scales by shifting from mono-layered to multi-layered stands. These changes were mainly driven by increasing mortality rates of canopy trees in the late 1960s, which caused numerous canopy gaps and created conditions conducive to regeneration over large spatial scales. As a result the volume of dead wood considerably increased from 1967 to 2002 in the permanent plot (4 to 107 m^3 ha^{-1}) [32]. Thus, the current rotated sigmoid diameter distribution (Fig. 1) is mainly a function of self-thinning and mortality processes of old trees [34].

The canopy is dominated by *F. sylvatica* (96%). The other 4% is composed of about 3% Scots pine (*Pinus sylvestris*) and 1% Sessile oak (*Quercus petraea*). The understorey consists almost entirely of *F. sylvatica* (S1 Table). The age of the overstorey trees varied between 200 and 240 years with maximum values of 116 cm in diameter at breast height (DBH) and 44 m in height. The mean structural characteristics (initial conditions in 2002) are as follows [32]: stand volume 605 m^3 ha^{-1}, stand basal area 32.72 m^2 ha^{-1} and stand density 263 stems ha^{-1}. The mean height of the overstorey and understorey trees was 34.3 m and 11.2 m, respectively. The top height (the average height of the 20% largest-DBH trees) amounted to 38.4 m in the overstorey, and to 16.5 m in the understorey.

Another old-growth feature is the high abundance of large-sized (>60 cm in DBH) beech trees, which account for 40 stems per hectare (57% of the canopy dominants). Those trees were regularly distributed in the study plot at spatial scales of approx. 13 m, whereas for neighbourhood scales > 13m the tree spatial pattern became more random (Fig. 2). As a result the impact of large-diameter (> 60 cm) trees on the local growing conditions within a neighborhood scale of 20 m was almost equally high for all canopy dominants with a DBH $\leq$ 60 cm (Fig. 3A). In contrast, understory trees tended to aggregate in areas with low neighbourhood densities of large-diameter trees (Fig. 3B).

Growth data

The research permission was provided by the administration of the Müritz National Park, Mecklenburg Vorpommern, Germany. No specific permissions were required for our activities. Our field studies did not involve any endangered species.

For all living trees with a DBH $\geq$ 7 cm in the study plot, stem diameter at 1.30 m, species, spatial position and crown class (dominant, co-dominant and suppressed) [35] were recorded (S2 Table). Annual basal area growth (BAI) was determined from two DBH measurements in 2002 and 2009, which represent a seven year growing period. An allometric equation describing tree height as a function of DBH was calibrated based on a subset of 243 height measurements of *F. sylvatica*. For *P. sylvestris* and *Q. petraea* the height of all trees within the study plot

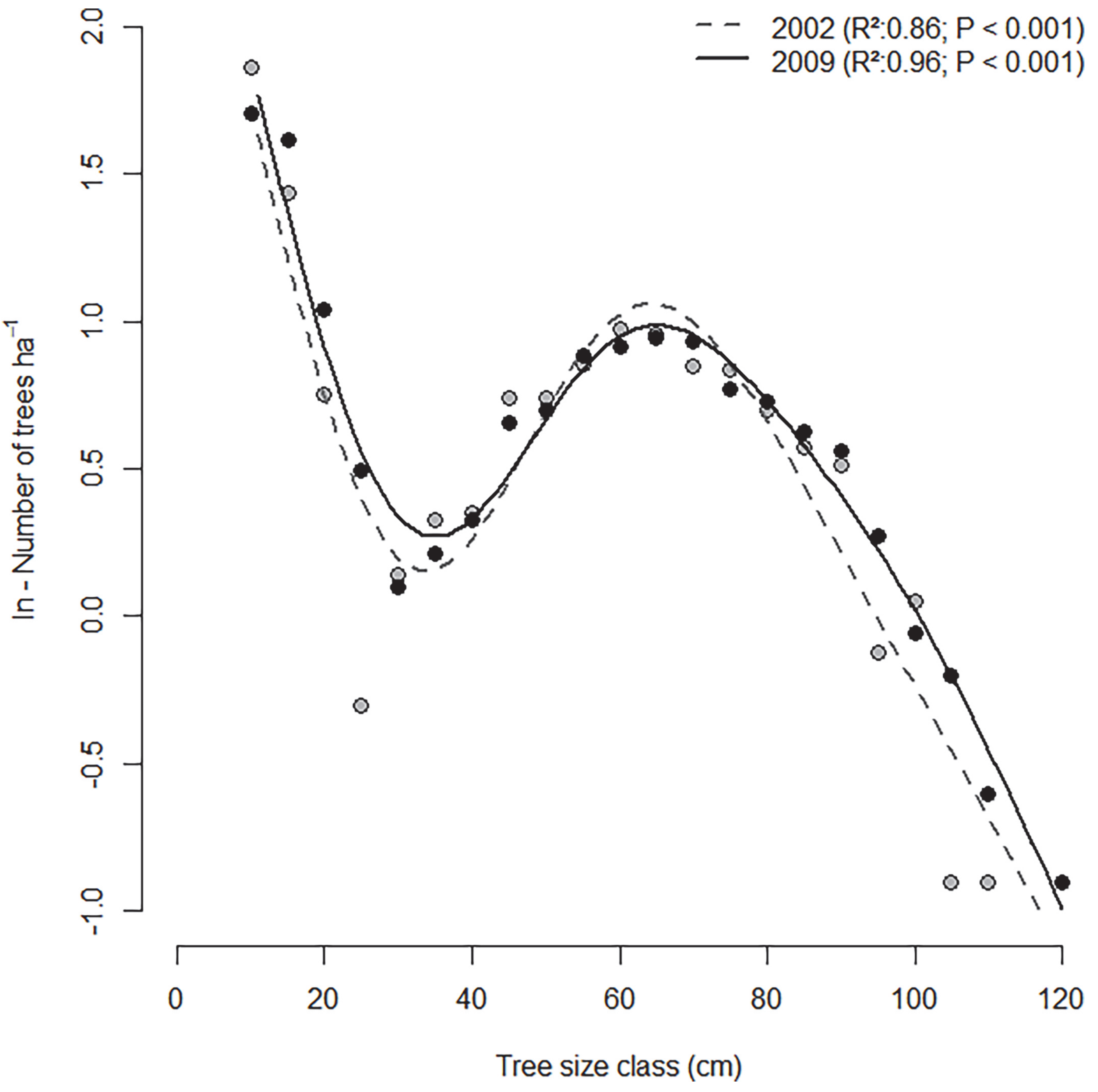

Fig 1. Stand structure of the investigated old-growth beech forest. The x-axis represents the upper boundaries of the tree size (DBH)-class. Regresssion lines were obtained by fitting generalized additive models (*gam* function in R, with five degrees of freedom). Grey dots: investigation year 2002; black dots: investigation year 2009.

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was recorded. Height measurements were determined with a Forestor VERTEX Hypsometer (Haglöf, Sweden).

Growth analyses focused on 545 dominant and co-dominant canopy beech trees (target trees). To account for edge effects, only target trees within a buffer zone of 20 m (see below) to the borders of the 8 ha plot were considered. The minimum radial distance of the study plot to

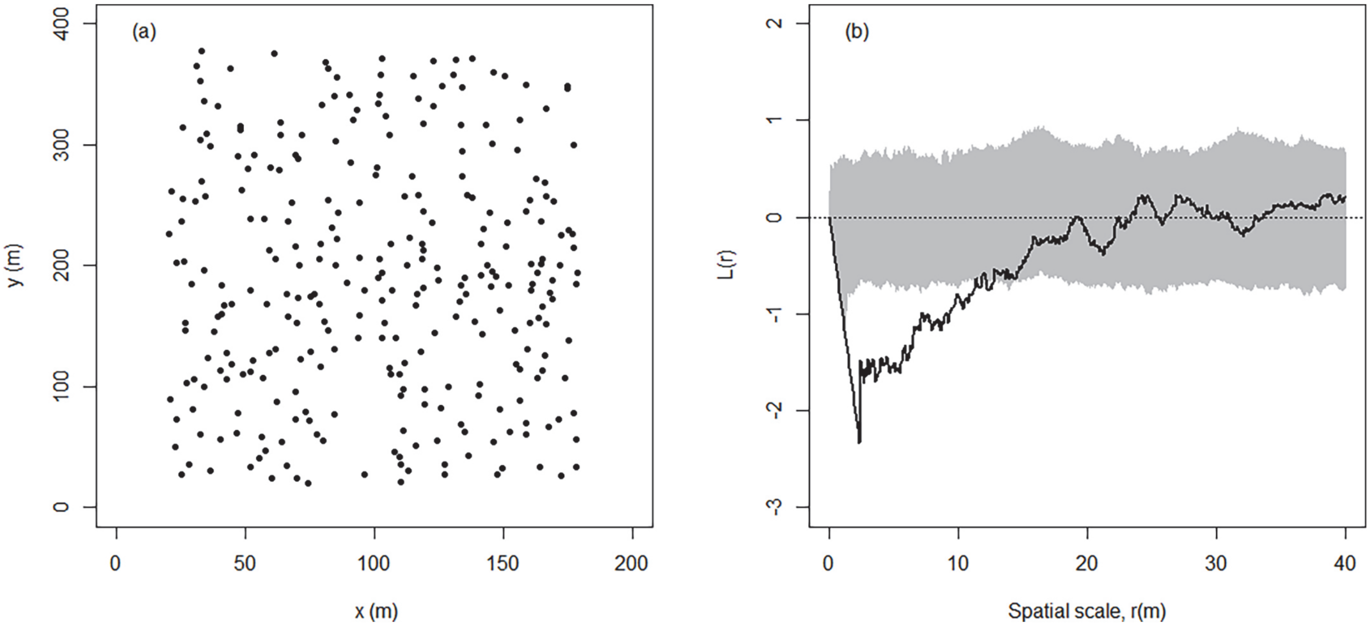

Fig 2. Spatial pattern (a) and corresponding spatial analysis (Ripley's *L* function; (b)) of large-sized (DBH > 60 cm) beech trees in 2002. Values of *L* (r) above the 95% confidence envelope (determined by 199 Monte Carlo simulations; grey area) indicate spatial aggregation, those within the envelope indicate spatial randomness and those below the envelope indicate spatial regularity. The spatial tree pattern was analysed in R using the package *spatstat*.

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forest edges was 150 m. As a result, the core zone amounted to 5.76 ha, and the buffer zone to 2.24 ha. All other individuals (n_{total} = 2770) were considered as neighbourhood trees (Table 1).

Competition indices

For distinguishing between above- (shading) and belowground (crowding) competition, we applied two competition indices (CI) according to [23]: An index of shading (CIS) was calculated as the total initial basal area of trees larger than the target tree (BAL) within a specified radius of the target tree. This index assumes that competing trees intercept light in relation to their stature, which typically results in a disproportionally higher light interception of larger trees compared to smaller neighbours [17]. An index of crowding (CIC) was calculated as the total initial basal area of all trees (BA) within this radius. This index assumes that all trees irrespective of their size compete for belowground resources (e.g. nutrients) and represents a proxy measure of belowground competition among trees when used in the same model as the other competition index that accounts more for aboveground competition [23]. In this context, it is worth mentioning the indirect assessment of belowground competition in our study, because we could not directly relate growth rates to measured root parameters such as fine root biomass or productivity. However, distant-dependent and distant-independent indices for crowding are assumed to act as proxies for belowground competition in tree growth studies, which account for both shading and crowding effects (e.g., [5,14,15,23]). To account for the distance-dependency of competition effects, we used a fixed radial distance approach. BAL and BA were computed for different radii (10, 15 and 20 m) and any tree within this distance was included as a neighbour. The optimum neighbourhood radius was determined by calculating the R^2 of the relationship between ln(BAI) and competition effects (BAL and BA). The area with a 20 m radius explained the highest amount of variation in BAI (R^2_{10m}: 0.15; R^2_{15m}: 0.22; R^2_{20m}: 0.31) and was therefore selected for further analysis. To facilitate comparisons between shading and

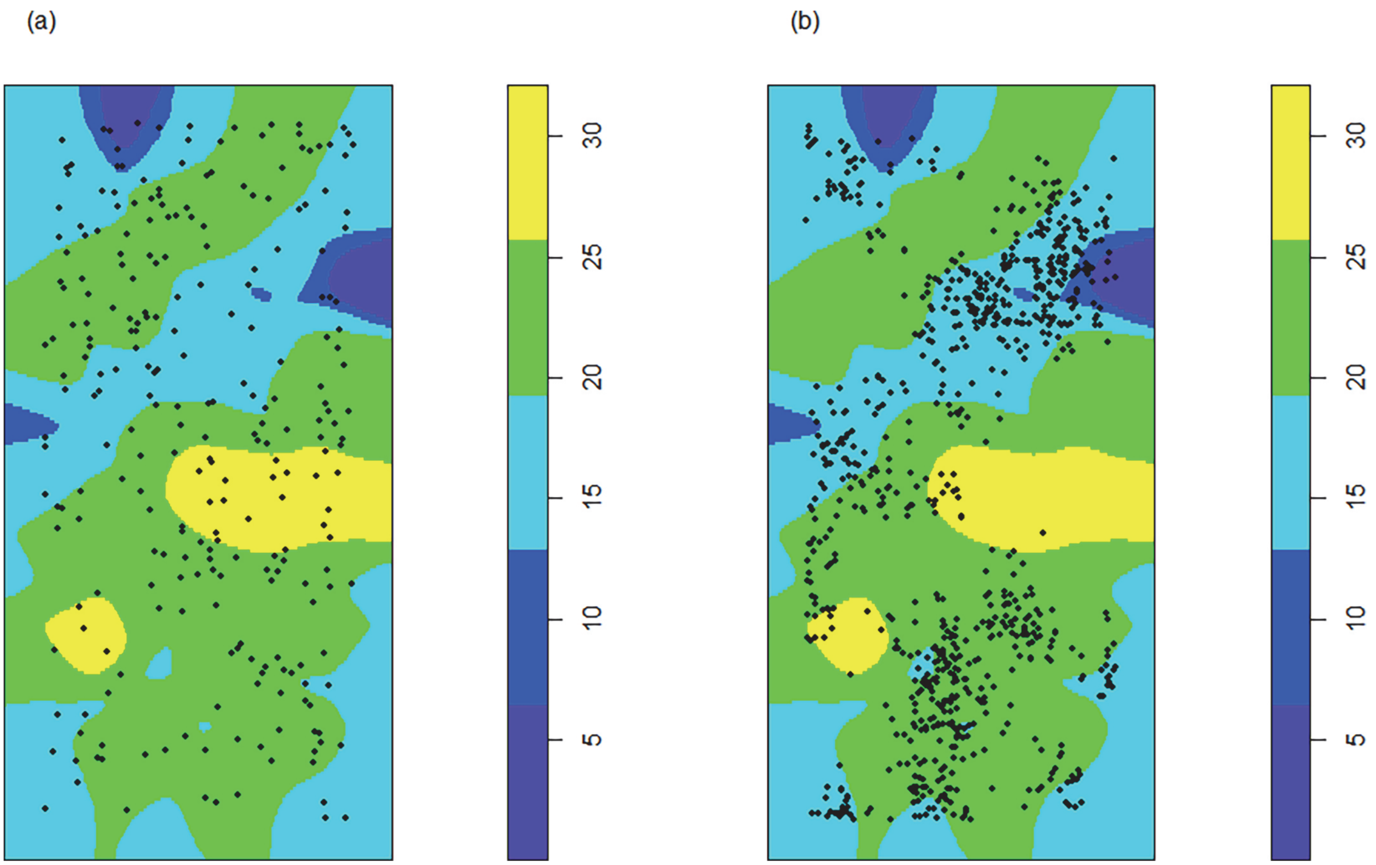

Fig 3. Local neighbourhood densities of large-sized (DBH > 60 cm) beech trees within a spatial distance of 20 m. Yellow and dark blue colours indicate highest and lowest densities of large-diameter trees. Tree densities were obtained by using the *localL* function (R package *spatstat*) with r = 20 m. Black dots indicate the initial spatial pattern of (a) dominant and co-dominant canopy beech trees with a DBH ≤ 60 cm and (b) beech trees growing in the understorey of the 8 ha study plot.

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Table 1. Summary statistics of the investigated old-growth beech forest in north-eastern Germany.

	Overstorey trees		**Understorey trees**	
	Mean (SD)	Min.–Max.	Mean (SD)	Min.–Max.
Diameter at 1.30 m (cm)	61.5 (15.9)	25.7–115.5	9.7 (2.8)	7.0–22.7
Tree height (m)	35.4 (3.5)	24.9–43.7	13.2 (3.4)	7.9–24.0
Basal area growth (cm^2 $year^{-1}$)	31.3 (25.3)	0.7–178.7	5.0 (5.4)	0.2–36.1
Basal area all trees (m^2 ha^{-1}) ^{A}	33.8 (7.6)	17.0–60.1	29.7 (7.2)	9.4–60.2
Basal area larger trees (m^2 ha^{-1}) ^{A}	20.7 (12.0)	0.0–52.7	28.1 (7.7)	6.1–60.0
Crowding index ^{A}	0.56 (0.13)	0.28–1.00	0.49 (0.12)	0.10–1.00
Shading index ^{A}	0.35 (0.20)	0.00–0.88	0.47 (0.13)	0.16–1.00
n_{trees}	545		815	

Values refer to the initial growing conditions in the core zone (5.76 ha) in 2002 of the modeling data set.

^{A} values refer to a neighbourhood radius of 20 m

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crowding effects, the competition indices were standardised by:

$$\mathrm{CI-shading\ (CIS_{\mathit{i}})\ =\ BAL_{\mathit{i}}/\,BAL_{\mathit{max}}}$$
$$\mathrm{CI-crowding\ (CIC_{\mathit{i}})\ =\ BA_{\mathit{i}}/\,BA_{\mathit{max}}}$$

where BAL_i and BA_i are the cumulative basal area of trees larger than the target tree and all neighbours within a 20 m radius of a target tree *i*, and BAL_{max} and BA_{max} are the maximum values for BAL_i and BA_i recorded in the study plot. Thus, CIs vary between 0 and 1 and indicate the minimum and maximum neighbourhood interactions observed for any target tree.

Growth model

To assess the size and competition dependence of radial growth of dominant and co-dominant canopy beech trees, we applied a parametric growth function using a generalised least squares framework (GLS) [36]. This weighted linear regression approach was preferred, because it retains the structure of the data while accounting for a heteroscedastic variance and correlated within-group errors, and thus avoids biased inferences associated with logarithmic transformations [37].

Basal area growth of target tree *i* (growth_i) was modelled as a functional relationship between tree size and the tree's competitive status:

$$\mathrm{growth}_i = \alpha + \beta_1 \mathrm{DBH}_i + \beta_2 \mathrm{DBH}^2{}_i + \beta_3 \mathrm{CIS}_i + \beta_4 \mathrm{CIC}_i$$

where α is the mean basal area growth rate and $\beta_{1,2,3,4}$ are estimated parameters of initial tree size (linear: DBH; non-linear: DBH^2), shading (CIS, aboveground competition) and crowding effects (CIC, belowground competition). The importance of above- and belowground processes for basal area growth was assessed by fitting several alternative models accounting for size or size and competition effects. Moreover, we considered interaction terms between explanatory variables (Table 2).

To address the skewed response and heteroscedasticity of the growth data, the residual error of the *i*-th target tree (ϵ_i) was modelled using a variance function based on the power of tree

Table 2. Model selection statistics.

Predictor	ΔAIC	w_i	R^2
DBH	58.0	0.000	0.25
DBH + DBH^2	55.4	0.000	0.26
DBH + CIS	9.7	0.004	0.31
DBH + DBH^2 + CIS	26.6	0.000	0.33
DBH + CIC	11.2	0.002	0.30
DBH + DBH^2 + CIC	25.5	0.000	0.34
DBH + CIS + CIC	11.6	0.002	0.31
DBH + DBH^2 + CIS + CIC	13.2	0.001	0.30
DBH + CIS + CIC + DBH x CIS	13.6	0.001	0.31
DBH + DBH^2 + CIS + CIC + DBH x CIS + DBH^2 x CIS	10.1	0.004	0.30
DBH + CIS + CIC + DBH x CIC	11.1	0.002	0.32
DBH + DBH^2 + CIS + CIC + DBH x CIC+ DBH^2 x CIC	9.9	0.004	0.30
DBH + CIS + CIC + CIS x CIC	**0.7**	**0.400**	**0.33**
DBH + DBH^2 + CIS + CIC + CIS x CIC	**0.0**	**0.576**	**0.31**

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size [36].

$$\mathrm{var}(\epsilon_i) = \sigma^2 |\mathrm{DBH}_i|^{2\delta}$$

where δ is a parameter to be estimated, which allows the variance to increase with tree size. Moreover, preliminary analyses indicated strong spatial correlation of the residuals. We therefore additionally included an exponential correlation structure in the variance-covariance terms [38]:

$$\gamma\,(s,\rho) = \begin{cases} c_0 + (1 - c_0)\left(1 - e^{\frac{s}{\rho}}\right), & \text{if } s > 0 \\ 0 \qquad\qquad\qquad\qquad , & \text{if } s = 0 \end{cases}$$

where ρ is the estimated range, s the estimated distance and c_0 the estimated nugget effect.

Models were selected based on the Akaike Information Criterion (AIC) and maximum likelihood (ML) estimations. Parameter estimates of the best-fitting model were based on the restricted maximum likelihood (REML) method [38]. Only models with an AIC difference (ΔAIC) ≤ 2 (compared with the best-fitting model) were considered as models with substantial support [39]. Models were fitted using the *gls* function from the *nlme* package in R [40].

The 14 candidate models describing basal area growth of dominant and co-dominant canopy beech (*Fagus sylvatica*) trees as a function of initial tree size (diameter at breast height, DBH), aboveground (shading, CIS) and belowground competition (crowding, CIC). The best-fitting models are highlighted in bold. ΔAIC is the difference in AIC (Akaike Information Criterion) with respect to the best-fitting model (lowest value of AIC). The Akaike weight (w_i) is the relative likelihood of each model to be the best-fitting model, given the complete set of candidate models. R^2 is the variance explained by the model.

Competition effects

We analysed changes in competition effects with various levels of shading and crowding by predicting the decline in potential growth of a target tree (expressed as the growth rate in the absence of competitors) as a function of the degree of competition. This allowed us to test whether target trees are more sensitive to changes in above- or belowground competition.

To more fully understand the mechanisms of biotic interactions, we further analysed how the intensity of tree–tree interactions was affected by competition. The intensity of competition was quantified for each target tree using the log response ratio [41]:

$$\mathrm{LnRR} = \ln(\mathrm{G}_{-\mathrm{N}}/\mathrm{G}_{+\mathrm{N}})$$

where G denotes the radial growth of a target tree either in absence (−) or presence (+) of local neighbourhood competitors. Positive LnRR-estimates indicate competition, while negative estimates imply that tree–tree interactions are facilitative. In the case of $\mathrm{G}_{-\mathrm{N}}$, CI was set at 0. In the case of $\mathrm{G}_{+\mathrm{N}}$, we used the average value of CIS and CIC (see Table 1) to account for potential differences in the strength of each competition mode (shading/crowding). $\mathrm{G}_{-\mathrm{N}}$ and $\mathrm{G}_{+\mathrm{N}}$ were predicted for every target tree based on our best-fitting model and LnRRs were calculated separately for each mode of competition. To evaluate changes in the response of neighbourhood interactions at various levels of above- and belowground competition, we predicted LnRRs at low (CI of 0.1) and high (CI of 0.6) levels of competitive stress. We predicted changes in LnRR as a function of tree size to further analyse tree size-related changes in the outcomes of competition. We distinguished between (i) medium-sized trees: DBH 30–60 cm, and (ii) large-sized trees:

DBH 61–100 cm. Differences in LnRR between the levels of competition (high/low) were tested by analysis of variance (ANOVA). All statistical analyses were performed using R [40].

Results

The minimum adequate models (MAM) according to the AIC included a tree size effect and interacting effects of shading and crowding (Akaike model weights of 0.40 and 0.58; Table 2). Thus, both above- and belowground competitive processes drive changes in individual tree growth patterns. However, comparisons of ΔAIC and R^2 indicated that the simpler MAM containing a linear size effect had substantially greater support than the MAM including a marginally significant non-linear response of basal area growth with tree size (DBH^2: $L = 2.71$, $P = 0.10$; ΔAIC for the MAM with a non-linear size effect was only 0.7 points lower than for the model with a linear size effect; Table 2). Consequently, the model with a linear BAI-DBH relationship was considered as the best-supported growth model (Table 3). Simpler, alternative models that excluded the effects of either competition or the interplay between shading and crowding showed much larger AIC values. Graphical validation plots indicated unbiased estimates (S1 and S2 Figs). The best-supported model explained 33% of the variance in BAI, and the mean prediction error was -1.87 cm^2 $year^{-1}$.

Effects of size on tree radial growth

Mean annual growth rates of beech increased continuously with DBH (Fig. 4A). For instance, the predicted growth of a large-sized tree with a DBH of 100 cm was 58% higher compared to a tree of 50 cm. Although growth pattern largely varied among individual trees of the same size (Fig. 4A), a distinct increase in average growth was obvious for trees > 75 cm (Fig. 4B). Mean annual growth was 32.6 cm^2 $year^{-1}$ in the 70–75 cm DBH range, 49.6 cm^2 $year^{-1}$ in the 75–80 cm DBH range and 98.8 cm^2 $year^{-1}$ in the 95–100 cm DBH range.

Effects of above- and belowground competition on tree radial growth

Overall, radial growth decreased with increasing competition, although growth rates were immensely variable among trees experiencing the same level of competitive stress (Figs. 5A and 5B). Beech trees were less sensitive to changes in crowding conditions compared to variation in shading (Fig. 5C). Mean growth reduction due to local shading effects was 3.5-times higher

Table 3. Parameter estimates of the best-supported growth model for dominant or co-dominant canopy beech (*Fagus sylvatica*) trees obtained by generalized least squares (GLS) regression.

	Estimate	SE	*P*-value
Fixed effects			
Intercept	53.692	9.542	<0.001
DBH	0.323	0.089	<0.001
CIS	–104.003	20.081	<0.001
CIC	–44.234	15.984	0.006
CIS * CIC	97.586	27.059	<0.001
Random effects			
δ	1.315		<0.001
ρ	17.559		<0.001
c_o	0.650		<0.001
$\sigma_{(resid.\ error)}$	0.084		

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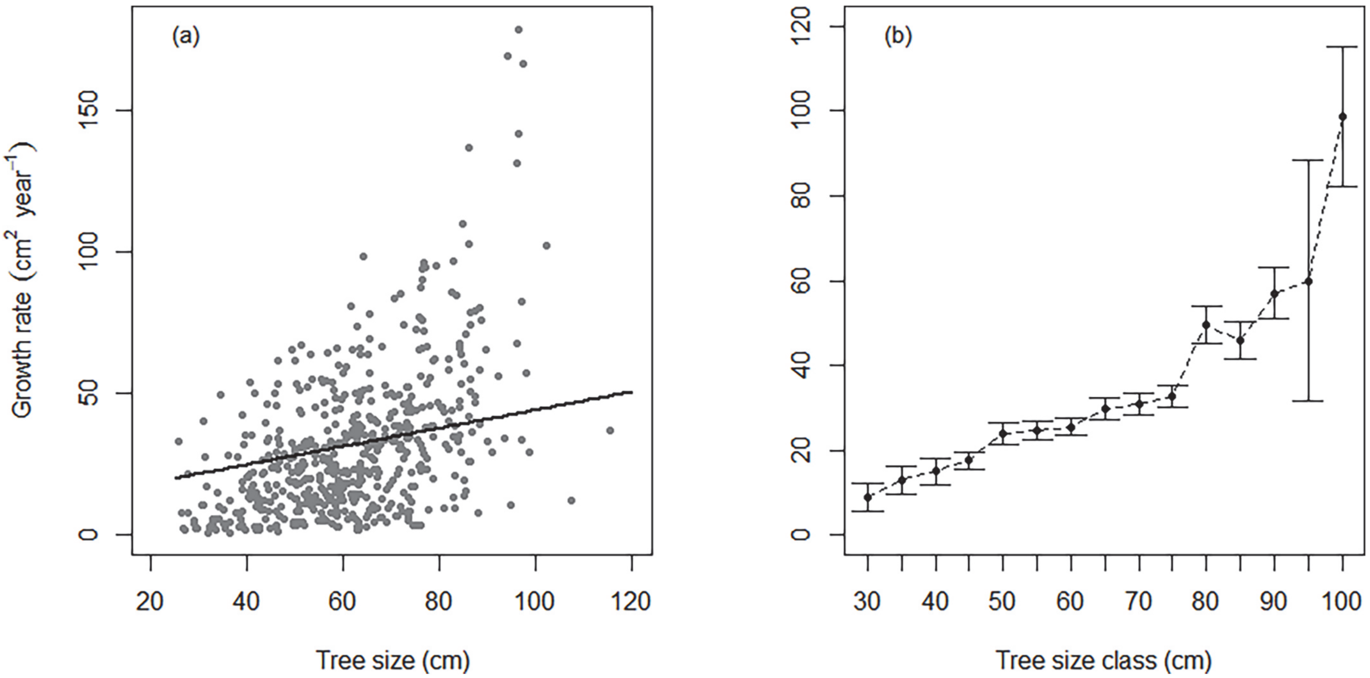

Fig 4. Radial growth rate as a function of tree size. (a) Predicted monotonic increase of basal area growth of dominant and co-dominant canopy beech (*Fagus sylvatica*) trees with trunk diameter ($\beta = 0.323 \pm 0.089$; $P < 0.001$). Competition effects were kept fixed at their means (see Table 1). (b) Observed growth rates (mean ± SE) against tree size classes. The x-axis represents the upper boundaries of the tree size (DBH)-class.

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than effects of crowding by neighbouring trees (*F*: 26.39, $P < 0.001$; Fig. 5D). However, the sensitivity to shading and crowding varied with the level of competitive stress. Changes in radial growth with increasing shading were less obvious at a high level of crowding (Fig. 6A). There was evidence of a shift to belowground facilitation for trees experiencing a high level of shading, where growth rates increased with increasing crowding (Fig. 6B).

We found antagonistic interactions between shading and crowding effects in which increasing competition for belowground resources was associated with decreased aboveground competition and vice versa (the light grey columns are always larger than the dark grey columns in Fig. 7). For example, LnRR (shading) was 34% (medium-sized trees) to 38% (large-sized trees) lower at high compared to low levels of crowding (both comparisons $P < 0.001$; Fig. 7A). Furthermore, at high levels of shading, radial growth was actually facilitated by a high density (crowding) of neighbouring trees (i.e., LnRR crowding showed negative values; both comparisons $P < 0.001$; Fig. 7B). There was also size-dependency in the magnitude of tree–tree interactions. Neighbourhood effects (LnRR shading and LnRR crowding) on target tree growth declined with tree size and tree size-related changes were most pronounced for crowding effects of trees experiencing a high level of shading (Fig. 7B). The decline in mean shading intensity with tree size was higher at a high (26%) compared to a low (21%) level of crowding (Fig. 7A).

Discussion

We evaluated the effects of tree size and above- and belowground competition on individual radial tree growth of dominant and co-dominant beech canopy trees in an unmanaged old-growth forest. Our results provide evidence that growth rates generally decreased with increasing competition, but each mode of competition mitigates the effect of the other. In this context,

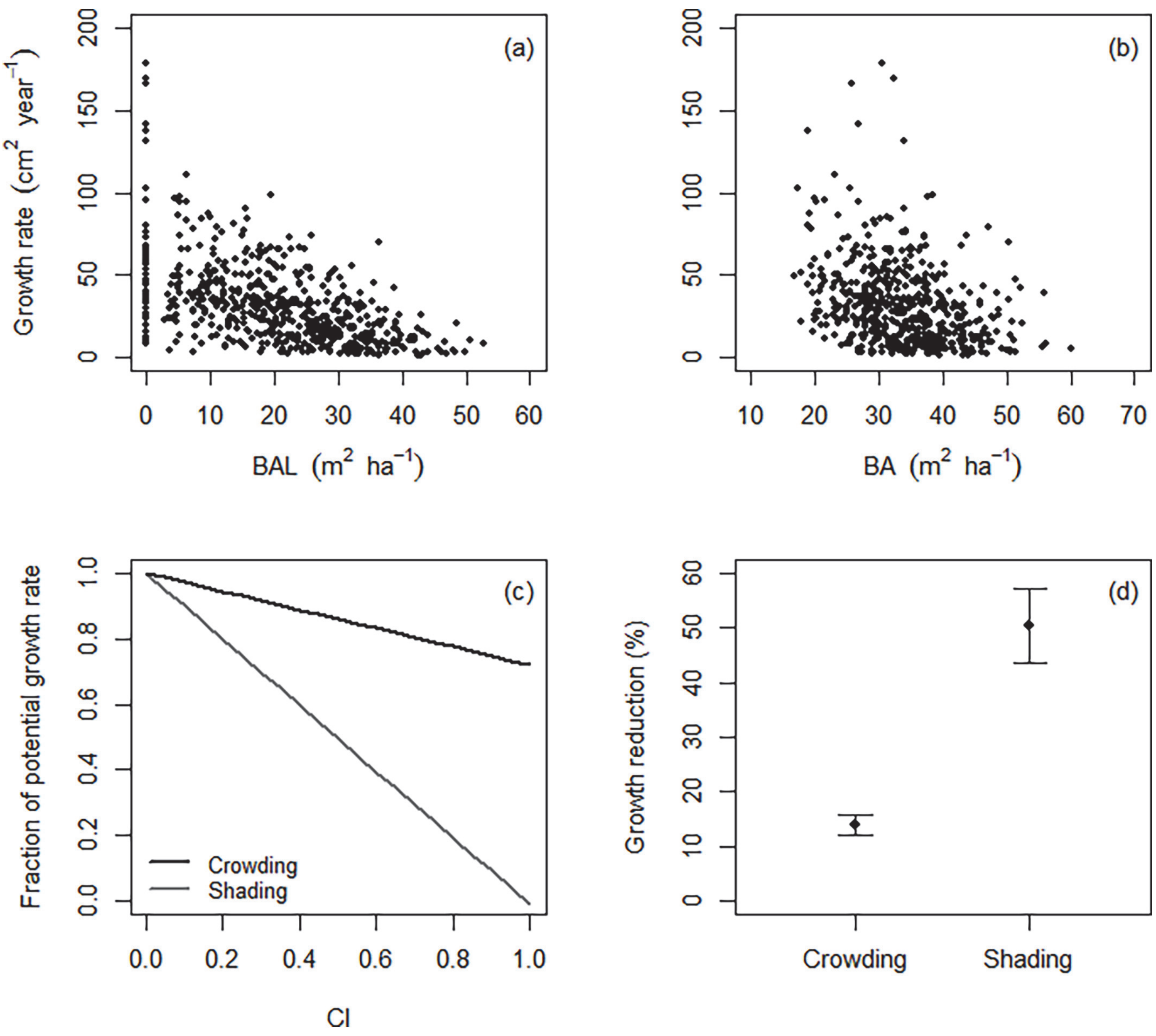

Fig 5. Effects of shading and crowding on radial growth. Growth rates of canopy dominants (*Fagus sylvatica*) in response to the cumulative basal area of (a) trees larger than the target tree (BAL; shading) and (b) all neighbours (BA; crowding) within a 20 m radius around a target tree. (c) Changes in competition response of canopy dominants with various levels of local neighbourhood competition. The response curve represents the predicted proportional decline in basal area growth as a function of shading and crowding effects, respectively. Competition effects are calculated for an overstorey beech tree of mean size and mean crowding or shading levels, while varying CI (see Table 1). (d) Relative growth reduction (mean ± SE) due to competition effects. Mean values were derived from the competition response curve in panel (c).

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we found that shading and crowding become less important with increasing tree size indicating size-asymmetry in both above- and belowground neighbourhood interactions. Here, we discuss the ecological significance of the observed growth strategies and their implications for forest community dynamics.

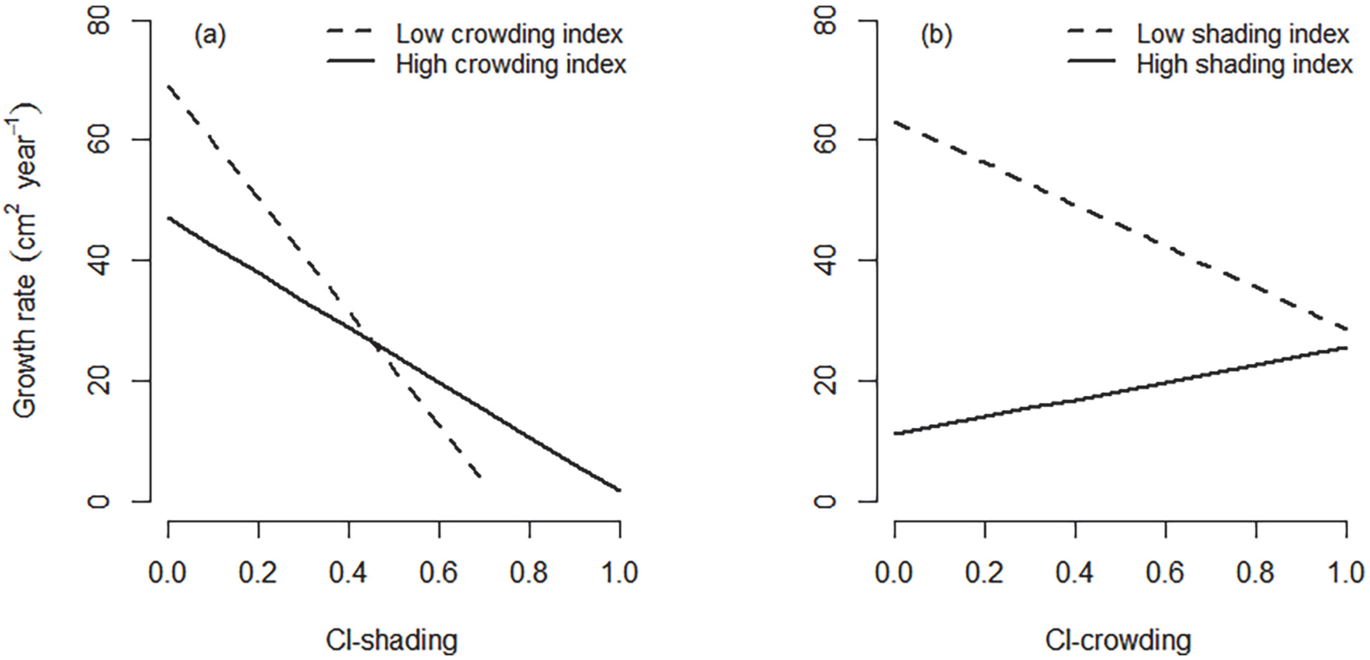

Fig 6. Variation in the effects of shading (a) and crowding (b) on radial growth rate at high and low level of competitive stress. The regression lines represent the estimated basal area growth for beech (*Fagus sylvatica*) of mean size growing in the overstorey (see Table 1) as predicted by the GLS-model.

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Competitive interactions are less prevalent in the presence of large trees

Our results indicate that not only environmental gradients, but also the mode of competition (above- vs. belowground) and their interacting effects are important factors that determine the intensity and the outcome of inter–tree competition. Growth reduction due to shading was significantly lower for trees experiencing a high level of crowding. In contrast, beech trees were able to grow faster in neighbourhoods with high abundance of larger neighbours (i.e., high level of shading) due to facilitative effects of belowground interactions. These characteristics might partly result from the spatial arrangement of large and vigorous trees and their proximity to conspecific smaller neighbours, respectively. The regular-random spatial distribution of large-sized (> 60 cm in DBH) trees in our study and their high density strongly suggest that those individuals have a disproportional impact on the local shading and crowding conditions for a focal tree (see Figs. 2 and 3A). Natural late successional forests are associated with a wide range of tree sizes at a small spatial scale [42], thus high shading or crowding intensities (high values of BAL and BA) of structurally diverse stands depend primarily on the presence of large-diameter trees and not on a high abundance of smaller stems. This indicates that the importance of competition effects may vary with forest structure and larger trees may benefit or stimulate smaller neighbours. For example, competition intensity was found to be strongly related to the stand-level tree spatial pattern in an old growth boreal forest, where tree clustering locally intensified competition [16]. Moreover, old and large trees can operate as strong organizers of spatially-structured tree recruitment through competitive interactions [43] or facilitate regeneration establishment by integrating seedlings in existing mycorrhizal networks [44].

There are two plausible explanations for the observed higher radial increment of beech trees in more dense above- and belowground neighbourhoods as compared to BAI rates at low shading or crowding intensities. First, lower competition intensities for light at high levels of crowding likely arise as a result of a higher habitat heterogeneity induced by morphological

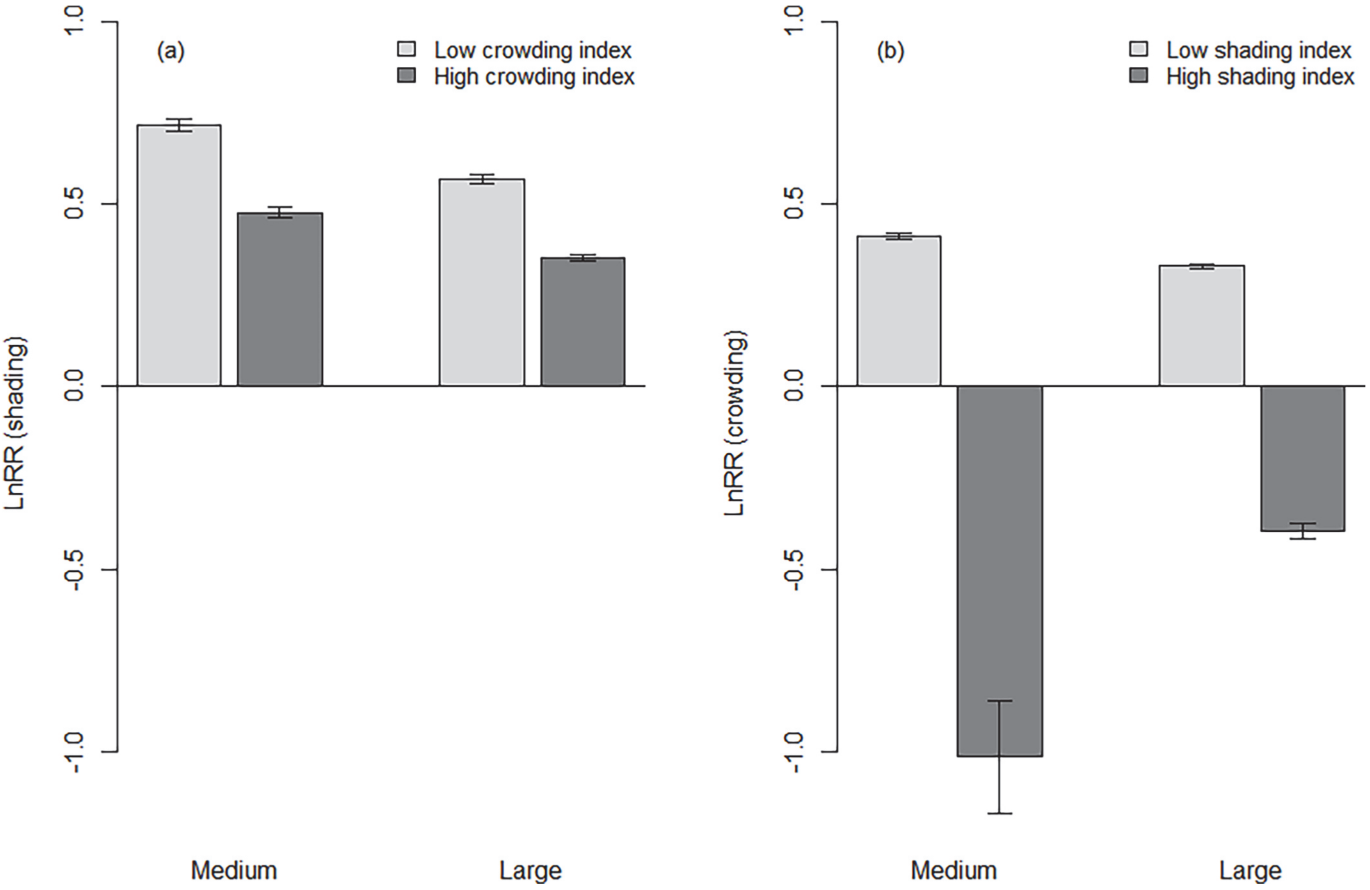

Fig 7. Variation in the intensity of neighbourhood interactions (LnRR) with tree size. (a) aboveground effects (shading), (b) belowground effects (crowding). Positive LnRR-values indicate competitive interactions, while negative values indicate facilitative interactions for medium-sized (DBH 30–60 cm) and large-sized (DBH 61–100 cm) dominant and co-dominant canopy beech (*Fagus sylvatica*) trees at low and high levels of competitive stress. Error bars represent 95% confidence intervals. Non-overlapping confidence intervals denote significant differences ($P < 0.001$) between stress levels.

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adjustments and a long continuity in tree-tree interactions [30]. Morphological plasticity enables trees to reduce competitive pressure from neighbours [45,46,47,48], and thus improve their light absorption [12]. In the Serrahn forest, Schröter et al. [49] found that this adaptation mechanism also holds for old beech trees, which in turn would allow for shifts in carbon allocation pattern (i.e. allocation to the trunk instead of an allocation to branches) even at late-successional stages. Such shifts were observed in long-term unmanaged beech forests where crown efficiency (defined as growth per unit crown area) of *F. sylvatica* increased with increasing length of non-forestry use and stand density, particularly in the presence of allospecific neighbours [50]. We therefore assume that the lower importance of aboveground competition with increasing belowground competition is probably linked to an optimal light resource partitioning as a result of a higher structural complexity in crown sizes and shapes. Similar patterns were observed for adult trees in mixed-species forests [48]. Thus, optimal partitioning theory may explain the interacting effects between shading and crowding where high crowding intensities mitigate response to light limitations. This might hold for both medium- and large-sized trees, since we observed a size-independent plasticity of canopy dominants (*F. sylvatica*), as indicated by the similar decline in net shading effects with increasing belowground competition (see Fig. 7). However, the stimulating role of large-sized trees might not be evident in stands with a low growing stock and high anthropogenic disturbance intensity and frequency because morphological adjustments are minor as the system homogeneity is increased. The second possible explanation for large trees facilitating smaller trees is them being the primary contributors of a common mycorrhizal network or of an improved access to soil resources (e.g. by accelerating rates of nutrient cycling) [30,44,51]. There is evidence that those networks are involved in belowground transfers of carbon, nutrients (e.g. nitrogen, phosphorous) and water between ectomycorrhizal tree species (e.g. *F. sylvatica*), and thus can alter net competition effects [52,53,54]. However, the actual magnitude of such interplant transfers through directly connected fungal hyphae does not seem to be well understood [54]. We found that tree size-related changes in the intensity of neighbourhood interactions were context-specific (mode of competition) and varied when the interactions were dominated by above- or belowground processes (high or low level of the other mode). In our study belowground facilitation was caused by a high level of shading. Specifically, canopy dominants that were smaller in stature (DBH 30–60 cm; Fig. 7B) tended to have disproportionately higher facilitative effects belowground indicating that these trees mostly benefit from a spatial aggregation of larger trees in their local neighbourhood. Thus, in agreement with similar facilitative effects observed between seedlings and adult trees [44,55], we suggest that common mycorrhizal networks could be an important mechanism promoting growth rates of adult trees in conspecific neighbourhoods. Moreover, allocational plasticity enables canopy dominants to balance optimal production of root and canopy structures (e.g. optimising efficiencies of light interception and use vs. maximal depletion of shared soil resources to intensify competitive effects) [56,57,58]. As a result, adult trees can receive benefit from their neighbouring larger trees (high shading or crowding intensities) to achieve higher growth rates [59].

Large trees play a key role for ecosystem functioning

The abundance of large-sized ($>$ 60 cm in DBH) beech trees in our study cover a representative range of late-successional stages. However, we found no evidence for a size-related decline of growth rates during tree maturation (up to 100 cm in DBH). Instead, regardless of competitive stress, basal area growth of *F. sylvatica* continuously increased with size, which is in agreement with a continuous increase of BAI with age of mature beech trees (160–265 years) [60]. Enhanced CO_2 levels in the recent decades might have contributed to increasing radial growth rates as trees age [61]. Similar results were found for long-living tree species (*Eucalyptus regnans* and *Sequoia sempervirens*) in old-growth forests located in Australia and North America, where aboveground wood production of un-suppressed individuals increased with size and age during the tree's lifetime (largest and oldest trees: '*E. regnans*' 299 years / DBH 92 cm; '*S. sempervirens*' 1847 years / DBH 648 cm) [62]. Given the close correlation between basal area and diameter growth rates (R^2 = 0.89; S3 Fig) in our study, larger trees are assumed to be those which accumulate carbon in the trunk at even faster rates as they mature. Thus, suggesting that not only the amount of carbon, but also the rate of carbon sequestration is highest in old, large-sized trees [63]. However, the observed monotonic increase in growth rates with size might not necessarily be valid on the level of an individual tree, as individual-specific time series were not available [64]. In this context, we found a comparably low amount of variation in growth rates (33%) explained either directly or indirectly (via tree size) by competition. Similar results were observed for temperate tree species in a mixed-species primeval *Abieto-Fagetum* forest [65] and tropical tree species in an unmanaged old-growth forest [66]. This suggests that competition effects on tree radial growth are considerably less important in tree communities with a long continuity of population dynamics compared to frequently anthropogenic disturbed stands. Consequently, our results strongly highlight the importance of the abundance and spatial distribution of large-diameter trees in near-natural managed forests for the maintenance of ecosystem functioning.

Conclusions

Interactions between neighbouring trees in long-term unmanaged communities may be more complex than commonly assumed, even at the intraspecific level. Recent studies have found evidence of such patterns in old-growth conifer forests [16,67]. Nonrandom demographic (density-dependent mortality and aggregated tree recruitment) processes can maintain tree patterns in a dynamic equilibrium [67], demonstrating that competitive interactions continue to affect forest structure and community processes over centuries [16,67]. Our research also has demonstrated that spatial aggregation of large-sized individuals could benefit growth of smaller conspecifics. It can therefore be considered that species competitive ability and neighbourhood competition intensity further depend on spatial aggregation patterns [16,68]. Thus, other factors such as forest structure or continuity of species interactions play a key role in regulating tree growth pattern and community dynamics in (near-) natural forest ecosystems.

Large-diameter and old trees are crucial components for maintaining biomass accumulation, carbon sequestration [62,63], structural heterogeneity [43], forest biodiversity [69] and forest integrity [70]. Our results additionally suggest that large-diameter trees have an important functional role for regulating biotic filtering processes. Moreover, the largest trees in our study were associated with the highest absolute radial growth rates, which might be a crucial mechanism for the maintenance of wood accumulation during stand development of old-growth forests [62]. This in turn emphasizes the need to reconsider the importance of large-diameter trees in (near-)natural forests to understand more fully interactions among conspecifics and allospecific neighbours, and thus forest community dynamics.

Supporting Information

S1 Fig. Residual plot of the best-fitting generalised least squares (GLS) regression model.
(PDF)

S2 Fig. Semivariogramm of the standardised residuals obtained by the best-fitting GLS model.
(PDF)

S3 Fig. Relationship between basal area and diameter growth rate of target trees.
(PDF)

S1 Table. Tree and stand characteristics of the 8 ha study plot of 2002 and 2009.
(PDF)

S2 Table. Observed growth rates and tree attributes of the modeling data set.
(PDF)

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Author Contributions

Conceived and designed the experiments: GVO WH. Performed the experiments: GVO. Analyzed the data: AF DIF. Contributed reagents/materials/analysis tools: GVO WH. Wrote the paper: AF DIF GVO WH KS.

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Part IV

Conservation biology

Chapter 18

Safeguarding the rare woodland species *Gagea spathacea*: understanding habitat requirements is not sufficient

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ORIGINAL ARTICLE

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Safeguarding the rare woodland species *Gagea spathacea*: Understanding habitat requirements is not sufficient

Andreas Fichtner[1] | **Werner Härdtle**[1] | **Diethart Matthies**[2] | **Volker Arnold**[3] | **Alexandra Erfmeier**[4,5] | **Tanja Hemke**[6] | **Doris Jansen**[7] | **Silke Lütt**[8] | **Marcus Schmidt**[9] | **Knut Sturm**[10] | **Goddert von Oheimb**[5,11] | **Bettina Ohse**[1]

[1]Institute of Ecology, Department of Landscape Ecology and Nature Conservation, Leuphana University of Lüneburg, Germany

[2]Department of Ecology, Faculty of Biology, Philipps-University Marburg, Marburg, Germany

[3]Museum for Archaeology and Ecology, Albersdorf, Germany

[4]Institute for Ecosystem Research/Geobotany, Kiel University, Kiel, Germany

[5]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany

[6]Nature Conservation Foundation Kurt und Erika Schrobach-Stiftung, Kiel, Germany

[7]Jansen & Rickert, Neumünster, Germany

[8]Department of Biodiversity, State Agency for Agriculture, Environment and Rural Affairs, Flintbek, Germany

[9]Northwest German Forest Research Station, Department A (Forest Growth), Section Forest Conservation and Natural Forest Research, Göttingen, Germany

[10]Community Forest Lübeck, Lübeck, Germany

[11]Institute of General Ecology and Environmental Protection, Technische Universität Dresden, Tharandt, Germany

Correspondence
Andreas Fichtner, Institute of Ecology, Department of Landscape Ecology and Nature Conservation, Leuphana University of Lüneburg, Universitätsallee 1, 21335 Lüneburg, Germany.
Email: fichtner@leuphana.de

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Abstract

A large proportion of temperate forest plant diversity is found in the herb layer. However, for many of its species, little is known about their autecology, which makes it difficult to assess potential threats and efficiently safeguard the diversity of understorey herbaceous communities. This also applies to *Gagea spathacea* (Liliaceae), a globally rare spring geophyte, which mainly occurs in deciduous forests of northern Central Europe. We investigated the causal relationships between population characteristics of *G. spathacea* and abiotic site conditions across different forest communities in the center of its distributional range. Leaf length (a surrogate of the species' vegetative propagation) was positively related to soil moisture and soil nitrogen. Consequently, mean leaf length was highest in moist forest communities of the alliance Alno-Ulmion. Moreover, mean variability in leaf length was lowest in those forests, indicating a higher and more stable vegetative propagation via bulbils. We found no support for a significant relationship between leaf length and leaf density or between leaf length and flower formation. Population density varied strongly among forest sites, but was not related to soil moisture and hardly influenced by soil nitrogen. Our results suggest that soil water and nutrient supply play a vital role in determining the species' vegetative propagation, whereas the duration of habitat continuity is most likely an important determinant of population size and density. Conservation strategies therefore require a better understanding of the complex interrelationships between abiotic site conditions and the historical context-dependency of habitats.

KEYWORDS

ash dieback, biodiversity, dispersal, habitat continuity, herbaceous layer

1 | INTRODUCTION

Habitat loss and habitat degradation are some of the main drivers of global decline in biodiversity (Maxwell, Fuller, Brooks, & Watson, 2016), and subsequent changes in species communities are expected to critically alter the functioning of ecosystems, thus diminishing the benefits that people obtain from nature (Cardinale et al., 2012; Isbell et al., 2017). Biodiversity conservation is therefore becoming a vital societal task in the context of global environmental change (Griggs et al., 2013). To address these challenges, National Biodiversity Strategies and Action Plans have been implemented within the framework of the Convention on Biological Diversity (Chandra & Idrisova, 2011). These national strategies also include lists of species for which individual countries have a particular responsibility (Schnittler & Günther, 1999), based on their global distribution and local abundance. However, our understanding of the habitat requirements of many of these species remains limited, thus limiting the development of effective conservation measures for remaining populations, particularly in the context of global environmental changes.

In temperate forests, the herb layer hosts a large proportion of plant diversity (Gilliam, 2007), and *Gagea spathacea* (Hayne) Salisb. is one of those temperate woodland plant species for which Germany has a national and international conservation responsibility (Ludwig, May, & Otto, 2007). More than 75% of the species' contiguous world range lies within northern Central Europe (Schnittler, Pfeiffer, Harter, & Hamann, 2009), with the largest populations occurring in the lowlands of northern Germany (Diekmann, Härdtle, & Stoltenberg, 2014; Timukhin, Tuniyev, & Levichev, 2010). The species has been categorized as "vulnerable" in Central Europe (Schnittler & Günther, 1999) and Germany (Metzing, Hofbauer, Ludwig, & Matzke-Hajek, 2018). Moreover, *G. spathacea* has been assigned the "National responsibility category II," meaning that Germany is responsible for the species to a very high degree, and an extinction in this core area would have very serious consequences for its global population (Gruttke, 2004).

G. spathacea shows hardly any genetic variation, is virtually sterile (Pfeiffer, Klahr, Heinrich, & Schnittler, 2011) and propagates only vegetatively by daughter bulbs ("bulbils;" Pfeiffer, Klahr, Peterson, Levichev, & Schnittler, 2012; Schnittler et al., 2009). The development of bulbils, however, is strongly related to the size of the parent bulb, which in turn is determined by the size of the leaves (Schnittler et al., 2009). Consequently, leaf length can be used as a surrogate for the species' vegetative propagation and dispersal capacity. The fact that the species is confined to ancient forests (Schmidt et al., 2014; Wulf, 1997), i.e., to forests that have been continuously wooded for several hundred years, is largely the result of its extremely low dispersal capacity (dispersal rates of <0.25 cm year^{-1}; Arnold & Fichtner, 2018; Brunet & von Oheimb, 1998). Moreover, *G. spathacea* is a highly stenoecious woodland species (Diekmann et al., 2014) that is confined to eutrophic and mesotrophic forest communities of the alliances Alno-Ulmion, Carpinion and Fagion (sensu Leuschner & Ellenberg, 2017). However, environmental change-induced shifts in canopy tree species composition might critically alter abiotic site conditions in these forests (Maes et al., 2019). This is particularly relevant for common ash (*Fraxinus excelsior*), as this species is currently threatened in many parts of Europe (Coker et al., 2019; Needham et al., 2016) and is one of the most abundant tree species in forests hosting *G. spathacea* populations (Diekmann et al., 2014; Härdtle, 1995). Previous studies provided knowledge on the species' genetics (Pfeiffer et al., 2011, 2012; Schnittler et al., 2009; Westergård, 1936), but how changes in habitat conditions influence the performance and fitness of *G. spathacea* has remained unclear.

This study aimed to provide a better understanding of the autecology of *G. spathacea*, and thus to identify potential threats to this rare woodland species. We first tested whether the species' performance depends on forest type (Alno-Ulmion, Carpinion and Fagion). We further explored multiple relationships between abiotic site conditions and plant performance measures of *G. spathacea* by using path models. Specifically, we hypothesized (a) that increasing water and nutrient supply promotes leaf length, and (b) that abiotic site conditions (water, nutrient and light availability) influence leaf length indirectly by altering leaf density and flower formation.

2 | MATERIALS AND METHODS

2.1 | Study area and sampling design

The study was conducted in temperate deciduous forests of northern Germany (Schleswig-Holstein, Mecklenburg-Western Pomerania and Lower Saxony) located within the core distribution area of *G. spathacea*. Forty populations of *G. spathacea* were investigated in different forest communities (sensu Leuschner & Ellenberg, 2017): Fagion (Hordelymo-Fagetum and Galio-Fagetum), Carpinion (Stellario-Carpinetum) and Alno-Ulmion (Crepis paludosa-Fraxinus excelsior community and Alno-Fraxinetum). Across forest communities, *Anemone nemorosa* (90%) and *Ficaria verna* (86%) were the most frequent spring geophytes. The frequency of other spring geophytes, however, was comparably low: *Adoxa moschatellina* (10.5%), *Gagea lutea* (8%), *Anemone ranunculoides* (3%), *Corydalis cava* (3%), *Allium ursinum* (2%) and *Arum maculatum* (2%). The most frequent summer herbs were *Stellaria holostea* (71.5%) and *Galeobdolon luteum* agg. (68%). In each forest, we sampled one to three populations (Figure S1). The sampling of several populations by forest occurred when a forest comprised different community types. Within each population five plots (0.5 m × 0.5 m) were randomly selected and the corners of the plots were marked with iron bars. To characterize the "optimum" habitat conditions within a population, one plot was located within the area of maximum abundance of *G. spathacea* (based on visual estimates) and the remaining plots were located in areas that capture (potential) small-scale heterogeneity in habitat conditions within a population. This allowed us to explore how changes in habitat conditions (both within and between populations) affect the performance of *G. spathacea*.

All populations (except for one: afforestation c. 1800) occurred at ancient forest sites with a continuity of forest cover for at least 250 years, as indicated by the historical maps of Schleswig-Holstein (Vahrendorfsche Landesaufnahme, 1789–1796), Mecklenburg-Western Pomerania (Schmettausches Kartenwerk, 1767–1787) and Lower Saxony (Kurhannoversche Landesaufnahme, 1764–1786). Stand age varied from 95 to 180 years. The predominant soil types were (stagnic) Luvisols, stagnic Gleysols and (humic) Gleysols. The predominant humus type was mull. Soils originated from geological substrates of the Weichselian or Saale glaciation.

2.2 | Measurements of plant performance

In 2015 and 2016, the performance of *G. spathacea* was recorded from mid-March to the beginning of April in each plot using the number of leaves as a measure of plant density. Moreover, we determined leaf length and the proportion of plants flowering. Average leaf length per plot was quantified as the mean leaf length of at least 30 individuals. To avoid sampling bias, each plot was further divided into 25 subplots (0.1 m × 0.1 m) and for all individuals within a central subplot leaf length was measured from the aboveground base of the leaf to the terminal leaf tip with a ruler. Note that the number of recorded subplots depended on the abundance of leaves, resulting in 30 to 57 (maximum) measurements per plot. Variability of leaf length was calculated as the coefficient of variation (CV), which is the ratio of the standard deviation of all leaf measurements to the mean leaf length within each plot. We also counted the number of flowering plants (with open or closed flowers) within each plot. Because of the extremely low proportion of plants flowering, which is typical for *G. spathacea* (Diekmann et al., 2014; Schnittler et al., 2009), we did not analyze the number of flowering plants per plot, but instead the probability that at least one plant per plot produced a flower.

2.3 | Measurements of abiotic habitat conditions

In each plot, soil samples were collected from the upper 5 cm of the mineral soil layer (i.e., within the growing zone of the bulbs) at the four corners of the plot. For subsequent analyses the four subsamples were thoroughly mixed to obtain one composite sample per plot. The samples were analyzed for total carbon (C) and nitrogen (N) concentrations, C/N ratio, exchangeable base cation concentration (EBC), base saturation (BS), cation exchange capacity (CEC) and pH value (measured in a 1:5 soil:water suspension). Total C and N concentrations were determined with a gas chromatographic analyzer (Vario EL, Elementar, Hanau, Germany). Determination of BS, CEC and pH followed standard procedures (Steubing & Fangmeier, 1992).

Local soil water availability was characterized by the mean Ellenberg indicator value for soil moisture (EIV-m) based on the composition of the vegetation that was sampled in 5 × 5-m survey plots placed around each plot (note that there was no overlap between vegetation survey plots within a given population). In each vegetation survey plot, we recorded the cover (%) of all vascular plant species (<1.5 m in height) and of all terricolous bryophytes by visual estimates. Vegetation surveys were conducted in 2015 or 2016 (March/April and June), depending on the sampling date of a specific forest. Each species was assigned an EIV according to Ellenberg et al. (2001) and for each plot we calculated the mean EIV for soil moisture, weighting by species' cover. Mean EIVs characterize the realized ecological niche of a given species along environmental gradients and are commonly applied as surrogates for environmental conditions in vegetation ecology in the absence of directly measured environmental variables (Diekmann, 2003; Schaffers & Sýkora, 2000).

Local light availability at the forest floor during the growing season of *G. spathacea* was quantified by taking hemispherical canopy photos at 1 m above the center of the plot with a digital camera (Nikon Coolpix 4500, Nikon, Tokyo, Japan) with a fisheye lens (Nikon FC-E8 0.21tx). The images were analyzed using the software Optimas 6.5 (Schwalbe, Maas, Kenter, & Wagner, 2009; Wagner, 1998). The program estimates the proportion of total solar radiation penetrating the canopy.

2.4 | Data analysis

We used linear mixed-effects and generalized mixed-effects models to assess the effect of forest type on leaf length (log-transformed), leaf variability, leaf density and flower formation of *G. spathacea*. Forest (to account for differences in the spatial dependency of populations within the same forest and with the same sampling date) and population (to account for differences in the spatial dependency of plots within the same population) were used as nested random effects. Leaf length and leaf density were modeled assuming a Gaussian error distribution, whereas a binomial error distribution with a logit link was used to model the probability of flowering. Differences in plant performance measures (leaf length, variability in leaf length, leaf density and probability of flower formation) among forest types were further evaluated by a Tukey test. Model validation was assessed and confirmed according to Zuur, Ieno, Walker, Saveliev, and Smith (2009).

We used path analysis (Grace, 2006) based on linear mixed-effects and generalized mixed-effects models to explore possible causal relationships between plant performance (endogenous variables) and abiotic site conditions (exogenous variables). This approach allowed us to explore more mechanistically how linkages between different aspects of plant performance were directly and indirectly affected by changes in the local water, nutrient and light regime. Moreover, we tested if an increase in leaf density or flower formation would result in a reduction of leaf length due to increased intraspecific competition for abiotic resources or increased allocation of resources to flowers. To avoid collinearity between predictors of abiotic site conditions (C, N, C/N-ratio, EBC, BS, CEC and pH value), we selected those covariates that showed no critical correlation according to the variance inflation factor (VIF; Zuur et al., 2009). All VIFs of the selected predictors (N, C/N-ratio, EBC, EIV-m and light) were <1.7. We evaluated different candidate models, each including different combinations of abiotic drivers (N, C/N-ratio, EBC, EIV-m and light). We sequentially dropped non-informative pathways, if their removal resulted in a reduction of the Akaike information criterion (AIC; Grace, 2006; Kline, 2016). The path model was fitted using a piecewise approach allowing for the simultaneous implementation of non-normal distributions and random effects (using the same error structure and error distribution as in the mixed-effects models described above) by combining multiple separate models into a single network using local estimation (Lefcheck, 2016). Path coefficients were standardized to compare their relative importance in the models. Leaf density and soil N concentration were log-transformed prior to analysis to meet model assumptions. Model fit was evaluated based on Fisher's *C*-statistics with associated *p*-value ($p > 0.05$ indicates that sample and observed covariance matrices are not statistically different and thus an adequate fit to the data) (Lefcheck, 2016). All analyses were conducted in R (v3.5.1; http://www.R-project.org) with the packages "lme4" (Bates, Maechler, Bolker, & Walker, 2015), "multcomp" (Hothorn, Bretz, & Westfall, 2008) and "piecewiseSEM" (Lefcheck, 2016).

3 | RESULTS

Across forest types, mean leaf length was 9.3 cm (standard deviation [*SD*], 2.7 cm), mean leaf density (per 0.25 m^2) was 338.5 (*SD*, 239.7) and mean number of flowering plants (per 0.25 m^2) was 1.5 (*SD*, 3.3).

Leaf length and leaf density increased in the order Fagion (FA)—Carpinion (CA)—Alno-Ulmion (AU; Figure 1). On average, leaf length was 29% higher in AU ($p_{adj.} < 0.001$) than in FA and 16% ($p_{adj.} = 0.052$) higher than in CA. In contrast, variability in leaf length was 25% higher in FA ($p_{adj.} < 0.001$) and 13% ($p_{adj.} < 0.058$) higher in CA compared to AU. Mean density of leaves in AU was 75% ($p_{adj.} = 0.019$) higher than in FA and 32% ($p_{adj.} = 0.498$) higher than in CA. The mean probability of flower formation was nearly three times higher in AU than in FA ($p_{adj.} = 0.010$) and CA ($p_{adj.} = 0.021$). In contrast, FA and CA did not significantly differ in the response variables leaf length ($p_{adj.} = 0.514$), variability in leaf length ($p_{adj.} = 0.214$), leaf density ($p_{adj.} = 0.549$) and probability of flower formation ($p_{adj.} = 0.959$). As

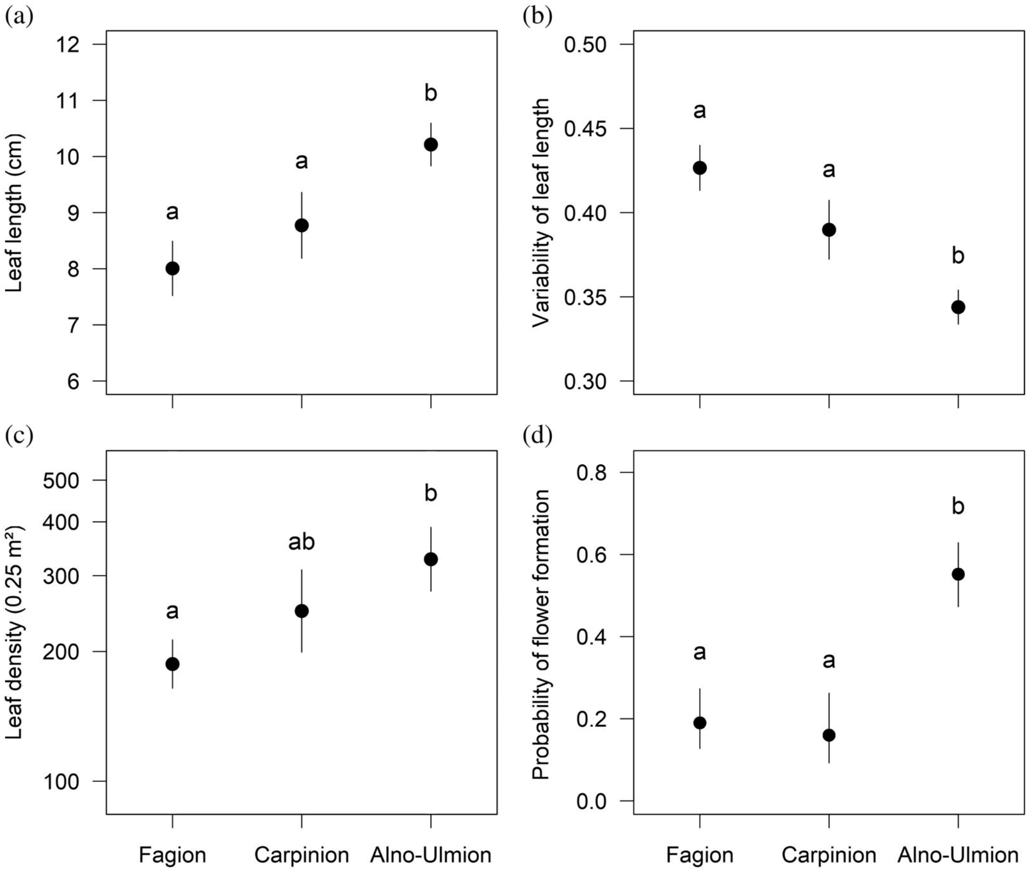

FIGURE 1 Variation in (a) leaf length and (b) variability of leaf length, (c) leaf density and (d) probability of flower formation of *Gagea spathacea* with forest type (Fagion: Hordelymo-Fagetum and Galio-Fagetum; Carpinion: Stellario-Carpinetum; Alno-Ulmion: Crepis paludosa-Fraxinus excelsior community and Alno-Fraxinetum). Predicted responses obtained from mixed-effects models. Error bars indicate standard errors. Different letters indicate significant differences among forest types ($p \leq .05$, Tukey test)

TABLE 1 Habitat characteristics of *Gagea spathacea* populations

	Across forest types	Fagion	Carpinion	Alno-Ulmion
Ellenberg indicator value for soil moisture	5.81 (0.04)	5.50 (0.05)^{a}	5.43 (0.06)^{a}	6.11 (0.05)^{b}
Light availability (%)	50.30 (0.67)	47.37 (1.31)^{a}	46.26 (1.55)^{a}	53.32 (0.78)^{b}
Species richness	22.22 (0.47)	18.80 (0.69)^{a}	19.37 (0.91)^{a}	25.12 (0.67)^{b}
Soil chemical properties				
pH (water)	4.83 (0.51)	4.81 (0.09)^{ab}	4.53 (0.09)^{a}	4.93 (0.08)^{b}
Carbon concentration (C) (%)	6.48 (0.21)	5.54 (0.33)^{a}	5.15 (0.34)^{a}	7.45 (0.29)^{b}
Nitrogen concentration (N) (%)	0.49 (0.15)	0.40 (0.02)^{a}	0.37 (0.02)^{a}	0.57 (0.02)^{b}
C/N ratio	13.25 (0.10)	13.54 (0.24)^{a}	13.89 (0.21)^{a}	12.87 (0.11)^{b}
Exchangeable base cation concentration (mval 100 cm^{-3})	9.24 (0.32)	8.52 (0.44)^{a}	6.52 (0.47)^{a}	10.55 (0.49)^{b}
Base saturation (%)	60.15 (1.53)	57.16 (2.30)^{a}	53.06 (3.18)^{a}	64.22 (2.30)^{b}
Cation exchange capacity (mval 100 cm^{-3})	15.62 (0.36)	15.24 (0.64)^{a}	12.70 (0.68)^{b}	16.81 (0.49)^{ab}
n (forests)	29	10	6	18
n (populations)	40	12	7	21
n (plots)	200	60	35	105

Note: Soil chemical properties refer to the upper mineral horizon (0–5 cm). Light intensity refers to the forest floor and species richness refers to the ground layer species (vascular plants and terricolous bryophytes) within a 25-m^2 plot. Values are means and their standard errors (in brackets). Different letters indicate significant differences among forest types ($p < .05$, Tukey test).

expected, soil moisture (expressed as EIV-m) and nutrient availability (N, C/N-ratio, EBC and BS), light availability and species richness were significantly (all comparisons $p_{\text{adj.}} < 0.05$) higher in AU than in FA and CA (Table 1).

The best-fitting path model included soil moisture, soil N concentration and light availability as habitat characteristics that significantly influenced the performance of *G. spathacea* (Figure 2). The effects of soil C/N ratio and exchangeable base cation concentration on leaf length, leaf density and probability of flowering were not significant (Table S1). Soil moisture (7%), soil N concentration (2%), light availability (1%) and flower formation (1%) accounted for 11% of the variation in leaf length. Leaf length increased with soil moisture ($p = .003$) and soil N concentration ($p = .033$). In contrast, light availability had no statistically significant direct ($p = .233$) or indirect effect (via promoting flower formation; $p = .154$) on leaf length. Leaf density was positively associated with soil N concentration ($p = .088$), but not with soil moisture ($p = .513$). The influence of soil N concentration on leaf density, however, was small (explained variation, 2%) relative to the effect of population identity, which accounted for 47% of the variation in leaf density. There was no significant relationship between leaf length and leaf density ($p = .719$). Light availability ($p = .013$) and soil moisture ($p = .009$) had strong positive effects on flowering, whereas the positive effect of soil N concentration was less influential ($p = .039$).

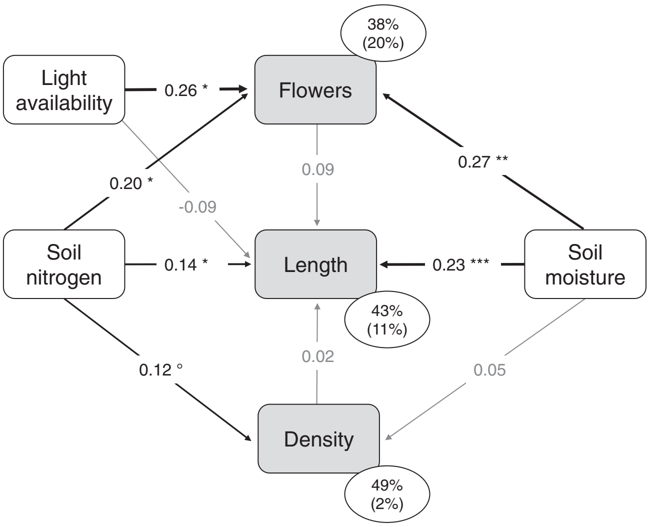

FIGURE 2 The best-fitting path model linking plant performance ("length", leaf length; "density", leaf density; "flowers", probability of flower formation) and local habitat conditions (soil nitrogen concentration, soil moisture and light availability). Black and gray arrows denote significant (°$p < .10$, *$p < .05$, ** $p < .01$, *** $p < .001$) and non-significant ($p > .10$) pathways, respectively. Numbers at arrows are standardized path coefficients indicating the effect size of the relationship and arrow width is proportional to the effect size. Percentage values are explained variances of endogenous variables of fixed and random effects; explained variances of fixed effects alone are in brackets. The model provided a good fit to the data (Fisher $C = 3.19$, degrees of freedom [*df*] = 4, $p = .53$)

4 | DISCUSSION

This study provides insights into the autecology of a rare woodland species by showing that soil water and nitrogen are important determinants regulating the leaf length of *G. spathacea*, and thus its vegetative propagation. Soil water and nitrogen were also identified as key habitat characteristics explaining variation in the species' vitality (i.e., leaf density and flower formation). Variation in leaf density, however, was to a large degree explained by population identity, suggesting that factors other than the recorded abiotic site conditions might have a strong impact on the abundance of *G. spathacea*.

4.1 | The role of abiotic site conditions and habitat legacies in the performance of *Gagea spathacea*

Soil nutrient supply is highly important for bulbous plants with a short vegetation cycle (Weeda, 2006), which lasts for *c.* 3 months in the case of *G. spathacea*. The species has a high nitrogen demand and is characterized by an exceptionally efficient resorption of nitrogen from senescing leaves and reallocation to bulbs, leading to a twofold increase of the bulbs' biomass at the end of the growing season (Fichtner et al., 2018). This efficient recycling of nitrogen allows the species to avoid nitrogen losses via litter (Aerts, 1990; Thornton & Millard, 1993), and therefore quickly form leaves and new bulbs during its short active growth phase. This explains why leaf length and leaf density increased with increasing soil N concentration. Surprisingly, the concentration of exchangeable base cations and soil C/N ratio were not directly linked with changes of the species' performance, which is likely to be the result of soil moisture-induced changes in the nutrient regime and availability of the soil. In deciduous forests in northern Germany (particularly in stands on ancient moraines), nutrient supply is often confounded with soil moisture (Härdtle, von Oheimb, Meyer, & Westphal, 2003). Thus, forest sites with moist soils are associated with high base supply and low soil C/N ratios in our study (Table 1; Figure S2). On the one hand, a high base supply supports litter turnover, and therefore the provision of nutrients (Härdtle, von Oheimb, Meyer, & Westphal, 2003). On the other hand, increasing soil moisture favors the abundance of tree species such as ash (*F. excelsior*) and alder (*Alnus glutionosa*), both of which are characterized by low leaf litter C/N ratios (the latter one due to symbiotic nitrogen fixation). Our finding of increasing leaf length with increasing soil moisture and nitrogen therefore suggests that the relative importance of soil moisture in determining leaf length is largely the result of an increase in soil fertility (in terms of both nitrogen and base supply) via increasing water supply.

G. spathacea develops more bulbils as leaves grow larger in size (up to a maximum of 54 bulbils per plant; Schnittler et al., 2009). Thus, larger plants should be associated with a higher vegetative propagation and therefore with an improved dispersal capacity. Consequently, leaf length should be positively linked to leaf density. Alternatively, it is conceivable that leaf density has a negative effect on leaf length, as increasing intraspecific competition for resources can result in smaller plants and an increase in size inequality (Silvertown & Charlesworth, 2007). Although leaf length decreased with increasing leaf density in FA (Figure S3), we found no evidence for a significant leaf size–density relationship in CA, AU and across forest types. This shows that an increase in leaf length (due to high water and nutrient supply) is less influential in explaining contemporary leaf density of *G. spathacea*. However, the high importance of population identity, which explained almost half of the variance in leaf density, suggests that habitat continuity is an important determinant of population density. The dispersal capacity of *G. spathacea* (a plant exclusively relying on subterraneous bulbils for its dispersal; Pfeiffer et al., 2011) is extremely low, because bulbils are generally dispersed over short distances by ants (Graae, 2000; Hermy, Honnay, Firbank, Grashof-Bokdam, & Lawesson, 1999;), by soil translocation through moles and mice (Arnold & Fichtner, 2018) or by uprooting trees (Pfeiffer et al., 2012). Digging by wild boars (Schnittler et al., 2009) and prehistorical farming practices (Arnold & Fichtner, 2018) are further assumed to promote the dispersal of *G. spathacea*. Stochastic processes that promote effective long-distance dispersal, however, might play a minor role in explaining the species' abundance and population size. For example, studies on temperate forests in northern Germany found that game is an important vector for the endozoochorous and epizoochorous dispersal of vascular plants that are restricted to open landscapes or for species growing in forests as well as in the open landscape, but not for those strongly associated with forests (Heinken, Schmidt, von Oheimb, Kriebitzsch, & Ellenberg, 2006; Schmidt, Sommer, Kriebitzsch, Ellenberg, & von Oheimb, 2004). Given the extremely low dispersal capacity of *G. spathacea*, it would take a long time to develop a large and dense population from a single bulbil or few founder bulbils. This indicates that the temporal extent of habitat continuity, and therefore the population age, is an important factor influencing the size and density of *G. spathacea* populations. Although data on the duration of habitat continuity were not available for each study site, we found that the largest and densest population of *G. spathacea* was at a site with a continuous forest cover of *c.* 2,500 years (Arnold & Fichtner, 2018; Figure S4). Population density might also be regulated by interspecific competition during the vegetation cycle of *G. spathacea*, but leaf density of *G. spathacea* was not significantly affected by the mean cover of other spring geophytes in our study (Figure S5).

We found no support for a trade-off between leaf length and flower formation. Although increasing light availability in combination with an ample water and nutrient supply promoted flowering, a higher probability of flowering does not result in a decline of leaf length (i.e., carbon allocation to leaves; Figure 2) or bulb growth (Schnittler et al., 2013). For example, Schnittler et al. (2009) reported that *G. spathacea* continues to allocate resources to bulbs during flowering. In this context, however, it should be noted that an increase in light availability due to natural or anthropogenic disturbances can favor the growth of winter-green plants (e.g., *Rubus* spec., *G. luteum*), that in turn might suppress *G. spathacea*. This is especially problematic in the Atlantic climate of Schleswig-Holstein, where more frequent mild winters and soil acidification through nitrogen deposition already promote *Rubus fruticosus* agg., and where *G. spathacea* has its largest populations. Moreover, closed tree canopies have been demonstrated to be vital for mitigating warming-induced changes in the composition of understorey herbaceous communities, and thus for safeguarding temperate forest plant diversity in the context of climate change (De Frenne et al., 2015).

4.2 | Implications for conservation management

Our results demonstrate the important role of soil water and nutrients in determining leaf length (as a surrogate of vegetative propagation) of *G. spathacea*. Hence, habitat changes that directly or indirectly impair soil water and nutrient availability could have detrimental impacts on the species' reproductive success. For example, a decrease in the abundance of ash due to ash dieback (Münster Mitchell et al., 2014; Needham et al., 2016) is likely to be associated with a decrease in soil nutrients (Münster Mitchell et al., 2014; Thomas, 2016). This is particularly relevant for moist forests, such ash and alder-ash forests, as we found that the largest and most vital populations of

G. spathacea are currently located in those forests, and alder-ash forests were identified to be most vulnerable to ash dieback (Erfmeier et al., 2019). The ecological consequences of ash dieback for temperate forest biodiversity and ecosystem functioning, however, remain unclear and require further investigation.

The Central European lowland populations of *G. spathacea* are confined to deciduous forests on ancient forest sites (Schmidt et al., 2014; Wulf, 1997). Hence, the species' occurrence is generally associated with a high diversity of forest species (e.g., Härdtle, von Oheimb, & Westphal, 2003; Nordén et al., 2014; Stefańska-Krzaczek, Kacki, & Szypuła, 2016). Given that within the core distribution area of *G. spathacea* ancient deciduous forests are rare, it is of vital importance to avoid the conversion of these remaining forests into coniferous or deciduous–coniferous stands (Kriebitzsch et al., 2013). Moreover, results from long-term observations of vegetation in a south Swedish deciduous forest suggest that regular soil disturbance by wild boar has a positive effect on the frequency of *G. spathacea* via reducing the mean cover of more competitive spring geophytes (e.g., *A. nemorosa*, *A. ranunculoides* and *F. verna*; Amelung, 2019; Brunet, Hedwall, Holmströn, & Wahlgren, 2016). Further studies that focus on the impacts of moderate soil disturbance on the performance of *G. spathacea* may therefore provide improved insight into effective conservation strategies. Our findings highlight that the maintenance of habitat continuity and favorable abiotic site conditions are among the most important measures to safeguard *G. spathacea*, a species of special conservation interest. This includes, (a) avoiding drainage, and thus preventing soil acidification, (b) promoting autochthonous deciduous tree species in the canopy to maintain a high availability of nutrients, and (c) maintaining closed tree canopies to reduce interspecific competition by winter-green plants and to ensure favorable forest-floor microclimate conditions.

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ORCID

Andreas Fichtner https://orcid.org/0000-0003-0499-4893

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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Chapter 19

Nitrogen cycling and storage in *Gagea spathacea* (Liliaceae): ecological insights for protecting a rare woodland species

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Nitrogen cycling and storage in *Gagea spathacea* (Liliaceae) – ecological insights for protecting a rare woodland species

Andreas Fichtner[a], Diethart Matthies[b], Malin Armbrust[a], Doris Jansen[c], Knut Sturm[d], David Walmsley[a], Goddert von Oheimb[e,f], Werner Härdtle[a]

[a]Leuphana University of Lüneburg, Institute of Ecology, Faculty of Sustainability, Universitätsallee 1, 21335 Lüneburg, Germany; [b]Philipps-University Marburg, Department of Ecology, Faculty of Biology, Karl von Frisch Str 8,35043 Marburg, Germany; [c]Jansen & Rickert, Heinrich-Wittorf-Strasse 31, 24539 Neumünster, Germany; [d]Community Forest Lübeck, Alt-Lauerhof 1, 23568 Lübeck, Germany; [e]Technische Universität Dresden, Institute of General Ecology and Environmental Protection, Pienner Str. 7, 01735 Tharandt, Germany; [f]German Centre of Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5E, 04103 Leipzig, Germany

Corresponding author: W. Härdtle, haerdtle@uni-lueneburg.de

Abstract

Strategies to globally protect biological diversity are often hampered by an insufficient ecological knowledge about target species. This also applies to *Gagea spathacea* (Liliaceae), a 'vulnerable' woodland spring geophyte with a distribution largely restricted to the lowlands of Central Europe. We studied whether the species' linkage to highly fertile forest soils is related to its high nitrogen (N) demands during its short developmental cycle. We hypothesized that the species exhibits a highly efficient N (re)cycling strategy, characterized by efficient resorption of N from the leaves and reallocation to bulbs at the end of the growing season. To test this assumption, we conducted a ^{15}N tracer experiment and quantified ^{15}N flows between soil, leaves, bulbs, and roots. Our findings support our hypothesis that *G. spathacea* is exceptionally efficient in recycling N, shown by the resorption of 68% of leaf N and its reallocation to bulbs at the end of the growing season. After six weeks of growth the plant showed a distinct shift in its N metabolism: The C:N ratio of leaves strongly increased and those of bulbs decreased, leaf ^{15}N enrichment and recovery started to decrease, while total plant ^{15}N recovery remained constant, indicating no further N uptake from the soil. Leaf N reallocation to bulbs was accompanied by a two-fold increase of the bulbs' biomass. Because of the stenoecious behavior of *G. spathacea,* a careful protection and sustainable management of *G. spathacea* forest habitats is necessary, particularly in its Central European core area.

Keywords: Ancient woodland, Convention on Biological Diversity, Nitrogen allocation, Nitrogen recycling, ^{15}N, Stable isotope

INTRODUCTION

The global loss of biodiversity is considered one of the most pressing environmental problems (Betts et al. 2017), and quite a number of political commitments have been adopted to counteract this development. The first global agreement aiming at the long-term conservation and sustainable use of biological diversity is the "Convention on Biological Diversity" (CBD), which came into force in 1993 and was subject to latest revision during the Nagoya-Conference in 2010 (Chandra and Idrisova 2011). Being a framework and legally binding instrument, the CBD provides general provisions at the international level, but also demands efforts at the national level to make them operational (Chaytor et al. 2002). As a consequence, one important means for the implementation of the CBD was the development of "National Biodiversity Strategies and Action Plans" (NBSAP; Chandra and Idrisova 2011), including the provision of lists for both habitats and species that are considered nationally endangered, and for which a focal country has an outstanding responsibility from a worldwide conservation perspective (Schnittler and Günther 1999).

The implementation of the NBSAP, however, faces several problems, for example an insufficient knowledge about the ecology of endangered species and the mechanisms underlying a proceeding decline of their populations (Balmford et al. 2005; Chandra and

Idrisova 2011; Joppa et al. 2013). Therefore, an improved and species-specific understanding of drivers of habitat change is critical in the guidance of policy, landscape management and conservation efforts.

A list of vascular plants requiring priority conservation measures in Central Europe has been compiled by Schnittler and Günther (1999). This list was based on an evaluation of the worldwide range of species and their (national) threat status (i.e. Red List category). One of the priority species in this list is the rare woodland plant *Gagea spathacea* (Hayne) Salisb., which is considered "vulnerable". Several Central European countries, and Germany in particular, have a large responsibility for the long-term protection of *G. spathacea* populations (Schnittler and Günther 1999), because more than 75% of the contiguous world range of the species lies within Central Europe (Schnittler et al. 2009). Its largest populations are restricted to the lowlands of northern Germany (Schlechtendal et al. 1851; Krause 1889, Meusel et al. 1965; Haeupler and Muer 2000; Levichev et al. 2010; Diekmann et al. 2014; Romahn 2015). The lowland populations of *G. spathacea* are associated with highly specific site conditions: Populations appear exclusively on soils developed from deposits from the Saale and Weichselian glaciation, and all sites are characterized by an ample supply of water as well as a high base and nitrogen (N) availability (Härdtle et al. 2003). As a consequence, *G. spathacea* is a highly stenoecious woodland species (Diekmann et al. 2014) that is confined to alder-ash- and ash-beech forests of the alliances Alno-Ulmion and Fagion (sensu Leuschner and Ellenberg 2017), respectively. These forest types represent the natural plant communities at the sites.

Recent studies have analyzed the phylogeny of the genus *Gagea* (Peruzzi et al. 2011; Peterson et al. 2009; Peterson et al. 2004; Peterson et al. 2011) and the reproductive biology and genetic diversity of populations of *G. spathacea* (Schnittler et al. 2009; Pfeiffer et al. 2011, 2012; Schnittler et al. 2013). The studies found that *G. spathacea* is a virtually sterile, non-apomictic species that relies on vegetative propagation by means of daughter bulbs ("bulbils"; Schnittler et al. 2009, Pfeiffer et al. 2012). Consistent with this propagation strategy is the finding that all populations in Central Europe can be assigned to a single clone with a virtual absence of a spatial genetic structure (Pfeiffer et al. 2012). It has been suggested that *G. spathacea* thus could be of hybridogenous origin (Levichev et al. 2010; Pfeiffer et al. 2012), and has colonised its current area of distribution by the dispersal of its bulbils.

The dispersal of plants exclusively relying on subterraneous bulbils is often poor (Šerá 2008). In the case of G. spathacea, mechanisms such as substrate translocation (e.g. in the case of uprooted tress) or bulbil transport by digging or wallowing animals (Pfeiffer et al. 2012) could result in short-distance dispersal. Moreover, former anthropogenic bulbil transport to hedges is possible, since trees (with roots and soil) were transplanted from forest sites. However, it is unlikely that all these mechnisms might ensure an effective long-distance dispersal to appropriate new sites. This assumption is supported by the fact that Central European lowland populations of *G. spathacea* are confined to ancient forests and are absent from young forests (Wulf 1997; Schmidt et al. 2015; Stefańska-Krzaczek et al. 2016).

Highly specific habitat preferences and poor dispersal may increase the extinction risk of a species when environmental conditions change (Keith 1998; Keith et al. 2008). The main factors altering the conditions in lowland moist forests in northern Germany, the core of the Central European range of *G. spathacea*, are drainage and the planting of non-autochthonous tree species (e.g. conifers or poplar; Härdtle et al. 2003). Moreover, the progressing ash-dieback due to fungal deseases (with *Hymenoscyphus fraxineus*) has caused dramatic changes in the biotic and abiotic environment of *G. spathacea* in recent years (Goberville et al. 2016; Kjaer 2017).

Given the shifts in site conditions, their possible negative impact on *G. spathacea* populations, and a limited autecological knowledge, the present study seeks to contribute to a better understanding of the species' habitat requirements. Since *G. spathacea* is characterized by a short developmental cycle including the formation of leaves and replacement/daughter bulbs to ensure assimilation and propagation, it is likely that plants have high nutrient demands (particularly for N) during its growing season. This in turn would explain the species' restriction to highly fertile forest soils. High N demands could be satisfied by both N uptake from soils and N recycling from the bulbs. We therefore hypothesize that the species shows a highly efficient N recycling, i.e. an N resorption from senescing leaves and reallocation to bulbs to avoid N losses via litter (Aerts 1990; Thornton and Millard 1993; Silla and Escudero 2003). To test this hypothesis, we conducted a ^{15}N tracer experiment to analyze N cycling and storage in *G. spathacea* over one growing season, and quantified flows of ^{15}N between and allocation to the compartments soil, roots, bulbs, and leaves.

METHODS

Morphological characterization of the study species

G. spathacea is a spring geophyte with a short annual developmental cycle of c. three months. Leaves start to develop usually at the beginning of March and senescence already at the end of May. Detailed morphological and anatomical studies on *G. spathacea* were conducted by Schnittler et al. (2009, 2013). According to these studies, a subterraneous parent bulb stores resources supporting the current-year plant growth (leaf formation) and develops a replacement bulb supporting the plants' growth in the following year. In addition, large parent bulbs develop one to many daughter bulbs (bulbils), depending on its size and thus its storage capacity for nutrients. The threshold bulb diameter above which bulbils are produced is c. 2.4 mm, and up to 54 bulbils may be produced by one plant per year (Schnittler et al. 2009). Due to its sexual sterility, the formation of bulbils is crucial for the propagation of the species.

As a consequence, the parent bulbs of *G. spathacea* support two crucial processes in the plants' development, the formation of assimilatory tissue and bulbils, both of which strongly depend on the availability of a sufficient amount of nutrients stored by the parent bulb (Schnittler et al. 2009). For a better understanding of the growth and propagation of the species it is, therefore, vital to gain insights into its nutrient cycling and storage strategies, particularly with regard to the (co-)limiting macronutrient N.

Experimental design

At the beginning of March, immediately after the first leaves were visible, 100 plants of *G. spathacea* were sampled randomly across one of the largest population in northern Germany (c. 1 Mio. plants) in the municipal forest of Lübeck (297 ha in size; Schleswig-Holstein, N-Germany; 53°46'N 10°35'E; forest type: alder-ash-forests (of the alliance Alno-Ulmion) on gley soils with high nutrient and year-round ample water supply; soil chemical properties of the A-horizon: pH(H_2O): 4.9, C:N ratio: 11.7, base saturation: 60%). To study individuals of similar size, we sampled individuals with only one leaf per bulb (two-leaved plants usually have significantly higher bulb diameters; Schnittler et al. 2009). Adhering soil was removed carefully and the plants were transferred individually into pots (5.5 cm diameter, 5 cm height, lined with a plastic foil at the bottom) filled with cultivation substrate (Substrate ED73, Uetersen, Germany). The plants were kept in an unheated greenhouse in the experimental garden of the University of Lüneburg. On the 9th March 2016 the initial leaf length of all plants was measured. Mean leaf length was 4.71 cm (SD = 1.55 cm). Plants were regularly watered and the position of the pots was re-randomized every week to avoid position effects. Because *G. spathacea* is a shade-tolerant species (indicator value for light: 2; Ellenberg et al. 1992), the pots were covered by a tent made from shade cloth that reduced illumination to 25% of that of the environment to ensure optimal growing conditions.

^{15}N tracer application

After plants were transferred to pots, 90 out of the 100 pots immediately received 0.1188 mg $^{15}NH_4{}^{15}NO_3$ (99.22 at.% ^{15}N) dissolved in 2.4 ml deionized water (in the following referred to as labelled pots) by evenly pouring the solution onto the soil. The quantity of tracer applied, which is equivalent to 50 mg of $^{15}NH_4{}^{15}NO_3$ per m^2 of soil surface, aimed at a target ^{15}N enrichment of about 600‰ in the plants' leaf tissue and was too low to cause a fertilization effect (Friedrich et al. 2011). After tracer addition, the 10 remaining pots (non-labelled pots) received the same amount of water without ^{15}N tracer.

Plant harvest and measurement of response variables

The experiment was designed to quantify the course of N cycling, allocation and storage during the entire developmental cycle of the current year (i.e. from the start of foliation until leaf senescence), which was estimated to take place over a period of nine weeks. To this end, weekly harvests of a total of 10 plants were preformed, beginning with the harvest of the ten plants of the non-labelled pots at the first day of the experiment (9th March 2016), and continued for nine weeks until all plants of the remaining 90 labelled pots were harvested (random selection of respectively 10 plants per harvest date). In the ninth week we noticed that we underestimated the length of the current-year developmental cycle, because at least some plants still showed leaves with only partly leaf senescence/colouration. In order to extend the experiment's duration by one week, and thus to enable us to perform an analysis when an almost complete leaf senescence/leaf colouration had occurred, we harvested only five pots during the last two weeks of the experiment.

At each harvest, adhering soil material was carefully removed from the plants and four compartments per pot, namely roots, leaves, bulbs (including the replacement bulb and, in twelve cases, bulbils), and soil were analyzed individually. The following response variables were quantified for each compartment: C and N concentration, C:N ratio, $\delta^{15}N$ enrichment, and ^{15}N tracer recovery. In addition, we measured the leaf length (bulb emergence point to leaf apex, immediately after harvest) in order to calculate leaf increment (leaf $\text{length}_{\text{harvest}}$ – leaf $\text{length}_{\text{start}}$) and determined the mass of the leaves, bulbs, roots and soil within each pot, after 24h at 60 °C in a drying oven. For element analyses, samples were ground in a ball mill (MM 400, Retsch, Haan, Germany). Due to the very low root biomass available for analysis, we had to pool the roots of 3(-4) randomly selected plants per harvest date. Therefore, only three samples were available for root element analyses for the first nine weeks of the experiment (i.e. no root samples remained for the 10th week). Total C and N concentrations and $\delta^{15}N$ values of compartments were determined using a continuous flow elemental analyser-isotopic ratio mass spectrometer (vario El cube, Elementar, Hanau, Germany, coupled to an Isoprime IRMS, Isoprime Ltd., Cheadle Hulme, UK).

Calculation of $\delta^{15}N$ enrichment and ^{15}N tracer recovery

^{15}N concentrations from compartments are presented in the δ notation:

$$\delta^{15}N\,(‰) = (R_{\text{sample}}/R_{\text{standard}} - 1) * 1000 \qquad (1)$$

where R_{sample} is the ratio between ^{15}N and ^{14}N of the sample and R_{standard} that of the standard, for which by convention, atmospheric N_2 was used ($\delta^{15}N_{\text{atm}} = 0$; Coplen et al., 1992).

^{15}N enrichment expresses the per mille isotope enrichment in a compartment sample from a labelled pot ($\delta^{15}N_{\text{sample}}$) vs. a reference compartment sample from a non-labelled pot ($\delta^{15}N_{\text{ref}}$; Fry, 2006):

$$^{15}N \text{ enrichment } (‰) = [(\delta^{15}N_{\text{sample}} - \delta^{15}N_{\text{ref}}) / (\delta^{15}N_{\text{ref}} + 1000)] * 1000 \qquad (2)$$

^{15}N-tracer recovery in compartment N-pools was calculated as follows:

$$^{15}N_{\text{rec}} = m_{\text{pool}} * (\text{atom}\%^{15}N_{\text{pool}} - \text{atom}\%^{15}N_{\text{ref}}) / (\text{atom}\%^{15}N_{\text{tracer}} - \text{atom}\%^{15}N_{\text{ref}}) \qquad (3)$$

where $^{15}N_{\text{rec}}$ is the mass of ^{15}N tracer recovered in the compartment N-pool of labelled pots (g N m^{-2}), m_{pool} is the mass of the compartment N-pool of labelled pots (g N m^{-2}), $\text{atom}\%^{15}N_{\text{pool}}$ is the $\text{atom}\%^{15}N$ in the compartment N-pool of labelled pots, $\text{atom}\%^{15}N_{\text{ref}}$ is the $\text{atom}\%^{15}N$ in the compartment N pool of non-labelled pots, and $\text{atom}\%^{15}N_{\text{tracer}}$ is the $\text{atom}\%^{15}N$ of the added ^{15}N tracer (Nadelhoffer et al. 2004). ^{15}N tracer recoveries in percent ($\%^{15}N_{\text{rec}}$) represent masses of ^{15}N tracer recovered as percent of total ^{15}N tracer masses added to the labelled pots.

Statistical analysis

Preliminary analyses indicated non-linear relationships between response variables and time (week 0-10). We therefore applied generalized additive mixed models (GAMMs) with an identity link function and Gaussian errors to assess temporal shifts in plant traits and soil nitrogen during the course of the experiment. To minimize heteroscedasticity, a variance function based on the covariate time (i.e. the variance of the residuals was modelled as σ^2, multiplied with the power of the absolute value time; Zuur et al. 2009) was added in the covariance structure of the models (except for C:N ratio bulb, N-concentration leaf/bulb). The non-linear effect of time was modelled using a thin plate regression spline, and the optimal amount of smoothing was determined by cross-validation (Wood 2006). GAMMs were fitted for each response variable and compartment (leaf, bulb, root, total plant, soil) separately. Model assumptions were visually assessed following Zuur et al. (2009). We found no trends in the residuals. All analyses were conducted in R 3.3.1 (http://www.R-project.org) with the package mgcv (Wood, 2006).

RESULTS

Time had a significant effect (all $P < 0.001$) on all response variables and explained on average 63%

(minimum: 35%, maximum: 89%) of the variation in response variables (Table 1).

Growth of leaves, bulbs and roots

Leaf length increased almost linearly up to the fifth week of the experiment and remained more or less constant for the following five weeks (Fig. 1a). The mean bulb mass (including replacement bulbs and bulbils) was about 2 mg until the fourth week, but then strongly increased (particularly from the seventh week onwards) to a maximum of c. 11.8 mg, which corresponds to a six-fold higher mass compared to the start of the experiment (Fig. 1b). The mean root mass showed no trend during the course of the experiment, ranging from 0.2 to 0.7 mg depending on harvest date (Table S1).

N concentration and C:N ratio of compartments

Leaf N concentration was c. 5% in the first three weeks, and then declined until the ninth week to c. 2% (Fig. 1c). Thus, N concentration decreased by c. 60% during the developmental cycle of the leaves. Bulb N concentration decreased during the first four weeks (by 45%), and then remained unchanged for three weeks (Fig. 1c). After the seventh week, bulb N concentration increased to the initial value of c. 3%.

The C:N ratio of leaves and bulbs was inversely related to their N concentration. Leaf C:N ratio was low (7.7) at the beginning of the experiment and increased from the sixth week onwards to a maximum of 18.0 (i.e. values more than doubled; Fig. 1d). In contrast, bulb C:N ratio declined from a value of 23.3 (from the sixth week onwards) to a minimum of 14.7. The C:N ratio of roots was c. 20 at the beginning of the experiment, peaked in the sixth week at 29, and decreased to 23.5 by the end of the experiment (Table S1). The soil C:N ratio showed no temporal trend and varied from 34 to 37 (data not shown).

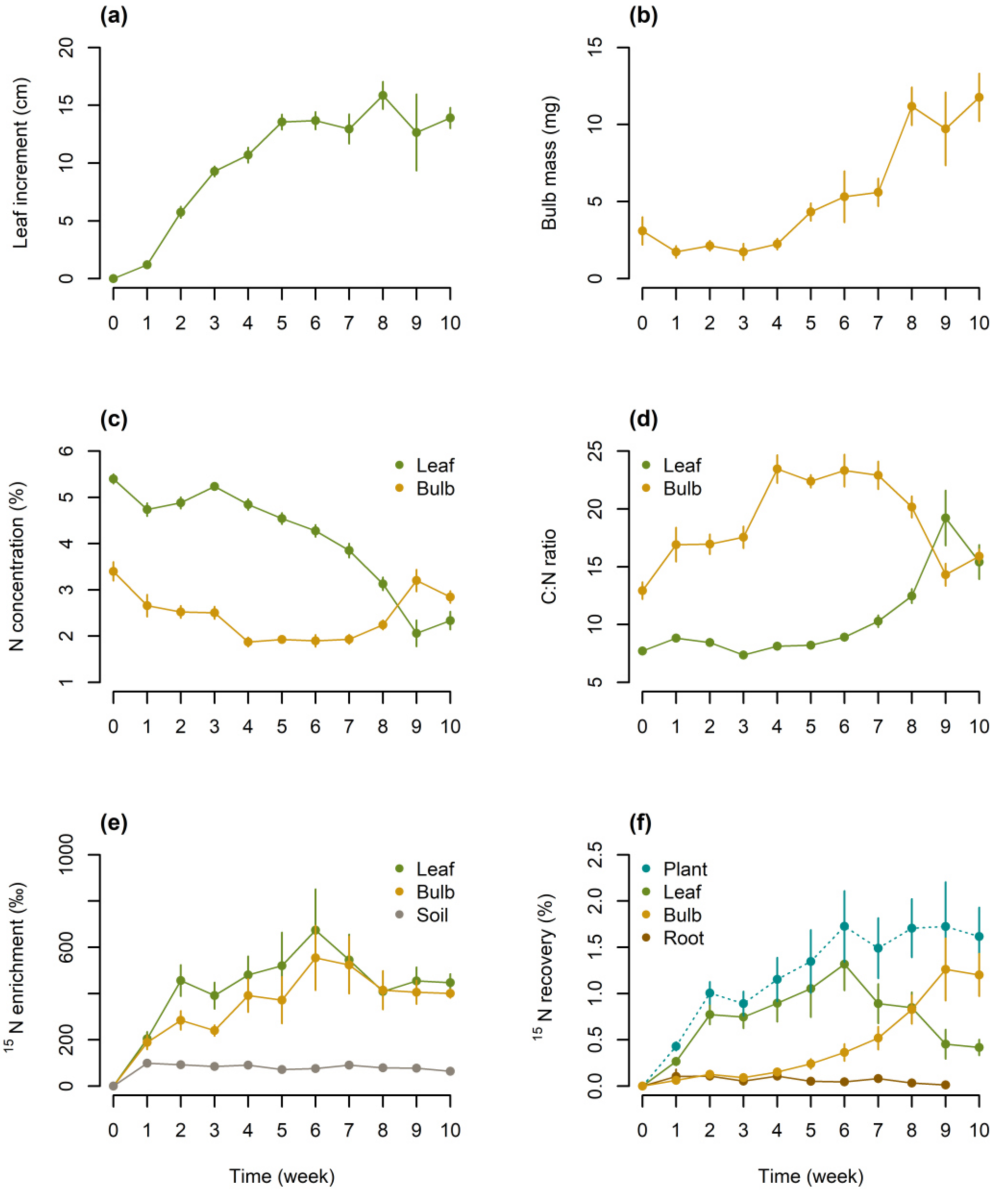
^{15}N enrichment and ^{15}N recovery in compartments

Leaf ^{15}N enrichment strongly increased during the first sixth weeks to 670‰, then decreased to a final value of c. 450‰ (Fig. 1e). Bulb ^{15}N enrichment showed a similar trend, but maximum values were lower and c. 550‰ in the sixth week (Fig. 1e). Root ^{15}N enrichment increased until the fourth week to c. 530‰ and then dropped to 130‰ at the end of the experiment (Table S1). Soil ^{15}N enrichment peaked in the first week at c. 100‰, and then slightly decreased to a final value of c. 64‰ (Fig. 1e).

Leaf ^{15}N recovery increased continuously until the sixth week to 1.32% and then decreased to a final value of 0.42% (Fig. 1f). This decrease of ^{15}N recovery in leaves coincided with a strong increase of ^{15}N recovery in bulbs. Here we found a continuous increase from the sixth week onwards and maximum values during the last two weeks (1.26% and 1.20%, respectively; Fig. 1f). Since total plant recovery showed no further increase from the sixth week onwards (Fig. 1f), the amount of ^{15}N withdrawn from senescing leaves was completely transferred to bulbs, corresponding to a transfer of 68% of leaf ^{15}N to bulbs (leaf $^{15}N_{max}$ - leaf $^{15}N_{final}$ = leaf $^{15}N_{transferred}$: 1.32% - 0.42% = 0.90%, 0.90% corresponds to 68% of leaf $^{15}N_{max}$). ^{15}N recovery from roots was negligible due to the low root biomass. A maximum value of about 0.1% was found during the first four weeks, and ^{15}N recovery dropped to a final value of 0.01% (Fig. 1f). The highest recovery was found in the soil (first week: 87%). This valued dropped to 61% at the end of the experiment (Table S1).

Table 1 Results from generalized additive mixed models for the effect of time (week 0 - 10) on various traits of *Gagea spathacea* and the ^{15}N soil enrichment and recovery. The estimated degrees of freedom (edf) indicate the amount of smoothing.

Response variable	edf	*F*-value	*P*-value	$R^2_{adj.}$
Leaf increment	6.0	326.7	<0.001	0.89
Bulb mass	3.1	34.0	<0.001	0.51
Leaf N concentration	7.7	64.1	<0.001	0.85
Bulb N concentration	7.3	14.2	<0.001	0.54
Leaf CN ratio	5.6	33.1	<0.001	0.62
Bulb CN ratio	7.0	13.8	<0.001	0.52
Leaf ^{15}N enrichment	3.2	73.2	<0.001	0.56
Bulb ^{15}N enrichment	3.5	60.3	<0.001	0.54
Soil ^{15}N enrichment	8.2	84.5	<0.001	0.87
Plant ^{15}N recovery	2.4	104.1	<0.001	0.55
Leaf ^{15}N recovery	3.2	70.5	<0.001	0.55
Bulb ^{15}N recovery	1.0	175.5	<0.001	0.35
Root ^{15}N recovery	1.0	21.9	<0.001	0.38
Soil ^{15}N recovery	8.2	75.6	<0.001	0.86



Fiure 1 Temporal shifts in leaf increment (a), bulb mass (b), leaf, and bulb N concentration) (c), leaf and bulb C:N ratio (d), leaf, bulb, and soil ^{15}N enrichment (e), and leaf, bulb, root, and total plant ^{15}N recovery (f). Means (± SE) for weekly sampled individuals of *Gagea spathacea*. For the sake of clarity, data for root ^{15}N enrichment are omitted from Figure 1e (see Table S1 for these data).

DISCUSSION

Nitrogen cycling and allocation strategy of *G. spathacea*

Plants may adopt several mechanisms to minimize or avoid nutrient losses, such as the (i) reduction of litter production, (ii) formation of low-nutrient tissues, or (iii) optimization of nutrient resorption from senescing leaves (Aerts 1990). As the leaves of *G. spathacea* are annual and characterized by low C:N ratios, plants can only avoid strong nutrient losses by being highly efficient in resorbing nutrients from their leaves (Aerts 1999). Our findings confirm our hypothesis that *G. spathacea* is exceptionally efficient in recycling N, shown by the resorption of about 68% of leaf N and its reallocation to bulbs at the end of the growing season. This resorption efficiency is remarkable, because such high resorption efficiencies are usually expected for plants of low-N environments, and resorption efficiency often decreases with increasing N-availability in the soil (Boerner 1984; Shaver and

Melillo 1984; Millard and Proe 1992). *Molinia caerulea*, for example, a typical grass of low-N environments, was found to resorb c. 65% of the N from senescing leaves and to store it in basal internodes (Aerts 1990; Friedrich et al. 2012). For deciduous-forest herbs, Rothstein and Zak (2001) found values between 21% and 70%, and Aerts (1996) calculated a mean N resorption efficiency of 50% for a total of 287 plant species (mean N resorption efficiency for forb species was 41%). For many tree species, leaf N resorption from senescing leaves amounts to about 50-60% (Niinemets and Tamm 2005; Tang et al. 2013; Zhang et al. 2015; Zhou et al. 2016; Bilgin and Guzel 2017).

Internally recycled N is a major source of the N needed for seasonal growth across different species and life forms (Aerts 1990; Millard and Proe 1992; Thornton et al. 1993; Millard 1996; Silla and Escudero 2003). In the case of *G. spathacea* the high resorption strategy suggests that plants have high N demands for both early seasonal leaf and (replacement/daughter) bulb formation to ensure assimilation and propagation. This is in contrast to other *Gagea* species with sexual reproduction and thus high investments into seeds (Schnittler et al. 2009, 2013; Beisenova et al. 2015; Schnittler et al. 2017). Highly efficient N resorption thus represents an important part of the life-history strategy of *G. spathacea*. In our experiment, the mobilization of bulb N in early spring to support the formation of leaves was shown by the strong decrease in bulb N concentration in the first four weeks of the experiment and the simultaneously increase in leaf length by 11 cm (Figs. 1c and a). In addition, the formation of bulbils also requires a high N supply, since N concentrations of bulbils are almost twice as high as in parent bulbs (Schnittler et al. 2009).

After six weeks of growth there was a marked shift in the N utilization and assimilation of *G. spathacea*: The C:N ratio of leaves strongly increased while that of bulbs decreased, enrichment and recovery no longer increased but instead decreased, and total plant recovery remained constant, indicating no further N uptake (i.e. no further ^{15}N was transferred from the soil to the plant, and shifts in leaf and bulk recovery were related to internal translocation processes). This is due to the onset of leaf senescence which is accompanied by decreasing water and thus nutrient uptake (Estiarte and Peñuelas 2015). Thus, the first six weeks of growth were characterized by N uptake from the soil (see below) and allocation of N from bulbs to leaves, whereas the last four weeks were characterized by N recycling (i.e. N reallocation from leaves to bulbs). This N recycling phase was accompanied by a doubling of the mass of the bulbs (Fig. 1b).

The patterns of ^{15}N enrichment and recovery found for *G. spathacea* indicate that N was also taken up from the soil from the very beginning of leaf formation. Therefore, N needed for early leaf growth was not only remobilized from bulbs but also absorbed from the soil N_{inorg} pool. Although total ^{15}N recovery at the plant level was comparatively low (about 1.7% at the end of the experiment), this value is in good agreement with that found in other ^{15}N tracer studies (e.g. for dwarf shrub *Calluna vulgaris*; Friedrich et al. 2011). Decreasing total recovery rates in the course of the experiment were comparable to those in other studies and probably due to losses with irrigation water or in gaseous form (Fang et al. 2015; Bähring et al. 2017).

Implications for species conservation

Plants of *G. spathacea* have high N requirements, but the high N resorption efficiency and storage in the bulb allows the species to quickly form leaves and new bulbs during its short active growth phase. The strong demand for N explains the stenoecious behavior of the species and its restriction to high N environments such as Alno-Ulmion (and partly Fagion) communities (Diekmann et al. 2014). High N availability at these sites with gley soils is correlated with an ample water supply (Härdtle et al. 2003), suggesting that soil drainage negatively affects the trophic condition of the sites. Typical tree species such as alder (*Alnus glutinosa*) may contribute to an improved N supply due to actinorhizal N fixation and the production of leaf litter with extremely low C:N ratios (McNeill et al. 1994). Replacement of alder with other tree species, due either to drainage or silvicultural measures (e.g. planting poplars), therefore, negatively affects the growth conditions for *G. spathacea* (e.g. hybrid poplar plantations cause a distinct reduction in groundwater recharge due to high transpiration rates; Petzold et al. 2011).

Another key species of the forests hosting large *G. spathacea* populations is common ash (*Fraxinus excelsior*), which is nowadays severely threatened by an emerging fungal disease caused by the ascomycete *Hymenoscyphus fraxineus*. This development has dramatic consequences for the *G. spathacea* populations, because affected forests experience shifts in both biotic and abiotic site conditions (e.g. light regime) with consequences for the dynamics of the herb layer (Pautasso et al. 2013a; b; Mitchell et al. 2014). The observation that some ash individuals are relatively resistant against the fungus calls for genetic studies to identify patterns of adaptive variation (i.e. genetic resistance or tolerance) across heterogeneous environments and landscapes (Gonzalez-Martinez et al. 2006). It is important that lightly or moderately damaged trees remain in the forest because of their potential tolerance against the pathogen, an important prerequisite for a possible recovery of ash populations (Pautasso et al. 2013b). A complete removal of all ash trees, in contrast, would have deleterious effects on the herb layer dynamics and the light environment of *G. spathacea* (Härdtle et al. 2003).

Further factors that might threaten populations of *G. spathacea* are habitat fragmentation (due to the species' low dispersal power; Šerá 2008), herbicide or nutrient inputs form adjacent agricultural fields (due to lateral transport; Gove et al. 2007) or habitat destruction (due to inappropriate forest management (Schmidt et al. 2014; Mölder et al. 2015). It is also conceivable that smaller population might be affected by heavy deer browsing or bulb excavation by wild boar (Romahn 2015).

G. spathacea is considered an "ancient woodland species" (Wulf 1997) and its occurence indicates a high diversity of typical forest species (Härdtle et al. 2003; Hofmeister et al. 2014; Stefańska-Krzaczek et al. 2016). Efficient protection and careful sustainable management of these '*G. spathacea*-forests' are, therefore, necessary to protect the rare woodland species *G. spathacea* and the biodiversity of these forest ecosystems.

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Chapter 20

Synthesis

GENERAL DISCUSSION AND CONCLUSIONS

Overall, the findings of this thesis point to the vital role of both biodiversity and ecological continuity in modulating the functioning of forest ecosystems in the context of global change by providing insight into the complex interrelationships between biodiversity, ecological continuity and ecosystem functioning and how these relationships are altered by multiple drivers of global environmental change. In this context, the thesis proposes several mechanisms by which forests associated with a high tree diversity and/or long ecological continuity may provide a more stable supply of multiple ecosystem services related to plant biomass (e.g. timber production, carbon sequestration and storage) than monocultures and/or intensely managed forests under ongoing environmental changes. The main findings and conclusions are grouped into five sections.

Neighbourhood diversity is a key determinant of forest productivity

Biodiversity loss is expected to decrease forest productivity worldwide, as tree species richness has been shown to foster key ecosystem functions such as primary productivity (Liang et al. 2016; Huang et al. 2018). Most studies in forests, however, analysed biodiversity effects at the community scale (stand level), but have rarely assessed those effects at the relevant scale where individuals and species interact – that is the local neighbourhood (Stoll & Weiner 2000). Consequently, we still have a limited understanding on mechanisms underlying biodiversity-productivity relationships in forests.

The thesis provides the first experimental support for the hypothesis that diversity-mediated interactions among local neighbours are a strong regulator of productivity in mixed-species tree communities by showing that local neighbourhood interactions explained over half of the variation (52%) on average in observed community productivity across biodiversity levels. Moreover, the thesis shows that the relative importance of local neighbourhood interactions in regulating forest productivity increases with community tree species richness. After five years, aboveground wood productivity of 24-species mixtures was more than twice as high (+122%) as those found in average monocultures. These are important findings, because they demonstrate that the previously reported positive biodiversity-productivity relationships in forests (Paquette & Messier 2011; Zhang et al. 2012; Liang et al. 2016; Huang et al. 2018) are largely the result of aggregated small-scale variations in diversity-mediated neighbourhood interactions, emphasising the significance of understanding mechanisms that operate at the local neighbourhood scale.

The BEF-studies presented in Part I demonstrate some principle mechanisms that explain positive biodiversity-productivity relationships at the local neighbourhood scale. For example, the finding that individual tree productivity increased with increasing local neighbourhood tree species richness is related to different mechanisms that depend on focal tree functional traits: For species with a conservative resource-use strategy net biodiversity effects were brought about by facilitation, and for species with acquisitive traits by competitive reduction. The results reported in this part also reveal a further mechanisms by which local species interactions translate into positive biodiversity effects at larger scales: Crown complementarity (i.e. resource partitioning in canopy space) was positively related to tree species richness at the local neighbourhood scale and emerged as the result of neighbour-driven shifts in branch morphology and wood volume allocation in favour of branches. This in turn allowed co-existing trees in species-rich neighbourhoods to use light resources more efficiently, and thus to be more productive than those growing with conspecific neighbours. Importantly, these effects became stronger through time and scaled up to promote community productivity. The observed diversity-mediated shifts in allocation pattern and crown morphology (i.e. crown size and shape with effects being stronger for crown shape) reveal a principal mechanism underlying positive biodiversity-productivity relationships in forest ecosystems and shed light upon the previously reported effects of crown complementarity and canopy packing on forest productivity (Pretzsch 2014; Jucker et al. 2015; Williams et al. 2017). Moreover, the thesis provides first experimental evidence that tree species richness stabilises forest productivity under varying climatic conditions, emphasising the high value of mixed-species forests in the context of climate change.

In summary, these findings are highly relevant for our understanding of biodiversity-ecosystem functioning relationships in forests and have important implications for the stable provisioning of ecosystem services (e.g. timber production) as well as for multispecies afforestation and forest restoration strategies. For example, mixing native tree species at the smallest spatial scale (i.e. at the local neighbourhood level) instead of mixing monospecific patches or forest stands at the stand or landscape scale could maximise the potential of forests to contribute to climate-change mitigation – particularly in highly diverse forest communities of the tropical and subtropical forest biomes (Fichtner & Härdtle 2020).

Neighbourhood diversity increases resistance of forests to drought

Nature-based climate solutions are becoming increasingly important to mitigate adverse impacts of climate change on the functioning of ecosystems (Seddon et al. 2019). Forests store immense amounts of carbon (Pan et al. 2011), and carbon sequestration by trees is assumed to be an important measure to remove carbon dioxide from the atmosphere (Griscom et al. 2017; Bastin et al. 2019; Pugh et al. 2019; but see Luyssaert et al. 2018; Popkin 2019). The future role of trees in contributing to total net primary production of forests, however, critically depends on how rates of tree carbon accumulation and tree vitality vary with the expected increase in severity and frequency of drought events (Ciais et al. 2005; Williams et al. 2013). Biodiversity is supposed to mitigate detrimental impacts of climate change on forest productivity (Hisano et al. 2018), but its functional role is still under debate and experimental evidence is rare. Specifically, our understanding of the mechanisms underlying mitigation effects remains limited, as existing work largely focuses on biodiversity effects related to the community scale (in particular in less diverse temperate and boreal forests). Using trait-based neighbourhood models, the thesis provide strong support for the hypothesis that mechanisms operating at the local neighbourhood scale are a key component for regulating forests responses to drought. Consistent with the prediction of the 'stress-gradient hypothesis' (Bertness & Callaway 1994; Maestre et al. 2009) the results of Chapter 5 show that positive biodiversity effects persist and became stronger in years with water deficits, indicating that local neighbourhood tree species richness has a strong potential to mitigate adverse impacts of climate change on individual tree productivity. Importantly, drought-sensitive species benefitted the most from growing in diverse neighbourhoods during drought, suggesting an important mechanism by which neighbourhood diversity increases the resistance of forests to drought via strengthening the weakest components of the system. Hence, this study provides for the first time experimental evidence that changes in trait-mediated neighbourhood interactions across biodiversity levels can critically regulate the response of forests to drought and advances our understanding on species interactions in highly diverse tree communities. This is an important finding, because it highlights that promoting high tree species diversity at the local neighbourhood scale is a promising way to secure high forest productivity and carbon sequestration even during periods of drought.

Ecological continuity mitigates climate change impacts on forest productivity

Previous work has demonstrated lasting impacts of land-use changes in the past on above- and belowground communities and related ecosystem functions (see Fraterrigo 2013 for a review), but the functional consequences for ecosystem responses to global environmental changes remain unclear (see Johnstone et al. 2016; Perring et al. 2016 for reviews). Specifically, we still lack empirical evidence on the role of forest continuity and continuity in natural stand dynamics in attenuating the effects of climate variability on forest productivity. The results reported in this thesis suggest that forest continuity and the (long-term) cessation of forest management enhances the resistance and resilience of forests to climate change. For example, forest continuity seems to increase ecosystem stability, as long-term (>100 years) interannual variation in tree-ring width of *Quercus petraea* was largely reduced in ancient forests. In contrast, oak trees in recent forests trees grew faster under favourable, but exhibited stronger growth decline under unfavourable climatic conditions. This opposite pattern of climate sensitivity might be linked to the finding of long-lasting impacts of land-use legacies on soil microbial community composition and nutrient cycling in *Q. petraea* forests (Chapter 8). Even after a century of reforestation, soil microbial community composition significantly differed between ancient and recent forest soils, while differences between forests on former arable land and former heathland were less distinct. This indicates that legacy effects of former land use are a major driver of soil microbial community dynamics, but that the land use itself, and not necessarily the type of land use, may be important for these legacy effects. On average, ancient forest soils were associated with higher proportions of saprotrophic and ectomycorrhizal fungi, but distinctly lower microbial biomass, actinobacteria and enzyme activities, which coincides with findings reported by Fraterrigo et al. (2006). The observed differences in nutrient cycling might explain why growth rates of oak trees in recent forests were on average higher, but less stable during the last century. For *Fagus sylvatica* forests, results of Chapter 10 show that forest continuity increased drought resistance of adult beech trees via increasing the standing fine root biomass and modulating fine root traits towards higher root tissue density, lower specific root length and area. These changes in the fine root system and fine root morphological properties are most likely the result of persistent soil legacies of former land use, as ancient forest soils still exhibited significantly lower levels of phosphorus, higher carbon to phosphorus and carbon to nitrogen ratios as compared to recent forest soils. Similarly, results of Chapter 14 provides first support that drought sensitivity of *F. sylvatica* is associated with forest management history. The finding of decreasing drought-induced growth decline with increasing length of forest management cessation is most likely the result of management legacies leading to modifications in crown size and total leaf area, and thus to an increase in the trees' water demand. In this way, former silvicultural interventions (e.g. logging-induced canopy gaps due to thinning and harvesting that trigger crown expansion) may enhance the contemporary risk of a temporal mismatch between water demand and water supply during drought events (structural overshoot; Jump et al. 2017). In this context, it is important to note that recommendations for sustainable forest management require a better understanding of the complex interrelationships among forest management intensity and multiple drivers of global change. However, the results presented in this thesis indicate that land-use legacies have persistent effects on tree growth for centuries with potential negative implications under climate extremes. Hence, forests associated with a long ecological continuity might be less sensitive to climate change than recent and/or (intensively) managed forests. A legacy-based perspective on forest ecosystems can therefore advance our mechanistic understanding of climate–growth relationships.

Nitrogen deposition increases sensitivity of forests to drought

Climate change and anthropogenic nitrogen deposition are some of the most significant threats for ecosystems (Galloway et al. 2008; Isbell et al. 2013; Greaver et al. 2016; Averill et al. 2018). However, interactions between global change drivers can differentially affect ecosystem response (Maes et al. 2019), making predictions on the net effects challenging. Sustainable forest management and conservation strategies therefore requires a better understanding of how drivers of global change interactively (e.g. non-additively) affect tree growth and forest productivity. The findings presented in Part II provide strong support that N enrichment increases the sensitivity of *F. sylvatica* to drought. Importantly, the results from Chapters 11–13 confirm non-additive effects across different life-history stages (saplings, young and adult individuals), which might be particularly relevant for early stages of forest succession due to the higher susceptibility of younger trees to environmental stress. These studies identified different mechanisms by which the combined effects of N and water deficits can lead to non-additive responses. First, N fertilisation induced shifts in allocation pattern towards less belowground biomass (i.e. less carbon is allocated to roots, which is in line with the 'resource optimisation hypothesis'; Thornley 1972; Ågren & Franklin 2003), leading to higher shoot:root ratios. Second, the results from Chapter 13 show that beech trees growing in nutrient-rich soils (those associated with recent forests) exhibited lower standing fine root biomass and higher fine-root dieback during periods of water deficits, most likely due to N-induced modifications in fine root traits (as described in the findings of the preceding section). Moreover, it is conceivable that N enrichment lead to decreasing mycorrhizal colonisation (Averill et al. 2018), and thus to reduced access to water and nutrients during drought events. The results from Chapter 12 also show that the positive effects of species-mixing on community productivity may diminish when forests experience combined effects of multiple drivers of global environmental change. For *F. sylvatica*–*Q. petraea* mixtures, complementarity effects (calculated based on Loreau & Hector

2001) significantly declined under combined effects of N fertilisation and drought, resulting in lower net biodiversity effects. However, this was not evident for other species-mixtures (i.e. *F. sylvatica–Pseudotsuga menziesii* and *F. sylvatica–Q. petraea–Pseudotsuga menziesii* mixtures), indicating that the functional composition rather than tree species richness per se regulate the response of young tree communities to multiple changes in environmental conditions. This suggests that simultaneous effects of different global change driver can counteract a successful tree regeneration, which is a critical stage in forest development. The results from Chapter 13 provides further support that high N loads increase the sensitivity of *F. sylvatica* to drought, but the magnitude of net effects for adult individuals depend on forest history and seasonality effects: While the response of beech to simultaneous effects of N deposition and summer water deficits was consistent across forest history types (up to fivefold higher growth decline under high N deposition), the magnitude of growth decline during spring water deficits and high N deposition was higher for trees in ancient compared to recent forests. However, this response might not inevitably be linked to water deficit-induced growth decline, as elevated N deposition can generate trade-offs between reproduction (resource allocation towards higher seed production) and trunk radial-growth rates (Hacket-Pain et al. 2018; Pesendorfer et al. 2019), in particular for *F. sylvatica* (Hacket-Pain et al. 2017). These findings suggest that non-additive effects of multiple global change drivers – ‘ecological surprises’ – can significantly alter the early recruitment stage as well as later forest development stages of temperate beech forests towards less vital and productive communities, emphasising the need to understand the complex interactions among forest history and co-occurring drivers of global environmental change. This in turn would advance our ability to predict how forests might respond to global change.

Forest management and global change: an ecosystem-based perspective

There is increasing concern that the functional integrity of forests declines by ongoing biodiversity loss and anthropogenic degradation (Erb et al. 2018; Watson et al. 2018), as key attributes for forest species conservation and ecological processes critically depend on management intensity (Brunet et al 2010). The current focus on economy alongside with the forest management intensification, however, runs the risk of failing global agreements on climate-change mitigation and biodiversity protection (IPCC 2018; IPBES 2019; Seddon et al. 2019). Thus, ecologists urge to shift silvicultural paradigms towards an ecosystem-based perspective (i.e. ecosystem-based forest management) that focus on ensuring the functional integrity (ecological processes and biome-specific forest biodiversity) of production forests (e.g. BfN 2019; Hlásny et al. 2019). While promoting mixed-species forests is invoked as a management option to improve the resilience of production forests in the context of global change (Pretzsch et al. 2017), the role of ecological continuity (and its potential interactions with global change) is overlooked. Mixed-species forests are often characterised by highly complex and densely packed canopies, leading to higher stand productivity compared to monocultures (e.g. Pretzsch 2014; Jucker et al. 2015). Although there is increasing understanding on the mechanisms why trees in mixture use canopy space more efficiently (Williams et al. 2017; Chapter 4), little is known about the interactive effects between tree diversity and continuity in anthropogenically unaltered tree-tree interactions on individual tree productivity. The results of Chapter 15 show that the positive effects of species mixing on crown efficiency (basal area growth per unit crown surface area) of *F. sylvatica* depend on the continuity of natural stand dynamics (managed, short-term and long-term unmanaged stands): In species mixtures, crown efficiency steadily increased with decreasing management intensity (increasing temporal extend of management cessation), while differences between management types were less distinct for monocultures. This allowed beech trees growing in (long-term) unmanaged stands to achieve similar growth rates by smaller crown sizes compared to those growing in managed stands. The results indicate that wood volume allocation patterns in unmanaged, mixed-species forests can shift towards an optimised trunk-crown relationship, which in turn leads to changes in the vertical distribution of trunk wood volume (Georgi et al. 2019). The results of Chapter 17 from long-term unmanaged beech forests also demonstrate that the spatial aggregation of large-diameter trees can benefit the growth of smaller neighbours. This suggests that radial growth rates do not exclusively depend on conspecific neighbour density, but on the aggregation of such large-diameter trees and their functional role for regulating biotic filtering processes. The finding that competitive tree-tree interactions are less prevalent in the presence of large-diameter trees is probably linked to resource partitioning in canopy space (induced by forest management abandonment as described above) and belowground facilitation. For example, large-diameter trees play a crucial role in connecting trees via common mycorrhizal mycelium (Beiler et al. 2010). Such mycorrhizal networks transfer carbon, water, nutrients and biochemical signals among trees (Simard et al. 1997; Gorzelak et al. 2015; Klein et al. 2016), and thereby alter tree-tree interactions or facilitate conspecific regeneration (Simard 2009; 2018). This implies that forest management intensification (in particular the intensive logging of large-sized trees – 'hub trees') runs the risk of disrupting mycorrhizal networks and of reducing the genetic diversity of fungal associates (Beiler et al. 2010), which may become increasingly important in the context of global change (Bingham & Simard 2012; Simard et al. 2012). The results presented in Chapter 17 also show that not only the amount of carbon, but also the rate of carbon accumulation is highest in large-diameter trees, emphasising the potential functional importance of those individuals for belowground networking and climate-change mitigation. The finding that competition intensity and importance varies with tree maturity across abiotic stress gradients (Chapter 16) lends additional support to minimise the frequency and intensity of thinning by accounting for the context-dependency of competition effects. This would promote tree longevity, stand maturity and the temporal extend of natural stand dynamics in production forests, which in turn would benefit synergies among multiple ecosystem services and biodiversity (Körner 2017; Felipe-Lucia et al. 2018; Lelli et al. 2019; Fichtner & Härdtle 2020).

Understorey plant communities are a major component of temperate forest plant diversity and play an important role for biotic interactions and ecosystem functioning (Gilliam 2007; Landuyt et al. 2018). However, for many of its species, little is known about their autecology, which makes it difficult to assess potential threats and to predict community dynamics under global change (Landuyt et al. 2019). In addition to the vital importance of increasing the total protected forest area across all forest biomes (including the strict preservation of primeval forests), the thesis also highlights that sustainable forest management schemes should focus on sustaining habitat continuity and habitat integrity in production forests, as many forest understorey plants are sensitive to changes in habitat conditions across spatial and temporal sales (Gilliam 2007). This also applies to *Gagea spathacea* – a plant species for which Germany has a national and international conservation responsibility. Given that its remaining large populations are confined to near-natural ancient deciduous forests, it is essential to avoid the conversion of these forests into coniferous or deciduous-coniferous stands (e.g. planting of *P. menziesii* as a current, economic-based management option in the context of global change). This in turn would benefit the biodiversity typical of (ancient) forest ecosystems. The results of Chapter 7 also show that plant diversity has a positive effect on insect diversity and abundance – both in short- (grasslands) and long-lived plant communities (forests). Species richness effects were strongly associated with functional and structural diversity, emphasising the pivotal role of ecosystem-based management of grassland and forest ecosystems (e.g. protection of biodiversity by promoting structural attributes associated with natural forest dynamics; Felipe-Lucia et al. 2018; Penone et al. 2019).

To increase the resilience of production forests to global change several management options have been proposed that focus on altering tree-tree interactions and ecological processes (e.g. reducing stand age by shortening rotation periods, reducing stand density and growing stocks and introducing non-native fast-growing tree species; e.g. D'Amato et al. 2013; Sohn et al. 2016; Jandel et al. 2019). The thesis extends the current debate on climate-change mitigation and biodiversity conservation by highlighting the functional importance of ecological continuity in mediating the response of forest ecosystems to global change. This includes (i) sustaining forest and habitat continuity, (ii) allowing trees and forest to mature, thereby sustaining the functional continuity within a stand, and (iii) minimising silvicultural interventions in production forests, thereby promoting natural stand dynamics (as a basis for the development of resource partitioning and facilitation effects). Given that each anthropogenic intervention alters ecological interactions that drive ecosystem functioning, the thesis offers an alternative, ecosystem-based perspective that prioritise the integrity of ecological functions and biome-specific forest biodiversity over economic interests and high-impact management options. In my view, this would be a promising way to meet United Nations Sustainable Development Goals in a changing world.

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The studies were conducted in various ecosystem types, such as forests, grasslands and heathlands, and are grouped into five reserach fields:

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