The importance of ecological continuity for ecosystem functions of beech forests

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‘Life can only be understood backwards; but it must be lived forwards.’
Søren Kierkegaard

Dedicated to Quintus

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Summary

Forest ecosystems significantly contribute to global carbon (C) sequestration and therefore play a crucial role for climate change mitigation. At the same time, forests were and are subjected to past and current environmental changes with consequences for the functioning of forest ecosystems and their associated ecosystem services.

Forests in Central Europe are highly influenced by former settlement activities and land-use changes, as well as silvicultural management measures. Until the beginning of the 19th century anthropogenic activities caused a tremendous decline of the forest area. The resulting timber shortage led to large scale afforestations on previously agriculturally used land (e.g. heathlands, grasslands and croplands) during the 19th and 20th century. Widespread afforestation programs created recent forest ecosystems (i.e. young forest systems in terms of their development history). Despite the positive effect of increasing the forest area of Central Europe, the ecological effects of these land-use changes on forest ecosystems remain poorly understood. In addition, most forests in Central Europe are under silvicultural management, while the knowledge about the consequences of management measures on forest ecosystem functioning, particularly in the face of ongoing global environmental changes, is also still limited.

In order to increase the understanding of ecosystem processes in forests, an assessment of conceivable shifts in ecosystem functions caused by former land-use changes and forest management is required. By analysing aboveground growth rates of European beech (*Fagus sylvatica* L.) in response to environmental change drivers, such as climate extremes and nitrogen (N) deposition, the presented thesis aims to assess the role of land-use and management legacies in modulating present responses to drivers of environmental change.

To this end, annual radial growth rates of individual trees were measured in mature beech stands. The investigated stands differed either in their land-use history (i.e. ancient forest sites with a forest continuity > 230 years versus recent forests afforested on former arable land ~ 100 years ago) or their forest management history (i.e. managed forest sites versus short-term and long-term unmanaged forest sites). Measurements of radial growth rates were complemented by analyses of the fine root systems, soil chemical properties and crown projection areas to gain insights into the mechanisms underlying alterations in tree growth. Within the projects of the presented thesis, shifts in the climate-growth relationships driven by land-use and management legacies were analysed. In addition, land-use legacy mediated differences in the climate-nitrogen-growth relationships were assessed.

The key findings are: **(I)** Soil legacy driven alterations in the fine root systems cause a higher sensitivity of radial increment rates to water deficits in summer for trees growing on recent forest sites than for trees growing on ancient forest sites. **(II)** Management legacies (in terms of tree release) enhance the sensitivity of beech's radial growth to water deficits in spring through changes in crown sizes. **(III)** Interacting effects of spring water deficits and co-occurring high deposition of reactive N compounds lead to stronger radial growth declines in trees growing in ancient forests. This is likely caused by resource allocation processes towards seed production, which is, in turn, mirrored by decreasing radial growth rates. In this context, high N deposition likely boosts mass fructification in beech trees.

Overall, it has been demonstrated that the ecological continuity plays a crucial role in modulating both climate sensitivity and the growth response to interacting effects of water deficits and nitrogen deposition in beech trees. The presented thesis identified a trade-off between the climate sensitivity and maximised growth rates within beech trees, depending on forest history. The results show that the growth of beech in ancient, unmanaged beech forests is less sensitive to water deficits than in recent and managed beech forests. Additionally, interacting effects of spring water deficits and N deposition likely increase the reproductive effort of beech trees, particularly in ancient forests. Thus, the results of this thesis once again underpin the uniqueness of ancient, unmanaged beech forests, whose importance for the conservation of biodiversity has been widely acknowledged. In summary, the presented thesis highlights the need to consider the ‘ecological memory’ of forest ecosystems when predicting responses to current and future environmental changes.

Keywords: Dendroecology ● Ecological continuity ● European beech ● Fine root inventory
Global environmental change ● Land-use legacies ● Management legacies
Reproduction-growth trade-off ● Soil legacies ● Structural overshoot

Zusammenfassung

Waldökosysteme tragen wesentlich zur globalen Kohlenstoff (C) -speicherung bei und spielen daher eine entscheidende Rolle für den Klimaschutz. Gleichzeitig werden die ökologischen Prozesse in Wäldern durch aktuelle und vergangene Klima- und Umwelteinflüsse verändert. Diese Prozessveränderungen wiederum beeinflussen die gegenwärtigen und zukünftigen Funktionen in Waldökosystemen und damit auch die durch sie bereitgestellten Ökosystemdienstleistungen.

Die Wälder in Mitteleuropa sind stark von historischen Landnutzungs- und Siedlungsaktivitäten sowie waldbaulichen Bewirtschaftungsmaßnahmen geprägt. Bis zum Beginn des 19. Jahrhunderts führten diese Aktivitäten zu einem erheblichen Rückgang der bewaldeten Fläche. In Folge einer zunehmenden Holzknappheit kam es im 19. und 20. Jahrhundert zu großflächigen Aufforstungen auf ehemals landwirtschaftlich genutzten Flächen (z.B. Heide-, Grünland- und Ackerflächen). Im Zuge dieser Aufforstungsprogramme entstanden rezente Waldökosysteme, also im Hinblick auf ihre Entwicklungsgeschichte vergleichsweise junge Wälder. Trotz des generell positiven Effekts einer Zunahme der Waldfläche in Mitteleuropa sind die ökologischen Auswirkungen dieser Landnutzungsänderungen für die Waldökosysteme selbst nach wie vor kaum verstanden. Darüber hinaus werden die meisten Wälder in Mitteleuropa waldbaulich bewirtschaftet, wobei das Wissen über die Folgen von Bewirtschaftungsmaßnahmen für die Waldökosystemfunktionen, insbesondere angesichts fortschreitender globaler Umweltveränderungen, noch immer begrenzt ist.

Für ein verbessertes Verständnis von Ökosystemprozessen in Wäldern ist eine Bewertung der möglichen Veränderungen der Ökosystemfunktionen durch frühere Landnutzung und Waldbewirtschaftung erforderlich. Anhand der Analyse des oberirdischen Wachstums von Rotbuchen (*Fagus sylvatica* L.) untersucht diese Arbeit, inwiefern vergangene Landnutzungsänderungen und waldbauliche Maßnahmen die gegenwärtigen Reaktionen auf globale Umweltveränderungen, wie Klimaextreme und Stickstoff (N) -deposition, beeinflussen.

Zu diesem Zweck wurden die jährlichen Zuwachsraten einzelner Bäume in hiebsreifen Buchenbeständen gemessen. Die untersuchten Bestände unterschieden sich entweder in ihrer Landnutzungsgeschichte (d.h. historisch alte Wälder, welche durch eine Bestockungskontinuität von mehr als 230 Jahren charakterisiert sind im Vergleich zu rezenten Wälder, die auf ehemaligen landwirtschaftlichen Nutzflächen vor etwa 100 Jahren aufgeforstet wurden) oder ihrer Bewirtschaftungsgeschichte (d.h. bewirtschaftete Bestände im Vergleich zu kurz- und langfristig unbewirtschafteten Beständen). Ergänzend zu den Messungen des Radialzuwachses wurden Analysen der Feinwurzelsysteme, der chemischen Bodeneigenschaften und Messungen der Kronen-projektionsflächen genutzt, um neue Erkenntnisse über die Mechanismen zu gewinnen, welche die auf ehemaliger Landnutzung und ehemaligem Management beruhenden Veränderungen in der klimagesteuerten Wachstumsreaktion erklären.

Die wichtigsten Erkenntnisse der durchgeführten Studien sind: **(I)** Die durch ehemalige Landnutzung hervorgerufenen Unterschiede in den chemischen Bodeneigenschaften bedingen

Unterschiede in den Feinwurzelsystemen der untersuchten Bestände. Dies führt dazu, dass die Klimasensitivität bei Bäumen auf rezenten Waldstandorten stärker ausgeprägt ist als bei Bäumen, welche an historisch alten Waldstandorten wachsen. **(II)** Eine Bewirtschaftung, also eine Freistellung einzelner Bäume durch Einschlagsereignisse, erhöht die Empfindlichkeit des radialen Zuwachses von Buchen gegenüber Frühjahrswasserdefiziten durch managementbasierte Änderungen der Kronengröße. **(III)** Wechselwirkungen zwischen Wasserdefiziten im Frühjahr und gleichzeitig auftretenden hohen Einträgen reaktiver N-Verbindungen führen zu einem höheren Rückgang des radialen Zuwachses der Bäume in historisch alten Wäldern. Dies wird wahrscheinlich durch Allokationsprozesse zu Gunsten einer erhöhten Buchecker-Produktion verursacht, welche sich wiederrum in geringeren Radial-zuwächsen widerspiegeln. In diesem Zusammenhang scheinen hohe N-Depositionen eine erhöhte Samenproduktion in der Buche zu fördern.

Insgesamt wurde gezeigt, dass die ökologische Kontinuität eine entscheidende Rolle bei der Ausprägung der Klimasensitivität als auch der Wachstumsreaktion auf interagierende Wasserdefizite und Stickstoffdepositionen in Buchen spielt. Die vorliegende Arbeit hebt eine gegenläufige Abhängigkeit zwischen Klimasensitivität und maximierten Radialzuwächsen bei der Buche hervor, wobei ihre Ausprägung nachweislich von der Waldgeschichte beeinflusst wird. Die Ergebnisse zeigen, dass das Wachstum von Buchen in historisch alten, nicht bewirtschafteten Buchenwäldern weniger empfindlich auf Wasserdefizite reagiert als in rezenten und bewirtschafteten Buchenwäldern. Darüber hinaus erhöhen interagierende Effekte von Frühjahrswasserdefiziten und N-Deposition wahrscheinlich die Reproduktionsanstrengungen von Buchen, insbesondere an historisch alten Waldstandorten. Somit unterstreichen die Ergebnisse der vorliegenden Arbeit einmal mehr die Sonderstellung von historisch alten, unbewirtschafteten Buchenwäldern, welche schon durch ihre Funktion für die Erhaltung der typischen Biodiversität von Buchenwäldern bekannt sind. Zusammenfassend hebt die vorliegende Arbeit die Notwendigkeit hervor, das „ökologische Gedächtnis“ von Waldökosystemen zu berücksichtigen, wenn Reaktionen auf globale Umweltveränderungen vorhergesagt werden.

1. General Introduction

1.1 Background: The socioeconomic importance of forest ecosystems

Since the 1990s there has been a noticeable increase of public and political interest in ecosystem functions. Ecosystem functions describe structures and processes of ecosystems as fundamental ecosystem properties, potentially providing desirable ecosystem services (Gómez-Baggethun et al. 2010). Ecosystem services, which are grouped in provisioning, regulating, cultural and supporting services, are defined as the benefit people gain from ecosystems (MEA 2005).

With regard to forest ecosystems, the highest socioeconomic importance has been attributed to their regulating (i.e. climate regulation) and provisioning (i.e. food, water, raw materials and medicinal resources) services, followed by their cultural and supporting ecosystem services (De Groot et al. 2012). Especially the ability of forest ecosystems to act as a carbon sink has fostered a public debate about the importance of forest protection and sustainable forest management (Naudts et al. 2016; Luyssaert et al. 2018; Box 1). Forests have the potential to sequester as much as 30% of annual global anthropogenic CO_2 emissions, hence forest productivity directly contributes to climate warming mitigation and climate regulation (Bellassen and Luyssaert 2014). Beyond carbon sequestration, forests are known to provide a wealth of further services. On one hand, the formal forest sector employs about 13.2 million people across the world and accounts for about 0.9% of the global economy (SOFO 2014). On the other hand, non-wood forest products play a crucial role for food security across the globe, especially for the livelihood of many people in the tropics and subtropics (SOFO 2018). In addition, forest ecosystems play an important role for recreation, especially in densely populated regions (e.g. Central Europe). Many cultural and spiritual sites are associated with forests as well (FOREST EUROPE, UNECE and FAO 2011). Of outstanding importance is the exceptional value of (intact) forest ecosystems in terms of biodiversity conservation (Watson et al. 2018). Forest ecosystems host the majority of terrestrial biodiversity across the globe (MEA 2005). Beside the intrinsic importance of biodiversity there is evidence that tree species richness supports important ecosystem functions such as tree productivity (Fichtner et al. 2018).

Box 1

Productivity, measured as the annual change in aboveground wood biomass, is one of the most important functions of forest ecosystems and has always been an integral part of silviculture (Boisvenue and Running 2006). Moreover, the increased awareness of forests acting as a carbon sink has led to a broader interest in forest productivity as a measure of carbon sequestration rates in above- and belowground biomass (Bellassen and Luyssaert 2014). Within this thesis annual tree-ring width (TRW) measurements were used as a proxy for individual tree aboveground productivity.

Overall, forest ecosystems are key for mitigating climate warming, for providing timber and food for the livelihood of billions of people, for protecting the planet’s biodiversity and for supporting the maintenance of human health and cultural heritage. Thus, a deeper understanding of forest ecosystem functioning, defined as the complex network of interactions and processes which sustain the system and its trajectory (Jax 2005), is crucial for assessing and securing forest ecosystem services for future generations in the face of unprecedented environmental changes.

1.2 Forest ecosystems in the midst of global environmental changes

The constant growth of the world population and its increasing impact on the earth and atmosphere underlines the central role of mankind in geology and ecology. This has been emphasised by naming the current geological epoch ‘anthropocene’ (Crutzen and Stoemer 2000). This epoch is characterised by such anthropogenic pressure that abrupt global environmental changes (‘tipping points’) cannot be excluded (Rockström et al. 2009). Increasing global anthropogenic greenhouse gas emissions (e.g. carbon dioxide, methane and nitrous oxide), for example, have led to profound changes in the climate system, including an increase of the mean global surface temperature and more frequent climate extremes (e.g. warm temperature extremes; IPCC 2013).

The ongoing climate change has profound consequences for forest ecosystems in particular, as trees are long-living individuals, unable to rapidly adapt to climate change via fast generational change (Lindner et al. 2010; Greenwood et al. 2017). Increased warm-season vapour-pressure deficit, which is largely controlled by temperature, was identified to be a key driver of forest drought-stress caused by climate change (Williams et al. 2013). Particularly at generally dry sites, drought-induced physiological stress (and therefore tree mortality) has been observed for different tree species across the world with fundamental consequences for tree species composition, forest structure and thus forest ecosystem functioning (Allen et al. 2010; Steinkamp and Hickler 2015). In fact, the increased frequency of extensive droughts during the last decades has led to decreasing growth rates of many tree species. This might hold true not only for a tree species’ distribution edge, since – in the case of *Fagus sylvatica* – susceptibility to drought was found to be highest in the core of the species’ distribution range (Cavin and Jump 2016). Moreover, drought-mediated bark-beetle infestations have caused tree-dieback of overstorey trees on subcontinental scales (Breshears et al. 2005). Further threats are large-scale wild-fires following dry periods which destroy millions of forest hectares every year (San-Miguel-Ayanz et al. 2018).

In contrast to these negative effects, a few positive effects of climate change on forest ecosystem productivity were documented. Due to climate warming a shift in the phenology of different tree species was reported (Chmielewski and Rötzer 2001). The inherent sensitivity of phenology to temperature has caused a longer vegetation period (i.e. climate warming causes an earlier bud break in spring and later leaf fall in autumn), thereby increasing the net carbon uptake of forests ecosystems (Keenan et al. 2014). Furthermore, a fertilising effect of elevated carbon dioxide concentrations of the atmosphere is discussed but a lasting effect has not been proven yet (Gedalof and Berg 2010; Norby et al. 2010).

Next to climate change, the excessive synthetical fixation of nitrogen (N) and its usage as fertiliser has contributed to many environmental problems such as eutrophication, acidification and biodiversity loss (Galloway et al. 2003). In fact, a European cost-benefit analysis of reactive N losses (caused by the increased use of reactive N as fertiliser in agriculture) showed that the overall environmental costs in the form of negative effects on the environment outweigh the direct economic benefit in agriculture (Sutton et al. 2011). Since the peak of reactive N emissions in Europe occurring in the 1980s, political interventions and new technologies have led to a decrease in emissions during the past decades (Sutton et al. 2011). Nevertheless, N deposition was shown to be the main driver of changes in species composition across all ecosystem types by driving the competitive interactions that lead to composition change (Bobbink et al. 2010). In forest ecosystems, species compositional changes are mainly limited to the shrub/herb layer and epiphytic lichens (Bobbink et al. 1998; Clark et al. 2013). Moreover, atmospheric N deposition was shown to be one key environmental variable influencing large-scale ectomycorrhizal fungi diversity in forests (Van der Linde et al. 2018), thus having an indirect effect on tree growth, as tree growth depends on interconnected mycorrhizal networks (Helgason et al. 1998; Simard et al. 2012). Trees of the temperate and boreal zone were shown to respond to atmospheric N addition with increased aboveground biomass production (Ferretti et al. 2014; Gentilesca et al. 2018; Schulte-Uebbing and De Vries 2018).

Studies on the combined effects of climate change and N deposition on ecosystem functions remain rare, although a physical and chemical interaction of theses drivers in the atmosphere can cause a variety of environmental impacts on different spatial scales (Bytnerowicz et al. 2007; Gaudnik et al. 2011). The understanding of ecosystem responses to these combined global change drivers is crucial for predicting future forest growth and adapting management strategies (Greaver et al. 2016). For forests ecosystems in particular, the interactive effects of climate change and N deposition are assumed to impact soil processes, tree growth, species composition and distribution, as well as the plants’ susceptibility to other stressors (Bytnerowicz et al. 2007; Law 2013). Multifactorial studies on tree growth showed that alternations in allocation processes (caused by higher nutrient availability through N deposition) increased the susceptibility to drought (Dziedek et al. 2017; Hess et al. 2018). Moreover, non-additive impacts of combined environmental change drivers on fruit production patterns of beech trees are under debate (e.g. Müller-Haubold et al. 2015; Braun et al. 2017; Hacket-Pain et al. 2018).

1.3 Forests of Central Europe: The uniqueness of European beech forests

In Central Europe, forest development has strongly been linked to the history of human settlement after the last glacial period. In the Holocene, Central Europe was reforested as a result of the immigration of different tree taxa which had survived the ice age in their southern refuges (Ellenberg and Leuschner 2010). Woody species of early successional stages such as birch (*Betula*), pine (*Pinus*) and hazelnut (*Corylus*) were most frequent in the Boreal, until oaks (*Quercus*) and other broadleaved taxa arrived in the Atlantic. As the last step of reforestation European beech (*Fagus sylvatica* L.) became the dominant tree species in large parts of Central Europe 3,300 years ago (Härdtle et al. 2008).

Due to its ecological, morphological and geographical plasticity, European beech is superior against other tree species, and beech forests are the potential natural vegetation in large parts of Central Europe (Ellenberg and Leuschner 2010). About one quarter of the total natural area of European beech forests is located in Germany, the centre of the distribution area of European beech. However, due to anthropogenic influences in recent centuries, forests dominated by European beech actually cover only a small fraction of their potential area (Knapp et al. 2008). The substantial and permanent use of the forests in Central Europe led to a degradation of many forest areas, but also to a fundamental change in forest structure and tree species composition (Ellenberg and Leuschner 2010). Shortage in timber and firewood occurring in the middle of the 18th century caused a wave of afforestation in Central Europe, but mainly with fast growing coniferous species (Härdtle et al. 2008). As a consequence, ancient forest sites (dominated by deciduous trees) are rare in Central Europe, and remnants of primeval forests did not survive at all in Central Europe (Glaser and Hauke 2004; Box 2).

The uniqueness of European beech forests is reflected by the recognition of ancient beech forest areas across ten European countries as a UNESCO World Heritage called 'Ancient and Primeval Beech Forests of the Carpathians and Other Regions of Europe' (UNESCO 2017). Ancient beech forests are of high nature conservation value (Westphal et al. 2004). For example, more than 5,000 animal species are associated with these beech forests (Assmann et al. 2007). Moreover, ancient beech forests are often associated with a high number of typical forest species and the occurrence of relict species (Fichtner and Lüderitz 2013). These species are characterised by low dispersion rates like ant-dispersed species with a dispersal rate of 30 cm per year (Brunet and von Oheimb 2008). There are also numerous stenotopic species among epiphytic bryophytes and lichens, as well as saproxylic

Box 2

In this context, *ecological continuity* is defined as the continuity in forest cover and soil development of a given site, thus focusing on the continuity of forest ecosystem development regarding anthropogenic disturbances (e.g. former land-use changes or degree of natural forest development). Consequently, ecological continuity (in terms of forest history or management history) is assumed to have long-lasting impacts on forest ecosystem processes.

insects and fungi with high demands on the quality and continuity of their habitats because of low dispersion rates (Fritz et al. 2008; Brunet et al. 2010). Many of these species, particularly fungal species, are of high importance for ecosystem processes and functions (Dighton 2003).

In contrast to the remaining patches of ancient forests, most of the forested areas in Central Europe are characterised by recent forests, which were planted during the last two centuries on former arable lands, grasslands or heathlands. The resulting disruption in forest continuity is reflected in the current diversity (species and genetic diversity) as well as in the ecological-biogeochemical and microbial conditions in recent forests (e.g. Fraterrigo et al. 2006; von Oheimb et al. 2008; Baeten et al. 2010). Even if suitable habitats are available in recent forests, low dispersion rates of typical forest species hamper a successful recolonisation (Flinn and Vellend 2005). There are also indications of a long-lasting effect of ecological continuity interruption in relation to different soil variables and related microbial communities, and thus on essential ecosystem processes (e.g. N and C cycles; Fraterrigo et al. 2005; von Oheimb et al. 2008; Fichtner et al. 2014; Blondeel et al. 2018; Box 2). Above all, context-dependent elevated levels of phosphorus (P) were found in formerly used soils, associated with lower C:P and C:N ratios in recent forest soils compared to ancient forest soils (Blondeel et al. 2018). Even 250 years after reforestation these land-use legacies were shown to be still present (Dupouey et al. 2002).

1.4 Objectives, research questions and methods

Legacy effects are known to alter the contemporary state of an ecosystem and system dynamics (Perring et al. 2016). However, it is largely unknown how legacy effects and environmental changes (e.g. climate change, atmospheric N deposition) interact. Therefore, revealing interactions of legacy effects and current global environmental change is crucial for predicting future ecosystem functioning under ongoing environmental changes. The overall objective of the presented thesis is to assess the importance of ecological continuity for ecosystem functions in beech forests in the midst of climate and environmental changes.

The following questions were addressed:

I) Are beech trees growing in ancient forests (i.e. sites associated with a long forest continuity) less sensitive to climate extremes (i.e. water deficits) than those growing on sites afforested on former farmland?

II) Are tree growth responses to negative climatic water balances modulated by legacy effects of forest management, and is the sensitivity to water deficits mediated by the length of abandonment of forest management?

III) Does forest history (in terms of former land-use legacies) alter the response of adult beech trees to interacting effects of water deficits and N deposition?

IV) Which mechanisms can explain potential differences in climate-growth and climate-nitrogen-growth relationships?

Two types of ecological continuity (i.e. continuity of forest cover and degree of natural forest development) were used to detect differences in continuity-mediated climate-growth and climate-nitrogen-growth relationships in beech forests in Northern Germany. In all studies presented in this thesis, tree-ring width (TRW) measurements were used to infer annual aboveground biomass productivity. The effects of forest continuity on climate-growth (paper I) and climate-nitrogen-growth (paper III) dynamics were assessed by using TRW chronologies of 243 adult beech trees growing in eight beech stands differing in ecological continuity (recent forests versus ancient forests). Additionally, annual records of mast intensity were used to take aboveground allocation patterns into account. Land-use legacy effects (Box 3) were characterised by analysing soil chemical properties. To explore possible mechanisms explaining differences in climate-(nitrogen)-growth relationships, analyses of the fine root system (i.e. root biomass and morphology; for a conceptual framework see Fig. 1.1) were conducted.

Box 3
Legacy effects: Within this thesis legacy effects of former land-use (land-use legacies) and management intensity (management legacies) were investigated. *Legacy effects* are defined as the long-lasting effects of anthropogenic disturbances on forest ecosystem processes.

The effects of management legacies on the climate-growth relationships (paper II) were identified by using 118 TRW chronologies from four more mature beech stands along a management intensity gradient (i.e. long-term unmanaged versus short-term unmanaged versus managed stands). In addition to the analyses of the soil chemical properties, measurements of the crown projection areas were used to identify possible mechanisms causing differences in the climate-growth response of trees growing on forest sites with different management histories.

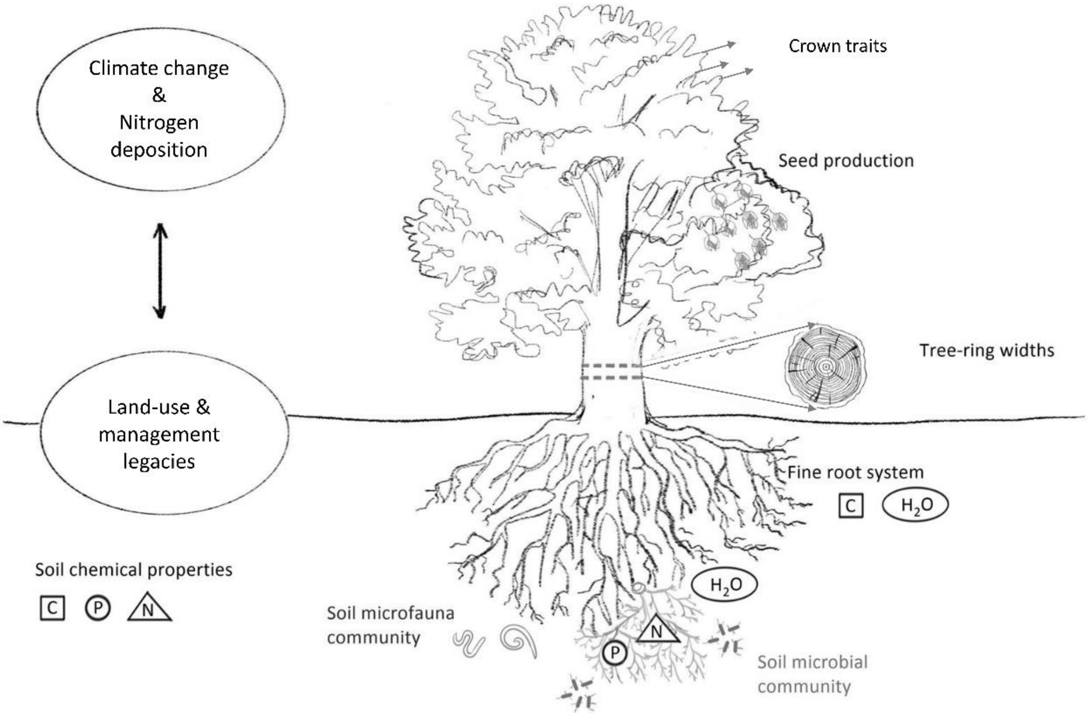

Figure 1.1 Conceptual framework illustrating how legacy effects of former land-use and forest management might modulate the response of trees to climate change and nitrogen deposition. Climate extremes influence a tree’s radial-growth pattern (tree-ring width), and climate and nitrogen are key drivers for the frequency of seed production (masting). Such growth responses, however, might be modulated by effects of former land-use: Land-use changes can impose long-lasting impacts on abiotic and biotic soil characteristics, such as changes in soil carbon and soil nutrient contents and changes in the soil microfauna and microbial communities. Altered edaphic conditions in turn can modulate the fine root system, which is crucial for a tree’s nutrient and water uptake (sensitivity to water deficits). Thus, land-use legacies can impact a tree’s susceptibility to adverse climatic conditions by influencing the root biomass or root morphology. Legacies of forest management can impose long-lasting impacts on crown traits of trees (such as crown size). Crown size is considered as a key parameter for tree growth by controlling photosynthetic carbon gain and transpiration water loss due to its relation to leaf area. Thus, management legacies can influence climate-growth relationships indirectly by altering the evaporative demand of a tree in managed forests. Illustration by Carolina Levicek.

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

Published article
Katharina Mausolf, Werner Härdtle, Kirstin Jansen, Benjamin M. Delory, Dietrich Hertel, Christoph Leuschner, Vicky M. Temperton, Goddert von Oheimb and Andreas Fichtner, *Oecologia*, 187, 825–837.

2.1 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.

Keywords: Climate change ● European beech ● Fine roots ● Forest continuity ● Plant-climate interactions

2.2 Introduction

Forest ecosystems significantly contribute to global carbon sequestration (Bellassen and Luyssaert 2014), and tree species' above- and belowground 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 belowground to climate variation via modifications of their fine root system (Bardgett et al. 2014; Fig. A1). 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 belowground community composition (Foster et al. 2003; Flinn and Vellend 2005; Fraterrigo 2013; Fig. A1). 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 fertilisation 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. A1). 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 to 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 belowground responses (i.e. fine root biomass and root morphological traits) allowing us to explore processes underlying climate-growth relationships.

2.3 Material and Methods

2.3.1 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 A1). Within each forest, we randomly selected 2-5 study plots (40 m × 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 A1).

2.3.2 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 4.69 k, 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 standardised. Standardisation 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 5-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 A2). Plot chronologies are shown in Fig. A2.

2.3.3 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).

2.3.4 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 into 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.

2.3.5 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 2017a, 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 1993-2013 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.

2.3.6 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 versus 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 standardised (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 A1). 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, 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 past 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 standardised (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 A3), 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), standardised 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).

2.4 Results

2.4.1 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 A1).

2.4.2 Legacy effects of land-use on trees' aboveground response

On average, standardised 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 past two decades (1994-2013; Table A2). The importance of land-use legacies as a driver of climate-growth relationships during the past 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 A4). 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. 2.1a). 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).

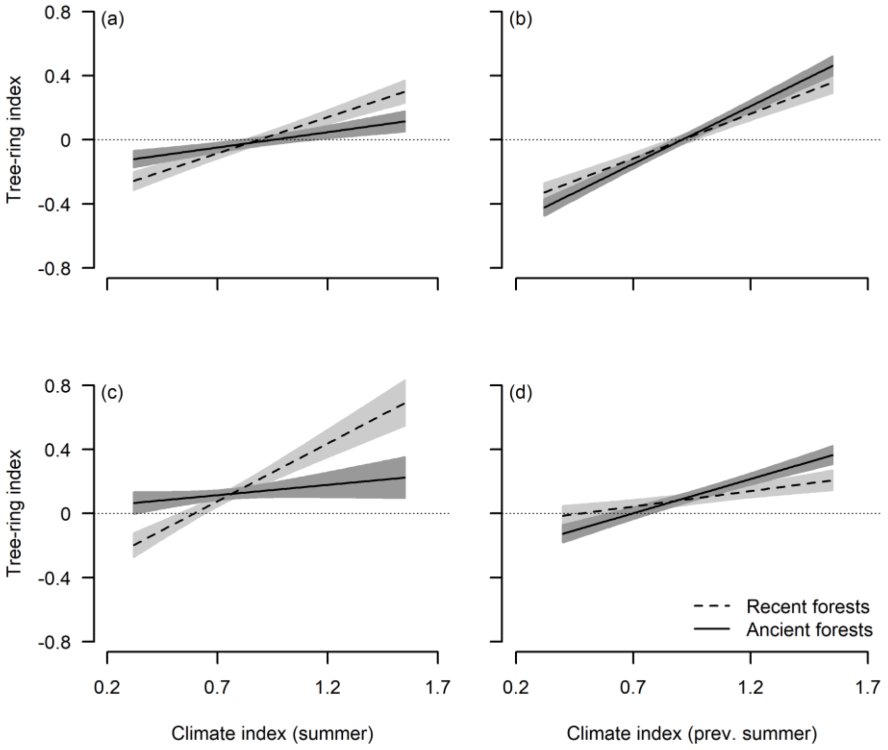

Figure 2.1 Effect of former land-use type (ancient versus recent forests) on the growth (tree-ring width index, TRI) responsiveness of European beech (*Fagus sylvatica* L.) to interannual fluctuations in climate during the last two decades (1994-2013) considering (**a, b**) all years ($n = 20$) and (**c, 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.

In contrast, growth rates of trees from recent forest sites declined under adverse climatic summer conditions (Fig. 2.1 a, c). 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. 2.1). 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 standardised regression coefficients; Table A4).

2.4.3 Legacy effects of land-use on trees' belowground 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. 2.2).

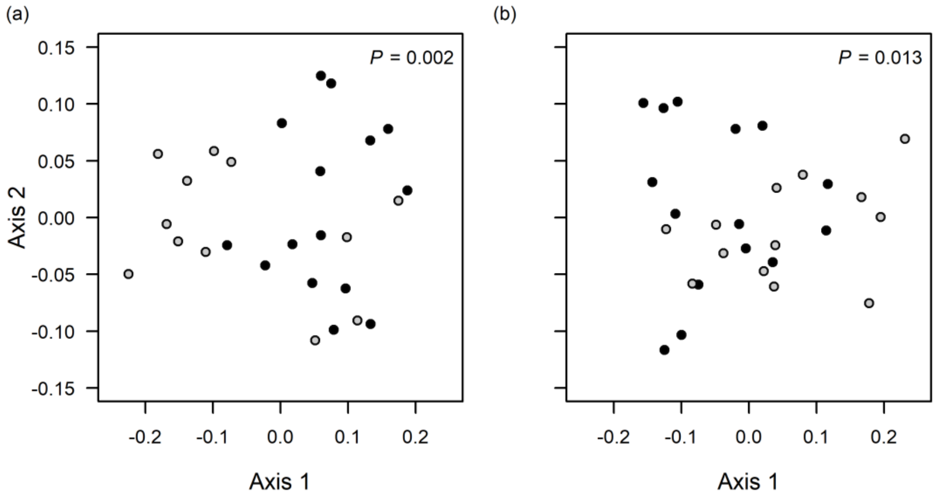

Figure 2.2 Non-metric multidimensional scaling (NMDS) ordination of fine root traits of *Fagus sylvatica* in **a**) 0-10 cm and **b**) 10-30 cm soil depth. The NMDS ordination was based on Bray-Curtis dissimilarities and used two dimensions (stress: 0.04 for 0-10 cm and 0.05 for 10-30 cm). The linear 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.

Former land-use types were clearly separated along the first NMDS axis, while the land-use effect was less evident along axis 2 (Table A5). 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% (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 2.1).

Table 2.1 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, *RAI* root area index

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 characterised 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 A1). 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 A6). Note that NMDS axis 1 score configuration differed between the two soil depths (Fig. 2.2).

2.4.4 Linking above- and belowground 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. A3).

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. 2.3 a). 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, 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. A4), 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 (χ^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. 2.3 b). 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. A5 a). Note that using total P concentration, which had the strongest effect on drought resistance, resulted in an unstable model (Fig. A5 b). 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.

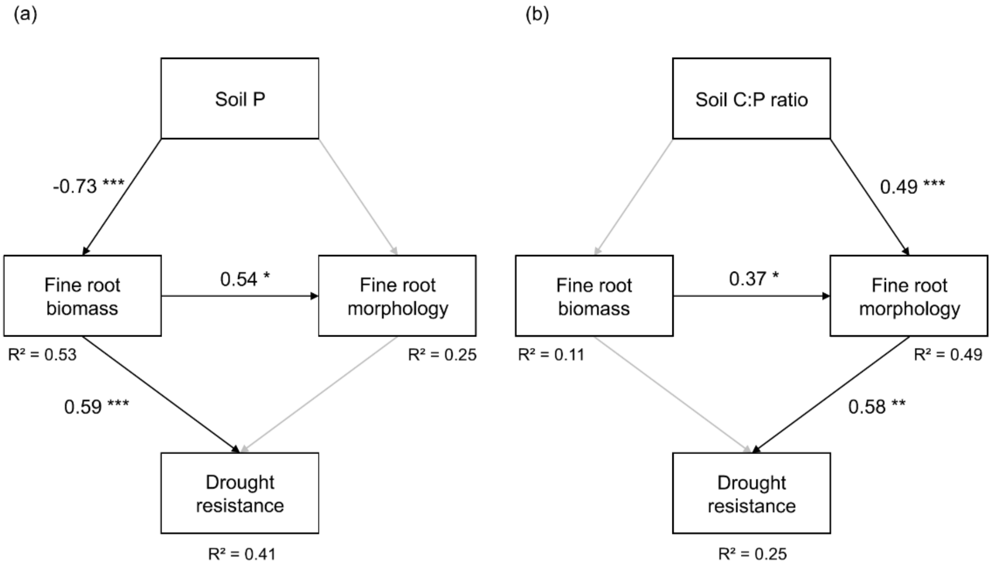

Figure 2.3 Structural equation models linking drought resistance, soil nutrient availability and fine root traits (biomass and morphology) in **a**) 0-10 cm and **b**) 10-30 cm soil depth. Fine root tissue density was selected as an indicator for morphology. Black lines denote significant and grey lines non-significant pathways. Numbers at arrows are standardised 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.

2.5 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 fertilisation (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 belowground 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 remobilization 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 A1), 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 A1). 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 A1 and A3), 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 and Chen 2010). Clearly, deep roots may be more decisive for maintaining tree water uptake in periods of drought (Meier et al. 2017), 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 aboveground (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 were 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 twenty-first 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.

A Supplementary Material

Supplementary Methods

Assessing climate sensitivity To assess the effect of climate extremes on individual tree productivity, we used drought resistance as a measure of climate sensitivity. For each target tree, we quantified drought resistance as the ratio between the individual growth rate during drought and before a drought event (Lloret et al. 2011). We used non-mast years with the lowest (i.e. strongest summer drought) and highest (i.e. lowest summer drought) climate indices for current summer conditions (DMI-summer) as drought (2003, which coincides with the pan-European drought years; see Zang et al. 2014) and pre-drought (2001) years. Drought resistance was calculated based on standardised annual basal area increment (SBAI, cm^2 cm^{-2} $year^{-1}$) to account for differences in tree age between the former land-use types. SBAI was obtained by dividing annual basal area increment at time t by the basal area of each target tree at time t_{-1}. To examine the effect of former land-use on drought resistance, we used a mixed-effects model with plot as random factor and a variance function allowing for different variances per former land-use type (Zuur et al. 2009).

Table A1 Summary statistics of structural and edaphic properties of the 28 study stands. Values are means and their standard deviation (in brackets). Significant ($P < 0.05$) differences between former land-use types are highlighted in bold. Note that the effects of former land-use on total P (0-10 cm) and C:P ratio (10-30 cm) were marginally significant ($P \leq 0.1$).

	Recent forests	Ancient forests
Forest continuity (years)	100-140	> 230
Elevation (m)	53.31 (18.54)	57.53 (11.51)
Stand density (stems ha^{-1})	198.08 (51.37)	177.94 (72.05)
Stand basal area (m^2 ha^{-1})	34.41 (7.44)	34.48 (6.75)
$Age_{target\ trees}$ (years)	**101.30 (23.98)**	**126.90 (17.14)**
Mean diameter at breast height (cm)	41.79 (6.73)	43.61 (14.82)
Species composition (%)		
beech	91.70 (11.07)	95.84 (5.25)
other deciduous species	3.57 (6.20)	4.16 (5.25)
other coniferous species	4.74 (9.64)	0
Soil type	(pseudogleyic) Luvisol	(pseudogleyic) Luvisol
pH (H_2O)		
0-10 cm	4.36 (0.59)	4.22 (0.76)
10-30 cm	4.57 (0.63)	4.47 (0.44)
pH ($CaCl_2$)		
0-10 cm	3.50 (0.63)	3.40 (0.76)
10-30 cm	3.91 (0.76)	3.75 (0.35)
Total C (%)		
0-10 cm	4.55 (1.72)	5.25 (1.24)
10-30 cm	1.33 (0.49)	1.49 (0.41)
Total N (%)		
0-10 cm	0.27 (0.08)	0.31 (0.06)
10-30 cm	0.09 (0.03)	0.08 (0.02)
Total P (mg g^{-1})		
0-10 cm	0.36 (0.16)	0.28 (0.09)
10-30 cm	**0.26 (0.14)**	**0.17 (0.06)**
C:N ratio		
0-10 cm	16.31 (1.56)	17.06 (1.74)
10-30 cm	**14.55 (2.97)**	**17.64 (3.41)**
C:P ratio		
0-10 cm	**140.50 (49.50)**	**201.30 (64.68)**
10-30 cm	69.43 (43.53)	102.11 (58.84)
N_{pa} (mg g^{-1})		
0-10 cm	0.05 (0.02)	0.04 (0.02)
10-30 cm	n.a.	n.a.
CEC (mmol kg^{-1})		
0-10 cm	11.59 (2.80)	11.05 (1.82)
10-30 cm	8.35 (3.83)	7.61 (2.18)
BS (%)		
0-10 cm	34.35 (19.61)	25.70 (6.40)
10-30 cm	41.35 (7.57)	43.24 (14.18)
n(plots)	13	15

C carbon, *N* nitrogen, *P* phosphorus, N_{pa} amount of plant available nitrogen (total NH_4^+ and NO_3^- concentration), *CEC* cation exchange capacity, *BS* base saturation, *n.a.* not available.

Table A2 Tree-ring series characteristics of target trees (*Fagus sylvatica*) for their entire lifespan and during the last two decades (1994-2013). Significant (P < 0.05) differences between former land-use types are highlighted in bold; *P*-values were obtained from mixed-effects models using study plot as random effect.

	Recent forests		Ancient forests	
	Mean (SE)	CV (%)	Mean (SE)	CV (%)
Entire lifespan				
Mean TRW (mm)	**2.79 (0.06)**	22.2	**2.33 (0.03)**	14.6
Maximum TRW (mm)	**5.52 (0.10)**	19.5	**4.87 (0.07)**	16.2
Minimum TRW (mm)	**0.82 (0.04)**	54.1	**0.54 (0.02)**	39.6
SD (TRW)	**1.00 (0.02)**	21.2	**0.89 (0.02)**	19.7
AC (TRW)	0.70 (0.01)	16.0	0.67 (0.01)	18.0
1994 to 2013				
Mean TRW (mm)	**2.52 (0.06)**	35.5	**2.09 (0.08)**	32.2
Maximum TRW (mm)	**4.16 (0.12)**	30.0	**3.61 (0.08)**	25.9
Minimum TRW (mm)	**1.14 (0.07)**	62.9	**0.75 (0.03)**	53.6
SD (TRW)	0.82 (0.02)	29.3	0.80 (0.02)	25.7
AC (TRW)	0.28 (0.02)	85.9	0.21 (0.02)	108.4
n(trees)	109		134	

BAI annual basal area increment, *SBAI* standardised annual basal area increment, *TRW* tree-ring width, *SE* standard error, *CV* coefficient of variation, *SD* standard deviation *AC* first-order autocorrelation, expressing the interannual TRW persistence.

Table A3 Pairwise relationships (Pearson correlation coefficients based on log-transformed traits) between three key morphological fine root traits in 0-10 cm and 10-30 cm soil depth. *SRA* specific root area, *SRL* specific root length, *RTD* root tissue density.

0-10 cm	SRA	SRL	RTD
SRA	1.00	0.94	-0.96
SRL		1.00	-0.82
RTD			1.00
10-30 cm	SRA	SRL	RTD
SRA	1.00	0.97	-0.87
SRL		1.00	-0.78
RTD			1.00

Table A4 Standardised regression coefficients from the best-fitting mixed-effects models for tree-ring width index (TRI) of European beech (*Fagus sylvatica*). The magnitude of the estimates is proportional to the effect size in the model. Note that the effect of tree age was not significant (all years: $P = 0.897$; non-mast years: $P = 0.546$).

	All years (1994-2013)		Non-mast years (1994-2013)	
	Estimate (SE)	*P*-value	Estimate (SE)	*P*-value
Intercept	-0.018 (0.013)	0.176	0.118 (0.015)	< 0.001
DMI-MAM	0.195 (0.010)	< 0.001	0.286 (0.012)	< 0.001
DMI-JJA	0.058 (0.013)	< 0.001	0.026 (0.015)	0.095
DMI-JJA$_p$	0.220 (0.012)	< 0.001	0.157 (0.015)	< 0.001
Former land-use type (RF)	0.004 (0.020)	0.849	-0.022 (0.023)	0.341
DMI-JJA × former land-use type (RF)	0.079 (0.019)	< 0.001	0.119 (0.023)	< 0.001
DMI-JJA$_p$ × former land-use type (RF)	-0.049 (0.019)	0.009	-0.086 (0.022)	< 0.001

Table A5 Results from analysis of variance (ANOVA) testing the effect of former land-use (ancient versus recent forests) on fine root trait composition (NMDS axes scores) in 0-10 cm and 10-30 cm soil depth.

	F-value	*P*-value
Axis 1		
0-10 cm	11.95	0.002
10-30 cm	6.83	0.015
Axis 2		
0-10 cm	0.49	0.491
10-30 cm	1.03	0.321

Table A6 Correlation between NMDS axes scores of fine root traits and chemical soil properties for 28 mature beech (*Fagus sylvatica*) stands in 0-10 cm and 10-30 cm soil depth. Values indicate Pearson coefficients and significant (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$) correlations are highlighted in bold.

	0-10 cm				10-30 cm			
	Axis 1		Axis 2		Axis 1		Axis 2	
pH (H_2O)	-0.21		-0.18		0.02		-0.25	
pH ($CaCl_2$)	-0.13		-0.17		0.02		-0.20	
Total C (%)	-0.08		0.00		**-0.43**	*	0.07	
Total N (%)	-0.08		-0.02		-0.21		-0.35	
Total P (mg g^{-1})	**-0.66**	***	0.22		-0.22	**	**-0.38**	*
C:N ratio	0.05		0.03		**-0.60**	*	**0.44**	**
C:P ratio	**0.56**	**	-0.10		**-0.43**		0.37	
N_{pa} (mg g^{-1})	-0.30		0.29		n.a.		n.a.	
CEC (mmol kg^{-1})	0.08		-0.20		-0.31		-0.01	
BS (%)	-0.25		-0.14		0.15		-0.26	

For abbreviations see Table A1.

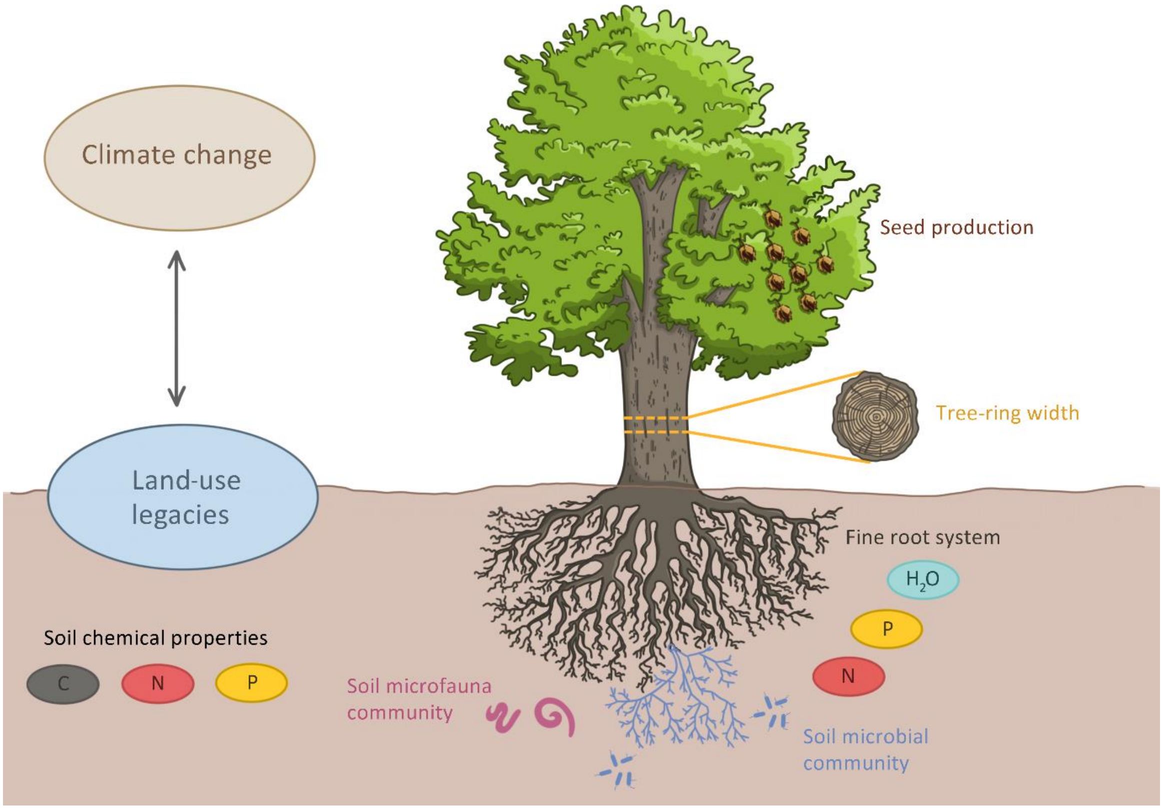

Figure A1 Conceptual framework illustrating how land-use legacies might modulate the response of trees to climate change. Climate extremes influence a trees' radial-growth pattern (tree-ring width) and frequency of seed production (masting). Such growth responses, however, might be modulated by effects of former land-use: Land-use changes can impose long-lasting impacts on abiotic and biotic soil characteristics, such as soil carbon and nutrient changes and changes in soil microfauna and microbial communities. These altered edaphic conditions in turn can modulate the fine root system, which is crucial for a trees' nutrient and water uptake (drought resistance). Thus, land-use legacies can impact a trees' susceptibility to adverse climatic conditions indirectly through influencing the composition of root traits. Illustration by Carolina Levicek.

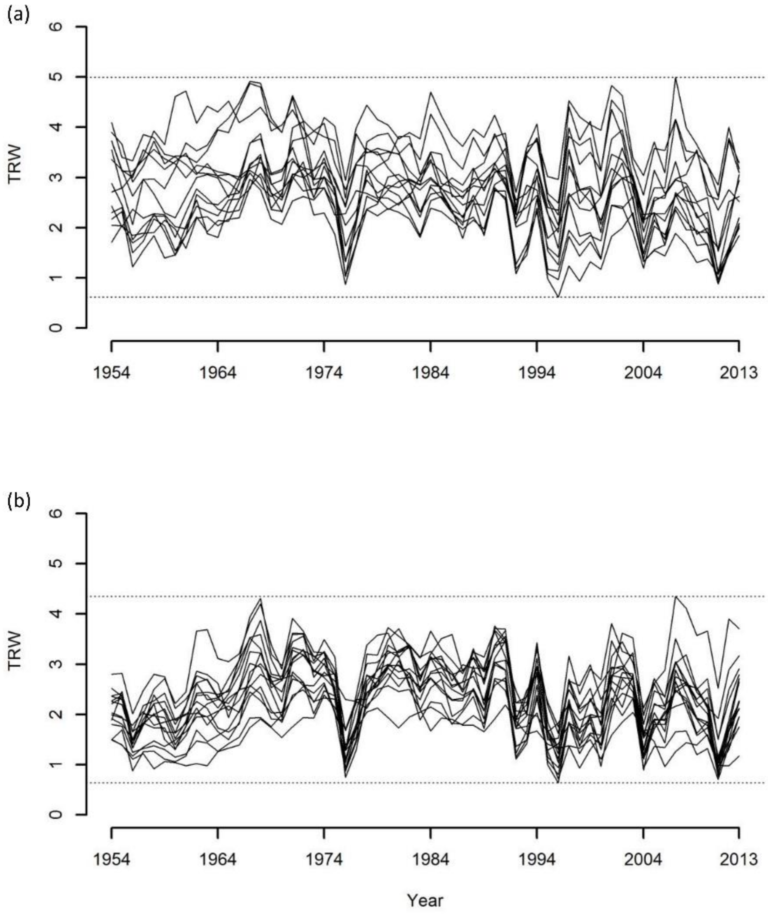

Figure A2 Temporal variation in tree-ring width (TRW) of European beech growing in (a) recent and (b) ancient forests. Data represent plot chronologies for the common interval (1954-2013) based on 243 target trees (recent forests: *n*(plots) = 13, *n*(trees) = 109; ancient forests: *n*(plots) = 15, *n*(trees) = 134). Dotted lines correspond to minimum and maximum values of TRW.

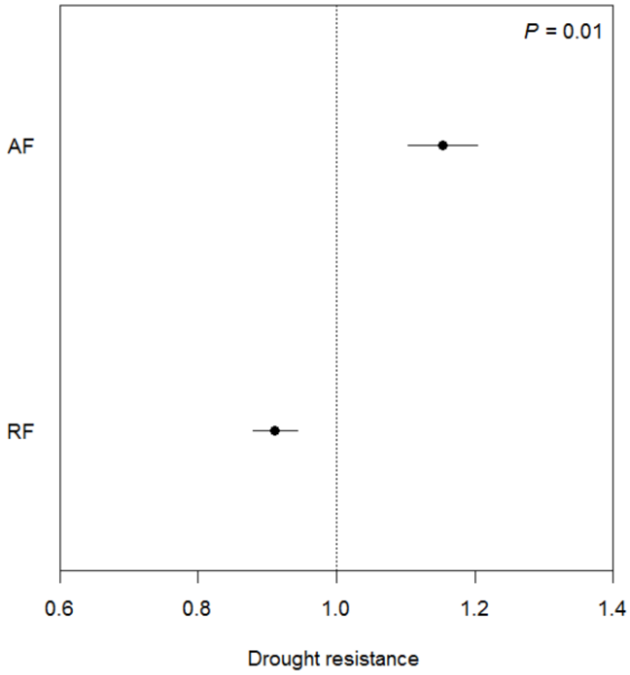

Figure A3 Differences in mean (± SE) drought resistance of European beech growing in stands with different forest continuity (*AF* ancient forests, *RF* recent forests). The dotted line indicate equivalent growth rates in drought and pre-drought years; *n*(target trees): 243.

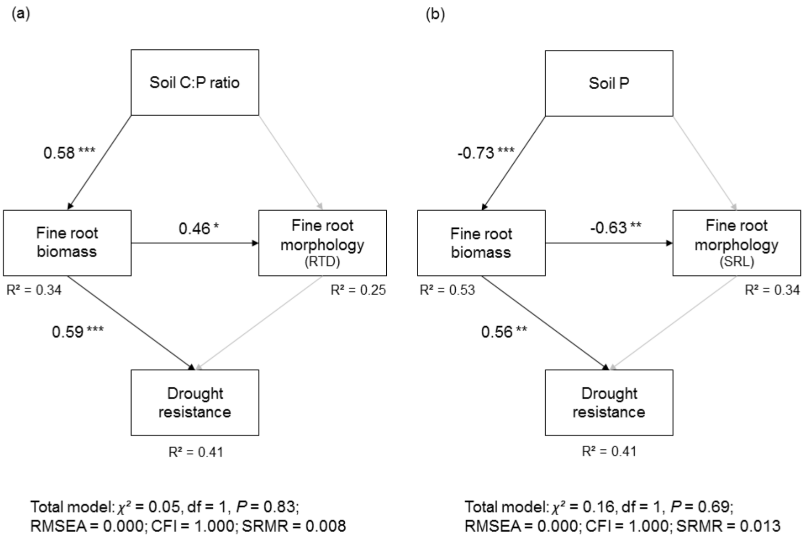

Figure A4 Structural equation models assessing the effects of soil nutrient availability and fine root traits (biomass and morphology) on drought resistance in 0-10 cm soil depth. Black lines denote significant and grey lines non-significant causal pathways. Numbers at arrows are standardised regression coefficients. 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. (**a**) C:P ratio as an indicator for soil nutrient availability, (**b**) specific root length (SRL) as an indicator for fine root morphology. *RTD* root tissue density, *C* total carbon concentration, *P* total phosphorus concentration.

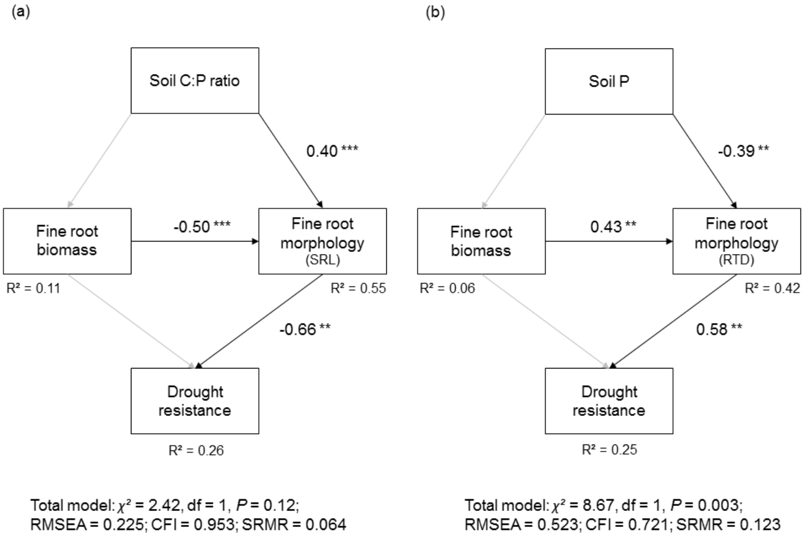

Figure A5 Structural equation models assessing the effects of soil nutrient availability and fine root traits (biomass and morphology) on drought resistance in 10–30 cm soil depth. Black lines denote significant and grey lines non-significant causal pathways. Numbers at arrows are standardised regression coefficients. 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. (**a**) specific root length (SRL) as an indicator for fine root morphology (b) P as an indicator for soil nutrient availability. Note that the model in (**b**) provided a poor fit to the data. *RTD* root tissue density, *C* total carbon concentration, *P* total phosphorus concentration.

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

Published article

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3.1 Highlights

- Climate sensitivity of beech is strongly related to forest management history.
- Drought-induced growth decline is critically higher in managed stands.
- Management legacies have long-lasting impacts on climate-growth relationships.
- Trade-off between maximum individual tree growth and drought resistance.
- Management legacies and climate change drivers are interacting.

3.2 Graphical Abstract

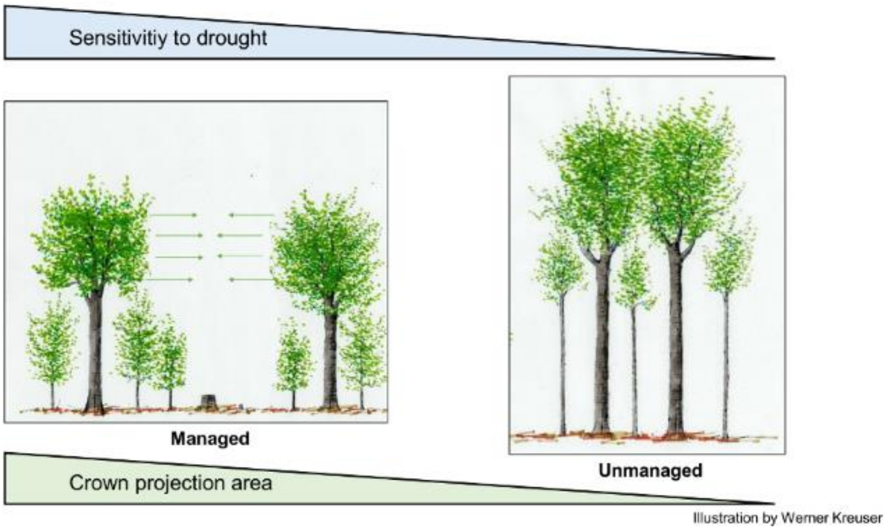

Illustration by Werner Kreuser

3.3 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 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 maximising 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

3.4 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 and 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 and Jump 2016; 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 versus forest) and forest continuity (Mausolf et al. 2018a). 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?

3.5 Material and Methods

3.5.1 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. B1). Elevation ranges from 0 to 90 m a.s.l. 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 2017b). 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. B1). 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 3.1) 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. 2018a), we chose study sites that had a forest continuity for at least 200 years according to Glaser and 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 type (Table 3.1). Tree age of the canopy trees ranged between 105 and 120 years (Table 3.2).

To characterise stand structure, we selected a representative 40 × 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. B2). 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 summarised in Table 3.1. Soil chemical properties did not significantly vary between managed and unmanaged stands (PERMANOVA: $F = 1.28$, $P = 0.292$; Fig. B3). 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 3.1).

3.5.2 Tree data

Within each study stand, we randomly selected 30 beech trees from the upper canopy with similar DBH (57-62 cm; Table 3.2) 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 (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 > 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.

3.5.3 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. 2018a 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. 2018a). Cross-dating was done following Mausolf et al. (2018a). Due to incomplete and broken wood cores, we omitted two trees from subsequent analyses.

Table 3.1 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 (Tukey-HSD: $P_{adj.} < 0.05$) 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^B	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

Table 3.2 Differences in target tree characteristics and tree-ring statistics of European beech growing in stands with different management history. Values are means and their standard error (in brackets). Different superscript letters indicate significant (Tukey-HSD: $P_{adj.} < 0.05$) differences between study sites. *DBH* diameter at breast height; *BAI* basal area increment; *TRW* tree-ring width; *AC* (TRW) 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

To minimise the effect of tree age on annual growth rates, TRW data of individual tree chronologies were standardised. Standardisation 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 3.2). 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).

3.5.4 Climate data

To quantify changes in climatic conditions, we used the standardised precipitation-evapotranspiration index (SPEI), which is a climatic water balance index that considers precipitation and potential evapotranspiration (Vincente-Serrano et al. 2010) and allows to study the effects of climate change for varying time scales (Bhuyan et al. 2017). Following Bhuyan 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 2017a). 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.

3.5.5 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 versus 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 standardised (mean= 0; SD = 1) before analysis.

We used Hedges' d effect size as a standardised measure to quantify the mean difference of the effects of forest management legacies on TRI during climate extremes (Hedges and 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 B1). 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 and Ripley 2002), nmle (Pinheiro et al. 2016) and vegan (Oksanen et al. 2016).

3.6 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 ($P_{adj.} < 0.05$; Fig. B3). 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 3.3). 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 3.3). 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 B2).

Growth stimulation (i.e. positive TRI-values) was higher in managed stands during years with ample water supply (i.e. positive SPEI-values; Fig. 3.1), but the benefit of trees growing in managed stands during climate extremes (extremely wet) was not significant (Hedges' d: 0.29; Fig. 3.2 a). 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 being stronger for drought events in spring (Fig. 3.1 a) than in previous summer (Fig. 3.1 b). 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. 3.2 b).

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 versus managed stands; $P < 0.05$) to 1.42 (long-term unmanaged versus managed stands; $P < 0.05$). Moreover, growth reduction during extreme drought in spring was positively related to crown projection area ($P < 0.01$; Fig. 3.3), 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 3.2), and growth decline was greater in the former.

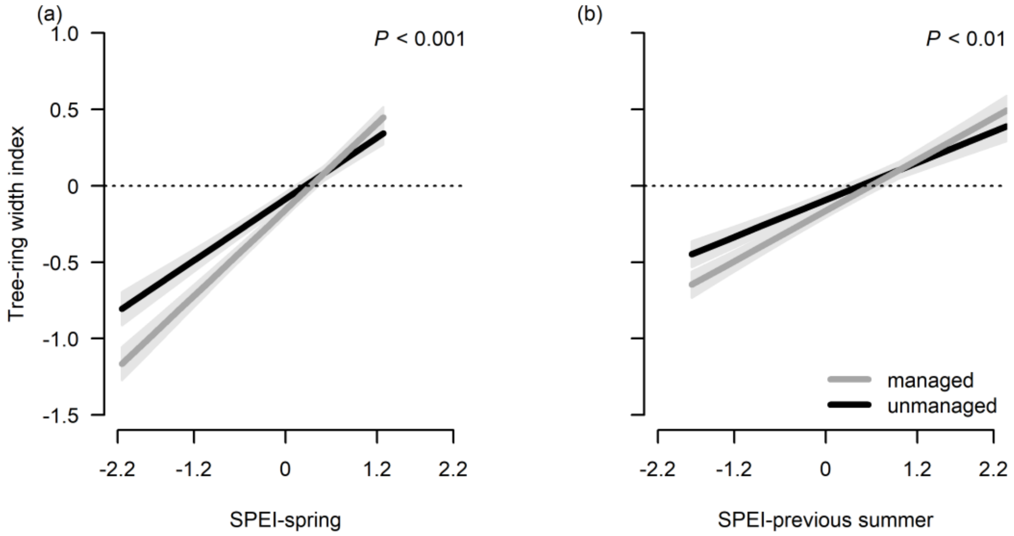

Figure 3.1 Effects of forest management history (managed versus unmanaged forests) on the growth (tree-ring width index, TRI) responsiveness of European beech (*Fagus sylvatica* L.) to interannual fluctuations in climate during the last two decades (1995-2014) considering (**a**) the response to the 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 standardised 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.

Table 3.3 Regression coefficients from the best-fitting mixed-effects model for tree-ring width index (TRI) of European beech (*Fagus sylvatica*). Predictor estimates were standardised, 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* standardised 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-prev. 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

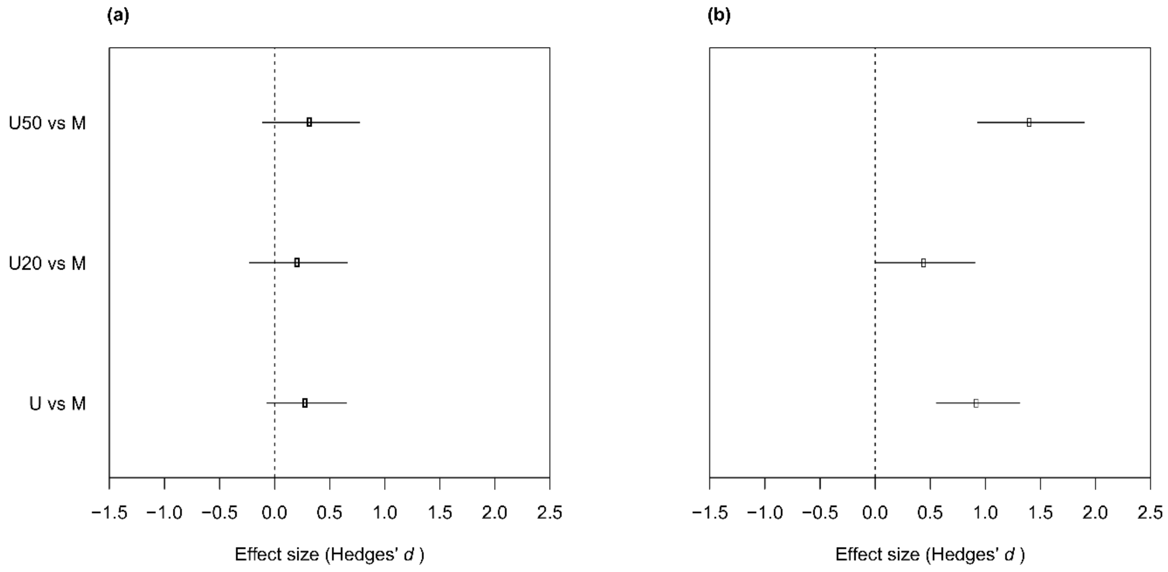

Figure 3.2 Effects of forest management history on (**a**) growth stimulation (i.e. positive tree-ring width indices) and (**b**) growth reduction (i.e. negative tree-ring width indices) of European beech (*Fagus sylvatica*) during climate extremes in spring (extremely dry or extremely wet events). Error 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.

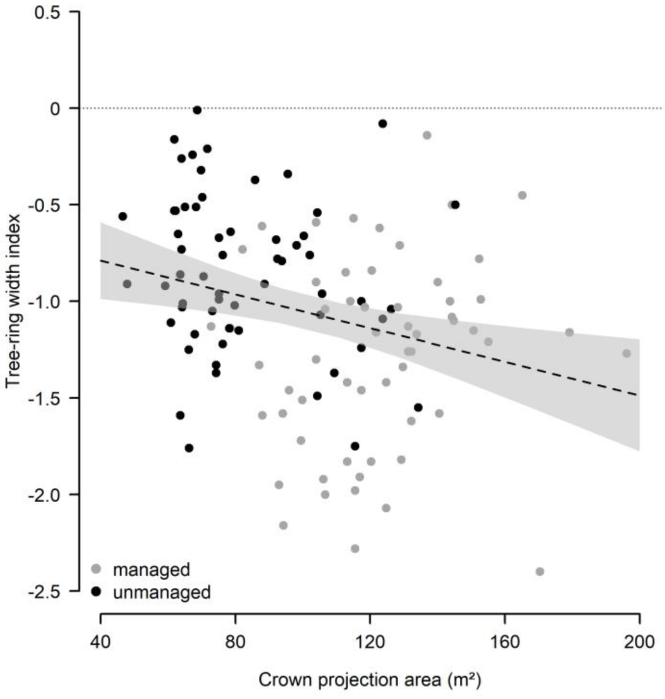

Figure 3.3 Relationship between tree-ring width index (TRI) and crown projection area (CPA) of European beech (*Fagus sylvatica*). Negative values of TRI indicate growth decline. The black line is a linear model fit ($P = 0.003$) and the shaded area indicates the 95% confidence interval. Points represent 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.

3.7 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 (Bréda et al. 1995; Sohn et al. 2016; Diaconu et al. 2016).

Beech has been identified as being relatively sensitive to summer drought and elevated summer temperatures (Geßler et al. 2007; Köcher et al. 2009; Packham et al. 2012), which may relate to its large shade crown and comparably high water consumption (Leuschner and 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. (2018a), 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 et al. 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 remobilisation 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 remobilised 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 > 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 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 and North 2009; Latif and 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.

3.8 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.

B Supplementary Material

Table B1 Values of the standardised precipitation-evapotranspiration index (SPEI) for spring, summer and previous summer during the last two decades. Data were obtained 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).

Year	SPEI-spring	SPEI-summer	SPEI-previous summer
1995	1.06403	-0.74063	1.01748
1996	-0.85495	-1.33328	-0.74063
1997	0.72708	0.17416	-1.33328
1998	0.69759	1.42614	0.17416
1999	-0.04300	-1.0332	1.42614
2000	-0.04581	-0.26454	-1.0332
2001	0.52093	0.8591	-0.26454
2002	0.55689	1.78939	0.8591
2003	-0.21258	-1.21287	1.78939
2004	-0.79137	0.3514	-1.21287
2005	-0.60397	0.28019	0.3514
2006	1.23882	-0.12167	0.28019
2007	0.47427	2.37145	-0.12167
2008	-0.27505	-0.03676	2.37145
2009	-0.22393	-0.53642	-0.03676
2010	0.99051	-0.08112	-0.53642
2011	-2.14309	1.99009	-0.08112
2012	-1.91999	-0.21823	1.99009
2013	1.27977	-1.75472	-0.21823
2014	1.01074	-0.81054	-1.75472

Table B2 Univariate relationships (Pearson correlation coefficients) between tree-ring width index (TRI) of single tree chronologies (timespan: 1995-2014) and climatic variables (current and previous year sum of precipitation and mean temperature for spring and summer) for trees growing in unmanaged and managed stands. Spring data include March, April and May, while summer data include June, July and August. To account for possible trends within the climatic variables, we used the same detrending procedure for climatic variables and tree-ring data (5-years-moving average provided by TSAP-Win; see Härdtle et al. 2013 for a related approach). Asterisks denote significant relationships (*** *P* < 0.001).

		Unmanaged	Managed
Precipitation			
Previous year	Summer	0.23 ***	0.23 ***
Current year	Spring	0.19 ***	0.26 ***
	Summer	0.19 ***	0.19 ***
Temperature			
Previous year	Summer	-0.20 ***	-0.25 ***
Current year	Spring	0.14 ***	0.13 ***
	Summer	0.28 ***	0.28 ***

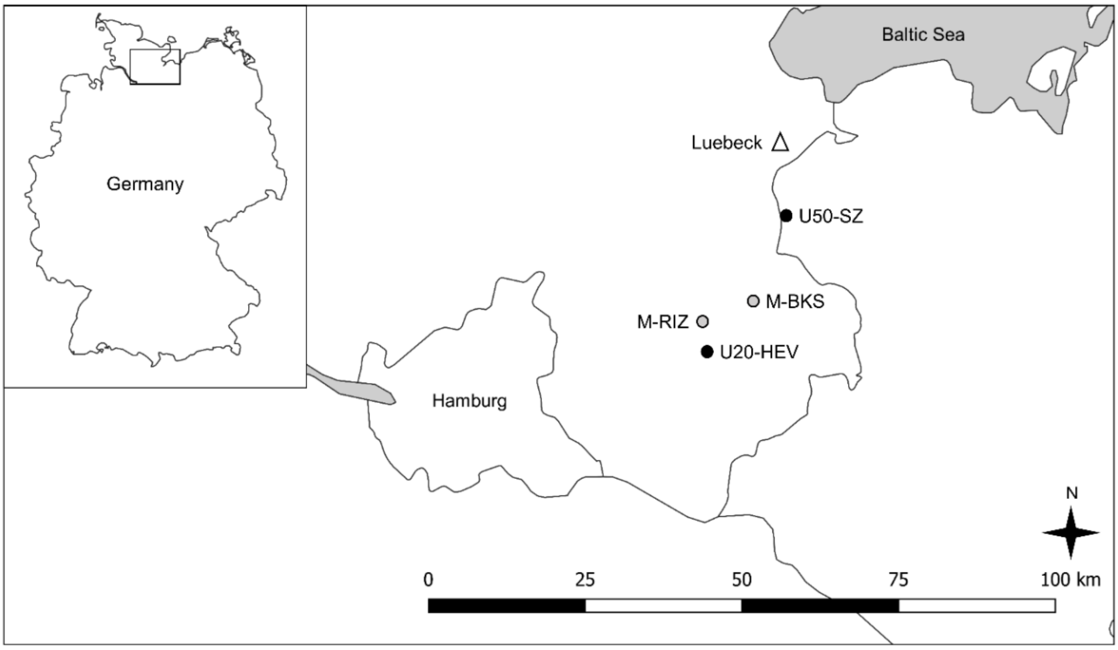

Figure B1 Location of the investigated forest sites in Northwest Germany. Grey circles indicate the managed stands (*M-BKS* ‘Berkenstrücken’, *M-RIZ* ‘Ritzerau’), black circles indicate the unmanaged stands (*U50-SZ* long-term unmanaged ‘Schattiner Zuschlag’, *U20-HEV* short-term unmanaged ‘Hevenbruch’).

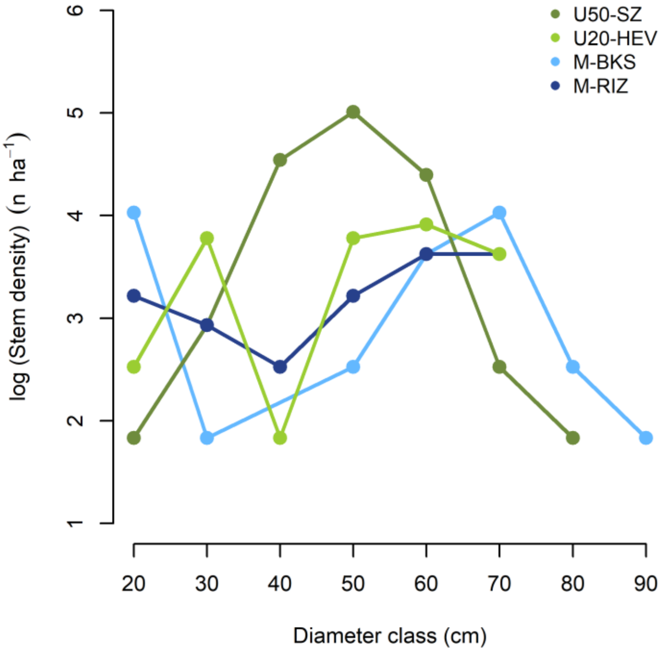

Figure B2 Stand structure of the beech stands investigated. The x-axis represents the upper boundaries of the tree size (DBH)-class. *M-RIZ* (‘Ritze-rau’), *M-BKS* (‘Berkenstrücken’): managed, *U50-SZ* (‘Schattiner Zu-schlag’): unmanaged > 50 years, *U20-HEV* (‘Hevenbruch’): unmanaged > 20 years.

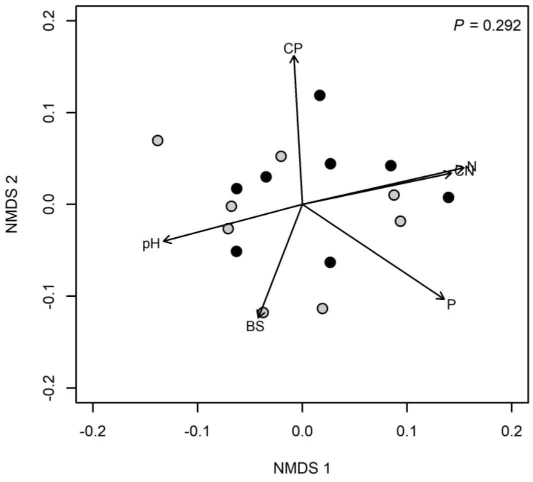

Figure B3 Non-metric multidimensional scaling (NMDS) ordination of soil chemical properties of study stands (four soil samples per stand). The NMDS ordination was based on Bray-Curtis dissimilarities and used two dimensions (stress: 0.10). The linear fit between ordination distances and root data ($R^2 = 0.94$) indicated an appropriate representation of the variation in fine root trait composition between study stands (black dots: unmanaged beech stands, grey dots: managed beech stands); the *P*-value indicates that differences in soil chemical properties between study stands were not significant. Arrows indicate significant ($P < 0.05$) joint axis correlations with soil properties (*C* total carbon content, *N* total nitrogen content, *P* resin-extractable phosphorus content; *CN* C:N-ratio, *CP* C:P-ratio, *BS* base saturation, *pH* pH-value measured in H_2O). Note that the arrow for C content was not displayed due to the close correlation ($r = 0.94$) between C and N.

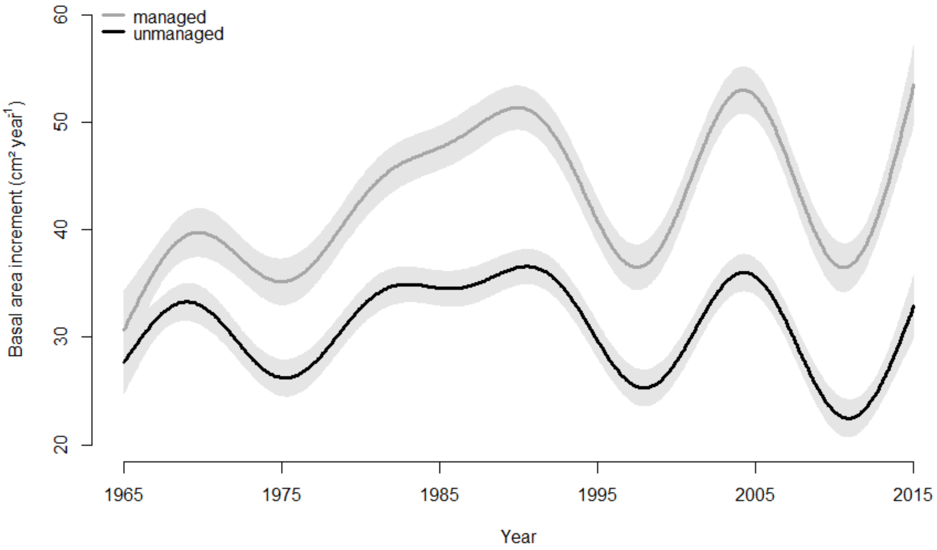

Figure B4 Temporal variation in basal area increment of European beech growing in managed and unmanaged forests. Lines correspond to the mean response for the last 50 years (1965-2015) based on 118 target trees (managed forests: $n = 59$; unmanaged forests: $n = 59$) as predicted by generalised additive models (GAMs). Shaded areas correspond to the 95% confidence interval. The non-linear time effect (both $P < 0.001$) was modelled using a cubic regression spline, and the optimal amount of smoothing was determined by cross-validation method.

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

Published article
Katharina Mausolf, Werner Härdtle, Dietrich Hertel, Christoph Leuschner and Andreas Fichtner, *Ecosystems*, https://doi.org/10.1007/s10021-019-00419-0

4.1 Manuscript Highlights

- Forest history modulates tree growth responses to co-occurring environmental changes
- N deposition affects resource allocation towards mass fructification of beech
- Legacy-mediated nutrient cycles affect growth response to water deficits and N deposition

4.2 Abstract

Revealing the interactive effects of multiple global 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 seems 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

4.3 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 et al. 2010; Greaver et al. 2016) and impose threats to forest biodiversity (Sala et al. 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 characterized by a long history of land-use changes, which in turn might affect their response to present changes in environmental conditions (Perring et al. 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 et al. 2015). The climate-growth response of beech was observed to vary with factors such as precipitation (Müller-Haubold et al. 2013), elevation (Di Filippo et al. 2007; Dulamsuren et al. 2017), forest management history (Mausolf et al. 2018b), and tree species composition of the stand (Metz et al. 2016).

There is evidence that N deposition (as a single driver of environmental change) has several effects on forest ecosystem functioning. According to Michel et al. (2018), atmospheric deposition of reactive N compounds in forest ecosystems enhances the risk of soil acidification, or has 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 et al. 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 et al. 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 et al. 2018).

For beech, experimental (Dziedek et al. 2016, 2017) and observational (Hess et al. 2018) studies demonstrated that the combined effects of multiple global 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 optimisation 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 fertilised plants can be attributed to both: changes in the fine root system (Dziedek et al. 2017; Hess et al. 2018) and higher evaporative demands aboveground (Meyer-Grünefeldt et al. 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 (for example, years with a high fruit production) in European beech stands has been identified as a cause of periodic growth declines (Hacket-Pain et al. 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 et al. 2015). Evidence exists that high temperatures or high solar radiation in the previous summer functions as triggers of high seed production (Müller-Haubold et al. 2015), suggesting a second pathway, through which future climate extremes could influence the radial growth of beech (Hacket-Pain et al. 2018). However, the impact of N deposition on seed production is still debated (Müller-Haubold et al. 2015; Braun et al. 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 global 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 et al. 2017; Maes et al. 2019). For example, former land-use such as past agricultural activity has been found to cause long-lasting shifts in soil chemical properties (Fraterrigo et al. 2005; von Oheimb et al. 2008; Kopecký and Vojta 2009; Blondeel et al. 2018) and soil microbiomes (Fichtner et al. 2014; De la Peña et al. 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 et al. 2014), mediated by changes in fine root biomass and morphology (Mausolf et al. 2018a).

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 hypothesised that (1) 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 (2) mast intensity plays a crucial role in mediating the growth response of beech to water deficits and N deposition.

4.4 Material and methods

4.4.1 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 characterised by a sub-oceanic climate with a mean annual precipitation of 777 mm and a mean annual temperature of 8.5°C (DWD 2017b). 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), characterised 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 (that is, mature, even-aged stands) on sites with similar topography (level terrain) and edaphic conditions (that is (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) above 7 cm were measured in 2014. For each measured tree, DBH and species identity were recorded.

4.4.2 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 et al. (2018a) 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 4.69 k, Rinntech, Heidelberg, Germany) to evaluate matches between the two cores of a tree. A CDI greater than 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 standardised for size- and age-related differences between trees. We used the moving-average standardisation procedure provided by the software TSAP-Win (Version 4.69k, Rinntech, Heidelberg, Germany) to retain as much as possible of the interannual climate signal within the chronologies. First, we calculated the 5-year moving average trend of each chronology. In a second step, tree-ring series were divided by the 5-year moving average trends, resulting in a dimensionless index of tree-ring width (TRI) (Dulamsuren et al. 2017). Descriptive dendrochronological statistics were based on individual tree chronologies and calculated using TSAP-Win (Table 4.1).

4.4.3 Climate, nitrogen deposition, and mast intensity data

We used the standardised 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 et al. 2010) and allows best to analyse the effects of climate change in beech tree-ring chronologies for variable time scales (Bhuyan et al. 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 et al. 2014; Hacket-Pain et al. 2015; Bosela et al. 2016). For each season, we used aggregated SPEI values based on a three-month period (that is, $\mathrm{SPEI}_{\mathrm{spring}}$ for March, April, May; $\mathrm{SPEI}_{\mathrm{summer}}$ for June, July, August; Figure C1).

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 et al. 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 between N_{dep}-values of different time scales 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 (Fig. C1).

Information about the frequency of beech masting was derived from Dammann et al. (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 generally occur synchronously over larger spatial scales (Packham et al. 2012), data from Dammann et al. (2016) were considered applicable for our study sites (see Hacket-Pain et al. 2018 for a similar approach).

4.4.4 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 (that is, colour, root elasticity and cohesion of the cortex, periderm and stele) following Hertel et al. (2013). Sorted fine roots were dried at 70°C for 24 h; afterwards dry matter of living and dead beech fine roots was 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 et al. 2018a (for a description of the methods see Mausolf et al. 2018a). 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 C1.

4.4.5 Data analysis

The time series of available N_{dep} data restricted our analyses to the period 2000-2013. In this interval, we found 6 years with positive and 8 years with negative $SPEI_{spring}$-values, whereas 8 years were characterised by positive and 6 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 C1). 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 et al. 2009). Competing models were evaluated by sequential comparison (backward selection) based on the Akaike Information Criterion (AIC) and maximum likelihood. Furthermore, we simplified the models with the lowest AIC value by removing non-significant terms. Parameter estimates of the final models were fitted using the restricted maximum likelihood (REML) method (Zuur et al. 2009). We fitted a global model containing climatic conditions during spring and summer to account for both effects simultaneously. All continuous predictors were standardised (mean=0, SD=1) before analysis.

To evaluate the linkage of N deposition during the growing season and tree growth, we performed confirmatory path analysis by using structural equation model (SEM) techniques (Grace et al. 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 et al. 2014) to our models (see Hacket-Pain et al. 2018 for a related approach). We hypothesised that the effect of N deposition on radial growth consists not only of a fertiliser effect, that is, a direct influence on tree growth, but there is also an indirect pathway of N deposition on tree growth mediated through masting intensity. Confirmatory path analysis was 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 generalised 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 et al. (2010) and model assumptions were visually checked and confirmed according to Zuur et al. (2009). All analyses were conducted in R (version 3.5.1) using the packages *MASS* (Venables and Ripley 2002), *nmle* (Pinheiro et al. 2016), *piecewiseSEM* (Lefcheck 2018) and *vegan* (Oksanen et al. 2016).

4.5 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 4.1). However, ancient forests showed a significantly lower mean minimum TRW than recent forests (0.88 mm vs. 1.25 mm, $P < 0.05$, Table 4.1). 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 4.2).

Table 4.1 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). 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 et al. (2018a). *TRW* Tree-ring width index, *SD* standard deviation, *AC* first-order autocorrelation.

	Ancient forests	Recent forests
	Mean (SE)	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)[1]	**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

1: values are related to cambial age at coring height

The best-fitting growth model showed a three-way interaction between N_{depGS}, $SPEI_{spring}$ and forest history type (Fig. 4.1; Table 4.2; $P = 0.006$). 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, that is, negative TRI values, due to water deficits was predicted to occur only in the trees of the ancient forests (Fig. 4.1a). 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. 4.1a). Moreover, the increase in radial growth rates was steeper in ancient forests than in recent forests under slightly negative $SPEI_{spring}$ values. Although 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. 4.1b). 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. C2; $P < 0.001$), 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 $\text{SPEI}_{\text{summer}}$ and forest history type ($P < 0.0572$). Due to the marginal significance, this interaction term was removed from the best-fitting growth model. In contrast to the effects of $\text{SPEI}_{\text{spring}}$, we found no significant three-way interaction between N_{depGS}, $\text{SPEI}_{\text{summer}}$ and forest history type.

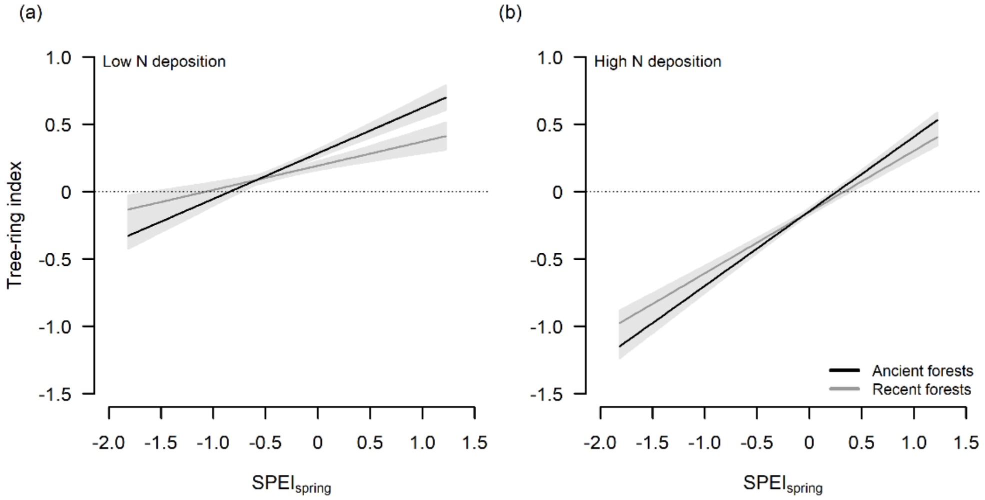

Figure 4.1 Effect of forest history type (ancient vs. recent forests) on the growth (tree-ring width index, TRI) response of European beech to interannual fluctuations in the climatic conditions during spring (2000-2013) considering **(a)** years with low nitrogen (N) deposition (30% quantile) and **(b)** 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.

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. 4.2). 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).

Table 4.2 Regression coefficients of the best-fitting mixed-effects models 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 standardised; hence, their magnitude is proportional to the effect size. Note that the intercept refers to the response of ancient forests, whereas 'RF' indicates recent forests. *SPEI*$_{spring}$ standardised precipitation-evapotrans-piration index aggregated for March, April and May, *SPEI*$_{summer}$ standardised 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

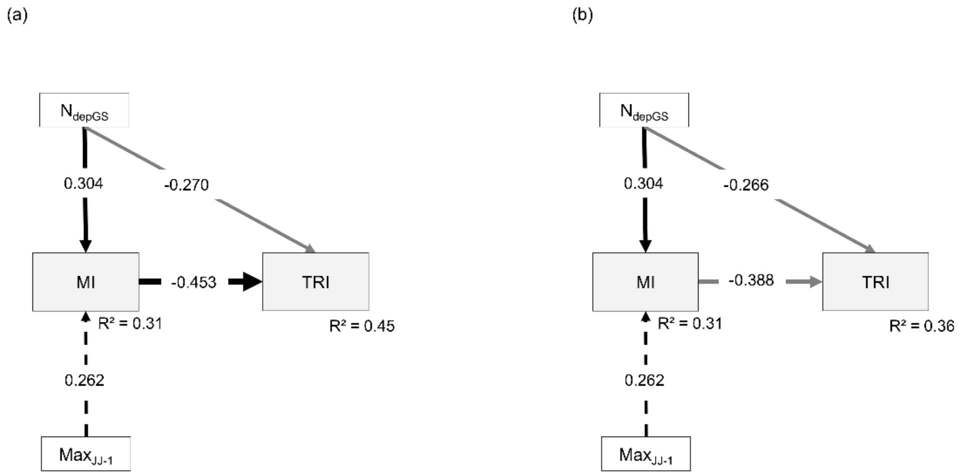

Figure 4.2 Confirmatory path analyses linking nitrogen (N) deposition and climate conditions, mast intensity and tree growth in **(a)** ancient forests and **(b)** recent forests across the years 2000-2013. Black solid, grey solid, and dashed lines indicate significant ($P < 0.05$), non-significant ($P > 0.1$) and marginal significant ($P < 0.1$) relationships, respectively. Positive and negative numbers at arrows are standardised 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.

4.6 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 envornmental 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.

4.6.1 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 high growing season temperatures on the radial growth of adult beech (that is, Braun et al. 2017; Hess et al. 2018). Hess et al. (2018) suggested that N fertilisation triggers an aboveground shift in plant-internal resource allocation which is in line with the predictions of the resource optimisation 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 in recent forests tended to be more sensitive to water deficits during summer than radial growth of trees in ancient forest stands (interaction $\text{SPEI}_{\text{summer}}$ × 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 changes in soil chemical properties through former land-use activities (Mausolf et al. 2018a, Table C1). 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 (Figure C3). Although 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.

4.6.2 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 3-6 years, which alternate with non-seed years (Packham et al. 2012). As high seed production comes at a high cost in terms of resource consumption, vegetative growth (that is, radial stem growth) in mast years, and sometimes in subsequent years as well, is lower than in non-mast years (Mund et al. 2010; Hacket-Pain et al. 2015; Müller-Haubold et al. 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 et al. 2007; Paar et al. 2011; Müller-Haubold et al. 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 et al. 2007; Müller-Haubold et al. 2015; Hacket-Pain et al. 2018; Lebourgeois et al. 2018). Additionally, pollination success during spring is a strong driver for the production of large amounts of seed crop (Pearse et al. 2016; Lebourgeois et al. 2018; Nussbaumer et al. 2018), as beech is a self-incompatible, wind-pollinated species (Packham et al. 2012). Because beech nuts are relatively rich in N, nitrogen availability in particular is discussed as a key driver of masting (Smaill et al. 2011; Bogdziewicz et al. 2017). In a study about the resource consumption with seed crop production in *Fagus crenata*, Abe et al. (2016) found that inner seed maturation highly depends on N availability. Furthermore, Miyazaki et al. (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 generalise results from short-term N deposition time series (that is, 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 (that is, radial stem growth) to reproductive growth (that is, seed production) thus seems to be stronger in trees growing in ancient forests. We hypothesise 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 et al. 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 et al. 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 et al. 2016), which should be more responsive in growth to reproduction-mediated effects of additional N input.

4.7 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 do 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.

C Supplementary Material

Table C1 Summary statistics edaphic properties of the 28 study stands published by Mausolf et al. (2018a). Values are means and their standard deviation (in brackets). Significant ($P < 0.05$) differences between former land-use types are highlighted in bold. Note that the effects of former land-use on total P (0-10 cm) and C/P ratio (10-30 cm) were marginally significant ($P \leq 0.1$).

	Recent forests	Ancient forests
Soil type	(pseudogleyic) Luvisol	(pseudogleyic) Luvisol
pH (H_2O)		
0–10 cm	4.36 (0.59)	4.22 (0.76)
10–30 cm	4.57 (0.63)	4.47 (0.44)
pH ($CaCl_2$)		
0–10 cm	3.50 (0.63)	3.40 (0.76)
10–30 cm	3.91 (0.76)	3.75 (0.35)
Total C (%)		
0–10 cm	4.55 (1.72)	5.25 (1.24)
10–30 cm	1.33 (0.49)	1.49 (0.41)
Total N (%)		
0–10 cm	0.27 (0.08)	0.31 (0.06)
10–30 cm	0.09 (0.03)	0.08 (0.02)
Total P (mg g^{-1})		
0–10 cm	0.36 (0.16)	0.28 (0.09)
10–30 cm	**0.26 (0.14)**	**0.17 (0.06)**
C:N ratio		
0–10 cm	16.31 (1.56)	17.06 (1.74)
10–30 cm	**14.55 (2.97)**	**17.64 (3.41)**
C:P ratio		
0–10 cm	**140.50 (49.50)**	**201.30 (64.68)**
10–30 cm	69.43 (43.53)	102.11 (58.84)
N_{pa} (mg g^{-1})		
0–10 cm	0.05 (0.02)	0.04 (0.02)
10–30 cm	n.a.	n.a.
CEC (mmol kg^{-1})		
0–10 cm	11.59 (2.80)	11.05 (1.82)
10–30 cm	8.35 (3.83)	7.61 (2.18)
BS (%)		
0–10 cm	34.35 (19.61)	25.70 (6.40)
10–30 cm	41.35 (7.57)	43.24 (14.18)
n(plots)	13	15

C carbon, *N* nitrogen, *P* phosphorus, N_{pa} amount of plant available nitrogen (total NH_4^+ and NO_3^- concentration), *CEC* cation exchange capacity, *BS* base saturation, *n.a.*: not available.

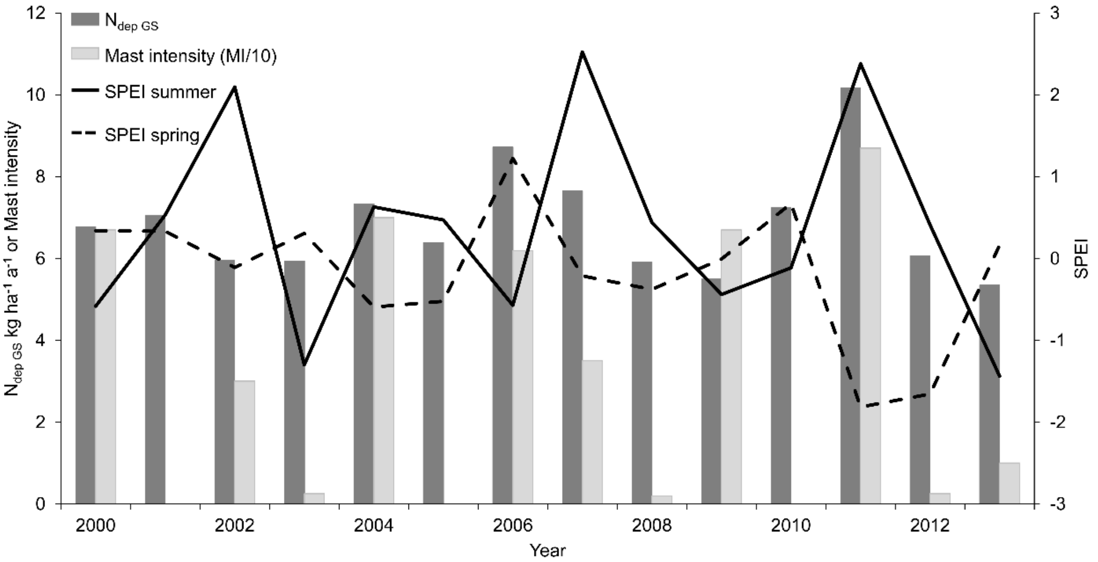

Figure C1 Seasonal (spring: March-May, dotted line; summer: June-August, solid line) standardised precipitation-evapotranspiration index (SPEI) for the study site. Negative values indicate water deficits. Dark grey bars show the amount of total nitrogen deposition during the growing season (April-October) for each year. Pale grey bars show the mast intensity for each year (for an easier visualisation mast intensity values were divided by 10).

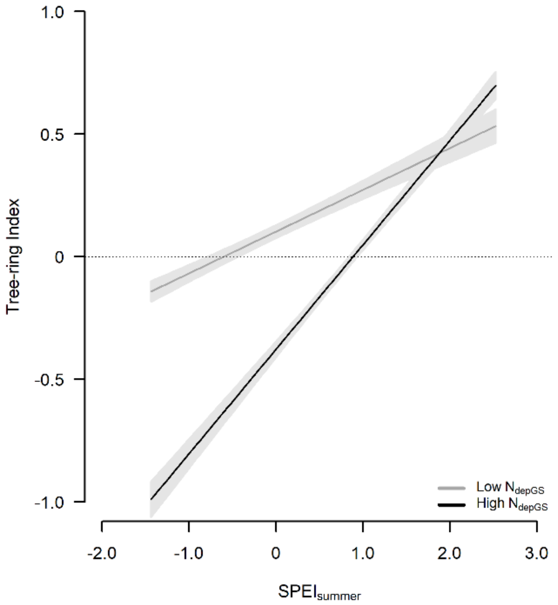

Figure C2 Effect of former land-use type (ancient vs. recent forests) on the radial growth (tree-ring width index, TRI) responsiveness of European beech (*Fagus sylvatica* L.) to the interacting effect of climate conditions and low (0.3 quantile) or high (0.7 quantile) nitrogen deposition on the growth response (tree-ring width index, TRI) of the trees of both forest history types. The climatic gradient is characterised by the standardised precipitation-evapotranspiration index (SPEI) aggregated for the month June-August. Negative SPEI-values display a negative climatic water balance, positive values display conditions with ample water supply. Lines correspond to the predicted response based on mixed-effects models and shaded areas indicate the 95% confidence interval.

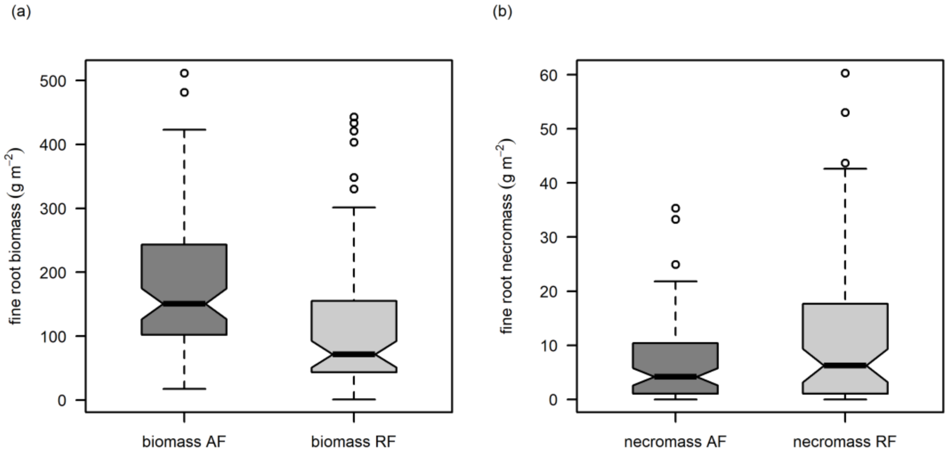

Figure C3 (**a**) Living fine root biomass (g m $^{-2}$) in ancient (AF) and recent (RF) forest and (**b**) fine root necromass (g m $^{-2}$) in ancient (AF) and recent (RF) sampled in October 2016. Mean values for ancient forests: 175.69 g m^{-2} (± 10.50) fine root biomass, 6.33 g m^{-2} (± 0.75) fine root necromass and mean values in recent forests: 113.76 g m^{-2} (± 12.20) fine root biomass, 12.23 g m^{-2} (± 1.62) fine root necromass. Differences between forest history types were tested by using linear mixed-effects models with ‘plot’ used as random effect. Values for fine root biomass differed significantly between types (P = 0.0295), as well as the values for fine root necromass (P = 0.0129).

5. SYNTHESIS AND CONCLUSIONS

5.1 Main findings

Many recent research approaches in ecosystem sciences have addressed the impact of human activities on the biosphere (Austin 2011). This has caused a shift in ecology from describing the actual state of ecosystems towards predicting their temporal dynamics taking ongoing environmental changes into account (Perring et al. 2018). More recently, there is an increasing awareness of the importance to include past anthropogenic ecosystem changes and the resulting legacy effects to understand present and future ecosystem responses to global environmental changes (Perring et al. 2016). Particularly, the evaluation of legacy effects on forest ecosystem processes are of high interest, as long-lived organisms, such as trees, are not able to adapt rapidly to abrupt environmental changes. In this context, the presented thesis analysed the growth dynamics of one of the ecologically and economically most important deciduous tree species (European beech) of Central Europe (Leuschner and Ellenberg 2017). Overall, the presented thesis provides evidence that forest history, in terms of former land-use history as well as management history, plays an important role in modulating present tree growth responses to drivers of environmental changes. Specifically, the presented thesis identified that:

I) Legacy effects of former land-use induce a greater susceptibility of beech tree growth to summer water deficits.

II) Legacy effects of former forest management cause a greater susceptibility of beech tree growth to spring water deficits.

III) Simultaneously acting water deficits in spring and high N deposition cause a stronger radial growth decline for beech trees located in ancient forests.

5.2 The underlying mechanisms

5.2.1 How legacy effects modulate tree growth response to water deficits

Beyond the identification of differences in the growth patterns of trees growing on sites which vary in their ecological continuity, the presented thesis aimed to identify the mechanisms underlying the observed differences in aboveground productivity of beech trees. Land-use legacies in recent forest soils were identified to cause changes in fine root biomass and morphology in recent forests. The fine root system related differences, in turn, modulate the climate-growth relationships of trees growing on afforested sites compared to trees growing on sites with a long ecological continuity. Under ample water supply (which is mostly the case in the sub oceanic climate of Schleswig-

Holstein's eastern moraine landscape) the observed alterations in fine root traits cause higher growth rates for the trees in recent forests. In contrast, the growth-optimised fine root systems in recent forests lead to higher growth declines when water deficits occur. (Fig. 5.1).

Here, the fine root biomass as well as the functional traits of the fine root system are crucial for buffering against environmental changes such as the more frequent occurrence of water deficits, as the fine root system determines a tree's growth via nutrient and water uptake. Although there is increasing evidence that fine root traits are multidimensional (Kramer-Walter et al. 2016), the fine root analyses carried out within the project of this thesis showed that within-species modifications in size and morphology of the fine root system may reflect differences in the whole-plant economics spectrum between trees growing in ancient and recent forests (Reich 2014). Specifically, the observed 55% higher standing fine root biomass in ancient forests shows that these trees likely invest a higher amount of C into their fine root systems. Moreover, the greater specific root length and lower root tissue density in recent forests probably explain – at least in part – differences in aboveground productivity. Indeed, trees with a higher specific root length generally have a higher hydraulic conductance (Huang and Eissenstat 2000), and it is thus likely that radial growth rates are higher during favourable climatic conditions, but lower during water deficits due to a greater susceptibility to cavitation and xylem dysfunction (Tyree 2003). Modifications in the fine root system (in terms of fine root biomass and morphology) are likely caused by a higher soil fertility (in particular phosphorus content) in recent forests due to former agricultural use.

The lower specific root length observed in ancient forests, however, might contribute to a greater root lifespan and a more diverse colonisation of fine roots by ectomycorrhizae (Comas et al. 2014; Reich 2014; Weemstra et al. 2016), as fungi are more diverse and abundant in ancient forest soils (Fraterrigo et al. 2006). Optimised mycorrhizal associations in ancient forest soils could therefore also explain the lower susceptibility of these trees to water deficits through an enhanced water transport capacity under low water availability (Brunner et al. 2015).

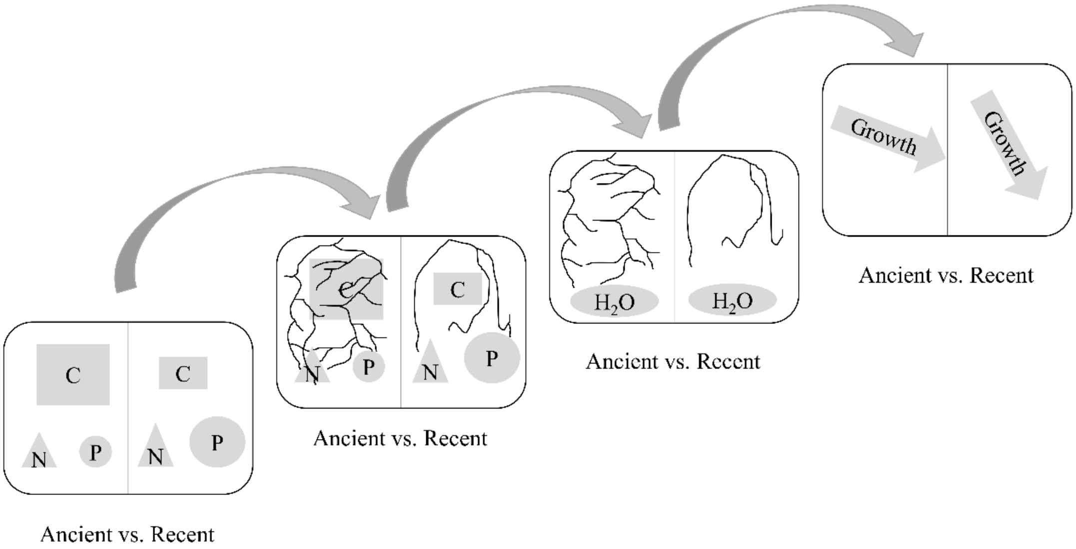

Figure 5.1 The land-use legacy effect cascade of former land-use on current tree growth. Past agricultural land-use causes long-lasting differences in soil chemical properties, particularly with regard to the phosphorus (P) content, the carbon (C) to nitrogen (N) ratio, and the C:P ratio in recent forest soils. These changes lead to differences in the nutrient availability and cause significant differences in the fine root biomass and the morphology of the fine root system. Differences in the size and morphology of the fine root system alter the amount of water and nutrients that can be taken up from the soil, causing higher growth declines for trees in recent forests under water deficits in summer.

Exploring the mechanisms underlying a higher susceptibility to spring water deficits of beech growing in managed compared to trees in unmanaged forests requires focusing on tree morphology. The presented thesis shows that tree morphology is modulated by forest management practice. In this context, structural overshoot has been identified as an important mechanism explaining the observed difference in climate-growth responses.

Structural overshoot designates the facilitation of tree growth via favourable environmental conditions (e.g. releasing trees via management) and the accompanied risk of a temporal mismatch between water demand and availability in times of water deficits (Jump et al. 2017). The tree morphology of beech responds sensitively to disturbance intensity (e.g. management history; Fichtner et al. 2013). For example, beech reacts quickly to improved light conditions by space filling via crown expansion (Lebourgeois et al. 2014). This is in line with the results of this thesis, where trees in managed forests are characterised by larger crown projection areas in comparison to trees in unmanaged stands. Due to the positive relation between crown size and a tree's leaf area, and thus an increase in photosynthetic activity and evapotranspiration, a higher water demand can be assumed for the trees in managed stands (Niinemets 2010).

Beyond the changes in crown size, it is likely that the released trees in managed forests also adapt their hydraulic system after logging activities (Noyer et al. 2017). Adaptions of the hydraulic system such as an increase in vessel diameter can lead to a higher risk of hydraulic failure and embolisms. In this case, a full restoration of the transport system usually occurs only after new ring formation the following year (Bréda et al. 2006). Thus, the higher water demand of trees growing in the local neighbourhood of management gaps, which is caused by adaptions of crown size to new environmental conditions, can explain the higher susceptibility to spring water deficits. Furthermore, a likely but time-lagged adaption of the trees' hydraulic systems might be another factor increasing – at least in the intermediate term – the sensitivity to spring water deficits. Conversely, radial growth is promoted under favourable climatic conditions.

5.2.2 Effects of simultaneously acting global change drivers: An ecological surprise?

Experimental studies on beech saplings proved a fertilising effect of N additions. Simultaneously, sensitivity to drought events increased due to an increase in shoot-to-root ratio (Dziedek et al. 2017). The 'resource optimisation hypothesis', which predicts that plants allocate less C to roots and increase their shoot-to-root ratio with higher nutrient availability (Thornley 1972; Ågren and Franklin 2003), can well explain the altered sensitivity of fertilised plants to water deficits through changes in the fine root system (Dziedek et al. 2017; Hess et al. 2018). Even for adult beech trees a (non-additive) negative effect of high N deposition and increasing summer temperatures on the radial growth was proven (Hess et al. 2018).

The presented thesis showed that the sensitivity to summer water deficits was enhanced by high N deposition in both forest history types, while soil legacy-mediated differences in the fine root system (e.g. necromass:biomass ratio) might explain the higher susceptibility of trees growing in recent forests to water deficits in summer. In contrast, growth declines in response to spring water deficits and high N deposition are higher for trees in ancient forests. This is, with respect to previous expectations, an ecological surprise (Filbee-Dexter et al. 2017; Box 4).

Box 4

Ecological surprises can be defined as situations in which expectations or predictions of natural system behavior deviate from observed ecosystem behavior, thus discovering something about an ecosystem that runs counter to previous knowledge (Filbee-Dexter et al. 2017).

Within paper III we were able to show that the interacting effects of spring water deficits and N deposition likely lead to an increasing investment of resources to reproduction (i.e. seed production), which also causes observable growth declines in beech ('reproduction-growth trade-off'; Hacket-Pain et al. 2015). In recent decades an increase in the frequency and intensity of mast events has been observed in beech stands across Germany (Paar et al. 2011), thus it can be assumed that a change in the drivers for mass fructification has taken place. In this context, nitrogen is discussed as a key resource and regulator for mass fruiting in the taxa *Fagus* (Miyazaki et al. 2014; Müller-Haubold et al. 2015). Apparently, the possible triggering function of high N deposition is stronger for trees growing in ancient forests. We assume that the phosphorus legacy effects of former land-use modifies the response in tree growth to multiple global change drivers.

Forest ecosystems with a low phosphorus availability, such as the investigated ancient forests, were shown to be associated with tight nutrient cycles (Lang et al. 2016). Moreover, the 55% higher standing fine root biomass in the uppermost soil layers offers a larger absorptive area, which may increase the responsiveness to additional N inputs. In this context, more research is required to test, for example, if there is a 'N availability threshold' for beech trees to switch to fruit investments. Possibly, this can help to explain the observed negative relationship between high N deposition (> 26 kg ha^{-1} a^{-1}) and basal area increment rates in beech (Braun et al. 2017).

More generally, the observed growth declines linked to global change stressors can be partly explained by allocation processes to reproduction. An increased resource investment to reproduction is not necessarily an indicator for a reduction in the vitality of trees. This is an important finding, as future dendroecological approaches need to keep in mind that tree-ring measurements of beech can reflect both growth declines caused by unfavourable growing conditions and resource allocation processes within the tree (i.e. towards reproduction and/or the root system).

5.3 Conclusions

Overall, the presented thesis emphasises the important role of ecological continuity in modulating the response of beech forests to global environmental changes. Forest history in terms of both former land-use and management was identified to critically alter radial growth rates of beech when facing drivers of global change.

In particular, soil phosphorus legacy effects have been shown to cause modifications in the fine root systems and thus explain altered growth patterns in trees growing on forest sites differing in their ecological continuity. These modifications of the fine root systems lead to a higher susceptibility to summer water deficits for beech trees growing on recent forest sites. Moreover, forest management legacies modulate the climate-growth response of adult beech trees to spring water deficits via changes in tree morphology caused by tree release in managed forests. This finding emphasises the need to consider trade-offs between maximised radial growth rates and climate sensitivity while evaluating forest management practices.

Combining the findings of papers I and II, it can be concluded that radial growth of beech in ancient, unmanaged forests is less sensitive to water deficits than in recent and managed beech forests. This can be of economic importance and of high relevance for political decisions as a lower sensitivity of growth to water deficits ensures continuous carbon sequestration rates. Thus, in the midst of global environmental changes, unmanaged, ancient Baltic beech forests hold a unique position in both hosting threatened animal, plant, and fungal species, and climate change mitigation.

While studying the combined effects of simultaneously acting global change drivers, the presented thesis provides evidence that tree-ring widths series of beech do not allow an unrestricted usage for assessing possible direct stress impacts on radial tree growth. In fact, the study conducted within this thesis shows that the effects of simultaneously acting global change drives, visible as growth declines in tree-ring series, are partly caused by allocation processes. This finding highlights the importance to consider possible confounding effects in tree-ring series when using them to assess growth responses to environmental change processes. Decreasing growth rates caused by increasing seed production do not necessarily reflect a reduction of tree vitality. On the contrary, the increased seed production might have a positive effect on natural forest regeneration in the investigated forests.

In summary, the presented thesis has shown that forest history modulates growth responses of beech to global environmental changes through legacy-mediated changes in the trees' above- and belowground morphology. This indicates that the 'ecological memory' of a forest is a crucial component in determining the forest ecosystem trajectory in the midst of global environmental changes.

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REFERENCES

Abe, T., Tachiki, Y., Kon, H., Nagasaka, A., Onodera, K., Minamino, K., Han, Q., Satake, A. (2016) Parameterisation and validation of a resource budget model for masting using spatiotemporal flowering data of individual trees. *Ecology Letters*, 19, 1129–1139.

Ågren, G.I., and Franklin, O. (2003) Root:shoot ratios, optimization and nitrogen productivity. *Annals of Botany*, 92, 795–800.

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H.T., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.-H., Allard, G., Running, S.W., Semerci, A., Cobb, N. (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*, 259, 660–684.

Ammer, C. (2017) Unravelling the importance of inter- and intraspecific competition for the adaptation of forests to climate change. In: Cánovas, F., Lüttge, U., Matyssek, R. (eds.) *Progress in Botany*, Vol. 78, Springer, Cham, Switzerland.

Anderegg, W.R.L., Schwalm, C., Biondi, F., Camarero, J.J., Koch, G., Litvak, M., Ogle, K., Shevlikova, E., Williams, A.P., Wolf, A., Ziaco, E., Pacal, S. (2015) Pervasive drought legacies in forest ecosystems and their implications for carbon cycle models. *Science*, 349, 528–532.

Anderson, M.J. (2001) A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, 26, 31–46.

Aranda, I., Gil-Pelegrín, E., Gascó, A., Guevara, M.A., Cano, J.F., De Miguel, M., Ramírez-Valiente, J.A., Peguero-Pina, J.J., Perdiguero, P., Soto, A., Cervera, M.T., Collada, C. (2012) Drought response in forest trees: From the species to the gene. In: Aroca, R. (ed.) Plant Responses to Drought Stress. Springer, Berlin, Heidelberg, Germany.

Assmann, T., Drees, C., Schröder, C., Ssymank, A. (2007) Mythos Artenarmut – Biodiversität von Buchenwälder – Low species diversity of beech forests – a myth. *Natur und Landschaft*, 82, 401–406.

Austin, A. (2011) Celebrating the ecosystem's three-quarter century: Introduction to a *Viral Special Issue* on Sir Arthur Tansley's ecosystem concept. *New Phytologist*, 192, 561–563.

Aussenac, G. (2000) Interactions between forest stands and microclimate: Ecophysiological aspects and consequences for silviculture. *Annals of Forest Science*, 57, 287–301.

Baeten, L., Hermy, M., Van Daele, Verheyen, K. (2010) Unexpected understorey community development after 30 years in ancient and post-agricultural forests. *Journal of Ecology*, 98, 1447–1453.

Bardgett, R.D., Mommer, L., De Vries, F.T. (2014) Going underground: root traits as drivers of ecosystem processes. *Trends in Ecology and Evolution*, 29, 692–699.

Bellassen, V., and Luyssaert, S. (2014) Managing forests in uncertain times. *Nature*, 506, 153–155.

Bergel, D. (1973) Formzahluntersuchungen an Buche, Fichte, europäischer Lärche und japanischer Lärche zur Aufstellung neuer Massentafeln. *Allgemeine Forst- und Jagdzeitung*, 144, 117–124.

Bhuyan, U., Zang, C., Menzel, A. (2017) Different responses of multispecies tree ring growth to various drought indices across Europe. *Dendrochronologia*, 44, 1–8.

Blondeel, H., Perring, M.P., Bergès, L., Brunet, J., Decocq, G., Depauw, L., Diekmann, M., Landuyt, D., Liira, J., Maes, S.L., Vanhellemont, M., Wulf, M., Verheyen, K. (2018) Context-dependency of agricultural legacies in temperate forest soils. *Ecosystems*, https://doi.org/10.1007/s10021-018-0302-9.

Bobbink, R., Hornung, M., Roelofs, J.G.M. (1998) The effects of air-borne nitrogen pollutants on species diversity in natural and semi-natural European vegetation. *Journal of Ecology*, 86, 717–738.

Boobink, R., Hicks, K., Galloway, J., Spranger, T., Alkemade, R., Ashmore, M., Bustamente, M., Cinderby, S., Davidson, E., Dentener, F., Emmett, B., Erisman, J.-W., Fenn, M., Gilliam, F., Nordin, A., Pardo, L., De Vries, W. (2010) Global assessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis. *Ecological Applications*, 20, 30–59.

Bogdziewicz, M., Crone, E.E., Steele, M.A., Zwolak, R. (2017) Effects of nitrogen deposition on reproduction in a masting tree: benefits of higher seed production are trumped by negative biotic interactions. *Journal of Ecology*, 105, 310–320.

Boisvenue, C., and Running, S.W. (2006) Impacts of climate change on natural forest productivity – evidence since the middle of the 20th century. *Global Change Biology*, 12, 862–882.

Bosela, M., Štefančík, I., Petráš, R., Vacek, S. (2016) The effects of climate warming on the growth of European beech forests depend critically on thinning strategy and site productivity. *Agricultural and Forest Meteorology*, 222, 21–31.

Bosela, M., Lukac, M., Castagneri, S. Sedmák, R., Biber, P., Carrer, M., Konôpka, B., Nola, P., Nagel, T.A., Popa, I., Roibu, C.C., Svoboda, M., Trotsiuk, V., Büntgen, U. (2018) Contrasting effects of environmental change on the radial growth of co-occuring beech and fir trees across Europe. *Science of the Total Environment*, 615, 1460–1469.

Bradford, M.A., Wood, S.A., Maestre, F.T., Reynolds, J.F., Warren II, R.J. (2012) Contingency in ecosystem but not plant community response to multiple global change factors. *New Phytologist*, 196, 462–471.

Braun, S., Schindler, C., Rihm, B. (2017) Growth trends of beech and Norway spruce in Switzerland: The role of nitrogen deposition, ozone, mineral nutrition and climate. *Science of the Total Environment*, 599-600, 637–646.

Bréda, N., Granier, A., Aussenac, G. (1995) Effects of thinning on soil and tree water relations, transpiration and growth in an oak forest (*Quercus petraea* (Matt.) Liebl.). *Tree Physiology*, 15, 295–306.

Bréda, N., Huc, R., Granier, A., Dreyer, E. (2006) Temperate forest trees and stands under severe drought: a review of ecophysiological reponses, adaption processes and long-term consequences. *Annals of Forest Science*, 63, 625–644.

Breshears, D.D., Cobb, N.S., Rich, P.M., Price, K.P., Allen, C.D., Balice, R.G., Romme, W.H., Kastens, J.H., Floyd, M.L., Belnap, J., Anderson, J.J., Myers, O.B., Meyer, C.W. (2005) Regional vegetation die-off in response to global-change-type drought. *PNAS*, 102, 15144–151148.

Brunet, J., and von Oheimb, G. (2008) Almsjuka och mördarsniglar: dramatik i Dalby Söderskog. *Svensk Botanisk Tidskrift*, 102, 27–38.

Brunet, J., Fritz, Ö., Richnau, G. (2010) Biodiversity in European beech forests – a review with recommendations for sustainable forest management. *Ecological Bulletins*, 53, 77–94.

Brunner, I., Herzog, C., Dawes, M.A., Arend, M., Sperisen, C. (2015) How tree roots respond to drought. *Frontiers in Plant Science*, 6, 547.

Buckley, D.H., and Schmidt, T.M. (2001) The structure of microbial communities in soil and the lasting impact of cultivation. *Microbial Ecology*, 42, 11–21.

Bürgi, M., Östlund, L., Mladenoff, D.L. (2017) Legacy effects of human land use: ecosystems as time-lagged systems. *Ecosystems*, 20, 94–103.

Buyan, U., Zang, C., Menzel, A. (2017) Different responses of multispecies tree ring growth to various drought indices across Europe. *Dendrochronologia*, 44, 1–8.

Bytnerowicz, A., Omasa, K., Paoletti, E. (2007) Integrated effects of air pollution and climate change on forests: A northern hemisphere perspective. *Environmental Pollution*, 147, 438–445.

Cavin, L., and Jump, A.S. (2016) Highest drought sensitivity and lowest resistance to growth suppression are found in the range core of the tree *Fagus sylvatica* L. not the equatorial range edge. *Global Change Biology*, 23, 362–379.

Carrer, M. (2011) Individualistic and time-varying tree-ring growth to climate sensitivity. *PLOS ONE*, 6, e22813.

Chambers, J.Q., Higuchi, N., Tribuzy, E.S., Trumbore, S.E. (2001) Carbon sink for a century. *Nature*, 410, 429.

Chmielewski, F.-M., and Rötzer, T. (2001) Response of tree phenology to climate change across Europe. *Agricultural and Forest Meteorology*, 108, 101–112.

Choat, B., Jansen, S., Brodribb, T.J., Cochard, H., Delzon S., Bhaskar, R., Bucci, S.J., Field, T.S., Gleason, S.M., Hacke, U.G., Jacobsen, A.L., Lens, F., Maherali, H., Martínez-Vilalta, J., Mayr, S., Mencuccini, M., Mitchell, P.J., Nardini, A., Pittermann, J., Pratt, R B., Sperry, J.S., Westoby, M., Wright, I.J., Zanne, A.E. (2012) Global convergence in the vulnerability of forests to drought. *Nature*, 491, 752–755.

Clark, C.M., Morefield, P.E., Gilliam, F.S., Pardo, L.H. (2013) Estimated loss of plant biodiversity in the United States from historical N deposition (1985-2010). *Ecology*, 94, 1441–1448.

Clark, J.S., Iverson, L., Woodall, C.W., Allen, C.D., Bell, D.M., Bragg, D.C., D'Amato, A.W., Davis, F.W., Hersh, M.H., Ibanez, I., Jackson, S.T., Matthews, S., Pederson, N., Peters, M., Schwartz, M.W., Waring, K.M., Zimmermann, N. E. (2016) The impacts of increasing drought on forest dynamics, structure, and biodiversity in the United States. *Global Change Biology*, 22, 2329–2352.

Comas, L.H., Callahan, H.S., Midford, P. (2014) Patterns in root traits of woody species hosting arbuscular and ectomycorrhizas: implications for the evolution of belowground strategies. *Ecology and Evolution*, 4, 2979–2990.

Compton, J.A., and Boone, R.D. (2000) Long-term impacts of agriculture on soil carbon and nitrogen in New England forests. *Ecology*, 81, 2314–2330.

Crutzen, P.J., and Stoermer, E.F. (2000) The "Anthropocene", In: Steffen, W. (ed.) The International Geosphere–Biosphere Programme (IGBP) Newsletter, 41, 17–18.

D'Amato, A.W., Bradford, J.B., Fraver, S., Palik, B.J. (2013) Effects of thinning on drought vulnerability and climate response in north temperate forest ecosystems. *Ecological Applications*, 23, 1735–1742.

Dammann, I., Paar, U., Weymar, J., Spielmann, M., Eichhorn, J. (2016) Waldzustandsbericht 2016 für Schleswig-Holstein. Printec Offset Kassel, Germany.

De Groot, R., Brander, L., van der Ploeg, S., Costanza, R., Bernard, F., Braat, L., Christie, M., Crossmann, N., Ghermandi, A., Hein, L., Hussain, S., Kumar, P., McVittie, A., Portela, R., Rodriguez, L.C., ten Brink, P., van Beukering, P. (2012) Global estimates of the value of ecosystems and their services in monetary units. *Ecosystem Services*, 1, 50–61.

De la Peña, E., Baeten, L., Steel, H., Viaene, N., De Sutter, N., De Schrijver, A., Verheyen, K. (2016) Beyond plant-soil feedbacks: mechanisms driving plant community shifts due to land-use legacies in post-agricultural forests. *Functional Ecology*, 30, 1073–1085.

De Martonne, E. (1926) Aréisme et indice d'aridité. *Comptes Rendus de l'Académie des Sciences*, 181, 1395–1398.

De Vries, W., Du, E., Butterbach-Bahl, K. (2014) Short and long-term impacts of nitrogen deposition on carbon sequestration by forest ecosystems. *Current Opinion in Environmental Sustainability*, 9–10, 90–104.

Diaconu, D., Stangler, D.F., Kahle, H.P., Spiecker, H. (2016) Vessel plasticity of European beech in response to thinning and aspect. *Tree Physiology*, 36, 1260–1271.

Di Filippo, A., Biondi, F., Cufar, K., De Luis, M., Grabner, M., Maugeri, M., Saba, E.P., Schirone, B., Piovesan, G. (2007) Bioclimatology of beech (*Fagus sylvatica* L.) in the Eastern Alps: spatial and altitudinal climatic signals identifies through a tree-ring network. *Journal of Biogeography*, 34, 1873–1892.

Dighton, J. (2003) Fungi in Ecosystem processes. In: Bennet, J.W. (ed.) Mycology Vol. 17, Marcel Dekker Inc., New York, US.

Dupouey, J.L., Dambrine, E., Laffite, J.D., Moares, C. (2002) Irreversible impact of past land use on forest soils and biodiversity. *Ecology*, 83, 2978–2984.

Drobyshev, I., Övergaard, R., Saygin, I., Niklasson, M., Hickler, T., Karlsson, M., Sykes, M.T. (2010) Masting behaviour and dendrochronology of European beech (*Fagus sylvatica* L.) in southern Sweden. *Forest Ecology and Management*, 259, 2160–2171.

Dulamsuren, C., Hauck, M., Kopp, G., Ruff, M., Leuschner, C. (2017) European beech responds to climate change with growth decline at lower, and growth increase at higher elevations in the center of its distribution range (SW Germany). *Trees*, 31, 673–686.

DWD Climate Data Center (CDC) (2017a) Historical monthly station observations (temperature, pressure, precipitation, sunshine duration, etc.) for Germany, version v005.

DWD (2017b) Klimareport Schleswig-Holstein. Deutscher Wetterdienst, Offenbach am Main, Germany.

Dziedek, C., Härdtle, W., von Oheimb, G., Fichtner, A. (2016) Nitrogen addition enhances drought sensitivity of young deciduous tree species. *Frontiers in Plant Science*, 7, 1100.

Dziedek, C., Fichtner, A., Calvo, L., Marcos, E., Jansen, K., Kunz, M., Walmsley, D., von Oheimb, G., Härdtle, W. (2017) Phenotypic plasticity explains response patterns of European beech (*Fagus sylvatica* L.) saplings to nitrogen fertilization and drought events. *Forests*, 8, 1–11.

Easterling, D.R., Meehl, G.A., Parmesan, C., Changnon, S.A., Karl, T.R., Mearns, L.O. (2000) Climate extremes: observations, modeling, and impacts. *Science*, 289, 2068–2074.

Ellenberg, H., and Leuschner, C. (2010) Die Vegetation Mitteleuropas mit den Alpen. Vol. 6, Ulmer, Stuttgart, Germany.

Eissenstat, D.M., and Yanai, R.D. (1997) The Ecology of Root Lifespan. *Advances in Ecological Research*, 27, 1–60.

Eissenstat, D.M., Wells, C.E., Yanai, R.D., Whitbeck, J.L. (2000) Building roots in a changing environment: implications for root longevity. *New Phytologist*, 147, 33–42.

Ferretti, M., Marchetto, A., Arisci, S., Bussotti, F., Calderisi, M., Carnicelli, S., Cecchini, G., Fabbio, G., Bertini, F., Matteucci, G., Cinti, B., Salvati, L., Pompei, E. (2014) On the tracks of Nitrogen deposition effects on temperate forests at their southern European range – an observational study from Italy. *Global Change Biology*, 20, 3423–3438.

Fichtner, A., and Lüderitz, M. (2013) Signalarten – ein praxisnaher Beitrag zur Erfassung der Naturnähe und Biodiversität in Wäldern – Signal species – a practical tool for the assessment of naturalness and biodiversity in forest ecosystems. *Natur und Landschaft*, 88, 392–399.

Fichtner, A., Sturm, K., Rickert, C., von Oheimb, G., Härdtle, W. (2013) Crown size-growth relationships of European beech (*Fagus sylvatica* L.) are driven by the interplay of disturbance intensity and inter-specific competition. *Forest Ecology and Management*, 302, 178–184.

Fichtner, A., von Oheimb, G., Härdtle, W., Wilken, C., Gutknecht, J.L.M. (2014) Effects of anthropogenic disturbances on soil microbial communities in oak forests persist for more than 100 years. *Soil Biology and Biochemistry*, 70, 79–87.

Fichtner, A., Härdtle, W., Bruelheide, H., Kunz, M., Li, Y., von Oheimb, G. (2018) Neighbourhood interactions drive overyielding in mixed-species tree communities. *Nature Communications*, 9:1144, 1–8.

Filbee-Dexter, K., Pittman, J., Haig, H.A., Alexander, S.T., Symons, C.C., Burke, M.J. (2017) Ecological surprise: concept, synthesis, and social dimensions. *Ecosphere*, 8, e02005.

Flinn, K.M., and Vellend, M. (2005) Recovery of forest plant communities in post-agricultural landscapes. *Frontiers in Ecology and the Environment*, 3, 243–250.

FOREST EUROPE, UNECE and FAO (2011) State of Europe's Forests 2011. Status and Trends in Sustainable Forest Management in Europe. FOREST EUROPE Liaison Unit, Oslo, Norway.

Foster, D., Swanson, F., Aber, J., Burke, I., Brokaw, N., Tilman, D., Knapp, A. (2003) The importance of land-use legacies to ecology and conservation. *BioScience*, 53, 77–88.

Fraterrigo, J.M., Turner, M.G., Pearson, S.M., Dixon, P. (2005) Effects of past land use on spatial heterogeneity of soil nutrients in southern Appalachian forests. *Ecological Monographs*, 75, 215–230.

Fraterrigo, J.M., Balser, T.C., Turner, M.G. (2006) Microbial community variation and its relationship with nitrogen mineralization in historically altered forests. *Ecology*, 87, 570–579.

Fraterrigo, J.M. (2013) Landscape legacies. In: Levin, S.A. (ed.) Encyclopedia of Biodiversity, Academic Press, Waltham, MA, US.

Freschet, G.T., Valverde-Barrantes, O.J., Tucker, C.M., Craine, J.M., McCormack, L., Violle, C., Fort, F., Blackwood, C.B., Urban-Mead, K.R., Iversen, C.M., Bonis, A., Comas, L.H., Cornelissen, H.C., Dong, M., Guo, D., Hobbie, S.E., Holdaway, R.J., Kembel, S.W., Makita, N., Onipchenko, V.G., Picon-Cochard, C., Reich, P.B., De la Riva, E.G., Smith, S.W., Soudzilovskaia, N.A., Tjoelker, M.G., Wardle, D.A., Roumet, C. (2017) Climate, soil and plant functional types as drivers of global fine-root trait variation. *Journal of Ecology*, 105, 1182–1196.

Fritz, Ö., Gustafsson, L., Larsson, K. (2008) Does forest continuity matter in conservation? – A study of epiphytic lichens and bryophytes in beech forests of southern Sweden. *Biological Conservation*, 141, 655–668.

Galloway, J.N., Dentener, F.J., Capone, D.G., Boyer, E.W., Howarth, R.W., Seitzinger, S.P., Asner, G.P., Cleveland, C.C., Green, P.A., Holland, E.A., Karl, D.M., Michaels, A.F., Porter, J.H., Townsend, A.R., Vörösmarty, C.J. (2003) Nitrogen cycles: past, present, and future. *Biogeochemistry*, 70, 153–226.

Gaudnik, C., Corcket, E., Clément, B., Delmas, C.J.E.L., Gombert-Courvoisier, S., Muller, S., Stevens, C.J., Alard, D. (2011) Detecting the footprint of changing atmospheric nitrogen deposition loads on acid grasslands in the context of climate change. *Global Change Biology*, 17, 3351–3365.

Gedalof, Z., and Berg, A.A. (2010) Tree ring evidence for limited direct CO_2 fertilization of forests over the 20th century. *Global Biogeochemical Cycles*, 24, GB3027.

Genet, H., Bréda, N., Dufrene, E. (2010) Age-related variation in carbon allocation at tree and stand scales in beech (*Fagus sylvatica* L.) and sessile oak (*Quercus petraea* (Matt.) Liebl.) using a chronosequence approach. *Tree Physiology*, 30, 177–192.

Gentilesca, T., Rita, A., Brunetti, M., Giammarchi, F., Leonardi, S., Magnani, F., van Noije, T., Tonon, G., Borghetti, M. (2018) Nitrogen deposition outweighs climatic variability in driving annual growth rate of canopy beech trees: Evidence from long-term growth reconstruction across a geographic gradient. *Global Change Biology*, 24, 2898–2912.

Geßler, A., Keitel, C., Kreuzwieser, J., Matyssek, R., Seiler, W., Rennenberg, H. (2007) Potential risks for European beech (*Fagus sylvatica* L.) in a changing climate. *Trees*, 21, 1–11.

Glaser, F.F., and Hauke, U. (2004) Historisch alte Waldstandorte und Hudewälder in Deutschland: Ergebnisse bundesweiter Auswertungen. BfN-Schr.-Vertrieb im Landwirtschaftsverlag, Münster, Germany.

Gómez-Baggethun, E., de Groot, R., Lomas, P.L., Montes, C. (2010) The history of ecosystem services in economic theory and practice: From early notions to markets and payment schemes. *Ecological Economics*, 69, 1209–1218.

Grace, J.B., Anderson, T.M., Oleff, H., Scheiner, S.M. (2010) On the specification of structural equation models for ecological systems. *Ecological Monographs*, 80, 67–87.

Grace, J.B., Schoolmaster, Jr. D.R., Guntesperger, G.R., Little, A.M., Mitchell, B.R., Miller, K.M., Schweiger, E.W. (2012) Guidelines for a graph-theoretic implentation of structural equation modeling. *Ecosphere*, 3, Article 73.

Greaver, T.L., Clark, C.M., Compton, J.E., Vallano, D., Talhelm, A.F., Weaver, C.P., Band, L.E., Baron, J.S., Davidson, E.A., Tague, C.L., Felker-Quinn, E., Lynch, L.A., Herrick, J.D., Liu, L., Goodale, C.L., Novak, K.J., Haeuber, R.A. (2016) Key ecological responses to nitrogen are altered by climate change. *Nature Climate Change*, 6, 836–843.

Greenwood, S., Ruiz-Benito, P., Martínez-Vilalta, J., Lloret, F., Kitzberger, T., Allen, C.D., Fensham, R., Laughlin, D.C., Kattge, J., Bönisch, G., Kraft, N.J.B., Jump, A.S. (2017) Tree mortality across biomes is promoted by drought intensity, lower wood density and higher specific leaf area. *Ecology Letters*, 20, 539–553.

Hacket-Pain, A.J., Friend, A.D., Lageard, J.A., Thomas, P.A. (2015) The influence of masting phenomenon on growth–climate relationships in trees: explaining the influence of previous summers' climate on ring width. *Tree Physiology*, 35, 319–330.

Hacket-Pain, A.J., Cavin, L., Friend, A.D., Jump, S. (2016) Consistent limitation of growth by high temperature and low precipitation from range core to southern edge of European beech indicates widespread vulnerability to changing climate. *European Journal of Forest Research*, 135, 897–909.

Hacket-Pain, A.J., Ascoli, D., Vacchiano, G., Biondi, F., Cavin, L., Conedera, M., Drobyshev, I., Liñán, I.D., Friend, A.D., Grabner, M., Hartl, C., Kreyling, J., Lebourgeois, F., Levanič, T., Menzel, A., van der Maaten E., van der Maaten-Theunissen, M., Muffler, L., Motta, R., Roibu, C.-C., Popa, I., Scharnweber, T., Weigel, R., Wilmking, M., Zang, C.S. (2018) Climatically controlled reproduction drives interannual growth variability in a temperate tree species. *Ecology Letters*, 21, 1833–1844.

Härdtle, W., Ewald, J., Hölzel, N. (2008) Wälder des Tieflandes und der Mittelgebirge, Ulmer, Stuttgart, Germany.

Härdtle, W., Niemeyer, T., Assmann, T., Baiboks, S., Fichtner, A., Friedrich, U., Lang, A.C., Neuwirth, B., Pfister, L., Ries, C., Schuldt, A., Simon, N., von Oheimb, G. (2013) Long-term trends in tree-ring width hand isotope signatures ($\delta^{13}C$, $\delta^{15}N$) of *Fagus sylvatica* L. on soils with contrasting water supply. *Ecosystems*, 16, 1413–1428.

Harris, I., Jones, P.D., Osborn, T.J., Lister, D.H. (2014) Updated high-resolution grids of monthly climatic observations – the CRU TS3.10 Dataset. *International Journal of Climatology*, 34, 623–642.

Hartmann, M., Niklaus, P.A., Zimmermann, S., Schmutz, S., Kremer, J., Abarenkov, K., Lüscher, P., Widmer, F., Frey, B. (2014) Resistance and resilience of the forest soil microbiome to logging-associated compaction. *The ISME Journal*, 8, 226–244.

Hedges, L.V., and Olkin, I. (1985) Statistical Methods for Meta-analysis. Academic Press, San Diego, US.

Helgason, T., Daniell, T.J., Husband, R., Fitter, A.H., Young, J.P.W. (1998) Ploughing up the wood-wide web? *Nature*, 394, 431.

Hentschel, R., Hommel, R., Poschenrieder, W., Grote, R., Holst, J., Biernath, C., Gessler, A., Priesack, E. (2016). Stomatal conductance and intrinsic water use efficiency in the drought year 2003: a case study of European beech. *Trees*, 30, 153–174.

Hertel, D., Strecker, T., Müller-Haubold, H., Leuschner, C. (2013) Fine root biomass and dynamics in beech forests across a precipitation gradient – is optimal resource partitioning theory applicable to water-limited mature trees? *Journal of Ecology*, 101, 1183–1200.

Hess, C., Niemeyer, T., Fichtner, A., Jansen, K., Kunz, M., Maneke, M., von Wehrden, H., Quante, M., Walmsley, D., von Oheimb, G., Härdtle, W. (2018) Anthropogenic nitrogen deposition alters growth responses of European beech (*Fagus sylvatica* L.) to climate change. *Environmental Pollution*, 233, 92–98.

Hoffmann, G. (1997) VDLUFA Methodenbuch Band I: Die Untersuchung von Böden. 4th Edition, Darmstadt, Germany.

Holmes, R.L. (1983) Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bulletin*, 43, 69–78.

Huang, B., and Eissenstat D.M. (2000) Root plasticity in exploiting water and nutrient heterogeneity, In: Wilkinson, R.E. (ed.) Plant-Environment Interaction, Vol. 2, Marcel Dekker Inc., New York, US.

IPCC (2013) Summary for Policymakers. In: T.F. Stocker et al. (eds.) Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, US.

Jax, K. (2005) Function and "functioning" in ecology: what does it mean? *OIKOS*, 111, 641–648.

Johnstone, J.F., Allen, C.D., Franklin, J.F., Frelich, L.E., Harvey, B.J., Higuera, P.E., Mack, M.C., Meentemeyer, R.K., Metz, M.R., Perry, G.L.W., Schoennagel, T., Turner, M.G. (2016) Changing disturbance regimes, ecological memory, and forest resilience. *Frontiers in Ecology and the Environment*, 14, 369–378.

Jump, A.S., Ruiz-Benito, P., Greenwood, S., Allen, C.D., Kitzberger, T., Fensham, R., Martínez-Vilalta, J., Lloret, F. (2017) Structural overshoot of tree growth with climate variability and the global spectrum of drought induced forest dieback. *Global Change Biology*, 23, 3742–3757.

Keenan, T.F., Gray, J., Friedl, M.A., Toomey, M., Bohrer, G., Hollinger, D.Y., Munger, J.W., O'Keefe, J., Schmid, H.P., Wing, I.S., Yang, B., Richardson, A.D. (2014) Net carbon uptake has increased through warming induced changes in temperate forest phenology. *Nature Climate Change*, 4, 598–604.

Keenan, R.J. (2015) Climate change impacts and adaptation in forest management: a review. *Annals of Forest Science*, 72, 145–167.

Kelly, D. (1994) The evolutionary ecology of mast seeding. *TREE*, 9, 465–470.

Kline, R.B. (2014) Principles and practice of structural equation modeling. Guilford Press, New York, US.

Knapp, H.D., Emde, F.-A., Engels, B., Lehrke, S., Hendrischke, O., Klein, M., Kluttig, H., Krug, A., Schäfer, H.-J., Scherfrose, V., Schröder, E., Schweppe-Kraft (2008) Naturerbe Buchenwälder – Situationsanalyse und Handlungserfordernisse. In: Knapp, H.D. (ed.) BfN-Skripten, Bonn-Bad Godesberg, Germany.

Knutzen, F., Dulamsuren, C., Meier, I.C., Leuschner, C. (2017) Recent climate warming-related growth decline impairs European beech in the center of its distribution range. *Ecosystems*, 20, 1494–1511.

Köcher, P., Gebauer, T., Horna, V., Leuschner, C. (2009) Leaf water status and stem xylem flux in relation to soil drought in five temperate broad-leaved tree species with contrasting water use strategies. *Annals of Forest Science*, 66, 101.

Köcher, P., Horna, V., Leuschner, C. (2012) Environmental control of daily stem growth patterns in five temperate broad-leaved tree species. *Tree Physiology*, 32, 1021–1032.

Kopecký, M., and Vojta, J. (2009) Land use legacies in post-agricultural forests in the Doupovské Mountains, Czech Republic. *Applied Vegetation Science*, 12, 251–260.

Koricheva, J., Gurevitch, J., Mengersen, K. (eds.) (2013) Handbook of Meta-Analysis in Ecology and Evolution. Princeton University Press, Princeton, US.

Kramer-Walter, K.R., Bellingham, P.J., Millar, T.R., Smissen, R.B., Richardson, S.J., Laughlin, D.C. (2016) Root traits are multidimensional: specific root length is independent from root tissue density and the plant economic spectrum. *Journal of Ecology*, 104, 1299–1310.

Kunz, J., Löffler, G., Bauhus, J. (2018) Minor European broadleaved tree species are more drought-tolerant than *Fagus sylvatica* but not more tolerant than *Quercus petraea*. *Forest Ecology and Management*, 414, 15–27.

Lang, F., Bauhus, J., Frossard, E., George, E., Kaiser, K., Kaupenjohann, M., Krüger, J., Matzner, E., Polle, A., Prietzel, J., Rennenberg, H., Wellbrock N. (2016) Phosphorus in forest ecosystems: new insights from an ecosystem nutrition perspective. *Journal of Plant Nutrition and Soil Sciences*, 179, 129–135.

Latif, Z.A., and Blackburn, G.A. (2010) The effects of gap size on some microclimate variables during late summer and autumn in a temperate broadleaved deciduous forest. *International Journal of Biometeorology*, 54, 119–129.

Law, B. (2013) Nitrogen deposition and forest carbon. *Nature*, 496, 307–308.

Lebourgeois, F., Eberlé, P., Mérian, P., Seynave, I. (2014) Social status-mediated tree-ring responses to climate of *Abies alba* and *Fagus sylvatica* shift in importance with increasing stand basal area. *Forest Ecology and Management*, 328, 209–218.

Lebourgeois, F., Delpierre, N., Dufrêne, E., Cecchini, S., Macé, S., Croisé, L., Nicolas, M. (2018) Assessing the roles of temperature, carbon inputs and airborne pollen as drivers of fructification in European temperate deciduous forests. *European Journal of Forest Research*, 137, 349–365.

Lefcheck, J.S. (2018) piecewiseSEM: Piecewise Structural Equation Modeling in R, version 2.0. http://CRAN.R-project.org/package=piecewiceSEM.

Lemoine, D., Jacquemin, S., Granier, A. (2002) Beech (*Fagus sylvatica* L.) branches show acclimation of xylem anatomy and hydraulic properties to increased light after thinning. *Annals of Forest Science*, 59, 761–766.

Leuschner, C., Backes, K., Hertel, D., Schipka, F., Schmitt, U., Terborg, O., Runge, M. (2001) Drought responses at leaf, stem and fine root levels of competitive *Fagus sylvatica* L. and *Quercus petraea* (Matt.) Liebl. Trees in dry and wet years. *Forest Ecology and Management*, 149, 33–46.

Leuschner, C., Hertel, D., Schmid, I., Koch, O., Muhs, A., Hölscher, D. (2004) Stand fine root biomass and fine root morphology in old-growth beech forests as a function of precipitation and soil fertility. *Plant and Soil*, 258, 43–56.

Leuschner, C., Wulf, M., Bäuchler, P., Hertel, D. (2014) Forest continuity as a key determinant of soil carbon and nutrient storage in beech forests on sandy soils in Northern Germany. *Ecosystems*, 17, 497–511.

Leuschner, C., and Ellenberg, H. (2017) Ecology of Central European Forests: Vegetation Ecology of Central Europe, Vol. 1. Springer, Switzerland.

Leuschner, C., and Meier, I.C. (2018) The ecology of Central European tree species: Trait spectra, functional trade-offs, and ecological classification of adult trees. *Perspectives in Plant Ecology, Evolution and Systematics*, 33, 89–103.

Lindner, M., Maroschek, M., Netherer, S., Kremer, A., Barbati, A., Garcia-Gonzalo, J., Seidl, R., Delzon, S., Corona, P., Kolström, M., Lexer, M.J., Marchetti M. (2010) Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. *Forest Ecology and Management*, 259, 698–709.

Lloret, F., Keeling, E.G., Sala, A. (2011) Components of tree resilience: effects of successive low-growth episodes in old ponderosa pine forests. *OIKOS*, 120, 1909–1920.

LLUR (2010) Atmosphärische Stoffeinträge in Schleswig-Holstein 2009 – Lufthygienische Überwachung Schleswig-Holstein. Landesamt für Landwirtschaft, Umwelt und ländliche Räume des Landes Schleswig-Holstein, Lufthygienische Überwachung, Itzehoe, Germany.

Luyssaert, S., Marie, G., Valade, A., Chen, Y.-Y., Dojomo, S.N., Ryder, J., Otto, J., Naudts, K., Lansø, A.S., Ghattas, J., McGarth, M.J. (2018) Trade-offs in using European forests to meet climate objectives. *Nature*, 562, 259–262.

Maes, S.L., Perring, M.P., Vanhellemont, M., Depauw, L., van den Bulke, J., Brümelis, G., Brunet, J., Decocq, G., den Ouden, J., Härdtle, W., Hédl, R., Heinken, T., Heinrichs, S., Jaroszewicz, B., Kopecký, M., Máliš, F., Wulf, M.,Verheyen K. (2019) Environmental drivers interactively affect individual tree growth across temperate European forests. *Global Change Biology*, 25, 201–217.

Mausolf, K., Härdtle, W., Jansen, K., Delory, B.M., Hertel, D., Leuschner, C., Temperton, V.M., von Oheimb, G., Fichtner, A. (2018a) Legacy effects of land-use modulate tree growth responses to climate extremes. *Oecologia*, 187, 825–837.

Mausolf, K., Wilm, P., Härdtle, W., Jansen, K., Schuldt, B., Sturm, K., von Oheimb, G., Hertel, D., Leuschner, C., Fichtner A. (2018b). Higher drought sensitivity of radial growth of European beech in managed than in unmanaged forests. *Science of the Total Environment*, 642, 1201–1208.

McCormack, M.L., Adams, T.S., Smithwick, E.A.H., Eissenstat, D.M. (2012) Predicting fine root lifespan from plant functional traits in temperate trees. *New Phytologist*, 195, 823–831.

McDowell, N.G., Fisher, R.A., Xu, C., Domec, J.C., Hölttä, T., Mackay, D.S., Sperry, J.S., Boutz, A., Dickman, L., Gehres, N., Limousin, J.M., Macalady, A., Martínez-Vilalta, J., Mencuccini, M., Plaut, J.A., Ogée, J., Pangle, R.E., Rasse, D.P., Ryan, M.G., Sevanto, S., Waring, R.H., Williams, A.P., Yepez, E.A., Pockman, W.T. (2013) Evaluating theories of drought induced vegetation mortality using a multimodel-experiment framework. *New Phytologist*, 200, 304–321.

MEA (2005) Ecosystems and Human Well-being: Biodiversity Synthesis. World Resources Institute, Washington, DC, US.

Meier, I.C., Knutzen, F., Eder, L.M., Müller-Haubold, H., Göbel, M., Bachmann, J., Hertel, D., Leuschner, C. (2017) The deep root system of *Fagus sylvatica* on sandy soil: structure and variation across a precipitation gradient. *Ecosystems*, 21, 280–296.

Metz, J., Annighöfer, P., Schall, P., Zimmermann, J., Kahl, T., Schulze, E.-D., Ammer, C. (2016) Site-adapted admixed tree species reduce drought susceptibility of mature European beech. *Global Change Biology*, 22, 903–920.

Meyer-Grünefeldt, M., Friedrich, U., Klotz, M., von Oheimb, G., Härdtle, W. (2013) Nitrogen deposition and drought events have non-additive effects on plant growth evidence from greenhouse experiments. *Plant Biosystems*, 149, 424–432.

Meyer-Grünefeldt, M., Calvo, L., Marcos, E., von Oheimb, G., Härdtle, W. (2015) Impacts of drought and nitrogen addition on *Calluna* heathlands differ with plant life-history stage. *Journal of Ecology*, 103, 1141–1152.

Michel, A., Seidling, W., Prescher, A.-K., (eds.) (2018) Forest Condition in Europe: 2018 Technical Report of ICP Forests. Report under the UNECE Convention on long-range transboundary air pollution (Air Convention). BFW-Dokumentation 25/2018 BFW Austrian Research Centre for Forests, Vienna, Austria.

Millard, P., and Grelet, G.-A. (2010) Nitrogen storage and remobilization by trees: ecophysiological relevance in a changing world. *Tree Physiology*, 30, 1083–1095.

Miyazaka, Y., Maruyama, Y., Chiba, Y., Kobayashi, M.J., Joseph, B., Shimizu, K.K., Mochida, K., Hiura, T., Kon, H., Satake A. (2014) Nitrogen as a key regulator of flowering in *Fagus crenata*: understanding the physiological mechanism of masting by gene expression analysis. *Ecology Letters*, 17, 1299–1309.

Mölder, I., and Leuschner, C. (2014) European beech grows better and is less drought sensitive in mixed than in pure stands: tree neighbourhood effects on radial increment. *Trees*, 28, 777–792.

Mommer, L., and Weemstra, M. (2012) The role of roots in the resource economics spectrum. *New Phytologist*, 195, 725–727.

Müller, A. (2007) Jahrringanalytische Untersuchungen zum Informationsgehalt von Holzkohle-Rückständen der historischen Meilerköhlerei. PhD thesis, Albert Ludwigs University of Freiburg, Freiburg, Germany.

Müller-Haubold, H., Hertel, D., Seidel, D., Knutzen, F., Leuschner, C. (2013) Climate responses of aboveground productivity and allocation in *Fagus sylvatica*: a transect study in mature forests. *Ecosystems*, 16, 1498–1516.

Müller-Haubold, H., Hertel, D., Leuschner, C. (2015) Climatic drivers of mast fruiting in European beech and resulting C and N allocation shifts. *Ecosystems*, 18, 1083–1100.

Mund, M., Kutsch, W.L., Wirth, C., Kahl, T., Knohl, A., Skomarkova, M.V., Schulze, E.-D. (2010) The influence of climate and fructification on the inter-annual variability of stem growth and net primary productivity in an old-growth, mixed beech forest. *Tree Physiology*, 30, 689–704.

Naudts, K., Chen, Y., McGrath, M.J., Ryder, J., Valade, A., Otto, J., Luyssaert, S. (2016) Europe's forest management did not mitigate climate warming. *Science*, 351, 597–600.

Niinemets, U. (2010) A review of light interception in plant stands from leaf to canopy in different plant functional types and in species with varying shade tolerance. *Ecological Research*, 25, 693–714.

Norby, R.J., Warren, J.M., Iversen, C.M., Medlyn, B.E., McMurtie, R.E. (2010) CO_2 enhancement of forest productivity constrained by limited nitrogen availability. *PNAS*, 107, 19368–19373.

Noyer, E., Lachenbruch, B., Dlouha, J., Collet, C., Ruelle, J., Ningre, F., Fournier, M. (2017) Xylem traits in European beech (*Fagus sylvatica* L.) display a large plasticity in response to canopy release. *Annals of Forest Science*, 74, 46.

Nussbaumer, A., Waldner, P., Aputhin, V., Aytar, F., Benham, S., Bussotti, F., Eichhorn, J., Eickenscheidt, N., Fabianek, P., Falkenried, L., Leca, S., Lindgren, M., Manzano Serrano, M.J., Neagu, S., Nevalainen, S., Pajtik, J., Potočik, N., Rautio, P., Sioen, G., Stakėnas, V., Tasdemir, C., Thomsen, I.M., Timmermann, V., Ukonmaanaho, L., Verstraeten, A., Wulff, S., Gessler A. (2018) Impact of weather cues and resource dynamics on mast occurrence in the main forest tree species in Europe. *Forest Ecology and Management*, 429, 336–350.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Michin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.M, Szoecs, E., Wagner, H. (2016) vegan: Community Ecology Package. R package, version 2.4-0. https://CRAN.R-project.org/package=vegan.

Ostonen, I., Helmisaari, H.-S., Borken, W., Tedersoo, L., Kukumägi, M., Bahram, M., Lindroos, A.-J., Nöjd, P., Uri, V., Merlä, P., Asi, E., Lõhmus, K. (2011) Fine root foraging strategies in Norway spruce forests across a European climate gradient. *Global Change Biology*, 17, 3620–3632.

Övergaard, R., Gemmel, P., Karlsson, M. (2007) Effects of weather conditions on mast year frequency in beech (*Fagus sylvatica* L.) in Sweden. *Forestr*y, 80, 555–565.

Ozbay, G., Khatiwada, R., Chintapenta, L.K., Handy, E.F., Smith, S.L. (2016) Sustainable farm practice: study of total and soluble phosphorus in a poultry farm equipped with heavy use area protection pads, Dover, Delaware. *Professional Agricultural Workers Journal*, 4, 1–17.

Paar, U., Guckland, A., Dammann, I., Albrecht, M., Eichhorn, J. (2011) Häufigkeit und Intensität der Fruktifikation der Buche. *AFZ-DerWald*, 6, 26–29.

Packham, J.R., Thomas, P.A., Atkinson, M.D., Degen, T. (2012) Biological flora of the British Isles: *Fagus sylvatica*. *Journal of Ecology*, 100, 1557–1608.

Pearse, I.S., Koenig, W.D., Kelly, D. (2016) Mechanisms of mast seeding: resources, weather, cues, and selection. *New Phytologist*, 212, 546–562.

Perring, M.P., De Frenne, P., Baeten, L., Maes, S.L., Depauw, L., Blondeel, H., Carón, M.M., Verheyen, K. (2016) Global environmental change effects on ecosystems: the importance of land-use legacies. *Global Change Biology*, 22, 1361–1371.

Perring, M.P., Bernhardt-Römermann, M., Baeten, L., Midolo, G., Blondeel, H., Depauw, L., Landuyt, D., Meas, S.L., De Lombaerde, E., Carón, M.M., Vellend, M., Brunet, J., Chudomelová, M., Decocq, G., Diekmann, M., Dirnböck, T., Dörfler, I., Durak, T., De Frenne, P., Gilliam, F.S., Hédl, R., Heinken, T., Hommel, P., Jaroszewicz, B., Kirby, K.J., Kopecký, M., Lenoir, J., Li, D., Máliš, F., Mitchell, F.J.G., Naaf, T., Newman, T., Petřík, P., Rectyńska, K., Schmidt, W., Standovár, T., Świerkosz, K., Van Calster, H., Vild, O., Wagner, E.R., Wulf, M., Verheiyen, K. (2018) Global environmental change effects on plant community composition trajectories depend upon management legacies. *Global Change Biology*, 24, 1722–1740.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., R Core Team (2016) nlme: linear and nonlinear mixed effects models. R package version 3.1-128, http://CRAN.R-project.org/package=nlme

Rambo, T.R., and North, M.P. (2009) Canopy microclimate response to pattern and density of thinning in a Sierra Nevada forest. *Forest Ecology and Management*, 257, 435–442.

Reich, P.B. (2014) The world-wide 'fast–slow' plant economics spectrum: a traits manifesto. *Journal of Ecology*, 102, 275–301.

Reyer, C., Lasch-Born, P., Suckow, F., Gutsch, M., Murawski, A., Pilz, T. (2014) Projections of regional changes in forest net primary productivity for different tree species in Europe driven by climate change and carbon dioxide. *Annals of Forest Science*, 71, 211–225.

Rockström, J., Steffen, W., Noone, K., Persson, Å., Chapin III, F.S., Lambin, E., Lanton, T.M., Scheffer, M., Folke, C., Schellnhuber, H.J., Nykvist, B., de Wit, C.A., Hughes, T., van der Leeuw, S., Rodhe, H., Sörlin, S., Snyder, P.K., Costanza, R., Svedin, U., Falkenmark, M., Karlberg, L., Corell, R.W., Fabry, V.J., Hansen, J., Walker, B., Liverman, D., Richardson, K., Crutzen, P., Foley, J. (2009) Planetary boundaries: Exploring the Safe Operating Space for Humanity. *Ecology and Society*, 14, 32.

Rosseel, Y. (2012) lavaan: an R package for structural equation modeling. *Journal of Statistical Software*, 48, 1–36.

Roumet, C., Birouste, M., Picon-Cochard, C., Ghestem, M., Osman, N., Vrigon-Brenas, S., Cao, K.-f., Stokes, A. (2016) Root structure-function relationships in 74 species: evidence of a root economics spectrum related to carbon economy. New Phytologist, 210, 815–826.

Sala, O.E., Chapin III, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M., Wall, D.H. (2000) Global diversity scenarios for the year 2100. *Science*, 287, 1170–1774.

San-Miguel-Ayanz, J., Durrant, T., Boca, R., Libertà, G., Branco, A., de Rigo, D., Ferrari, D., Maianti, P., Vivancos, T.A., Costa, H., Lana, F., Löffler,P., Nuijten, D., Ahlgren, A.C., Leray, T. (2018) Forest Fires in Europe, Middle East and North Africa 2017. Joint Research Centre, Ispra, Italy.

Scharnweber, T., Manthey, M., Criegee, C., Bauwe, A., Schröder, C. (2011) Drought matters – Declining precipitation influences growth of *Fagus sylvatica* L. and *Quercus robur* L. in north eastern Germany. *Forest Ecology and Management*, 262, 947–961.

Schenk, H.J. (2005) Vertical vegetation structure below ground: scaling from root to globe. *Progress in Botany*, 66, 341–373.

Schulte-Uebbing, L., and De Vries, W. (2018) Global-scale impacts of nitrogen deposition on tree carbon sequestration in tropical, temperate and boreal forests: A meta-analysis. *Global Change Biology*, 24, e416–e431.

Simard, S.W., Beiler, K.J., Bingham, M.A., Deslippe, J.R., Philip, L.J., Teste, F.P. (2012) Mycorrhizal networks: Mechanisms, ecology and modelling. *Fungal Biology Reviews*, 26, 39–60.

Skomarkova, M.V., Vaganov, E.A., Mund, M., Knohl, A., Linke, P., Boerner, A., Schulze, E.-D. (2006) Inter-annual and seasonal variability of radial growth, wood density and carbon isotope ratios in tree rings of beech (*Fagus sylvatica*) growing in Germany and Italy. *Trees*, 20, 571–586.

Smaill, S.J., Clinton, P.W., Allen, R.B., Davis, M.R. (2011) Climate cues and resources interact to determine seed production by a masting species. *Journal of Ecology*, 99, 870–877.

SOFO (2014) State of the World's Forests: Enhancing the socioeconomic benefits from forests. FAO, Rome, Italy.

SOFO (2018) State of the World's Forests: Forest pathways to sustainable development. FAO, Rome, Italy.

Sohn, J.A., Hartig, F., Kohler, M., Huss, J., Bauhus, J. (2016) Heavy and frequent thinning promotes drought adaptation in *Pinus sylvestris* forests. *Ecological Applications*, 26, 2190–2205.

Steinkamp, J., and Hickler, T. (2015) Is drought-induced forest dieback globally increasing? *Journal of Ecology*, 103, 31–43.

Steubing, L., and Fangmeier, A. (1992) Pflanzenökologisches Praktikum. Parey Verlag, Berlin, Germany.

Sturm, K. (1993) Prozeßschutz – ein Konzept für naturschutzgerechte Waldwirtschaft. *Zeitschrift für Ökologie und Naturschutz*, 2, 182–192.

Sutton, M.A., Howard, C.M., Erisman, J.W., Billen, G., Bleeker, A., Grennfeldt, P., van Grinsven, H., Grizzetti (eds.) (2011) The European nitrogen assessment: sources, effects, and policy perspectives. University Press, Cambridge, UK.

Temperton, V.M., Millard, P., Jarvis, P.G. (2003) Does elevated atmospheric carbon dioxide affect internal nitrogen allocation in the temperate trees *Alnus glutinosa* and *Pinus sylvestris*? *Global Change Biology*, 9, 286–294.

Thornley, J.H.M. (1972) A balanced quantitative model for root: shoot ratios in vegetative plants. *Annals of Botany*, 36, 431–441.

Tyree, M.T. (2003) Plant hydraulics: The ascent of water. *Nature*, 423, 923.

UBA Umweltbundesamt (2014) Modelling and mapping of atmospheric nitrogen and sulphur deposition and critical loads for ecosystem assessment of threats to biodiversity in Germany – PINETI (Pollutant INput and EcosysTem Impact). *UBA Texte 60*, Dessau-Roßlau, Germany.

UNESCO (2017) Decisions adopted during the 41st session of the World Heritage Committee, Krakow, Poland.

Van der Linde, S., Suz, L.M., Orme, C.D.L., Cox, F., Andreae, H., Asi, E., Atkinson, B., Benham, S., Carroll, C., Cools, N., De Vos, B., Dietrich, H.-D., Eichorn, J., Gehrmann, J., Grebenc, T., Gweon, H.S., Hansen, K., Jacob, F., Kristöfel, F., Lech, P., Manninger, M., Martin, J., Meesenburg, H., Merilä, P., Nicolas, M., Pavlenda, P., Rautio, P., Schaub, M., Schröck, H.-W., Seidling, W., Šrámek, V., Thimonier, A., Thomsen, I.M., Titeux, H., Vanguelova, E., Verstraeten, A., Vesterdal, L., Waldner, P., Wijk, S., Zhang, Y., Žlindra, D., Bidartondo, M.I. (2018) Environment and host as large-scale controls of ectomycorrhizal fungi. *Nature*, 558, 243–250.

Venables, W.N., and Ripley, B.D. (2002) Modern applied statistics with S. Fourth Edition. Springer, New York, US.

Vincente- Serrano, S.M., Beguería, S., López-Moreno, J.I., Angulo, M., El Kenawy, A. (2010) A new global 0.5° gridded dataset (1901-2006) of a multiscalar drought index: comparison with current drought index datasets based on the Palmer Drought Severity Index. *Journal of Hydrometeorology*, 11, 1033–1043.

Von Oheimb, G., Härdtle, W., Naumann, P.S., Westphal, C., Assmann, T., Meyer, H. (2008) Long-term effects of historical heathland farming on soil properties of forest ecosystems. *Forest Ecology and Management*, 255, 1984–1993.

Von Oheimb, G., Härdtle, W., Eckstein, D., Engelke, H.-H., Hehnke, T., Wagner, B., Fichtner, A. (2014) Does forest continuity enhance the resilience of trees to environmental change? *PLOS ONE*, 9, 1–18, e113507.

Wagner, S., Collet, C., Madsen, P., Nakashizuka, T., Nyland, R.D., Sagheb-Talebi, K. (2010) Beech regeneration research: from ecological to silvicultural aspects. *Forest Ecology and Management*, 259, 2172–2182.

Watson, J.E.M., Evans, T., Venter, O., Williams, B., Tulloch, A., Stewart, C. Thompson, I., Ray, J.C., Murray, K., Salazar, A., McAlpine, C., Potapov, P., Walston, J., Robinson, J.G., Painter, M., Wilkie, D., Filardi, C., Laurance, W.F., Houghton, R.A., Maxwell, S., Grantham, H., Samper, C., Wang, S., Laestadius, L., Runting, R.K., Silva-Chávez, G.A., Ervin, J., Lindenmayer, D. (2018) The exceptional value of intact forest ecosystems. *Nature Ecology & Evolution*, 2, 599–610.

Weemstra, M., Mommer, L., Visser, E.J.W., van Ruijven, J., Kuyper, T.W., Mohren, G.M.J., Sterck, F.J. (2016) Towards a multidimensional root trait framework: a tree root review. *New Phytologist*, 211, 1159–1169.

Westphal, C., Härdtle, W., von Oheimb, G. (2004) Forest History, Continuity and Dynamic Naturalness. In: Honnay, O., Verheyen, K.; Bossuyt, B., Hermy, M. (eds.): Forest Biodiversity: Lessons from History for Conservation. CAB International, Wallingford, UK.

Williams, A.P., Allen, C.D., Macalady, A.K., Griffin, D., Woodhouse, C.A., Meko, D.M., Swetman, T.W., Rauscher, S.A., Seager, R., Grissino-Mayer, H.D., Dean, J.S., Cook, E.R., Gangodagamage, C., Cai, M., McDowell, N.G. (2013) Temperature as a potent driver of regional forest drought stress and tree mortality. *Nature Climate Change*, 3, 292–297.

Yuan, Z.Y., and Chen, H.Y.H. (2010) Fine root biomass, production, turnover rates, and nutrient contents in boreal forest ecosystems in relation to species, climate, fertility, and stand age: literature review and meta-analyses. *Critical Reviews in Plant Science*, 29, 204–221.

Zang, C., Hartl-Meier, C., Dittmar, C., Rothe, A., Menzel, A. (2014) Patterns of drought tolerance in major European temperate forest trees: climatic drivers and levels of variability. *Global Change Biology*, 20, 3767–3779.

Zavaleta, E.S., Shaw, M.R., Chiariello, N.R., Mooney, H.A., Field, C.B. (2003) Additive effects of simulated climate changes, elevated CO_2, and nitrogen deposition on grassland diversity. *PNAS*, 100, 7650–7654.

Zeller, L. Ammer, C., Annighöfer, P., Biber, P., Marshall, J., Schütze, G., del Río Gaztelurrutia, M., Pretzsch, H. (2017) Tree ring wood density of Scots pine and European beech lower in mixed–species stands compared with monocultures. *Forest Ecology and Management*, 400, 363–374.

Zimmermann, J., Hauck, M., Dulamsuren, C., Leuschner, C. (2015) Climate warming-related growth decline affects *Fagus sylvatica*, but not other broad-leaved tree species in central European mixed forests. *Ecosystems*, 18, 560–572.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M. (2009) Mixed effects models and extensions in ecology with R. Springer, New York, USA.

Zuur, A.F., Ieno, E.N., Elphick, C.S. (2010) A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, 1, 3–14.

APPENDIX

List of publications

Mausolf, K., Härdtle, W., Jansen, K., Delory, B.M., Hertel, D., Leuschner, C., Temperton, V.M., von Oheimb, G., Fichtner, A. (2018a) Legacy effects of land-use modulate tree growth responses to climate extremes. *Oecologia*, 187, 825–837.

Mausolf, K., Wilm, P., Härdtle, W., Jansen, K., Schuldt, B., Sturm, K., von Oheimb, G., Hertel, D., Leuschner, C., Fichtner A. (2018b) Higher drought sensitivity of radial growth of European beech in managed than in unmanaged forests. *Science of the Total Environment*, 642, 1201–1208.

Mausolf, K., Härdtle, W., Hertel, D., Leuschner, C., Fichtner, A. (2019) Impacts of multiple environmental change drivers on growth of European beech (*Fagus sylvatica*): forest history matters. *Ecosystems*, https://doi.org/10.1007/s10021-019-00419-0

Article overview and authors' contribution to articles

Table D1. Overview of the articles in this thesis, my contribution, article publication status, and the authors' contribution to each article.

	Article		
	I	II	III
Title	Legacy effects of land-use modulate tree growth responses to climate extremes	Higher drought sensitivity of radial growth of European beech in managed than in unmanaged forests	Impacts of multiple global change drivers on growth of European beech (*Fagus sylvatica*): forest history matters
Journal (Impact factor)	Oecologia (3.127)	Science of the Total Environment (4.610)	Ecosystems (4.030)
Publication status	Published	Published	Published
Weighting factor for my contribution	predominant contribution (1.0)	predominant contribution (1.0)	predominant contribution (1.0)
Specific contribution of all authors			
Research question and design	KM, AF, WH, GvO, CL, VMT	KM, CL, DH, BS, KS, AF	KM, AF, CL, WH
Study design	KM, WH, DH	KM, AF, BS	KM, DH
Data collection	KM	PW	KM
Data analysis	KM, AF, DH, BMD, KJ	KM, AF	KM, AF
Manuscript preparation	KM, AF	KM, AF	KM, AF
Textualisation	all authors	all authors	all authors

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Erklärung

Ich versichere, dass alle in diesem Anhang gemachten Angaben jeweils einzeln und insgesamt der Wahrheit entsprechen.

Kiel, 20.11.2019

(Katharina Mausolf)

Erklärungen und Versicherungen

Hiermit erkläre ich, dass ich mich noch keiner Doktorprüfung unterzogen oder mich um Zulassung zu einer solchen beworben habe.

Ich versichere, dass die Dissertation mit dem Titel "The importance of ecological continuity for ecosystem functions of beech forests" noch keiner Fachvertreterin bzw. Fachvertreter vorgelegen hat, ich die Dissertation nur in diesem und keinem anderen Promotionsverfahren eingereicht habe und, dass diesem Promotionsverfahren keine endgültig gescheiterten Promotionsverfahren vorausgegangen sind.

Ich versichere, dass ich die eingereichte Dissertation "The importance of ecological continuity for ecosystem functions of beech forests" selbstständig und ohne unerlaubte Hilfsmittel verfasst habe. Anderer als der von mir angegebenen Hilfsmittel und Schriften habe ich mich nicht bedient. Alle wörtlich oder sinngemäß anderen Schriften entnommenen Stellen habe ich kenntlich gemacht.

Kiel, 20.11.2019 __________________________

(Katharina Mausolf)