

# **The role of plant biodiversity in modifying the structure and functioning of higher trophic levels in species-rich forests**

Kumulative Habilitationsschrift  
zur Erlangung der *venia legendi*  
für das Fach Ökologie

von

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## Contents

Summary	1
Chapter 1: Introduction and overview	3
Chapter 2: Plant traits affecting herbivory on tree recruits in highly diverse subtropical forests	21
published as: Schuldt A, Bruelheide H, Durka W, Eichenberg D, Fischer M, Kröber W, Härdtle W, Ma K, Michalski S, Palm WU, Schmid B, Welk E, Zhou H, Assmann T (2012) Plant traits affecting herbivory on tree recruits in highly diverse subtropical forests. <i>Ecology Letters</i> 15: 732-739	
Chapter 3: Functional and phylogenetic diversity of woody plants drive herbivory in a highly diverse forest	43
published as: Schuldt A, Assmann T, Bruelheide H, Durka W, Eichenberg D, Härdtle W, Kröber W, Michalski SG, Purschke O (2014) Functional and phylogenetic diversity of woody plants drive herbivory in a highly diverse forest. <i>New Phytologist</i> 202: 864-873	
Chapter 4: Early positive effects of herbivory in a large-scale forest biodiversity experiment	61
submitted as: Schuldt A, Assmann T, Bruelheide H, Härdtle W, Li Y, Ma K, von Oheimb G, Zhang J: Early positive effects of herbivory in a large-scale forest biodiversity experiment	
Chapter 5: Woody plant phylogenetic diversity mediates bottom-up control of arthropod biomass in species-rich forests	73
published as: Schuldt A, Baruffol M, Bruelheide H, Chen S, Chi X, Wall M, Assmann T (2014) Woody plant phylogenetic diversity mediates bottom-up control of arthropod biomass in species-rich forests. <i>Oecologia</i> 176: 171-182	
Chapter 6: Predator diversity and abundance provide little support for the enemies hypothesis in forests of high tree diversity	99
published as: Schuldt A, Both S, Bruelheide H, Härdtle W, Schmid B, Zhou H, Assmann T (2011) Predator diversity and abundance provide little support for the enemies hypothesis in forests of high tree diversity. <i>PLoS ONE</i> 6: e22905	
Chapter 7: Predator assemblage structure and temporal variability of species richness and abundance in forests of high tree diversity	115
published as: Schuldt A, Bruelheide H, Härdtle W, Assmann T (2012) Predator assemblage structure and temporal variability of species richness and abundance in forests of high tree diversity. <i>Biotropica</i> 44: 793-800	

<p><b>Chapter 8:</b> Tree diversity promotes functional dissimilarity and maintains functional richness despite species loss in predator assemblages</p> <p>published as: Schuldt A, Bruelheide H, Durka W, Michalski SG, Purschke O, Assmann T (2014) Tree diversity promotes functional dissimilarity and maintains functional richness despite species loss in predator assemblages. <i>Oecologia</i> 174: 533-543</p>	<p>131</p>
<p><b>Chapter 9:</b> Tree diversity promotes predator but not omnivore ants in a subtropical Chinese forest</p> <p>published as: Staab M, Schuldt A, Assmann T, Klein AM (2014) Tree diversity promotes predator but not omnivore ants in a subtropical Chinese forest. <i>Ecological Entomology</i>, DOI: 10.1111/een.12143</p>	<p>151</p>
<p><b>Chapter 10:</b> Ant community structure during forest succession in a subtropical forest in South-East China</p> <p>submitted as: Staab M, Schuldt A, Assmann T, Bruelheide H, Klein AM (submitted) Ant community structure during forest succession in a subtropical forest in South-East China</p>	<p>171</p>
<p><b>Chapter 11:</b> Effects of ants on the functional composition of spider assemblages increase with tree species richness in a highly diverse forest</p> <p>submitted as: Schuldt A, Staab M (submitted) Effects of ants on the functional composition of spider assemblages increase with tree species richness in a highly diverse forest</p>	<p>193</p>
<p><b>Chapter 12:</b> Scale-dependent diversity patterns affect spider assemblages of two contrasting forest ecosystems</p> <p>published as: Schuldt A, Assmann T, Schaefer M (2013) Scale-dependent diversity patterns affect spider assemblages of two contrasting forest ecosystems. <i>Acta Oecologica</i> 49: 17-22</p>	<p>211</p>
<p><b>Chapter 13:</b> Non-native tree species (<i>Pseudotsuga menziesii</i>) strongly decreases predator biomass and abundance in mixed-species plantations of a tree diversity experiment</p> <p>published as: Schuldt A, Scherer-Lorenzen M (2014) Non-native tree species (<i>Pseudotsuga menziesii</i>) strongly decreases predator biomass and abundance in mixed-species plantations of a tree diversity experiment. <i>Forest Ecology and Management</i> 327: 10-17</p>	<p>223</p>
<p><b>Chapter 14:</b> General discussion and conclusions</p>	<p>243</p>

Authors' contributions to manuscripts with multiple authors	255
Acknowledgements	257
List of publications	259
Declaration	263



## Summary

Biodiversity loss is one of the major components of global change, affecting and threatening the functioning and service provisioning of ecosystems worldwide. Although much progress has been made over the last decades in understanding the relationships between biodiversity and ecosystem functioning (BEF), much of our knowledge stems from simplified or relatively low-diverse agricultural and grassland systems. More complex systems such as forests, which play a crucial role in regulating global biogeochemical cycles and mitigating climate change effects, have received less attention in the context of BEF research until recently. This applies particularly to subtropical and tropical forests, which contribute substantially to primary production, carbon sequestration and climate regulation, and which harbor a large part of terrestrial biodiversity. Importantly, the functioning and biodiversity maintenance of these forests are often considered to be strongly affected by trophic interactions. Trophic complexity is increasingly being recognized as a key determinant of biodiversity-ecosystem functioning relationships in many ecosystems. And yet, it is poorly explored how higher trophic levels and their interaction effects on the structure and functioning of ecosystems are altered by biodiversity loss in species-rich systems such as (sub)tropical forest, where these interaction effects may be particularly relevant.

The studies united in this thesis address major aspects of these shortcomings and analyze the impacts of plant diversity and its loss on the diversity and functional impact of, and the potential interactions among, key functional groups of primary (herbivores) and secondary consumers (predators) in forests—with a primary focus on highly diverse subtropical forests. Particular attention is given to (near)natural forests, as they have the advantage of providing insight into ecosystem functioning based on established communities of plants and animals under natural conditions. Experimental studies in tree diversity experiments are used to back up and verify the causality of important observational

results. The analyses in this thesis go beyond the effects of mere species richness and, where possible, incorporate functional and phylogenetic data of the producer or consumer assemblages to help unveil the potential mechanisms and evolutionary dependencies underlying biodiversity effects.

The studies presented in this thesis identify key plant functional traits and multivariate trait complexes that determine herbivory levels within and among woody plant species, and they show that the functional and phylogenetic diversity of woody plant communities strongly promotes herbivore damage—indicating a strong impact of generalist herbivores that benefit from dietary mixing of different plant species. The extent to which the distribution and diversity of key palatability and defense traits in plant communities are affected by changes in plant diversity thus strongly determine the strength of plant diversity effects on herbivory. Likewise, a strong impact of plant phylogenetic diversity and, at the same time, a lack of effect of plant species richness on herbivore biomass and abundance in the studied forests indicate that the diversity-dependence of herbivore-mediated ecosystem processes may fundamentally depend on nonrandom associations among plant and herbivore species. Scenarios of random species loss may thus underestimate the consequences for ecosystem functions if these scenarios do not reflect the driving forces of community assembly. In contrast to herbivores, overall patterns in predator abundance and diversity appear to be little affected by plant diversity in the studied forest systems. The results suggest that predator top-down control is not necessarily promoted by higher plant diversity, neither in species-rich subtropical forests nor in less diverse temperate forests. However, differential responses of predator functional diversity and species richness to changes in plant diversity highlight the complexity of diversity patterns even within individual trophic levels. The results of this thesis indicate that this complexity could lead, via intraguild interactions among predators, to plant

## 2 SUMMARY

diversity-mediated shifts in the functional structure of important predatory guilds. These shifts, in turn, could potentially influence the overall strength of predator top-down effects.

Altogether the results of this thesis point to an important role of plant diversity in regulating particularly herbivore assemblage patterns and in mediating plant-herbivore interactions at the levels of both individual plant species and entire plant communities in species-rich subtropical forests. Herbivores and their functional effects in these forests appear to be strongly affected by bottom-up effects of plant diversity, whereas predators show an overall weak relationship with plant diversity. While intraguild interactions among predators might complicate the analysis of this relationship, the general findings of this thesis challenge the commonly held view that, at least for many forest systems, plant diversity promotes predator top-down effects on dominant herbivores. Rather, the results are in line with the expectation that plant diversity effects become weaker with increasing trophic level. This, in turn, means that the positive effects of plant diversity on herbivores and

herbivore damage observed in the studied forests can be expected to cause direct feedbacks on the producer level. Higher damage on more common than rare plant species might lead to a positive feedback loop of bottom-up controlled herbivores on plant diversity maintenance, and increasing damage levels with increasing plant diversity at the community-level are likely to affect the way plant diversity impacts on processes such as primary production and nutrient cycling.

This thesis makes an important contribution to better understanding biodiversity and ecosystem function relationships across trophic levels in forests— aspects that are still underrepresented in BEF research. Ongoing biodiversity loss can be expected to change important trophic interaction pathways in these ecosystems, making increased efforts in exploring the mechanisms underlying, and the drivers determining, the impact of trophic complexity on the relationships between biodiversity and ecosystem functioning a crucial objective for holistic approaches to BEF research.



# CHAPTER 1

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# Introduction and overview

## 1.1 Background

Humans have a long history of strongly impacting on, and modifying, their environment, with new technological developments and population expansions over the last millennia having led to increasing pressures on ecosystems and their biota (Goudie 2013). However, human impact on the environment has accelerated and reached a new level during the last centuries. Exponential population growth, increased mobility, globalized economic markets and the concomitant high resource demands have caused land transformations, changes in biogeochemical cycles, and impacts on biodiversity on a global scale (Vitousek 1994; Chapin III et al. 2000; Goudie 2013). These global changes are increasingly being recognized as threats to human well-being, and scientific research has been intensified over the last decades to better understand the consequences of these changes for the functioning and service-provisioning of ecosystems (Vitousek 1994; Foley et al. 2005; Schröter et al. 2005; Barnosky et al. 2012). Knowledge of how specific drivers of global change affect ecosystem functions and services is a prerequisite for the development of a sustainable management of resources and ecosystems (Chapin III et al. 2010; Naeem et al. 2012).

### Biodiversity loss

The loss of biological diversity is one of the drivers of global change that have been identified to substantially affect the functioning and service-provisioning of ecosystems (Cardinale et al. 2012; Hooper et al. 2012; Naeem et al. 2012). Worldwide, biodiversity is being affected by human impact, and current declines in biodiversity are even likened to the mass extinction events in Earth's history (Chapin III et al. 2000; Pimm and Brooks 2005; Barnosky et al. 2011). The effects of biodiversity loss rival, and may in some cases even exceed, the effects of environmental stressors that have received particular scientific and public attention in the

past, such as climate change and eutrophication (Hooper et al. 2012). Studies over the last two decades have significantly advanced our understanding of how biodiversity affects and often promotes many ecosystem functions and services (Cardinale et al. 2012). In particular, many studies have shown that species diversity increases the resource use efficiency and biomass production, and the temporal stability of these processes, in communities of primary producers (Cardinale et al. 2011). More recently, the focus has shifted to the effects of functional and phylogenetic diversity to unveil the mechanisms and evolutionary dependencies underlying biodiversity effects (Diaz and Cabido 2001; Cavender-Bares et al. 2009; Srivastava et al. 2012). Moreover, an increasing body of studies indicates that biodiversity effects can cascade through the food web to and from higher trophic levels and that interactions among trophic levels can significantly modify the overall response of ecosystem functions to changes in biodiversity (Duffy 2003; Duffy et al. 2007; Thebault et al. 2007; Hillebrand and Matthiessen 2009; Scherber et al. 2010). However, our general understanding of the relationships between biodiversity and ecosystem functioning (BEF) is hampered by the fact that in many cases much of our knowledge—particularly for highly diverse systems—stems from grassland studies in temperate and boreal regions or from artificial systems of low complexity (Srivastava and Vellend 2005; Hillebrand and Matthiessen 2009; Cardinale et al. 2011). More complex systems, such as forests in general and species-rich forests in particular, have only been thoroughly incorporated into BEF research relatively recently.

### Forests

Forests cover one third of the Earth's land surface (Bonan 2008) and assume a central role in global biogeochemical cycles, the mitigation of climate change effects, and the preservation of terrestrial biodiversity (Kremen et al. 2000; Bonan 2008). Forests are

characterized by long-lived plant individuals with specific life histories, a long-term development of structural components and trophic interactions, and an often knowledge of biodiversity-ecosystem function relationships from less complex systems such as (artificial) grasslands might not necessarily be transferable to forest systems. However, such knowledge is urgently needed. High rates of deforestation and forest degradation worldwide seriously threaten the functions and services provided by forests and cause increased rates of species extinctions (Kremen et al. 2000; Bala et al. 2007). At the same time, extensive reforestation and forest conversion efforts are being made (Li 2004; Chazdon 2008; Meyfroidt et al. 2010), but forest practitioners are unsure as to the benefits of stand diversification (see Knoke et al. 2008). The recent establishment of large-scale forest BEF experiments may help to shed more light on the ecosystem-level consequences of biodiversity loss and the benefits of promoting biodiversity for a sustainable forest management. However, most of these experiments are still at an early stage and thus do not yet reflect the qualities and dynamics of mature forests (Baeten et al. 2013; Bruelheide et al. 2014). Although older forest stages can be found in some forestry experiments, these experiments usually comprise only monocultures and tree species mixtures of very low diversity (usually two-species mixtures; Scherer-Lorenzen 2014). As such, they often confound tree species richness and tree species composition, and the species-poor communities of these experiments do not allow scaling up BEF relationships to more diverse forests (Nadrowski et al. 2010; Scherer-Lorenzen 2014). Non-additive diversity effects due to species interactions may often only become evident at higher levels of diversity (e.g. Loranger et al. 2013), and ecosystem (multi)functionality in space and time may require more species than often assumed (see e.g. Isbell et al. 2011; Gamfeldt et al. 2013). Therefore, insights from species-rich forests may be particularly informative for BEF research. Alarmingly, many of the world's regions with species-rich forests are strongly affected by human impact and biodiversity

heterogeneous vertical stratification of vegetation layers and associated heterotrophic organisms (Scherer-Lorenzen et al. 2005; Leuschner et al. 2009). Therefore, our loss (Kremen et al. 2000; Myers et al. 2000; Brooks et al. 2006), making biodiversity research in these regions a priority also from a conservation perspective.

### **(Sub)tropical forests and trophic interactions**

Most of the world's highly diverse forests are located in subtropical and tropical regions. These forests often belong to global hotspots of not only plant diversity, but of animal diversity as well (Myers et al. 2000; Basset et al. 2012). Of all forests worldwide, they contribute most to primary production, carbon sequestration and climate regulation (Bonan 2008). (Sub)tropical forests may thus be model systems to study how the functioning of complex ecosystems responds to high levels of biodiversity and to species loss at such high diversity levels. Even more importantly, they may also be model systems to study the role of trophic complexity in regulating ecosystem functions and their relationships with biodiversity. Interactions among primary producers, herbivores and predators/parasitoids result in higher complexity of diversity-functioning relationships than predicted from analyses restricted to only one (traditionally the producer level) trophic level (Thebault and Loreau 2005; Thebault and Loreau 2006). These trophic interactions thus need to be considered to obtain a more realistic picture of BEF relationships (Duffy et al. 2007; Hillebrand and Matthiessen 2009; Reiss et al. 2009; Cardinale et al. 2012). In species-rich (sub)tropical forests, herbivory and predation are often assumed to be particularly pronounced (Novotny et al. 2006; Schemske et al. 2009; Salazar and Marquis 2012), and strong impacts of trophic interactions on the structure and diversity of these forests have repeatedly been shown (see Terborgh 2012; Coley and Kursar 2014; Muller-Landau 2014). For instance, studies on density-dependent seedling mortality caused by specialist herbivores (e.g. Metz et al. 2010; Swamy and Terborgh 2010; Visser et al. 2011; Bagchi et al.

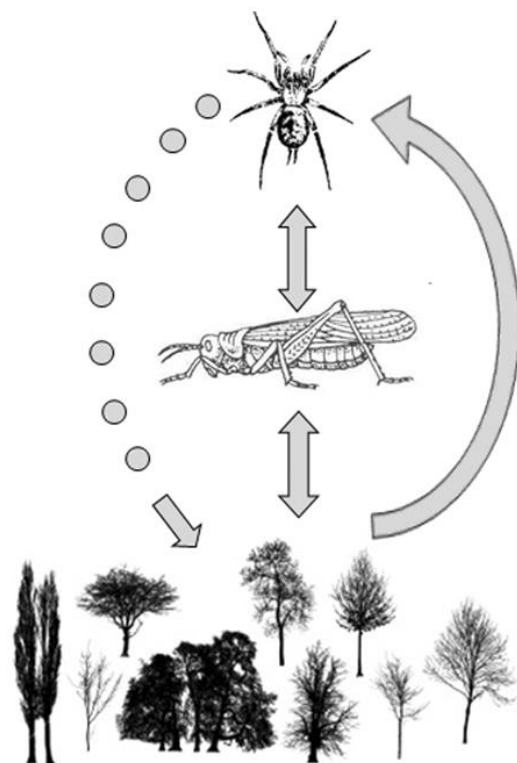
2014) indicate that resource-based mechanisms operate in these forests (Janzen 1970; Connell 1971) which are also relevant for our understanding of the relationship between plant diversity and herbivory (Root 1973; Jactel and Brockerhoff 2007). Likewise, predator top-down control could have stronger effects on herbivores in these systems than at higher latitudes (Novotny et al. 2006; Schemske et al. 2009), and predators could thus mediate the impact of herbivores on ecosystem functions (Root 1973; Haddad et al. 2009). Interestingly, however, the community-level effects of these interactions have rarely been linked up directly with BEF research in species-rich forests (see Scherer-Lorenzen 2014). The consequences of biodiversity loss on the strength and direction of trophic interaction effects in these systems thus remain poorly understood, as do the mechanisms responsible for potential biodiversity effects on these interactions.

## 1.2 Aims and hypotheses of this thesis

### Main objectives

The chapters of this thesis tackle important aspects of the above-mentioned shortcomings, with the aim to provide in-depth insight into the role of trophic complexity in mediating biodiversity-ecosystem function relationships in forests—and particularly in highly diverse and poorly studied subtropical forests. Specifically, this thesis focuses on the effects of plant diversity and the consequences of the loss of this diversity on the diversity and functional impact of, and the potential interactions among, key functional groups of primary (herbivores) and secondary consumers (predators) (Fig. 1.1). Both herbivores and predators have been shown to either directly or indirectly affect plant community structure and ecosystem processes, such as nutrient cycling and biomass production, that are central to ecosystem functioning (Weisser and Siemann 2004; Schmitz 2008; Schmitz et al. 2010; Schowalter 2012). Importantly, the analyses in this thesis go beyond the effects of mere species richness as a biodiversity metric. Where possible, they incorporate functional and phylogenetic data of the producer or consumer assemblages to help unveil the

potential mechanisms and evolutionary dependencies underlying the observed diversity effects (Reiss et al. 2009; Srivastava et al. 2012). The studies presented in this thesis make use of both (near)natural and experimentally assembled tree communities. Particular attention is given to (near)natural forests, as they have the advantage over the recently established tree diversity experiments of providing insight into ecosystem functioning based on established communities of plants and animals under natural conditions (Leuschner et al. 2009). A potential downside of these studies is that they are usually observational in character (see Vilà et al. 2005), and in this thesis experimental studies in tree diversity experiments are used to back up and verify the causality of important observational results. And even though the data from these experiments so far reflect conditions of early successional forest stages, they may be highly informative with regard to the development of sustainable management practices in plantation forests and reforestation projects.



**Figure 1.1.** Schematic representation of the potential bottom-up and top-down effects among plants, herbivores and predators addressed in this thesis

## Structure and main hypotheses of this thesis

The main chapters of this thesis can be grouped into three sections. The first two sections focus on diversity-dependent patterns and processes in highly diverse subtropical forests. They tackle important but so far poorly studied issues of the role of arthropod herbivory and herbivores in these forests in relation to woody plant diversity (**Section I**) and the impact of arthropod predators as top-down control agents and potential regulators of herbivore effects (**Section II**). The last section (**Section III**) provides an outlook on patterns and processes in temperate forests (again taking key arthropod predators as an example), which are characterized by much lower levels of producer and consumer diversity. Section III thus extends the geographic scope to regions where trophic interactions are often assumed to have a less severe impact on the structure and functioning of many ecosystems (Schemske et al. 2009; Rodriguez-Castaneda 2013; but see e.g. Petermann et al. 2008).

**Section I** (herbivory and herbivores in species-rich subtropical forests) consists of four chapters (Chapters 2-5):

### **Chapter 2: *Plant traits affecting herbivory on tree recruits in highly diverse subtropical forests***

This chapter analyzes which functional traits make woody plant species in highly diverse forests particularly susceptible to herbivory. Biodiversity effects are essentially driven by the (dis)similarity in the functional traits of the species making up a community (see Reiss et al. 2009), and trait-based approaches may thus help to gain a mechanistic understanding of biodiversity effects. While much work has been conducted on the effects of individual plant traits on the performance of individual herbivore species and vice versa, no general trends have been established so far and many of the plant traits commonly assumed to affect herbivores may have a relatively weak effect on overall herbivore damage

(Carmona et al. 2011; Garibaldi et al. 2011; Paine et al. 2012). Pluralistic approaches are required, but have rarely been applied so far. This chapter therefore analyses the combined effects of a large number of morphological, chemical and biogeographical characteristics, as well as the influence of phylogenetic relationships, on the herbivory levels of dominant tree and shrub species in highly diverse secondary forests in South-East China (see chapter 1.3). The results yield new insights into the relative importance and interdependence of the drivers that might cause differences in mean levels of herbivory and promote the maintenance of woody plant diversity in plant species-rich forests.

### **Chapter 3: *Functional and phylogenetic diversity of woody plants drive herbivory in a highly diverse forest***

This chapter follows up on the findings of the preceding chapter and evaluates the ecosystem-level consequences of the relationships between a multitude of plant traits and entire herbivore assemblages. There is a lack of detailed studies that analyze how trait variation and trait diversity in plant communities affect the relationship between herbivory, plant diversity and ecosystem functions. This is despite the fact that the impact of herbivores on resource-allocation patterns and the growth of plant species is known to vary with the plants' growth strategy (Lind et al. 2013), such that both species- and community-level effects of herbivory may depend on the species composition and functional diversity of a given plant community (Eskelinen et al. 2012). The study presented in this chapter analyzes herbivore damage in forest stands along a gradient from medium to high woody plant species richness and tests the extent to which functional and phylogenetic aspects of woody plant community composition contribute to improving our mechanistic

understanding of how biodiversity and its loss affect the impact of higher trophic levels on ecosystem functions.

**Chapter 4: *Early positive effects of herbivory in the world's largest forest biodiversity experiment***

Chapter 4 makes use of a newly established and large-scale tree diversity experiment in subtropical China (set up close to the near-natural forest sites in which the studies of chapters 1 and 2 were conducted, see chapter 1.3) to experimentally verify the causality of herbivory-woody plant diversity relationships unveiled in the observational study of naturally assembled woody plant communities in chapter 2. Moreover, as the experiment is still at a very early stage, it can provide insight into the extent to which herbivores contribute to the processes that drive the assembly and functioning of establishing tree communities in species-rich forests from the very start of forest succession. The study presented in this chapter is based on herbivory assessments in about 300 experimental study plots which feature gradients in tree species richness based on both random and nonrandom (trait-based) extinction scenarios (Bruehlheide et al. 2014). This further allows testing of how processes such as herbivory change in response to directed (for instance caused by anthropogenic disturbance) and random species loss, an issue that has rarely been addressed in biodiversity experiments so far.

**Chapter 5: *Woody plant phylogenetic diversity mediates bottom-up control of arthropod biomass in species-rich forests***

Chapter 5 shifts the focus to the herbivores responsible for the observed herbivore damage. It analyzes how herbivory patterns are reflected and explained by herbivore assemblage responses to changes in woody plant diversity. This study focuses on overall patterns and the functional divergence

in biomass distributions of important herbivore guilds (leaf chewers and sap suckers) in the same forest stands studied in chapters 1 and 2, and assesses the impact of woody plant species richness and phylogenetic diversity on the herbivore assemblages. Phylogenetic diversity may serve as a comprehensive metric of community trait space and potential evolutionary associations among herbivores and host plant lineages (Weiblen et al. 2006; Sanders and Platner 2007; Srivastava et al. 2012) and reveal nonrandom associations between herbivores and plant diversity that are not necessarily apparent from relationships with plant species richness. The analyses of this chapter also consider the natural enemies of the herbivores and thus directly lead over to the next section and the question of whether predator top-down control might affect herbivores and mediate herbivore effects in relation to plant diversity.

The **main hypotheses** addressed in the chapters of Section I are:

**H1:** Species-specific damage levels and the susceptibility of woody plant species to entire herbivore assemblages is determined by a complex of not only multiple chemical and morphological traits, but by biogeographical characteristics of the plant species as well. The relative importance and interdependence of the factors driving the differences in mean levels of herbivory among plant species can provide insight into the mechanisms that promote the maintenance of woody plant diversity in plant species-rich forests.

**H2:** At the community level, the trait (dis)similarities among plant species and the evolutionary dependencies of plants and herbivores will result in a change in overall herbivore damage with changes in plant diversity and community

composition. Both functional and phylogenetic community metrics will therefore explain the variation in observed herbivory within species better than woody plant species richness. In particular, multivariate indices of trait diversity may reveal non-additive effects that arise from interactions among species and traits and that are not necessarily apparent from single trait measures of community-weighted mean values and variability. Increasing loss of plant species, but in particular the concomitant loss of functional variability and phylogenetic information in a community, can thus be expected to change the impact of herbivores – with consequences for the herbivore-mediated regulation of ecosystem functions and properties.

**H3:** Plant diversity effects on herbivory arise at the very early stages of forest succession and thus play an important role in influencing the structure and functioning of establishing forest communities right from the start of forest development. Whether plant species are assembled and potentially lost in a random or nonrandom way will affect the strength and direction of diversity effects on herbivory

**H4:** Herbivore biomass and abundance increase with woody plant diversity. In particular generalist herbivores may benefit from increased resource availability and possibilities of dietary mixing in forest stands with higher plant diversity. Metrics of plant diversity that take into account the complexity of evolutionary and functional characteristics that may underlie diversity effects, such as plant phylogenetic diversity, are expected to be particularly informative in predicting herbivore assemblage patterns.

**Section II** (predators and top-down control in species-rich subtropical forests) consists of six chapters (Chapters 6-11):

**Chapter 6: *Predator diversity and abundance provide little support for the enemies hypothesis in forests of high tree diversity***

This chapter starts off the section on the relationships between woody plant diversity and secondary consumers, the latter of which might act via top-down control as mediators of herbivore effects. Despite extensive theory and experimental manipulation of predator diversity, our knowledge about the relationships between plant and predator diversity—and thus information on the relevance of experimental findings and the role of predators for ecosystem functioning—for species-rich, natural ecosystems is limited. This chapter analyzes the activity abundance and species richness of spiders—as one of the dominant generalist predators—across the gradient in tree species richness formed by the forest stands that were studied for herbivory and herbivores in the preceding chapters. Ecological theory predicts higher predator abundance and diversity, and concomitantly more effective top-down control of food webs, with increasing plant diversity (e.g. the ‘enemies hypothesis’). The results of this study have implications for evaluating the way in which theoretical predictions and experimental findings of functional predator effects apply to species-rich forest ecosystems, and they help to show whether stronger top-down control of food webs can actually be expected in the more plant diverse stands of such ecosystems.

**Chapter 7: *Predator assemblage structure and temporal variability of species richness and abundance in forests of high tree diversity***

Chapter 7 extends the analyses of the preceding chapter by adding a spatio-temporal dimension to the biodiversity relationships between woody plants and generalist predators. This chapter analyzes fine-scale spatial patterns of species composition (turnover and



habitat specificity within and among forest stands) and temporal changes in richness and abundance of spiders in relation to woody plant diversity. Diversity patterns have been shown to often exhibit scale-dependency, such that an analysis that considers multiple spatial scales can provide information for a differentiated understanding of diversity relationships. Likewise, temporal changes and the overall temporal stability of assemblage patterns may be important factors influencing the functional impact of species assemblages.

**Chapter 8: *Tree diversity promotes functional dissimilarity and maintains functional richness despite species loss in predator assemblages***

This chapter introduces a functional trait approach to analyzing predator assemblage structure and the potential functional impact of these assemblages in relation to woody plant diversity. It incorporates a variety of traits, related to the resource use of spiders, into complementary measures of functional diversity which allow for a thorough assessment of how the richness, evenness and divergence of functional traits within spider assemblages are affected by changes in woody plant diversity (in this case by plant species richness and plant phylogenetic diversity). Higher functional richness, but also higher functional evenness or divergence, would indicate a broader resource use within the spider assemblages and might, in consequence, lead to stronger prey control. This functional trait diversity is not necessarily a linear function of species richness (e.g. Mason et al. 2008). Previous studies have even found contrasting patterns of species and functional diversity, indicating that these two metrics may predict different facets of the diversity and strength of functional effects of species assemblages (Devictor et al. 2010;

Villéger et al. 2010). Similar patterns were also indicated by the results of chapter 6, i.e. functional effects of spiders in the subtropical study system might be opposed to species richness effects. Accounting for differences in the functional characteristics of species may thus help to better understand the potential effects, and the change in effects along environmental gradients, of predator assemblages on ecosystem functions.

**Chapter 9: *Tree diversity promotes predator but not omnivore ants in a subtropical Chinese forest***

Chapter 9 shifts the focus to ants, which form a second major group of secondary consumers in the studied forests and which are generally important keystone organisms in many ecosystems. Previous studies have shown that different groups of predators can show differential responses to changes in plant diversity (e.g. Koricheva et al. 2000; Vehviläinen et al. 2008). This may lead to a higher complexity of interaction effects on diversity relationships across trophic levels than often assumed, in particular considering that predatory taxa may interact with each other. Via intraguild effects they can modify the response of individual predatory taxa to changes in plant diversity. A thorough assessment and analysis of predator diversity and functional predator effects in relation to plant diversity will thus benefit from the consideration of multiple predatory taxa. Therefore, this chapter tests for relationships between ants and woody plant diversity, analogous to the analyses of spiders in chapter 6. Moreover, the analysis presented in this chapter differentiates between effects on strictly predatory ants and omnivorous ants, as differences in their trophic niches could lead to differences in their potential dependence on plant diversity (Scherber et al. 2010).

**Chapter 10: *Ant community structure during forest succession in a subtropical forest in South-East China***

Chapter 10 further adds to broadening our understanding of taxon-specific patterns of predator assemblage structures in species-rich subtropical forests by analyzing the spatial turnover and details of the species composition of ant assemblages in the near-natural subtropical study system. The results of this chapter also have implications for the conservation of biodiversity at the regional scale in such species-rich regions, which are often strongly threatened by habitat degradation and conversion due to human impact.

**Chapter 11: *Effects of ants on the functional composition of spider assemblages increase with tree species richness in a highly diverse forest***

This chapter investigates the potential interactions among the main predatory taxa of the subtropical study system, spiders and ants. The analysis in this chapter tests for the interactive effects of ant presence and tree species richness on the biomass and functional composition of spider assemblages. Relationships between ants and spiders at the level of whole plant communities are poorly studied, and thus knowledge of their ecosystem-level consequences is largely lacking. Moreover, the role that changes in plant diversity play in affecting the interactions between these major predator taxa is not known. Differential responses of these taxa to changes in woody plant diversity and the resulting effects on intraguild predation and interference competition might strongly modify and determine the overall effect of predators in relation to plant diversity. The findings of this study can thus help to better understand the complexity of biotic interactions in species-rich ecosystems.

The **main hypotheses** addressed in the chapters of Section II are:

**H5:** Predator abundance and species richness in time and space respond positively to higher structural heterogeneity and potentially increased prey availability in forest stands of high woody plant diversity, in accordance with the enemies hypothesis, and thus increase the potential of predators to exert top-down pressure on herbivores with increasing plant diversity. The strength of plant diversity effects, however, may differ among and within different predator taxa.

**H6:** Predator functional diversity will likewise increase with woody plant diversity. However, patterns may differ from those of predator species richness. Relationships with plant diversity may be stronger due to the fact that functional diversity may better reflect the variability and distribution of the traits that are affected by and respond to changes in plant diversity and composition and that determine the functional effect of predators. Likewise, plant diversity effects may be more effectively captured by plant phylogenetic diversity metrics that reflect potential plant functional trait effects and nonrandom species associations than by mere plant species richness.

**H7:** Intraguild interactions among different predator taxa will affect the overall effect of predators in relation to changes in woody plant diversity, emphasizing the complexity of trophic interaction effects in species-rich forests. For instance, ants may negatively impact on spiders and shift their functional composition at the plant community level. However, such interaction effects will be mediated by woody plant diversity. Depending on the strength of plant diversity effects on individual predator taxa, these interactions can be expected to result in

either negative or neutral effects on overall predator top-down control with increasing plant diversity.

**Section III** (predators in temperate forests) consists of two chapters (Chapters 12-13):

**Chapter 12: *Scale-dependent diversity patterns affect spider assemblages of two contrasting forest ecosystems***

Chapter 12 leads over from the species-rich subtropical forests to the much less diverse temperate forests. It compares species and family richness, functional diversity, and  $\alpha$ - and  $\beta$ -components of spiders in near-natural temperate and subtropical forests. While the strength of biotic interactions such as predation is generally considered to be more pronounced at lower latitudes, recent findings indicate that spider functional guild richness and diversity do not differ consistently between temperate and tropical regions, possibly due to higher functional redundancy in the species-rich tropics (Cardoso et al. 2011). These patterns might be scale-dependent, as latitudinal diversity patterns are often particularly pronounced at larger spatial scales (Hillebrand 2004). By testing for diversity patterns across different spatial scales, the study presented in this chapter can help to further our limited understanding of these issues.

**Chapter 13: *Non-native tree species (*Pseudotsuga menziesii*) strongly decreases predator biomass and abundance in mixed-species plantations of a tree diversity experiment***

Chapter 13 makes use of a tree diversity experiment in temperate Central Europe to test the extent to which tree species richness and the identity of the planted tree species affect the abundance, biomass, species richness and functional diversity of spiders. The experiment uses four of the economically most important broadleaved and coniferous tree species in Europe. The results of

this study may thus be very relevant for the management of forest plantations in this region. A mix of broadleaved and coniferous species as well as the inclusion of a non-native tree species that has become the economically most important exotic tree species in Europe (Douglas fir) reflects two important trends in forest management practices that are in need of further exploration in the framework of biodiversity and ecosystem functioning research.

The **main hypotheses** addressed in the chapters of Section III are:

**H8:** While temperate forests feature both a lower overall richness and a lower small-scale  $\alpha$ -richness of predators than subtropical forests, overall richness differences will be shaped particularly by a higher species turnover ( $\beta$ -richness) in subtropical than in temperate forests. With lower species richness in the temperate forests, functional diversity of predators—which can be indicative of higher predator pressure—may be lower in temperate forests as well.

**H9:** Even though temperate forests are much less diverse than many (sub)tropical forests, tree diversity nevertheless promotes the abundance, biomass, species richness and functional diversity of predators and thus enhances the pest-control potential of forest stands. However, tree species identity will play an important additional role that may be more pronounced at the low levels of tree diversity in temperate forests than in (sub)tropical forests.

### 1.3 The study systems

The studies presented in this thesis were conducted in forest systems at four different locations in subtropical South-East China and temperate Central Europe. The subtropical sites comprised a near-natural forest system (Gutianshan National Nature Reserve) and a large-scale tree diversity experiment (Main Experiment of the ‘BEF-China’ project).

Likewise, the temperate study sites comprised a semi-natural forest system (Hainich National Park) and a planted tree diversity experiment (BIOTREE Experiment Kaltenborn). In the following, the four sites will be introduced briefly to provide an overview of the study designs and environmental conditions under which the studies were conducted.

### Gutianshan National Nature Reserve

The Gutianshan Nature Reserve (29°14'N, 118°07'E) is located in the western part of Zhejiang Province in South-East China, about 350 km south-east of Shanghai. The area forms part of the Nanling mountain system, and the sloping terrain of the reserve covers elevations from 250 – 1260 m asl. The reserve was established as a forest reserve in 1975 and gained the status of a national nature reserve in 2001. The subtropical monsoon climate is characterized by a mean annual temperature of 15.3°C and a mean annual precipitation of 2000 mm (Hu and Yu 2008). Broadleaved evergreen tree species such as *Castanopsis eyrei* (Champ. ex Benth.) Tutch. and *Schima superba* Gardn. et Champ dominate the ca 80 km<sup>2</sup> of the nature reserve, and a total of 1426 seed plant species (258 of them woody) of 125 families have been recorded (Legendre et al. 2009; Bruelheide et al. 2011).

In 2008, 27 study plots of 30 x 30 m were established in the reserve, following a stratified selection process based on the age (ranging between < 20 and > 80 years) and woody plant species richness (ranging from 25 to 69 tree and shrub species) of the plots (Fig. 1.2). Plot locations were randomly chosen as far as possible, limited by inaccessibility and steep topography (areas with an inclination >55° were excluded) of parts of the reserve. Details on plot establishment and plot characteristics can be found in Bruelheide et al. (2011).

Most of the research reported in this thesis (chapters 2, 3, and 5-11) is based on assessments in the study plots of the Gutianshan National Nature Reserve, as they provide near-natural conditions in highly diverse forests with established plant and animal communities.

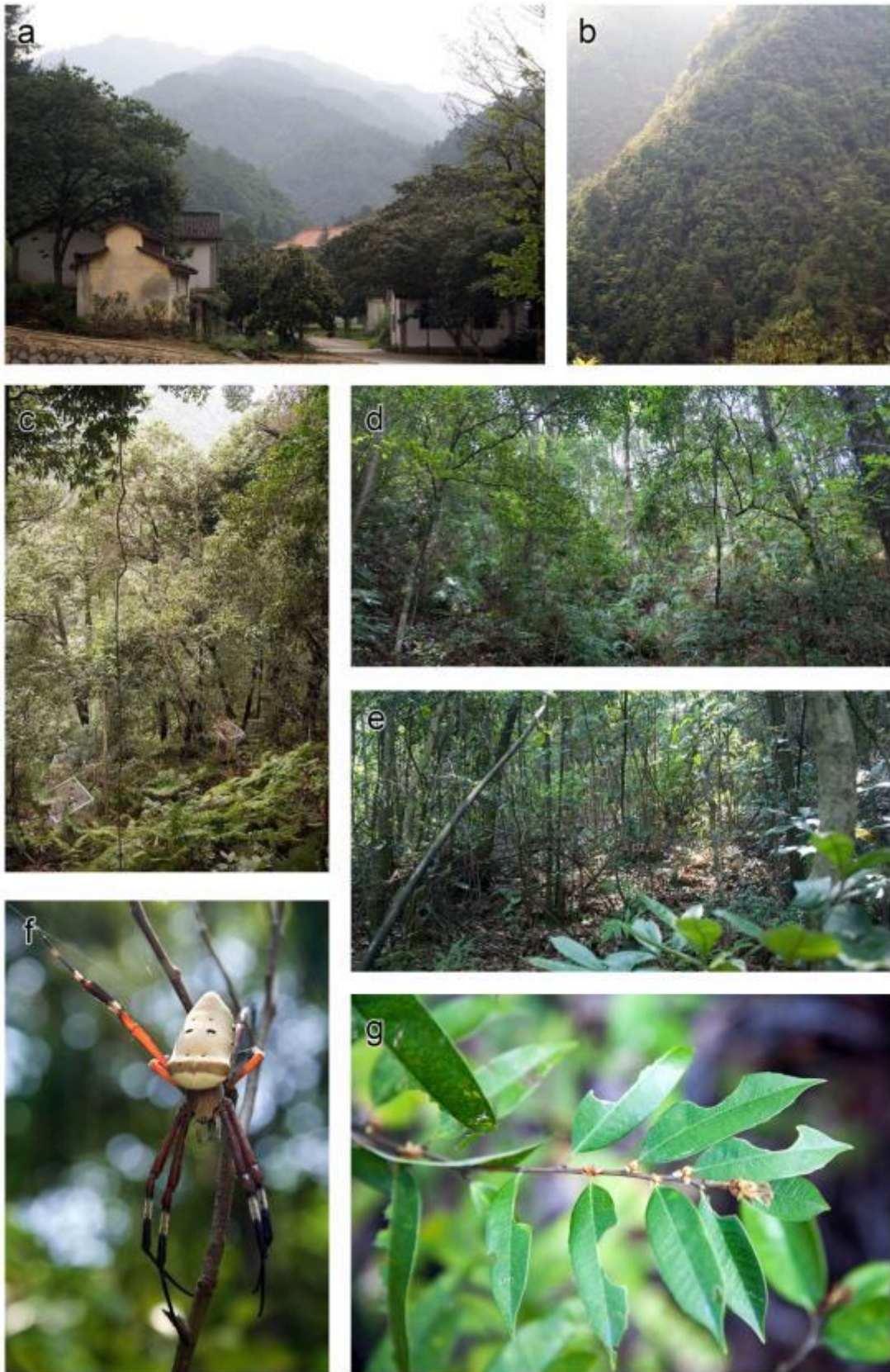
### BEF-China Main Experiment

The subtropical BEF-China tree diversity experiment is located close to Xingangshan, Jiangxi Province (29.08–29.11 N, 117.90–117.93 E), about 30 km east of the Gutianshan Nature Reserve. Mean annual temperature is 16.7°C and mean annual precipitation around 1800 mm (Yang et al. 2013). The experiment consists of two experimental sites (Site A and Site B) of ca 20 ha each, located in sloping terrain between 100 and 300 m asl (Fig. 1.3). Each site harbors 271 plots of ca 26 x 26 m (= 1 mu in the traditional Chinese areal unit) planted in 2009 (Site A)/2010 (Site B) with either monocultures or mixtures of 2, 4, 8, 16, or 24 tree species. The species composition of the mixtures followed either a random or one of two nonrandom (trait-oriented) extinction scenarios. Species compositions in the two nonrandom scenarios were based on local rarity and specific leaf area (SLA) of the tree species, respectively, with the rarest species or those with the highest SLA being sequentially eliminated with decreasing diversity of the species mixtures. Each of the experimental plots consists of 400 trees planted in a grid of 20 x 20 individuals with a 1.29 m horizontal planting distance, with species randomly assigned to individual planting positions within the plots. In total, 40 native broadleaved tree species were planted in the experiment, with the species pools of the two sites overlapping by eight species (planted in one of the random extinction scenario replicates of both sites). Details of the experimental design are provided in Bruelheide et al. (2014).

The experiment is still in a very early stage of development, and the study presented in chapter 4 of this thesis is one of the first to provide results on trophic interactions in this experiment.

### Hainich National Park

The Hainich National Park is located at a low mountain range in Thuringia, Germany, between the cities of Mühlhausen and Eisenach. Mean annual temperature averages from 7.5 to 8.0°C and mean annual precipitation is 600 mm, indicating a subatlantic climate with a slight subcontinental



**Figure 1.2.** The Gutianshan National Nature Reserve (a) covers 8000 ha of mixed broadleaved forest on sloping terrain (b). Study plots with medium to high tree diversity were established across a range of old (c), medium aged (d), and young (e) forest stands. Spiders are dominant predatory arthropods in this system (f: web-building Araneidae). Herbivorous insects cause substantial leaf damage (g: damage by lepidopteran caterpillars on *Castanopsis fargesii* Franch). Photos by A. Schuldt.



**Figure 1.3.** The BEF-China Main Experiment. The first of the two experimental sites (Site A) was prepared (a) and tree seedlings were planted (b) in the spring of 2009. Fast tree growth (c: 5 months after planting; d: four years after planting) leads to a fast development of the experimental plots. Lepidopteran caterpillars belong to the dominant herbivores (e). Photos by A. Schuldt.

impact in the eastern part (Mölder et al. 2006). The national park covers about 76 km<sup>2</sup> of deciduous forest, with *Fagus sylvatica* L., *Tilia platyphyllos* Scop., *Tilia cordata* L. and *Fraxinus excelsior* L. as dominant tree species and, due to former forest management, consists of a wide variety of very different deciduous forest stands on a small scale.

In 2005, nine study plots of 50 x 50 m,

with a stand age of 80–120 years, were established at about 300–370 m asl (51°1' N, 10°5' E), representing a tree diversity gradient ranging from 1 to 10 tree species (Fig. 1.4). Details are provided by Leuschner et al. (2009).

Chapter 12 of this thesis focuses on diversity patterns in this semi-natural forest system.

### BIOTREE Experiment Kaltenborn

The 'Kaltenborn' site of the BIOTREE tree diversity experiment is located in southwest Thuringia, Germany (50°47' N, 10°13' E). The study site is located at a height of 320-350 m asl and is characterized by a subatlantic climate. Mean annual temperature is 7.8°C and mean annual precipitation is 650 mm (Scherer-Lorenzen et al. 2007).

The experimental setup at the 'Kaltenborn' site consists of 16 study plots of 0.58 ha (120 m x 48 m), established in 2003/2004, which cover a total area of 20 ha under homogeneous site conditions (Fig. 1.4).

The 16 study plots comprise the monocultures (4 plots), all possible two (six plots) and three species mixtures (four plots),

and the four species mixture (2 plots) of four tree species: the broadleaved, deciduous *Fagus sylvatica* L. and *Quercus petraea* Liebl., and the coniferous *Picea abies* (L.) H. Karst. and *Pseudotsuga menziesii* (Mirb.) Franco. While the latter is an exotic species, all four tree species are commonly found in the surrounding forests and are economically highly important for local forestry. The plots are thus representative of large-scale forest diversity in the temperate and boreal parts of Europe. Details on the experimental design are provided by Scherer-Lorenzen et al. (2007).

Chapter 13 of this thesis makes use of the BIOTREE sites to assess diversity relationships in temperate forests under experimental conditions.



**Figure 1.4.** Study plots in the Hainich National Park (a: monoculture of *Fagus sylvatica* L.; b: species-rich forest stand with *F. sylvatica*, *Fraxinus excelsior* L., *Carpinus betulus* L., *Tilia* spec. and *Acer* spec.) and the BIOTREE tree diversity experiment (c: monoculture of *Picea abies* (L.) H. Karst.; d: mixture of *Quercus petraea* Liebl. and *Pseudotsuga menziesii* (Mirb.) Franco). Photos by A. Schuldt.

## References

- Baeten L et al. (2013) A novel comparative research platform designed to determine the functional significance of tree species diversity in European forests. *Perspectives in Plant Ecology, Evolution and Systematics* 15:281-291
- Bagchi R et al. (2014) Pathogens and insect herbivores drive rainforest plant diversity and composition. *Nature* 506:85-88
- Bala G et al. (2007) Combined climate and carbon-cycle effects of large-scale deforestation. *Proceedings of the National Academy of Sciences* 104:6550-6555
- Barnosky AD, Hadly EA, Bascompte J, Berlow EL, Brown JH (2012) Approaching a state shift in Earth's biosphere. *Nature* 486:52-58
- Barnosky AD et al. (2011) Has the Earth's sixth mass extinction already arrived? *Nature* 471:51-57
- Basset Y et al. (2012) Arthropod diversity in a tropical forest. *Science* 338:1481-1484
- Bonan GB (2008) Forests and climate change: forcings, feedbacks, and the climate benefits of forests. *Science* 320:1444-1449
- Brooks TM et al. (2006) Global biodiversity conservation priorities. *Science* 313:58-61
- Bruehlheide H et al. (2011) Community assembly during secondary forest succession in a Chinese subtropical forest. *Ecological Monographs* 81:25-41
- Bruehlheide H et al. (2014) Designing forest biodiversity experiments: general considerations illustrated by a new large experiment in subtropical China. *Methods in Ecology and Evolution* 5:74-89
- Cardinale BJ et al. (2012) Biodiversity loss and its impact on humanity. *Nature* 486:59-67
- Cardinale BJ et al. (2011) The functional role of producer diversity in ecosystems. *American Journal of Botany* 98:572-592
- Cardoso P, Pekar S, Jocque R, Coddington JA (2011) Global patterns of guild composition and functional diversity of spiders. *Plos ONE* 6:e21710
- Carmona D, Lajeunesse MJ, Johnson MTJ (2011) Plant traits that predict resistance to herbivores. *Functional Ecology* 25:358-367
- Cavender-Bares J, Kozak KH, Fine PVA, Kembel SW (2009) The merging of community ecology and phylogenetic biology. *Ecology Letters* 12:693-715
- Chapin III FS et al. (2010) Ecosystem stewardship: sustainability strategies for a rapidly changing planet. *Trends in Ecology and Evolution* 25:241-249
- Chapin III FS et al. (2000) Consequences of changing biodiversity. *Nature* 405:234-242
- Chazdon RL (2008) Beyond Deforestation: Restoring Forests and Ecosystem Services on Degraded Lands. *Science* 320:1458-1460
- Coley PD, Kursar TA (2014) On tropical forests and their pests. *Science* 343:35-36
- Connell JH (1971) On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In: den Boer PJ, Gradwell GR (eds) *Dynamics of populations*. Centre for Agricultural Publishing and Documentation, Wageningen, pp 298-312
- Devictor V, Mouillot D, Meynard C, Jiguet F, Thuiller W, Mouquet N (2010) Spatial mismatch and congruence between taxonomic, phylogenetic and functional diversity: the need for integrative conservation strategies in a changing world. *Ecology Letters* 13:1030-1040
- Diaz S, Cabido M (2001) Vive la différence: plant functional diversity matters to ecosystem processes. *Trends in Ecology and Evolution* 16:646-655
- Duffy JE (2003) Biodiversity loss, trophic skew and ecosystem functioning. *Ecology Letters* 6:680-687
- Duffy JE, Cardinale BJ, France KE, McIntyre PB, Thebault E, Loreau M (2007) The functional role of biodiversity in ecosystems: incorporating trophic complexity. *Ecology Letters* 10:522-538
- Eskelinen A, Harrison S, Tuomi M (2012) Plant traits mediate consumer and nutrient control on plant community productivity and diversity. *Ecology* 93:2705-2718
- Foley JA et al. (2005) Global consequences of land use. *Science* 309:570-574
- Gamfeldt L et al. (2013) Higher levels of multiple ecosystem services are found in forests with more tree species. *Nature Communications* 4:1340
- Garibaldi LA, Kitzberger T, Ruggiero A (2011) Latitudinal decrease in folivory within *Nothofagus pumilio* forests: dual effect of climate on insect density and leaf traits? *Global Ecology and Biogeography* 20:609-619
- Goudie AS (2013) *The human impact on the natural environment: past, present, and future*. John Wiley and Sons
- Haddad NM, Crutsinger GM, Gross K, Haarstad J, Knops JMH, Tilman D (2009) Plant species loss decreases arthropod diversity and shifts trophic structure. *Ecology Letters* 12:1029-1039
- Hillebrand H (2004) On the generality of the latitudinal diversity gradient. *American Naturalist* 163:192-211



- Hillebrand H, Matthiessen B (2009) Biodiversity in a complex world: consolidation and progress in functional biodiversity research. *Ecology Letters* 12:1405-1419
- Hooper DU et al. (2012) A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature* 486:105-108
- Hu Z, Yu M (2008) Study on successions sequence of evergreen broad-leaved forest in Gutian Mountain of Zhejiang, Eastern China: species diversity. *Frontiers of Biology in China* 3:45-49
- Isbell F et al. (2011) High plant diversity is needed to maintain ecosystem services. *Nature* 477:199-U196
- Jactel H, Brockerhoff EG (2007) Tree diversity reduces herbivory by forest insects. *Ecology Letters* 10:835-848
- Janzen DH (1970) Herbivores and the number of tree species in tropical forests. *American Naturalist* 104:501-528
- Knoke T, Ammer C, Stimm B, Mosandl R (2008) Admixing broadleaved to coniferous tree species: a review on yield, ecological stability and economics. *European Journal of Forest Research* 127:89-101
- Koricheva J, Mulder CPH, Schmid B, Joshi J, Huss-Danell K (2000) Numerical responses of different trophic groups of invertebrates to manipulations of plant diversity in grasslands. *Oecologia* 125:271-282
- Kremen C et al. (2000) Economic incentives for rain forest conservation across scales. *Science* 288:1828-1832
- Legendre P et al. (2009) Partitioning beta diversity in a subtropical broad-leaved forest of China. *Ecology* 90:663-674
- Leuschner C, Jungkunst HF, Fleck S (2009) Functional role of forest diversity: Pros and cons of synthetic stands and across-site comparisons in established forests. *Basic and Applied Ecology* 10:1-9
- Li WH (2004) Degradation and restoration of forest ecosystems in China. *Forest Ecology and Management* 201:33-41
- Lind EM et al. (2013) Life-history constraints in grassland plant species: a growth-defence trade-off is the norm. *Ecology Letters*:doi: 10.1111/ele.12078
- Loranger J et al. (2013) Predicting invertebrate herbivory from plant traits: Polycultures show strong nonadditive effects. *Ecology* 94:1499-1509
- Mason NWH, Irz P, Lanoiselee C, Mouillot D, Argillier C (2008) Evidence that niche specialization explains species-energy relationships in lake fish communities. *Journal of Animal Ecology* 77:285-296
- Metz MR, Sousa WP, Valencia R (2010) Widespread density-dependent seedling mortality promotes species coexistence in a highly diverse Amazonian rain forest. *Ecology* 91:3675-3685
- Meyfroidt P, Rudel TK, Lambin EF (2010) Forest transitions, trade, and the global displacement of land use. *Proceedings of the National Academy of Sciences* 107:20917-20922
- Mölder A, Bernhardt-Römermann M, Schmidt W (2006) Forest ecosystem research in Hainich National Park (Thuringia): first results on flora and vegetation in stands with contrasting tree species diversity.
- Muller-Landau HC (2014) Plant diversity rooted in pathogens. *Nature*
- Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. *Nature* 403:853-858
- Nadrowski K, Wirth C, Scherer-Lorenzen M (2010) Is forest diversity driving ecosystem functioning and service? *Current Opinion in Environmental Sustainability* 2:75-79
- Naeem S, Duffy JE, Zavaleta E (2012) The functions of biological diversity in an age of extinction. *Science* 336:1401-1406
- Novotny V et al. (2006) Why are there so many species of herbivorous insects in tropical rainforests? *Science* 313:1115-1118
- Paine CET et al. (2012) Phylogenetic density dependence and environmental filtering predict seedling mortality in a tropical forest. *Ecology Letters* 15:34-41
- Petermann JS, Fergus AJF, Turnbull LA, Schmid B (2008) Janzen-Connell effects are widespread and strong enough to maintain diversity in grasslands. *Ecology* 89:2399-2406
- Pimm SL, Brooks TM (2005) The sixth extinction: how large, where, and when? In: Raven PH (ed) *Nature and human society*. National Academy Press, Washington (D.C.), pp 46-62
- Reiss J, Bridle JR, Montoya JM, Woodward G (2009) Emerging horizons in biodiversity and ecosystem functioning research. *Trends in Ecology and Evolution* 24:505-514
- Rodriguez-Castaneda G (2013) The world and its shades of green: a meta-analysis on trophic cascades across temperature and precipitation gradients. *Global Ecology and Biogeography* 22:118-130
- Root RB (1973) Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). *Ecological Monographs* 43:95-124

- Salazar D, Marquis RJ (2012) Herbivore pressure increases toward the equator. *Proceedings of the National Academy of Sciences of the United States of America* 109:12616-12620
- Sanders D, Platner C (2007) Intraguild interactions between spiders and ants and top-down control in a grassland food web. *Oecologia* 150:611-624
- Schemske DW, Mittelbach GG, Cornell HV, Sobel JM, Roy K (2009) Is there a latitudinal gradient in the importance of biotic interactions? *Annual Review of Ecology Evolution and Systematics* 40:245-269
- Scherber C et al. (2010) Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. *Nature* 468:553-556
- Scherer-Lorenzen M (2014) The functional role of biodiversity in the context of global change. In: Burslem D, Coomes D, Simonson W (eds) *Forests and Global Change*. Cambridge University Press, Cambridge, pp 195-238
- Scherer-Lorenzen M, Körner C, Schulze ED (2005) The functional significance of forest diversity: a synthesis. In: Scherer-Lorenzen M, Körner C, Schulze ED (eds) *Forest diversity and function: temperate and boreal systems*. Springer, Berlin, Heidelberg, pp 377-389
- Scherer-Lorenzen M, Schulze ED, Don A, Schumacher J, Weller E (2007) Exploring the functional significance of forest diversity: A new long-term experiment with temperate tree species (BIOTREE). *Perspectives in Plant Ecology Evolution and Systematics* 9:53-70
- Schmitz OJ (2008) Herbivory from individuals to ecosystems. *Annual Review of Ecology Evolution and Systematics* 39:133-152
- Schmitz OJ, Hawlena D, Trussell GC (2010) Predator control of ecosystem nutrient dynamics. *Ecology Letters* 13:1199-1209
- Schowalter TD (2012) Insect herbivore effects on forest ecosystem services. *Journal of Sustainable Forestry* 31:518-536
- Schröter D et al. (2005) Ecosystem service supply and vulnerability to global change in Europe. *Science* 310:1333-1337
- Srivastava DS, Cadotte MW, MacDonald AAM, Marushia RG, Mirotnick N (2012) Phylogenetic diversity and the functioning of ecosystems. *Ecology Letters* 15:637-648
- Srivastava DS, Vellend M (2005) Biodiversity-ecosystem function research: Is it relevant to conservation? *Annual Review of Ecology Evolution and Systematics* 36:267-294
- Swamy V, Terborgh JW (2010) Distance-responsive natural enemies strongly influence seedling establishment patterns of multiple species in an Amazonian rain forest. *Journal of Ecology* 98:1096-1107
- Terborgh J (2012) Enemies maintain hyperdiverse tropical forests. *American Naturalist* 179:303-314
- Thebault E, Huber V, Loreau M (2007) Cascading extinctions and ecosystem functioning: contrasting effects of diversity depending on food web structure. *Oikos* 116:163-173
- Thebault E, Loreau M (2005) Trophic interactions and the relationship between species diversity and ecosystem stability. *American Naturalist* 166:E95-E114
- Thebault E, Loreau M (2006) The relationship between biodiversity and ecosystem functioning in food webs. *Ecological Research* 21:17-25
- Vehviläinen H, Koricheva J, Ruohomäki K (2008) Effects of stand tree species composition and diversity on abundance of predatory arthropods. *Oikos* 117:935-943
- Vilà M et al. (2005) Confounding factors in the observational productivity-diversity relationship in forests. In: Scherer-Lorenzen M, Körner C, Schulze ED (eds) *Forest diversity and function: temperate and boreal systems*. Springer, Heidelberg, pp 65-85
- Villéger S, Ramos Miranda J, Flores Hernandez D, Mouillot D (2010) Contrasting changes in taxonomic vs. functional diversity of tropical fish communities after habitat degradation. *Ecological Applications* 20:1512-1522
- Visser MD, Muller-Landau HC, Wright SJ, Rutten G, Jansen PA (2011) Tri-trophic interactions affect density dependence of seed fate in a tropical forest palm. *Ecology Letters* 14:1093-1100
- Vitousek PM (1994) Beyond global warming: ecology and global change. *Ecology* 75:1861-1876
- Weiblen GD, Webb CO, Novotny V, Basset Y, Miller SE (2006) Phylogenetic dispersion of host use in a tropical insect herbivore community. *Ecology* 87:S62-S75
- Weisser WW, Siemann E (2004) The various effects of insects on ecosystem functioning. In: Weisser WW, Siemann E (eds) *Insects and ecosystem function*. Springer, Berlin, Heidelberg, pp 3-24
- Yang X et al. (2013) Establishment success in a forest biodiversity and ecosystem functioning experiment in subtropical China (BEF-China). *European Journal of Forest Research* 132:593-606

# CHAPTER 2

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# Plant traits affecting herbivory on tree recruits in highly diverse subtropical forests

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## Abstract

Differences in herbivory among woody species can greatly affect the functioning of forest ecosystems, particularly in species-rich (sub)tropical regions. However, the relative importance of the different plant traits which determine herbivore damage remains unclear. Defense traits can have strong effects on herbivory, but rarely studied geographic range characteristics could complement these effects through evolutionary associations with herbivores. Here, we use a large number of morphological, chemical, phylogenetic and biogeographic characteristics to analyze interspecific differences in herbivory on tree saplings in subtropical China. Unexpectedly, we found no significant effects of chemical defense traits. Rather, herbivory was related to the plants' leaf morphology, local abundance and climatic niche characteristics, which together explained 70% of the interspecific variation in herbivory in phylogenetic regression. Our study indicates that besides defense traits and apparency to herbivores, previously neglected measures of large-scale geographic host distribution are important factors influencing local herbivory patterns among plant species.

**Key words:** BEF-China; ecosystem functioning; Gutianshan National Nature Reserve; latitudinal range; phenolics; phytochemical diversity; plant defense; plant–insect interaction; species richness; tannins

## Introduction

Herbivory can strongly affect plant communities and might play an important structuring role in species-rich subtropical and tropical forests (Wright 2007; Viola et al. 2010). However, little is known about the main drivers causing interspecific differences in herbivore damage among tree species.

It is often assumed that the extent of herbivore damage is driven primarily by morphological or phytochemical plant traits (Coley and Barone 1996; Marquis et al. 2001; Poorter et al. 2004). Primary metabolites, such as nitrogen compounds, and morphological traits related to high growth rates, such as

specific leaf area, increase nutritional quality and can make plants more susceptible to herbivory (Poorter et al. 2004). In contrast, the role of many secondary compounds not directly involved in primary metabolism, and the part played by many morphological characteristics, have often been attributed to chemical and physical defense against herbivores (Coley and Barone 1996). Tannins, total phenolics, or even overall phytochemical diversity, but also physical traits such as leaf toughness and dry matter content, are assumed to increase a plant's resistance to herbivory (Jones and Lawton 1991; Poorter et al. 2004). Yet, identifying general patterns across different species has proven difficult

because the vast majority of studies incorporated only a limited number of traits and plant species; thus, results have often been ambiguous (see Carmona et al. 2011). Moreover, the potential effects of the phylogenetic interdependence of these relationships must be accounted for, as these can be influenced by a common evolutionary history which affects the degree of trait similarity between species (Freckleton et al. 2011).

In addition to palatability and defense traits, characteristics relating to the abundance and geographic distribution of plants might also strongly affect local herbivory levels. Abundant plant species can experience greater herbivore damage due to the effects of negative density dependence, a process which has frequently been studied for local distribution patterns (e.g. Terborgh 2012). However, a more evolutionary, but so far neglected, perspective might equally suggest that larger-scale geographic distribution of a host plant also affects local herbivory levels. Widespread plants provide increased opportunities for host-specialization and should sustain more widely distributed populations of herbivores, thus reducing extinction probabilities and promoting the accumulation of herbivore species over time (Kennedy and Southwood 1984, Lewinsohn et al. 2005, Miller 2012). High herbivore diversity can intensify herbivore pressure not only via complementarity among herbivore species, but also by increasing the probability of important herbivores being present at local scales. Range characteristics probably also affect the long-term stability of these associations, as host range fragmentation and persistence in refugia during past glacial periods differed between plant species with different range sizes and geographic distributions (Qiu et al. 2011). Moreover, herbivores might cause greater damage at the hosts' geographic range margins. Plants often face stressful environmental conditions at the margins of their range (Brown 1984), which can affect their susceptibility to herbivory (Fine et al. 2004; Meyer et al. 2006). Range characteristics might thus mediate local herbivory patterns, but so far these aspects have not been incorporated into analyses of

the drivers that determine herbivore damage levels.

An improved understanding of the relative contribution and interdependence of these different characteristics to herbivore damage levels requires a pluralistic approach which incorporates the whole suite of different traits and characteristics that potentially affect plant resistance (Agrawal 2007; Carmona et al. 2011; Moles et al. 2011). In intraspecific comparisons morphological and life-history traits have recently been found to have a greater effect on herbivory levels than secondary compounds, and this could also apply to interspecific patterns (Carmona et al. 2011). These traits might in turn be influenced by the distributional characteristics of the plants: apparency theory predicts that plant species which are obvious to herbivores (such as those plants with high local abundance) will evolve mechanisms to reduce their nutritional attractiveness (Feeny 1976; Agrawal 2007). This evolutionary response might also be encountered at larger scales for plant species with a high regional spread, i.e. a large-scale geographic availability (Bryant et al. 1989; Scriber 2010). Local abundance and geographic range characteristics might thus covary with, and to some extent influence, physical or chemical defense mechanisms (e.g. Moles et al. 2011). However, direct effects of range-size related aspects on the species richness and composition of herbivore assemblages (Lewinsohn et al. 2005; Lavandero et al. 2009) could also cause increased herbivore pressure independent of, and even outweighing, the effects of plant defenses.

Here, we analyze the combined effects of a large number of morphological, chemical and biogeographic characteristics, as well as the influence of phylogenetic relationships, on the herbivory levels of saplings of 21 dominant tree and shrub species (representing 16 genera of 9 families) in an extraordinarily plant species-rich subtropical forest in southeast China. We focus on saplings (height range: 20–100 cm), as these recruits are particularly important for the long-term maintenance of tree and shrub diversity in these forests, forming future generations of the tree and shrub layers (Bruehlheide et al.

2011). We test which plant characteristics primarily determine mean levels of herbivore damage on tree recruits, and to what extent the effects of the various characteristics are complementary. While we expect to find (i) negative effects of defense traits and (ii) positive effects of traits that increase the plants' palatability to herbivores, we hypothesize that (iii) local abundance, range size and the marginality of climatic conditions at the study site (relative to the host species' overall climatic niche) positively, and in part independent of the effects of chemical and morphological traits, affect local herbivory levels.

## Methods

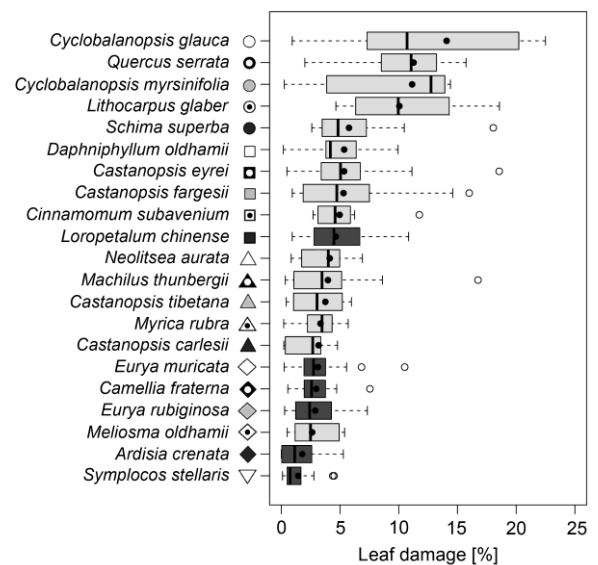
### Study plots

The study was conducted in the Gutianshan National Nature Reserve (29°14' N, 118°07' E), Zhejiang Province, in southeast China. The reserve covers about 8000 ha of semi-evergreen, broad-leaved subtropical forest. In 2008, 27 study plots (30 x 30 m) were established, distributed randomly across the whole reserve. Plot selection was based on stand age (ranging from < 20 to > 80 yr) and woody plant species richness (25–69 species per plot), allowing quantification of herbivory as a mean value over a range of abiotic and biotic local conditions. For further details on plot selection and general plot characteristics see Bruelheide et al. (2011).

### Herbivory assessment

We studied insect herbivory on leaves of saplings (height 20–100 cm) from 21 tree and shrub species (Fig. 2.1). The study species belonged to the dominant plants, accounting for 65% of the total biomass (as approximated by their local relative basal area) in the tree and shrub layers of the study plots. A maximum of ten saplings of each species were randomly sampled in each plot (see Appendix S1 in Supplementary Material). Insect herbivory was measured as standing levels of leaf damage (Ness et al. 2011) at the end of the rainy season in June/July 2008, which also marks the end of a major activity period for arthropods in these forests (personal observations). To ensure that the analysis was consistent among species, we only used young

leaves produced in the current growing season (time of leaf flush is very similar among the studied species (Teng Fang, unpubl. data) and did not affect herbivory levels:  $R^2 = 0.05$ ,  $P = 0.35$ ). Leaf damage was assessed as the cumulative percentage of leaf area lost due to chewing, mining, galling and (if visible) sucking insects. Damage was estimated by visual inspection using a pre-defined percentage system of six classes of photosynthetic tissue removal for each leaf (Appendix S1).



**Figure 2.1.** Leaf damage (%) on young, fully expanded leaves of 21 tree (light grey) and shrub (dark grey) species in subtropical forests of southeast China. Species are ordered by mean leaf damage levels. Filled circles indicate mean values, black lines show medians across the 27 study plots. Each species is assigned a unique symbol (next to species name) for identification in Fig. 2.2.

The validity of the estimates was checked using samples of randomly collected leaves; these were digitally scanned to determine the exact amount of leaf damage (expressed as the ratio of removed to estimated total leaf area). For the statistical analysis, we used the mean percentage of herbivory determined from the sampled and scanned leaves for each percentage class (see Appendix S1 and Schuldt et al. 2010 for details).

### Plant characteristics

We used a comprehensive set of morphological, chemical, biogeographic, and

phylogenetic characteristics of the plant species as predictors of species-specific levels of herbivory. Details of measurements and calculations of these variables are provided in Appendix S1.

The morphological leaf traits included in our analyses were leaf area, specific leaf area (SLA), leaf dry-matter content (LDMC), and leaf toughness. Larger leaves might attract more herbivores and thus show greater damage (Garibaldi et al. 2011). SLA, which is often positively related to plant growth rate and leaf quality, can have similar effects (Diaz et al. 2004). LDMC, on the other hand, is often considered to be related to leaf robustness and toughness (Poorter et al. 2009; Kitajima and Poorter 2010).

A wealth of phytochemical compounds and compound classes has been identified as potential defense against herbivores (Coley and Barone 1996). We tested for total phenolics and tannins as 'classical' chemical defenses (Coley and Barone 1996). However, a variety of compounds are effective against different herbivores and might also act together to affect herbivores (Rasmann and Agrawal 2011). Thus, we also used chemical diversity and chemical uniqueness (expressed as the Shannon Index and the proportion of unique retention time peaks, respectively, of leaf extracts in HPLC analysis) as measures of the general phytochemical diversity (Lavandero et al. 2009). The method records UV spectra of a multitude of both non-polar and weakly polar compounds, among them a large number of compounds with UV spectra that point to flavonoids such as kaempferol and quercetin derivatives. Herbivores might have difficulties dealing with chemical mixtures, and high phytochemical diversity or unique phytochemical features not shared by many other plants might thus reduce a plant species' overall susceptibility to herbivory (Jones and Lawton 1991; Lavandero et al. 2009; Rasmann and Agrawal 2011). As chemical traits that determine the nutritional quality of the plants, we included leaf C and N content (%) and the C/N ratio, which have often been used as measures of palatability to herbivores (Poorter et al. 2004).

As a measure of mean local

abundance, we used the total basal area (cm<sup>2</sup> per plot) of each species averaged across study plots (see Appendix S1 and Bruelheide et al. 2011).

Variables related to the plant species' geographic range were latitudinal range, minimum latitude of the species' range, geographic range size (approximated as the number of occupied 0.25 x 0.25' grid cells), climatic niche breadth (calculated from temperature and precipitation ranges of the occurrence data points) and marginality of climatic conditions at the study site, i.e. the minimum distance in PCA space to the margin of the species' niche (see below). Larger range size, latitudinal range and niche breadth might promote the accumulation of herbivore species adapted to a plant species over time (Lewinsohn et al. 2005). A lower minimum latitude of the plant species' range might have a similar effect, as it can indicate a higher long-term stability of plant-herbivore associations in historical time (see Discussion). Finally, deviations from the mean climatic niche conditions of the plant species (high niche marginality) at the study site might increase environmental stress and affect the plants' susceptibility to herbivory. Distribution data were derived from data bases, published range maps and regional floras (see Appendix S1 for a complete list of data sources). Species occurrence data were geo-referenced and digitized to calculate species ranges. Corresponding climate data (0.25 x 0.25' resolution) were extracted from the Worldclim database (<http://www.worldclim.org>). The niche position and niche breadth along climatic axes were quantified using a multivariate coinertia analysis computing an Outlying Mean Index (OMI) (Dolédec et al. 2000). The analysis results in species-specific descriptions of the niche ranges along the main principal components of the environmental data space of all considered species. In this context, the species-specific niche position is a measure of the deviations of the mean climatic conditions of the study location from the range-wide habitat conditions of each species, calculated as the mean of marginality distances on each principal components axis (see Appendix S1 for details).



Phylogenetic relationships between species were constructed from *rbcL* and *matK* sequences, downloaded from NCBI Genbank (<http://www.ncbi.nlm.nih.gov>; Table S2.2 in Appendix S1). Sequences were aligned in Bioedit, and a first phylogenetic hypothesis was generated using maximum likelihood (ML) in MEGA5 (Tamura et al. 2011). A second ultrametric tree was computed based on the ML tree (Fig. S2.1 in Appendix S1) using penalized likelihood. The branch lengths in this tree are a measure of divergence time. For each of our study species we also included the number of congenics growing in the 27 study plots as a measure of taxonomic isolation. This can provide further insight into plant community effects on interspecific patterns of herbivore damage (Ness et al. 2011).

### Data analysis

We used phylogenetic general least squares (PGLS) regression, based on the ultrametric phylogenetic tree, to test for the effects of biogeographic, morphological and chemical plant traits on insect herbivory levels. Damage was expressed as the mean leaf damage per species averaged across plots in order to match it with the explanatory variables, which were available in most cases only as species-level data (due to the nature of the data or because traits were measured from pooled samples). This also hinders the integration of potential effects of intraspecific trait variation on herbivory and phylogenetic relationships in our models (cf. Ives et al. 2007). This would have required trait measurements at the plot or individual level, and limits our analyses to an interspecific perspective based on mean trait values. However, variance components analysis of the herbivory data on the individual plant level (regressing herbivory on species and plots as random effects) revealed that 29.2% of the variation was explained by species, 5.5% by plots (pooled over species) and 65.3% was residual variation, indicating that intraspecific variation in herbivory due to changes in environmental conditions among the 27 study plots was low compared to interspecific variation in herbivory levels across species.

Phylogenetic analysis assumes that the

residual error of the regression (and not necessarily the independent and dependent variables) is affected by phylogenetic relationships among the species studied (Revell 2010). In many cases, the strength of this phylogenetic signal is not known *a priori* and thus it is not possible to determine in advance whether phylogenetically explicit modeling should be used (Freckleton 2009). We thus followed the approach suggested by Revell (2010) and simultaneously estimated the phylogenetic signal in the regression residuals with the regression parameters, quantifying Pagel's  $\lambda$  with a maximum likelihood approach. The value of  $\lambda$  is adjusted to, and optimized for, the strength of the phylogenetic signal in the error structure (where  $\lambda = 0$  indicates no phylogenetic signal and  $\lambda = 1$  a strong phylogenetic signal according to a Brownian motion model of trait evolution; Freckleton et al. 2011). This ensures that potential phylogenetic effects are adequately considered and reduces the risk of over- or underestimating this effect (Revell 2010; Freckleton et al. 2011). As the presence or absence of phylogenetic effects is already automatically accounted for in this regression, the approach statistically more straightforward than a comparison between phylogenetically corrected and uncorrected models (cf. Freckleton 2009). We also checked for the strength and significance of the phylogenetic signal in the regression residuals by calculating *K* statistics (Blomberg et al. 2003). For additional information on the individual variables see Table S2.1 in Appendix S1.

Prior to analysis, we checked for collinearity among explanatory variables. Minimum latitude, latitudinal range and distribution area were strongly correlated with the climatic niche breadth (Pearson's  $r = 0.75$ ,  $P < 0.001$ ;  $r = -0.68$ ,  $P < 0.001$ ; and  $r = 0.70$ ,  $P < 0.001$ , respectively), C/N ratio with N content ( $r = -0.93$ ,  $P < 0.001$ ), and phenolic content with tannins ( $r = 0.80$ ,  $P < 0.001$ ). To avoid problems of multicollinearity, we only retained those variables most strongly related to herbivory in each of the above-mentioned sets. Differences in the number of plant individuals sampled for herbivory (the 27 plots did not necessarily have 10 saplings from each of the 21 species) had no effect on mean

leaf damage ( $r = -0.19$ ,  $P = 0.935$ ) and we did not include this variable in the regression analyses. The full model thus included leaf area, SLA, LDMC, leaf toughness, chemical diversity, chemical uniqueness, C content, N content, tannin content, mean local abundance, climatic niche breadth, niche marginality, congeneric isolation, and growth form (tree or shrub) as predictors of the differences in herbivory levels between species (Table S2.1 in Appendix S1). Mean leaf damage, mean local abundance, leaf area and tannin content were log-transformed to increase normality of the data.

We used model simplification based on the Akaike Information Criterion ( $AIC_c$ , corrected for small sample sizes; Burnham and Anderson 2004). Variables were eliminated from the full model until a minimal, best-fit model with the lowest global  $AIC_c$  was obtained. Model residuals were checked for assumptions of normality and homoscedasticity. Variance partitioning (Legendre and Legendre 1998) was used to determine the independent and shared effects of the explanatory variables on mean levels of herbivore damage between the 21 tree and shrub species. Statistical analyses were performed with R 2.12.0 (<http://www.R-project.org>).

## Results

Overall, we assessed herbivory on 1602 individuals (on a total of 36,752 leaves) of the 21 tree and shrub species. Mean leaf damage by insect herbivores ranged from 1.4–14.1% per plant species (Fig. 2.1), with an overall mean of 5.3%.

The best PGLS-model ( $AIC_c = 24.9$ , compared to  $AIC_c = 159.6$  for the full model) accounted for 70.3% of the among-species variation in herbivory ( $F_{5,16} = 12.84$ ;  $P < 0.001$ ) and included LDMC ( $t = 4.4$ ;  $P < 0.001$ ), mean local abundance ( $t = 3.8$ ;  $P = 0.0016$ ), climatic niche breadth ( $t = 3.3$ ;  $P = 0.0049$ ) and niche marginality ( $t = 2.5$ ;  $P = 0.0233$ ) as predictors (Table 2.1). Simultaneous consideration of phylogeny with the regression parameters showed that there was no phylogenetic signal in the residual error of the regression model (Pagel's  $\lambda = 0$ ). This was also confirmed by an additional analysis of the residuals using  $K$

statistics as an alternative measure ( $K = 0.17$ ;  $P = 0.11$ ). Yet, results were essentially the same even when (incorrectly, see Revell 2010) assuming phylogenetic effects (with  $\lambda = 1$ ) due to signals in individual variables, thus underlining the robustness of our results (Table S2.3 in Appendix S2).

All four explanatory variables were significantly positively related to leaf damage by insects, i.e., mean herbivory levels increased with LDMC, local abundance, the breadth of the climatic niche, and niche marginality (Table 2.1; Fig. 2.2). Leaf chemical traits were not included in the minimal model and did not show significant correlations with leaf damage in single regressions (not shown). The only exception was C content, which was also not included in the minimal model, but showed a significant positive relationship with herbivory in single regressions ( $R^2 = 0.17$ ;  $P = 0.039$ ) and was correlated with LDMC (Pearson's  $r = 0.61$ ;  $P = 0.003$ ). In contrast, leaf toughness was not significantly related to herbivory ( $R^2 = 0.09$ ;  $P = 0.193$ ), nor was it correlated with LDMC ( $r = 0.09$ ;  $P = 0.674$ ).

**Table 2.1.** Regression results for the minimal-adequate phylogenetic general least squares model for mean herbivore damage levels (log-transformed) of 21 tree and shrub species in subtropical China

Variable	Estimate (standardised)	SE	$t$	$P$
(Intercept)	1.499	0.071	21.1	<0.001
Leaf dry matter content	0.335	0.076	4.4	0.0004
Mean local abundance (log-transf.)	0.282	0.074	3.8	0.0016
Climatic niche breadth	0.303	0.093	3.3	0.0049
Niche marginality	0.234	0.093	2.5	0.0233

Adjusted  $R^2 = 0.703$ ;  $F_{5,16} = 12.84$ ;  $P < 0.001$ .  
ML estimation of  $\lambda = 0$

Partitioning the total explained variance among the four predictors showed that LDMC, mean local abundance, and climatic niche breadth and niche marginality accounted for largely independent fractions of explained variance (Fig. 2.3). LDMC (32.3%) had the strongest independent effect on leaf damage

levels, followed by mean local abundance (23.5%). The independent effects of the range size variables climatic niche breadth and niche marginality accounted for 15% of the variance in the herbivory data (Fig. 2.3).

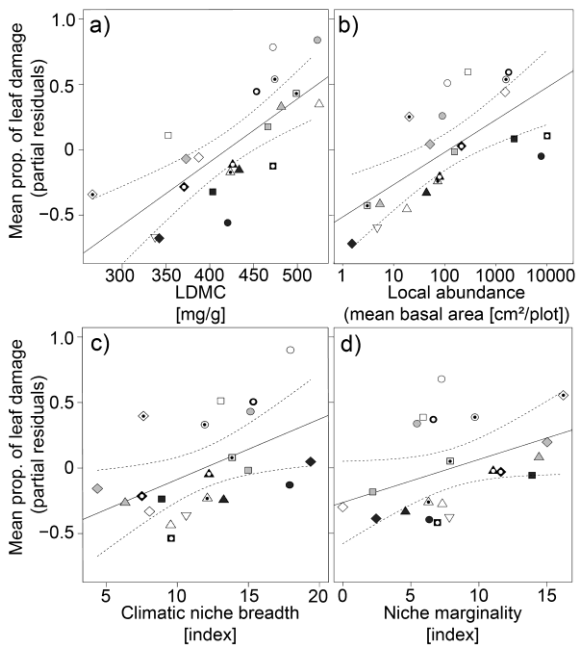
## Discussion

By incorporating rarely tested biogeographic characteristics and the large number of morphological and chemical traits of a large proportion of the dominant plant species, our study provides a more comprehensive analysis of interspecific herbivory patterns than previous studies. It thus yields new insights into the relative importance and interdependence of drivers that might cause differences in mean levels of herbivory and promote the maintenance of woody plant diversity in plant species-rich forests. Three major conclusions arise from our study: whereas i) our herbivory data do not reveal an effect of chemical compounds generally assumed to play an important role in plant defense, ii) distributional characteristics have strong effects on local herbivory patterns, and iii) these distributional characteristics are largely independent of palatability and defense traits.

Our finding (i) is in contrast to the results of many previous studies, which, however, often focused on either a single or on a few, and similar, plant species (e.g. Eichhorn et al. 2007; Lavandero et al. 2009; Muola et al. 2010). However, it corroborates recent results of a more global analysis which indicates that secondary metabolites are of less importance as a defense against herbivory than morphological and life-history traits (Carmona et al. 2011). Unfortunately, we were not able to consider potential effects of intraspecific variation in defense traits on our results (cf. Ives et al. 2007). Yet, intraspecific variation among study plots was low compared to variation in herbivory among species (see Methods). Moreover, Carmona et al. (2011) showed that general support for an impact of secondary metabolites is also weak for intraspecific patterns. We did not consider the full range of potential chemical defense compounds, but the compounds we measured are frequently considered to have a particularly strong effect on herbivory (Coley and Barone

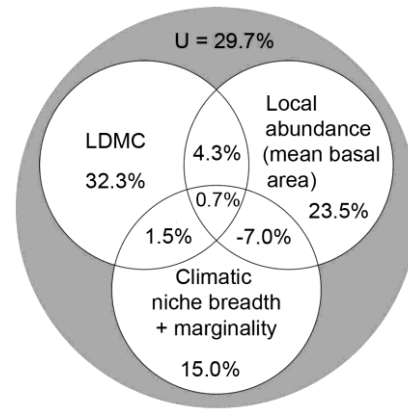
1996; Moles et al. 2011). Many specific chemical defense mechanisms might be overcome by the multitude of herbivore species adapted to, and able to deal with, phytochemical compounds of their hosts (see also Kurokawa and Nakashizuka 2008) to such an extent that in an interspecific context, other plant characteristics may have a stronger bearing on mean herbivore damage levels. Our study shows that even without finding a strong signal of chemical defense traits, a large proportion (70%) of the interspecific variation in herbivory can be explained by such alternative characteristics.

The strongest predictor in our analysis was leaf dry matter content (LDMC). However, although high values of LDMC and analogous measures are often related to traits that convey physical resistance to herbivores (i.e. leaf toughness: Coley and Barone 1996; Perez-Harguindeguy et al. 2003; Poorter et al. 2009), we found an increase in herbivory with LDMC. Our results indicate that effects other than physical toughness are responsible in our case: LDMC was not related to leaf toughness in our study, and our direct measure of leaf toughness had no effect on herbivory. Leaf toughness does not necessarily pose an obstacle to herbivores adapted to tough leaves. Herbivores with strong mouthparts, particularly external leaf chewers, such as many beetles (which also caused a large proportion of the overall damage in our system; Schuldt et al. 2010), are not constrained in their feeding by physical leaf structure and can thus select leaves on the basis of other criteria (see also Marquis et al. 2001; Perez-Harguindeguy et al. 2003). This may apply in particular to regions such as our subtropical forests, where the leaves of most plant species are generally relatively tough, and may explain the deviating results of other studies from, for instance, temperate regions (see also Marquis et al. 2001; Perez-Harguindeguy et al. 2003). In view of the lack of support for physical defense effects, the positive relationship of both LDMC and C content (which did not, however, enter the final regression model) to herbivory might point to a different underlying mechanism: higher C content, and concomitantly higher LDMC, can represent a higher amount of



**Figure 2.2.** Independent effects of a) leaf dry matter content (LDMC), b) mean basal area as a measure of local abundance, c) climatic niche breadth, and d) niche marginality on the mean proportion of leaf damage (partial residuals and 95% confidence bands with the effects of all other variables partialled out) by insect herbivores across 21 tree and shrub species in subtropical China. Niche breadth and marginality are dimensionless index values calculated from coinertia analyses (see Methods). All relationships are significant at  $P < 0.05$  (see Table 2.1). Each species is assigned a unique symbol (see Fig. 2.1).

structural components (Poorter et al. 2009). This, in turn, can cause herbivores to increase leaf consumption in order to compensate for lower nutrient content relative to structural compounds (Berner et al. 2005; Stiling and Cornelissen 2007). This may be particularly important as higher LDMC also means reduced leaf water content, which, in turn, can decrease nitrogen accumulation rates of herbivores (Scriber and Slansky 1981). We did not find a direct relationship between herbivory and traits such as leaf N content and C/N-ratio. Although N content is often related to leaf palatability (Coley and Barone 1996; Poorter et al. 2004), it can also include N-based compounds which are used as a defense against herbivores (Baraza et al. 2007). A lack of effects of N content on herbivory at an interspecific level has also been reported by several other studies (e.g. Berner et al. 2005; Eichhorn et al. 2007).



**Figure 2.3.** Partitioning of between-species variance in herbivory of young, fully expanded leaves of the 21 study species into independent and shared effects (percent explained variance) of morphological (LDMC), local (mean basal area as a measure of local abundance), and biogeographic (climatic niche breadth and niche marginality) variables. Shared effects are shown in the intersecting parts of the circles. U is the unexplained variation.

Most importantly, however, our findings (ii) and (iii) confirm our initial hypothesis that distribution characteristics also play a role in influencing local patterns of herbivory, independent of local abundance and other plant characteristics. Incorporation of biogeographic characteristics can thus improve our understanding of differences in the levels of herbivore damage among plant species. Our findings also provide little evidence for the assumption of the apparency theory that more apparent plants exhibit a higher degree of defensive traits or reduced palatability (see also Agrawal 2007). Leaf traits important for herbivory, such as LDMC, were little affected by local abundance in our study. Nor were they influenced by biogeographic characteristics. However, this also means that the local-abundance and biogeographic effects we found were not caused by covarying effects of morphological or chemical plant traits. Rather, they might be related to the direct effects of herbivores. Locally more apparent, or more widespread, plants should be more visible, or regionally more widely available, to herbivores and thus face higher herbivore pressure (Chew and Courtney 1991; Brändle and Brandl 2001; Terborgh 2012). Our measures of niche breadth and niche marginality highlight the factors potentially

underlying biogeographic effects that have also become evident in studies of latitudinal range effects on herbivore diversity and spatial patterns in herbivory (Jones and Lawton 1991; Brändle and Brandl 2001; Lavandero et al. 2009; Moles et al. 2011). Both of our measures incorporate temperature and precipitation and thus characterize not only the area of distribution but also the breadth of the plants' climatic niches. Plants covering a broader range of climatic conditions face a larger and more diverse set of herbivore species in their distribution ranges (Chew and Courtney 1991; Brändle and Brandl 2001; Lavandero et al. 2009). Besides higher encounter rates and the support of larger, less extinction-prone populations of herbivores across their ranges (Kennedy and Southwood 1984; Ness et al. 2011), widespread plant species might have had a higher probability of persisting (together with a larger proportion of their herbivores) in climatically suitable areas during past climatic changes. Niche breadth was strongly positively related to minimum latitude of the distribution range in our study (Pearson's  $r = 0.75$ ,  $P < 0.001$ ). This could indicate a higher long-term stability of plant–herbivore associations for these species, as glacial refuges for subtropical species were primarily located in southern China (Qiu et al. 2011). These large-scale geographic effects of host availability can influence local-scale patterns. Interrelations between regional and local species pools (Lewinsohn et al. 2005; Harrison and Cornell 2008) increase the probability of a locally more diverse set of herbivores adapted to these plants and concomitantly the likelihood that important herbivore species which increase herbivore pressure are present. Moreover, the observed positive relationship between herbivory and niche marginality indicates that plants are more susceptible to herbivory at their environmental range margins. One explanation would be that herbivory directly contributes to limiting the host species ranges. However, it is also conceivable that climatically marginal conditions at the study site affect plant physiology and morphology and make them more susceptible to herbivory (Fine et al. 2004; Meyer et al. 2006).

Although our study excludes very rare

species and their contribution to interspecific trait variability, mean local abundance of the studied species varied by several orders of magnitude. Likewise, the species showed high interspecific variation in their morphological, chemical and biogeographic characteristics (Table S2.1), such that our set of species is representative of a large part but obviously not all tree and shrub species occurring in the study region.

Our results were not affected by phylogenetic relationships among the studied species, which is in line with the results of related studies (cf. Brändle and Brandl 2001). Range size-related characteristics and abundances can be evolutionary labile and can differ strongly between closely related species (Losos 2011). On the other hand, convergent selection may have contributed to similar leaf morphology among species, with the majority of species in our forest ecosystem, for instance, having relatively tough leaves compared to species from more temperate regions.

## Conclusions

Variance partitioning showed that morphological traits, local abundance and biogeographic characteristics had largely independent effects on mean herbivory levels, but together explained a large proportion (70%) of the overall herbivory found among the 21 tree and shrub species. Effects on mean herbivory levels were thus complementary, with morphological traits and local abundance, for instance, being largely unaffected by the biogeographic characteristics of the plants (cf. Garibaldi et al. 2011). The latter also applied to chemical plant traits, which were of less importance in our study, but were in some cases correlated with morphological traits. A clear message from our findings is that distributional, morphological and chemical characteristics need to be considered simultaneously if we are to improve our understanding of interspecific patterns of herbivory. This approach has rarely been applied in previous studies, but can provide a better knowledge of the main drivers influencing herbivore damage levels. In addition to leaf traits that reflect palatability or defense, the apparency of plant species on

a local scale, and the availability to herbivores on a larger geographic scale emerge as important, but—in the case of geographic distribution measures—previously neglected, factors that influence mean herbivory levels. Apparency and range characteristics might thus potentially contribute to maintaining patterns of coexistence between plant species in ecosystems with high plant diversity.

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### Author contributions

AS, HB, MF, WH, KM, BS, TA designed the study. AS, WD, DE, WK, SM, WUP, EW, HZ collected and prepared the data. AS carried out statistical analyses and wrote the manuscript, with input from all coauthors.

### References

- Agrawal AA (2007) Macroevolution of plant defense strategies. *Trends in Ecology and Evolution* 22:103-109
- Baraza E, Zamora R, Hodar JA, Gomez JM (2007) Plant-herbivore interaction: beyond a binary vision. In: Pugnaire FI, Valladares F (eds) *Functional plant ecology*, 2nd edn. CRC Press, Boca Raton, pp 481-514
- Berner D, Blanckenhorn WU, Körner C (2005) Grasshoppers cope with low host plant quality by compensatory feeding and food selection: N limitation challenged. *Oikos* 111:525-533
- Blomberg SP, Garland T, Ives AR (2003) Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution* 57:717-745
- Brändle M, Brandl R (2001) Species richness of insects and mites on trees: expanding Southwood. *Journal of Animal Ecology* 70:491-504
- Brown JH (1984) On the relationship between abundance and distribution of species. *American Naturalist* 124:255-279
- Bruelheide H et al. (2011) Community assembly during secondary forest succession in a Chinese subtropical forest. *Ecological Monographs* 81:25-41
- Bryant JP, Tahvanainen J, Sulkinoja M, Julkunen-Titto R, Reichardt P, Green T (1989) Biogeographic evidence for the evolution of chemical defense against mammal browsing by boreal birch and willow. *American Naturalist* 134: 20-34.
- Burnham KP, Anderson DR (2004) *Model selection and multimodel inference: a practical information-theoretic approach*. Springer, New York
- Carmona D, Lajeunesse MJ, Johnson MTJ (2011) Plant traits that predict resistance to herbivores. *Functional Ecology* 25:358-367
- Chew FS, Courtney SP (1991) Plant apparency and evolutionary escape from insect herbivory. *American Naturalist* 138:729-750
- Coley PD, Barone JA (1996) Herbivory and plant defenses in tropical forests. *Annual Review of Ecology and Systematics* 27:305-335
- Diaz S et al. (2004) The plant traits that drive ecosystems: Evidence from three continents. *Journal of Vegetation Science* 15:295-304
- Dolédec S, Chessel D, Gimaret-Carpentier C (2000) Niche separation in community analysis: a new method. *Ecology* 81: 2914-2927.
- Eichhorn MP, Fagan KC, Compton SG, Dent DH, Hartley SE (2007) Explaining leaf herbivory rates on tree seedlings in a Malaysian rain forest. *Biotropica* 39:416-421
- Feeny PP (1976) Plant apparency and chemical defense. In: Wallace JW, Mansell RL (eds) *Recent Advances in Phytochemistry*. Plenum Press, New York, pp 1-40
- Fine PVA, Mesones I, Coley PD (2004) Herbivores promote habitat specialization by trees in amazonian forests. *Science* 305: 663-665.
- Freckleton RP (2009) The seven deadly sins of

- comparative analysis. *Journal of Evolutionary Biology* 22: 1367-1375.
- Freckleton RP, Cooper N, Jetz W (2011) Comparative methods as a statistical fix: the dangers of ignoring an evolutionary model. *American Naturalist* 178:E10-17
- Garibaldi LA, Kitzberger T, Ruggiero A (2011) Latitudinal decrease in folivory within *Nothofagus pumilio* forests: dual effect of climate on insect density and leaf traits? *Global Ecology and Biogeography* 20:609-619
- Harrison S, Cornell H (2008) Toward a better understanding of the regional causes of local community richness. *Ecology Letters* 11:969-979
- Ives A.R., Midford P.E. and Garland T., Jr. (2007) Within-species variation and measurement error in phylogenetic comparative methods. *Syst. Biol.*, 56, 252-270.
- Jones CG, Lawton JH (1991) Plant Chemistry and Insect Species Richness of British Umbellifers. *Journal of Animal Ecology* 60:767-777
- Kennedy CEJ, Southwood TRE (1984) The number of species of insects associated with British trees: a re-analysis. *Journal of Animal Ecology* 53: 455-478.
- Kitajima K, Poorter L (2010) Tissue-level leaf toughness, but not lamina thickness, predicts sapling leaf lifespan and shade tolerance of tropical tree species. *New Phytologist* 186:708-721
- Kurokawa H, Nakashizuka T (2008) Leaf herbivory and decomposability in a Malaysian tropical rain forest. *Ecology* 89:2645-2656
- Lavandero B, Labra A, Ramirez CC, Niemeyer HM, Fuentes-Contreras E (2009) Species richness of herbivorous insects on *Nothofagus* trees in South America and New Zealand: The importance of chemical attributes of the host. *Basic and Applied Ecology* 10:10-18
- Legendre P, Legendre N (1998) *Numerical ecology*, 2nd edn. Elsevier, Amsterdam
- Lewinsohn TM, Novotny V, Basset Y (2005) Insects on plants: Diversity of herbivore assemblages revisited. *Annual Review of Ecology Evolution and Systematics* 36:597-620
- Losos JB (2011) Seeing the forest for the trees: the limitations of phylogenies in comparative biology. *American Naturalist* 177:709-727
- Marquis RJ, Diniz IR, Morais HC (2001) Patterns and correlates of interspecific variation in foliar insect herbivory and pathogen attack in Brazilian cerrado. *Journal of Tropical Ecology* 17:127-148
- Meyer ST, Roces F, Wirth R (2006) Selecting the drought stressed: effects of plant stress on intraspecific and within-plant herbivory patterns of the leaf-cutting ant *Atta colombica*. *Functional Ecology* 20: 973-981.
- Miller Z. (2012) Fungal pathogen species richness: Why do some plant species have more pathogens than others? *American Naturalist* 179: 282-292.
- Moles AT, Bonser SP, Poore AGB, Wallis IR, Foley WJ (2011) Assessing the evidence for latitudinal gradients in plant defence and herbivory. *Functional Ecology* 25:380-388
- Muola A, Mutikainen P, Lilley M, Laukkanen L, Salminen JP, Leimu R (2010) Associations of plant fitness, leaf chemistry, and damage suggest selection mosaic in plant-herbivore interactions. *Ecology* 91:2650-2659
- Ness JH, Rollinson EJ, Whitney KD (2011) Phylogenetic distance can predict susceptibility to attack by natural enemies. *Oikos* 120:1327-1334
- Perez-Harguindeguy N, Diaz S, Vendramini F, Cornelissen JHC, Gurvich DE, Cabido M (2003) Leaf traits and herbivore selection in the field and in cafeteria experiments. *Austral Ecology* 28:642-650
- Poorter H, Niinemets Ü, Poorter L, Wright IJ, Villar R (2009) Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. *New Phytologist* 182:565-588
- Poorter L, de Plassche MV, Willems S, Boot RGA (2004) Leaf traits and herbivory rates of tropical tree species differing in successional status. *Plant Biology* 6:746-754
- Qiu YX, Fu CX, Comes HP (2011) Plant molecular phylogeography in China and adjacent regions: Tracing the genetic imprints of Quaternary climate and environmental change in the world's most diverse temperate flora. *Molecular Phylogenetics and Evolution* 59: 225-244.
- Rasmann S, Agrawal AA (2011) Latitudinal patterns in plant defense: evolution of cardenolides, their toxicity and induction following herbivory. *Ecology Letters* 14:476-483
- Revell LJ (2010) Phylogenetic signal and linear regression on species data. *Methods in Ecology and Evolution* 1:319-329
- Schuldt A et al. (2010) Tree diversity promotes insect herbivory in subtropical forests of southeast China. *Journal of Ecology* 98:917-926
- Scriber JM (2010) Integrating ancient patterns and current dynamics of insect-plant interactions: Taxonomic and geographic variation in herbivore specialization. *Insect Science* 17: 471-507.
- Scriber JM, Slansky F (1981) The nutritional ecology of immature insects. *Annual Review of*

Entomology 26 183-211.

Stiling P, Cornelissen T (2007) How does elevated carbon dioxide (CO<sub>2</sub>) affect plant–herbivore interactions? A field experiment and meta-analysis of CO<sub>2</sub>-mediated changes on plant chemistry and herbivore performance. *Global Change Biology* 13:1823-1842

Tamura K, Peterson D, Peterson N, Stecher G, Nei M, Kumar S (2011) MEGA5: Molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. *Molecular Biology and Evolution* 28:2731-2739

Terborgh J (2012) Enemies maintain hyperdiverse tropical forests. *American Naturalist* 179 303-314.

Viola DV et al. (2010) Competition-defense tradeoffs and the maintenance of plant diversity. *Proceedings of the National Academy of Sciences of the United States of America* 107:17217-17222

Wright SJ (2007) Plant diversity in tropical forests. In: Pugnaire FI, Valladares F (eds) *Functional plant ecology*, 2nd edn. CRC Press, Boca Raton, pp 351-367

## Supplementary Material

Additional Supplementary Material may be found in the online version of this article:

**Appendix S1** *Details of methods used in herbivory assessment and in measurements of plant characteristics*

**Table S2.1** *Summary statistics for leaf damage and predictor variables*

**Table S2.2** *Species and GenBank accession numbers for *rbcL* and *matK* sequences*

**Fig. S2.1** *Ultrametric phylogenetic tree of the 21 study species*

**Appendix S2** *PGLS results for regression with fixed lambda ( $\lambda = 1$ )*

**Table S2.3** *PGLS results for regression with fixed lambda ( $\lambda = 1$ )*

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## Supplementary Material

### Appendix S1: Details of methods used in herbivory assessment and in measurements of plant characteristics

#### Herbivory assessment

Leaf herbivory by insects was measured on 21 of the dominant tree (*Castanopsis carlesii* (Hemsl.), *Castanopsis eyrei* (Champ. ex Benth.), *Castanopsis fargesii* Franch., *Castanopsis tibetana* Hance, *Cinnamomum subavenium* Miq., *Cyclobalanopsis glauca* (Thunb.), *Cyclobalanopsis myrsinifolia* (Bl.), *Daphniphyllum oldhamii* (Hemsl.), *Lithocarpus glaber* (Thunb.), *Machilus thunbergii* Sieb. et Zucc., *Meliosma oldhamii* Maxim., *Myrica rubra* Sieb. et Zucc., *Neolitsea aurata* (Hayata), *Quercus serrata* Murray, *Schima superba* Gardn. et Champ.) and shrub species (*Ardisia crenata* Sims, *Camellia fraterna* Hance, *Eurya muricata* Dunn, *Eurya rubiginosa* H.T. Chang, *Loropetalum chinense* (R. Br.), *Symplocos stellaris* Brand).

A maximum of ten saplings per species were randomly sampled by crossing each of the study plots along parallel transects. The mean number of individuals analyzed per species was  $78.6 \pm 56.6$  SD, as the 27 plots did not necessarily all have 10 saplings of each of the 21 species. We distinguished between young (expanded in the current growing season) and older (expanded in previous growing seasons) leaves. In order to ensure a consistent analysis of plant traits, which might vary between leaves of different ages, we only used young leaves. The main damage patterns could clearly be attributed to major groups of insect herbivores, i.e., predominantly to lepidopterous larvae and several beetle families, observed during the herbivory census.

Insect herbivory was measured as standing levels of leaf damage (Llandres et al. 2010; Ness et al. 2011) in June/July 2008. The degree of leaf damage was estimated by visual inspection using a percentage system of six classes of photosynthetic tissue removal for each leaf (Eichhorn et al. 2007; Sobek et al. 2009; Llandres et al. 2010; Ness et al. 2011): 0%, < 1%, 1–5%, > 5–15%, > 15–35%, and > 35%. Absent leaves were only counted if the petiole was still present, as otherwise the reason for leaf abscission is difficult to

identify (Eichhorn et al. 2007). These six classes were defined beforehand and the appropriateness of the estimates was checked by analyzing samples of randomly collected leaves. These were digitally scanned to determine the exact amount of leaf damage as the ratio of removed to estimated total area of the leaves (Schuldt et al. 2010). For the statistical analysis, we used the mean percentage of herbivory determined from the sampled and scanned leaves for each percentage class (0%, 0.5%, 3%, 9%, 23%, and 55%).

#### Measurements of plant characteristics

**Morphological:** Morphological leaf traits can act as a physical defense against herbivores. In our analyses we included morphological traits widely used in similar studies, i.e. leaf area ( $\text{mm}^2$ ), specific leaf area (SLA [ $\text{m}^2/\text{kg}$ ]), leaf dry matter content (LDMC [ $\text{mg}/\text{g}$ ], and leaf toughness) (Table S2.1). The traits were measured for each species from leaves of five to seven plant individuals (seven leaves per individual, with only one individual per species collected per plot sampled) in the summer of 2008. Only completely developed leaves unaffected by herbivory were collected, stored in wet PVC bags and taken to the field lab for weighing and measuring. Leaves were digitally scanned, and leaf area ( $\text{mm}^2$ ) was determined using the software Win FOLIA Pro S (Regent Instruments Inc.). SLA ( $\text{m}^2/\text{kg}$ ) was calculated after oven-drying (48h at  $80^\circ\text{C}$ ) of the fresh leaves as leaf area divided by leaf dry mass; LDMC was calculated as the ratio of leaf dry weight to fresh weight ( $\text{mg}/\text{g}$ ). Leaf toughness was measured as leaf tensile strength on five individuals (four leaves per individual) per plant species in 2011, using a modified ‘tearing apparatus’ developed after Hendry and Grime (1993). A leaf fragment of 5 mm width was cut from the central part of the leaves (not including the midrib) along the longitudinal axis and positioned between two clamps in the tearing apparatus. The part of the fragment to be torn apart did not include

any main veins. The clamps were slowly pulled apart, and the force needed to tear apart the leaf fragment was measured with a spring balance (Cornelissen et al. 2003).

*Chemical:* Phytochemicals determine both the nutritional quality and the chemical defense mechanisms of plant species. We determined leaf C and N content (%) and the C/N ratio, phytochemical diversity and uniqueness (expressed as the Shannon-Wiener Index and the proportion of unique retention time peaks, respectively, of leaf extracts in HPLC analysis), and the total phenolic and tannin content of the leaves of the 21 tree and shrub species (Table S2.1).

Five saplings of each species were sampled in August 2009, with six undamaged, young but fully expanded leaves collected per plant individual. Samples were pooled per species, leaves were air dried in shade and ground for further analyses. C and N content as well as C/N ratio were determined with an elemental analyzer (vario El cube, Elementar, Hanau, Germany). For measurements of phytochemical diversity and uniqueness, ground leaves were extracted in methanol / water (cf. Rasmann et al. 2009) and analyzed by HPLC with a gradient of acetonitrile, phosphoric acid and water. For the analyses, 25 mg of dried and ground leaves were extracted with 1.5 ml of 80% methanol / 20% water on a planary shaker for 2 h. After centrifugation, samples were analyzed by HPLC (Agilent 1100 with quaternary pump and DAD-detector; column NUCLEODUR C8ec, 4.6x100 mm, particle size 3 $\mu$ m, Macherey-Nagel). The 10  $\mu$ l injection was eluted at a constant flow of 1 ml/min with a gradient of water, acetonitrile and 0.005 M phosphoric acid. The fraction of phosphoric acid was always held constant at 5%, the gradient of water / acetonitrile was as follows: start with 65% water and 30% acetonitrile, 0-25 min linear gradient to 90 % acetonitrile, 25-26 min linear gradient back to 30% acetonitrile and hold for 6 minutes. Peaks were detected by a diode array detector at 280 nm. We used 1-bromo-4-fluorobenzene (c = 32 mg/L, RT=16.5 min) as internal standard for the retention times of leaf-chemical compounds in the chromatogram. Two

boundary conditions were applied in the analysis of HPLC-chromatograms: (a) peak-retention times of individual compounds were used above an arbitrary cut-off of 2 minutes to exclude signals around the dead time of the column and (b) peaks with absorbances below 1 mAU were rejected and not used in the analysis. Chemical diversity ( $D$ ) was recorded as the Shannon index of the number of peaks in retention time and their respective standardized peak areas for each species. Chemical uniqueness ( $u$ ) was calculated following Jones and Lawton (1991) as

$$u = \sum_1^d 1/P_i d,$$

with  $P_i$  being the proportion of all studied species containing the compound  $i$ , and  $d$  representing the number of retention time peaks.

In addition, total phenolics and tannin content were determined from oven dried (48h at 80°C) leaves. About 50 mg of dried leaf-powder were extracted, as described by Torti et al. (1995), four times in each 5 ml 50% aqueous acetone. Total phenolics were determined using the Modified Prussian Blue Method as described by Hagerman (1992). Total tannin concentrations were determined by the Radial Diffusion Assay for increased sensitivity (Hagermann 1987; Salminen and Karonen 2011), modified by using 0.75% agarose gels as well as 0.016% BSA (Bovine Serum Albumin) as standard protein. Stained gels were digitized using a desk scanner. Image processing was carried out using ImageJ 1.44p (Rasband 2011) and inverted white-balance modification. Both assays were calibrated against tannic acid (Carl Roth, Germany, charge nr. 250153788) and concentrations are expressed in tannic acid equivalents (TAE) in mg/g on a dry mass basis.

*Local abundance:* As a measure of mean local abundance, we included the total basal area of the 21 species averaged across all 27 study plots. Diameter at breast height (d.b.h.) was recorded for all trees and shrubs >10 cm d.b.h. in the whole plot and for all individuals >3 cm d.b.h. in a central plot of 10 x 10 m. From these data, we calculated sums of species-specific basal area per plot and species.

Basal area measurements were carried out in 2008 (see Bruelheide et al. 2011).

*Biogeographic:* Variables related to the plant species' distribution were: latitudinal range, minimum latitude of the species' range, geographic range size (approximated as the number of occupied 0.25' x 0.25' grid cells), size of the climatic niche (calculated from temperature and precipitation data of the occurrence data points) and marginality of climatic conditions at the study site in comparison to the overall climatic niche of the species.

While the mechanisms causing differences in the range size attributes of the individual species might, to some extent, influence chemical and morphological characteristics of the plants (Moles et al. 2011), a plant's range size can also give indications as to the size of the regional and local herbivore species pool adapted to this plant species (Lewinsohn et al. 2005).

Distribution data for the studied tree and shrub species were compiled using as many data sources as available. Specimen location data was obtained from the Global Biodiversity Information Facility (GBIF 2010) and the Chinese Virtual Herbarium (CVH 2010). Published distribution range maps (Kurata 1964-1973; Horikawa 1972-1976; Menitsky 2005) were geo-referenced and digitized using ArcMap (ESRI). Additionally, GIS datasets of county occurrence data for China were obtained from Fang et al. (2010). Recording localities for SE Asia as listed in Aubréville (1960-1996) and Soepadmo et al. (Soepadmo and Wong 1995; Soepadmo et al. 1998; Soepadmo and Saw 2000; Soepadmo et al. 2002, 2004; Soepadmo et al. 2007) were geo-referenced using web-based gazetteers (NGA GEONet Names Server, 2010; Global Gazetteer 2.2, 2010). The resulting spatial data for each species range were used to extract climate data from the Worldclim database (Hijmans et al. 2005) using the extract functionality of ArcMap (ESRI) and climate layers of a spatial resolution of 2.5 arc minutes (0.25' x 0.25' grid cells). The size of the distribution area was approximated as the number of 0.25' x 0.25' grid cells occupied by the respective species. Latitudinal range was calculated as the difference between the

lowest and highest latitude at which each species was recorded. We also included the minimum latitude of occurrence of each species to test whether potential effects of latitudinal range were influenced by the degree to which distributions extended into the tropics, which can be indicative of the stability of host-herbivore associations over historical time (see Discussion).

To assess whether potential effects of range size are driven by climatic characteristics of the plant species' distribution area, we also included a measure of the species' climatic niche breadth and an index of the marginality of the climatic conditions at the study site (which might affect herbivory; Vergeer and Kunin 2011) in comparison to the overall climatic niche of the species. The niche position and niche breadth along climatic axes were quantified using a multivariate coinertia analysis computing an Outlying Mean Index (OMI) (Dolédec et al. 2000) as implemented in the "ade4" package for the statistical software R (Thioulouse and Dray 2007). The analysis results in species-specific descriptions of the niche ranges along the main principal components of the environmental data space of all considered species. In this context, the species-specific niche position of the study site is captured by a marginality index, which is a measure of the deviations of the mean climatic conditions of the study location from the range-wide habitat conditions of each species. As a first step, the distance is calculated along the PCA axes of the study sites' environmental position to the nearest marginal value of the species. The niche marginality index of the study site for each species was calculated as the mean of the marginality distances on each PCA axis. Species with high mean distances from their niche margins to the study site conditions obtain low marginality values. The study site represents a typical combination of climatic conditions for those species and they are expected to be well adapted and regionally common, whereas species that have high marginality values are expected to be rare. Although the approach to niche position and breadth presented here does not account for idiosyncrasies and constraints due to biotic interactions or species' dispersal limitation, it

represents a methodological step toward a more exhaustive analysis of plant-herbivore relationships.

*Phylogenetic.* Due to common evolutionary history, plant traits are not independent of the phylogenetic relationships among species, which therefore have to be considered in interspecific trait analyses (Harvey and Pagel 1991). We constructed phylogenetic relationships from *rbcL* and *matK* sequences, downloaded from NCBI Genbank (Benson et al. 2005), for the species of interest or for their closest available relatives and aligned the sequences with ClustalW in Bioedit (Table S2.2). *Pinus massoniana* (Lamb) was used as an outgroup. Total alignment length was 466 bp for *rbcL* and 630 bp for *matK*. Based on the combined alignment, a first phylogenetic hypothesis was generated using maximum likelihood (ML) in MEGA5 (Tamura et al. 2011) applying the Tamura-Nei model of base substitution, uniform mutation rates, complete deletion of gaps and tree inference by nearest-neighbor-interchange. Branch lengths in the ML tree are a direct measure of the number of base substitutions. Based on the ML tree, a second ultrametric tree was computed (Fig. S2.1) using penalized likelihood (Sanderson 2002) as implemented in function *chronopl* in ape 2.7.2. (Paradis 2006).  $\lambda$  was set to  $10^{2.666}$ . The branch lengths in this tree are a measure of divergence time. Additionally, for each of our study species we included the number of congenics growing in the 27 study plots.

## References

- Aubréville A (1960-1996) Flore du Cambodge, du Laos et du Viêt Nam. Muséum national d'Histoire naturelle, Paris
- Benson DA, Karsch-Mizrachi I, Lipman DJ, Ostell J, Wheeler DL (2005) GenBank. *Nucleic Acids Research* 33: D34-D38
- Bruelheide H et al. (2011) Community assembly during secondary forest succession in a Chinese subtropical forest. *Ecological Monographs* 81:25-41
- Cornelissen JHC et al. (2003) A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* 51:335-380
- CVH (2010) Chinese Virtual Herbarium. <http://www.cvh-beta.org>. accessed online 02/2010
- Dolédéc S, Chessel D, Gimaret-Carpentier C (2000) Niche separation in community analysis: a new method. *Ecology* 81:2914-2927
- Eichhorn MP, Fagan KC, Compton SG, Dent DH, Hartley SE (2007) Explaining leaf herbivory rates on tree seedlings in a Malaysian rain forest. *Biotropica* 39:416-421
- Fang J, Wang Z, Tang Z (2010) Atlas of Woody Plants in China. Higher Education Press, Beijing
- GBIF (2010) Global Biodiversity Information Facility. <http://www.data.gbif.org>. accessed online 02/2010
- Graham HD (1992) Stabilization of the Prussian Blue Color in the Determination of Polyphenols. *Journal of Agricultural and Food Chemistry* 40:801-805
- Hagermann AE (1987) Radial diffusion method for determining tannin in plant extracts. *Journal of Chemical Ecology* 13:437-449
- Harvey PH, Pagel MD (1991) The comparative method in evolutionary biology. Oxford Univ. Press, Oxford
- Hendry G, Grime J (1993) Methods in comparative plant ecology: a laboratory manual. Chapman and Hall, London
- Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25:1965-1978
- Horikawa Y (1972-1976) Atlas of the Japanese Flora: an Introduction of Plant Sociology of East Asia. Gakken, Tokyo
- Jones CG, Lawton JH (1991) Plant Chemistry and Insect Species Richness of British Umbellifers. *Journal of Animal Ecology* 60:767-777
- Kurata S (1964-1973) Illustration of Japanese forest trees 1-4. Chikyu Shuppan, Tokyo
- Lewinsohn TM, Novotny V, Basset Y (2005) Insects on plants: Diversity of herbivore assemblages revisited. *Annual Review of Ecology Evolution and Systematics* 36:597-620
- Llandres AL, A. R-GM, Dirzo R (2010) Plant stages with biotic, indirect defences are more palatable and suffer less herbivory than their undefended counterparts. *Biological Journal of the Linnean Society* 101:536-543
- Menitsky YL (2005) Oaks of Asia. Komarov Botanical Institute, Science Publishers, Enfield NH
- Moles AT, Bonser SP, Poore AGB, Wallis IR, Foley WJ (2011) Assessing the evidence for

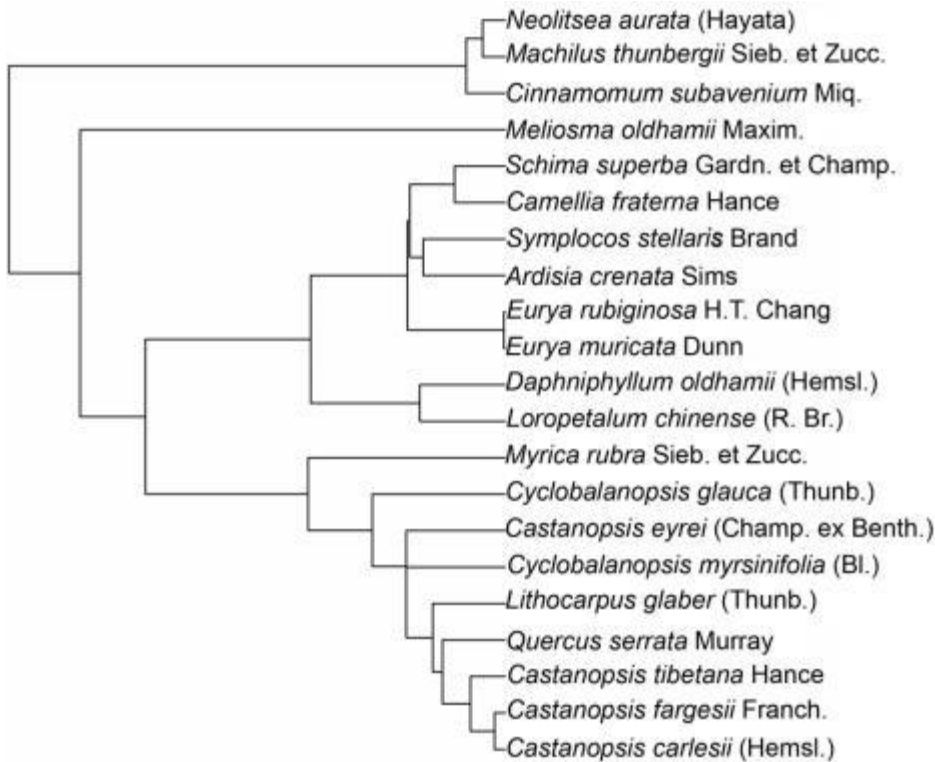
- latitudinal gradients in plant defence and herbivory. *Functional Ecology* 25:380-388
- Ness JH, Rollinson EJ, Whitney KD (2011) Phylogenetic distance can predict susceptibility to attack by natural enemies. *Oikos* 120:1327-1334
- Paradis E (2006) *Analysis of Phylogenetics and Evolution with R*. Springer, New York
- Rasband WS (2011) ImageJ, U. S. National Institutes of Health, Bethesda, Maryland, USA, <http://imagej.nih.gov/ij/>, 1997-2011.
- Rasmann S, Johnson MD, Agrawal AA (2009) Induced Responses to Herbivory and Jasmonate in Three Milkweed Species. *Journal of Chemical Ecology* 35:1326-1334
- Salminen JP, Karonen M (2011) Chemical ecology of tannins and other phenolics: we need a change in approach. *Functional Ecology* 25:325-338
- Sanderson MJ (2002) Estimating absolute rates of molecular evolution and divergence times: a penalized likelihood approach. *Molecular Biology and Evolution* 19:101-109
- Schuldt A et al. (2010) Tree diversity promotes insect herbivory in subtropical forests of south-east China. *Journal of Ecology* 98:917-926
- Sobek S, Scherber C, Steffan-Dewenter I, Tschamtkke T (2009) Sapling herbivory, invertebrate herbivores and predators across a natural tree diversity gradient in Germany's largest connected deciduous forest. *Oecologia* 160:279-288
- Soepadmo E, Saw LG (eds) (2000) *Tree Flora of Sabah and Sarawak*. Volume 3. Malaysian Nature Society, Kuala Lumpur
- Soepadmo E, Saw LG, Chung RCK (eds) (2002) *Tree Flora of Sabah and Sarawak*. Volume 4. Malaysian Nature Society, Kuala Lumpur
- Soepadmo E, Saw LG, Chung RCK (eds) (2004) *Tree Flora of Sabah and Sarawak*. Volume 5. Forest Research Institute Malaysia, Kuala Lumpur
- Soepadmo E, Saw LG, Chung RCK, Kiew R (eds) (2007) *Tree Flora of Sabah and Sarawak*. Volume 6. Forest Research Institute Malaysia, Kuala Lumpur
- Soepadmo E, Wong KM (eds) (1995) *Tree Flora of Sabah and Sarawak*. Volume 1. Forest Research Institute Malaysia, Kuala Lumpur
- Soepadmo E, Wong KM, Saw LG (eds) (1998) *Tree Flora of Sabah and Sarawak*. Volume 2. Forest Research Institute Malaysia, Kuala Lumpur
- Tamura K, Peterson D, Peterson N, Stecher G, Nei M, Kumar S (2011) MEGA5: Molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. *Molecular Biology and Evolution* 28:2731-2739
- Thioulouse J, Dray S (2007) Interactive Multivariate Data Analysis in R with the ade4 and ade4TkGUI Packages. *Journal of Statistical Software* 22:1-14
- Torti SD, Dearing MD, Kursar TA (1995) Extraction of Phenolic compounds from fresh leaves: A comparison of methods. *Journal of Chemical Ecology* 21:117-125
- Vergeer P, Kunin WE (2011) Life history variation in *Arabidopsis lyrata* across its range: effects of climate, population size and herbivory. *Oikos* 120:979-990

**Table S2.1.** Summary statistics (minimum, maximum and mean values, standard deviation, and  $K$ -statistics with  $P$  values as a measure for the strength of the phylogenetic signal in each variable) for leaf damage and morphological, chemical and biogeographic plant characteristics included in the full model. The phylogenetic signal was tested separately for each variable (see main text for details)

Variable	Min	Max	Mean	$SD$	$K$	$P$
Mean leaf damage [%]	1.4	14.1	5.34	3.49	0.37	0.004
Leaf area [cm <sup>2</sup> ]	48	1012	238	242	0.19	0.162
SLA [m <sup>2</sup> /kg]	7.82	18.68	10.87	2.55	0.08	0.613
LDMC [mg/g]	266	525	424	67	0.46	0.001
Leaf toughness [N/mm]	3.39	13.65	8.36	2.79	0.08	0.001
Chemical diversity [Shannon Index]	1.06	3.12	2.21	6.05	0.03	0.742
Chemical uniqueness [# retention time peaks]	4.1	11.3	6.84	1.74	0.03	0.837
Tannin content [mg/g]	6.47	206.7	66.37	62.77	0.34	0.038
C content [%]	44.56	53.39	49.62	2.5	0.36	0.003
N content [%]	1.05	1.87	1.36	0.23	0.52	0.001
Mean local abundance (based on basal area) [cm <sup>2</sup> /plot]	1.5	10122.8	1243.4	2671.4	0.06	0.609
Climatic niche breadth [index]	4.4	19.4	12.1	4.1	0.09	0.373
Niche marginality [index]	0	16.2	8.1	4.3	0.01	0.993
Congeneric isolation [# of congeners]	0	5	1.9	1.8	0.34	0.021

**Table S2.2.** Species and GenBank accession numbers for rbcL and matK sequences

Species	Family	rbcL	
<i>Pinus massoniana</i>	Pinaceae	gi 332015285 gb HQ427243.1	<i>Pinus massoniana</i>
<i>Cinnamomum subavenium</i>	Lauraceae	gi 332015320 gb HQ427266.1	<i>Cinnamomum subavenium</i>
<i>Machilus thunbergii</i>	Lauraceae	gi 332015308 gb HQ427257.1	<i>Machilus thunbergii</i>
<i>Neolitsea aurata</i>	Lauraceae	gi 331704431 gb HQ415213.1	<i>Neolitsea aurata</i>
<i>Meliosma oldhamii</i>	Sabiaceae	gi 332015234 gb HQ427213.1	<i>Meliosma oldhamii</i>
<i>Loropetalum chinense</i>	Hamamelidaceae	gi 332015155 gb HQ427163.1	<i>Loropetalum chinense</i>
<i>Daphniphyllum oldhamii</i>	Daphniphyllaceae	gi 332015154 gb HQ427162.1	<i>Daphniphyllum oldhamii</i>
<i>Castanopsis carlesii</i>	Fagaceae	gi 332015174 gb HQ427175.1	<i>Castanopsis carlesii</i>
<i>Castanopsis eyrei</i>	Fagaceae	gi 332015160 gb HQ427167.1	<i>Castanopsis eyrei</i>
<i>Castanopsis fargesii</i>	Fagaceae	gi 332015170 gb HQ427173.1	<i>Castanopsis fargesii</i>
<i>Castanopsis tibetana</i>	Fagaceae	gi 332015168 gb HQ427172.1	<i>Castanopsis tibetana</i>
<i>Cyclobalanopsis glauca</i>	Fagaceae	gi 332015162 gb HQ427168.1	<i>Quercus glauca</i>
<i>Cyclobalanopsis myrsinifolia</i>	Fagaceae	gi 332015165 gb HQ427170.1	<i>Quercus myrsinifolia</i>
<i>Lithocarpus glaber</i>	Fagaceae	gi 332015172 gb HQ427174.1	<i>Lithocarpus glaber</i>
<i>Quercus serrata</i>	Fagaceae	gi 332015167 gb HQ427171.1	<i>Quercus serrata</i>
<i>Myrica rubra</i>	Myricaceae	gi 332015300 gb HQ427253.1	<i>Morella rubra</i>
<i>Ardisia crenata</i>	Myrsinaceae	gi 332015325 gb HQ427270.1	<i>Ardisia crenata</i>
<i>Camellia fraterna</i>	Theaceae	gi 332015250 gb HQ427224.1	<i>Camellia fraterna</i>
<i>Eurya muricata</i>	Theaceae	gi 332015257 gb HQ427228.1	<i>Eurya muricata</i>
<i>Eurya rubiginosa</i>	Theaceae	gi 332015247 gb HQ427222.1	<i>Eurya rubiginosa</i>
<i>Schima superba</i>	Theaceae	gi 332015261 gb HQ427230.1	<i>Schima superba</i>
<i>Symplocos stellaris</i>	Symplocaceae	gi 332015272 gb HQ427236.1	<i>Symplocos stellaris</i>
Species	Family	matK	
<i>Pinus massoniana</i>	Pinaceae	gi 332015610 gb HQ427386.1	<i>Pinus massoniana</i>
<i>Cinnamomum subavenium</i>	Lauraceae	gi 332015653 gb HQ427408.1	<i>Cinnamomum subavenium</i>
<i>Machilus thunbergii</i>	Lauraceae	gi 60495427 emb AJ247180.	<i>Persea grijsii</i>
<i>Neolitsea aurata</i>	Lauraceae	gi 332015657 gb HQ427410.1	<i>Neolitsea aurata</i>
<i>Meliosma oldhamii</i>	Sabiaceae	gi 332015560 gb HQ427360.1	<i>Meliosma oldhamii</i>
<i>Loropetalum chinense</i>	Hamamelidaceae	gi 332015466 gb HQ427312.1	<i>Loropetalum chinense</i>
<i>Daphniphyllum oldhamii</i>	Daphniphyllaceae	gi 332015464 gb HQ427311.1	<i>Daphniphyllum oldhamii</i>
<i>Castanopsis carlesii</i>	Fagaceae	gi 332015487 gb HQ427323.1	<i>Castanopsis carlesii</i>
<i>Castanopsis eyrei</i>	Fagaceae	gi 332015471 gb HQ427315.1	<i>Castanopsis eyrei</i>
<i>Castanopsis fargesii</i>	Fagaceae	gi 332015483 gb HQ427321.1	<i>Castanopsis fargesii</i>
<i>Castanopsis tibetana</i>	Fagaceae	gi 332015481 gb HQ427320.1	<i>Castanopsis tibetana</i>
<i>Cyclobalanopsis glauca</i>	Fagaceae	gi 332015473 gb HQ427316.1	<i>Quercus glauca</i>
<i>Cyclobalanopsis myrsinifolia</i>	Fagaceae	gi 332015475 gb HQ427317.1	<i>Quercus myrsinifolia</i>
<i>Lithocarpus glaber</i>	Fagaceae	gi 332015485 gb HQ427322.1	<i>Lithocarpus glaber</i>
<i>Quercus serrata</i>	Fagaceae	gi 332015479 gb HQ427319.1	<i>Quercus serrata</i>
<i>Myrica rubra</i>	Myricaceae	gi 332015629 gb HQ427396.1	<i>Morella rubra</i>
<i>Ardisia crenata</i>	Myrsinaceae	gi 332015661 gb HQ427412.1	<i>Ardisia crenata</i>
<i>Camellia fraterna</i>	Theaceae	gi 332015588 gb HQ427374.1	<i>Camellia chekiangoleosa</i>
<i>Eurya muricata</i>	Theaceae	gi 332015586 gb HQ427373.1	<i>Eurya muricata</i>
<i>Eurya rubiginosa</i>	Theaceae	gi 332015576 gb HQ427368.1	<i>Eurya rubiginosa</i>
<i>Schima superba</i>	Theaceae	gi 332015590 gb HQ427375.1	<i>Schima superba</i>
<i>Symplocos stellaris</i>	Symplocaceae	gi 332015597 gb HQ427379.1	<i>Symplocos stellaris</i>



**Figure S2.1.** Ultrametric phylogenetic tree of the 21 study species obtained using penalized likelihood. Branch lengths indicate relative divergence time.

## Appendix S2: PGLS results for regression with fixed lambda ( $\lambda = 1$ )

**Table S2.3.** Regression results of the minimal-adequate PGLS model **with fixed lambda ( $\lambda = 1$ )**, i.e. assuming *a priori* a strong phylogenetic signal that might affect variable selection) for mean herbivore damage levels (log-transformed) of 21 tree and shrub species in subtropical China. Adjusted  $R^2 = 0.64$ ;  $F_{5,16} = 9.73$ ;  $P < 0.001$ . See main text for details

Variable	Estimate	Std.Error	<i>t</i>	<i>P</i>
(Intercept)	1.553	0.367	4.2	0.0006
Leaf dry matter content	0.336	0.098	3.4	0.0035
Mean local abundance (log-transf.)	0.247	0.069	3.6	0.0024
Climatic niche breadth	0.279	0.073	3.8	0.0015
Niche marginality	0.170	0.037	4.6	0.0003



# CHAPTER 3

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# Functional and phylogenetic diversity of woody plants drive herbivory in a highly diverse forest

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## Abstract

Biodiversity loss may alter ecosystem processes such as herbivory, a key driver of ecological functions in species-rich (sub)tropical forests. However, the mechanisms underlying such biodiversity effects remain poorly explored, as mostly effects of species richness—a very basic biodiversity measure—have been studied. Here, we analyze to what extent the functional and phylogenetic diversity of woody plant communities affect herbivory along a diversity gradient in a subtropical forest. We assessed the relative effects of morphological and chemical leaf traits and of plant phylogenetic diversity on individual-level variation in herbivory of dominant woody plant species across 27 forest stands in south-east China. Individual-level variation in herbivory was best explained by multivariate, community-level diversity of leaf chemical traits, in combination with community-weighted means of single traits and species-specific phylodiversity measures. These findings deviate from those based solely on trait variation within individual species. Our results indicate a strong impact of generalist herbivores and highlight the need to assess food-web specialization for determining the direction of biodiversity effects. With increasing plant species loss, but particularly with the concomitant loss of functional and phylogenetic diversity in these forests, the impact of herbivores will likely decrease—with consequences for the herbivore-mediated regulation of ecosystem functions.

**Key words:** BEF China; biodiversity; ecosystem functioning; functional traits; negative density dependence; plant-insect interactions; species richness

## Introduction

The realization that global change alters the biotic composition of ecosystems has spawned a wealth of research showing that biodiversity loss significantly affects ecosystem functions and services (Cardinale *et al.*, 2012, Naeem *et al.*, 2012). However, our understanding of the mechanisms underlying observed diversity effects is still limited, since many studies have focused on species richness as a very basic measure of biodiversity (Hillebrand and Matthiessen, 2009). More recently, the awareness that species' functional traits (e.g. morphological or physiological features that determine an organism's

performance) play a central role in determining many of these diversity effects has led to a stronger focus on the functional dimensions of biodiversity and a more thorough investigation into the role of specific traits for individual functions (Diaz *et al.*, 2007, Reiss *et al.*, 2009). However, while progress in our understanding of functional diversity effects has been made particularly for processes within single trophic levels (primarily the producer level), it is increasingly being recognized that in many cases trophic interactions are key modifiers of these relationships (Reiss *et al.*, 2009, Cardinale *et al.*, 2012). Herbivory may be particularly crucial in this respect.

Herbivory strongly influences nutrient cycles, productivity and the diversity maintenance of ecosystems (Schmitz, 2008, Schowalter, 2012, Terborgh, 2012). Moreover, the strength of herbivory effects has been shown to vary with plant diversity (e.g. Jactel and Brockerhoff, 2007, Schuldt *et al.*, 2010, Cardinale *et al.*, 2012). However, we still lack a mechanistic understanding of the relationship between herbivory and plant diversity. Some plant traits commonly assumed to determine levels of herbivory within and among species, such as secondary metabolites, have been found to perform poorly in predicting overall damage levels under natural conditions (Carmona *et al.*, 2011, Schuldt *et al.*, 2012; see also Paine *et al.* 2012) and the general pattern seems to be that several traits act in combination to make a plant attractive to herbivores or repel them (e.g. Agrawal and Fishbein, 2006, Loranger *et al.*, 2012). Multivariate trait indices or even an estimation of functional trait space by phylogenetic diversity (Srivastava *et al.*, 2012) might thus be stronger predictors than single traits. Phylogenetic diversity incorporates the evolutionary history of species relationships and may thus not only capture phylogenetically conserved dissimilarity of (often unmeasured) traits among species. It also indicates shared evolutionary relationships between herbivores and their host plants (Cavender-Bares *et al.*, 2009, Srivastava *et al.*, 2012) and has been shown to predict herbivory-induced seedling mortality in some cases better than the diversity of functional traits commonly considered to be important for herbivores (Paine *et al.*, 2012). Moreover, non-additive effects of increasing plant species richness on herbivory patterns indicate that not only a focal plant species' traits but also community properties play an important role in determining herbivore damage levels (Loranger *et al.*, 2013).

Accounting for the functional and phylogenetic diversity of plant communities may thus be key to explaining the variation in herbivory along environmental gradients, in particular along gradients of decreasing plant species richness. This knowledge is of crucial importance in developing a better understanding of how biodiversity and its loss affect the impact of higher trophic levels on

ecosystem functions. This is particularly relevant for species-rich subtropical and tropical forests, as they assume an important role in global biogeochemical cycles and climate regulation (Bonan, 2008), and for which the effects of herbivores are considered key modifiers of ecosystem processes (Schemske *et al.*, 2009). Interestingly, while current theory on herbivore effects often emphasizes the role of specialists (see Cardinale *et al.*, 2012), there is evidence that the impact of generalist herbivores can prevail over and differ from that of specialists in such highly diverse systems (Schuldt *et al.*, 2010). Previous work in such forests has highlighted traits that might be particularly relevant in determining overall differences in herbivory levels among woody plant species (Schuldt *et al.*, 2012). However, so far no study has attempted to mechanistically relate changes in species-specific herbivore damage with increasing woody plant diversity to functional trait and phylogenetic information of species-rich woody plant communities.

Here, we analyze to what extent functional and phylogenetic aspects of woody plant community composition contribute to improving our understanding of the role of biodiversity for herbivory patterns in highly diverse ecosystems. Our analysis builds on, and mechanistically extends, previous findings of increasing levels of herbivore damage on individuals of dominant tree and shrub species with increasing woody plant species richness in a subtropical forest system (Schuldt *et al.*, 2010), and a particular focus of our study is on the performance of functional and phylogenetic diversity measures in explaining herbivory patterns relative to species richness effects. Effects of the former are usually not simply a reflection of the latter (e.g. Mason *et al.*, 2008, Devictor *et al.*, 2010). We study the relative effects of morphological and chemical leaf traits commonly considered to affect herbivory and the impact of woody plant phylogenetic diversity on species-specific herbivory levels across 27 forest stands in south-east China. We account for effects of community-weighted means, trait diversity (based on single and multiple traits) and phylogenetic diversity, as well as of species-specific diversity measures. The relative

impact of these different facets of community composition and diversity on ecosystem functions is only poorly known in natural systems (Mouillot *et al.*, 2011). By focusing on these community-level measures, our approach takes into account the major sources of trait variation in these forest stands, since compared to strong effects of interspecific variation, intraspecific trait variation within species was previously found to play a very minor role for trait-environment relationships across the 27 study plots (Kröber *et al.* 2012). We hypothesize that i) both functional and phylogenetic community metrics will explain the individual-level variation in observed herbivory better than woody plant species richness, ii) not only individual traits, but multivariate diversity indices that combine the interactive effects of different traits will also be important predictors, and iii) unlike in systems with specialized herbivore communities, the expected dominance of generalist herbivores in our study system (see Schuldt *et al.*, 2010, 2012) is likely to promote positive interactions between herbivory and functional and phylogenetic diversity—which would be in contrast to predictions of general ecological theory for such highly diverse forests (see also Novotny *et al.*, 2012).

## Methods

### Study site and herbivory assessment

The study was conducted in the Gutianshan National Nature Reserve (29°14' N; 118°07' E) in south-east China. The reserve covers about 80 km<sup>2</sup> of semi-evergreen, broadleaved forest, with *Castanopsis eyrei* and *Schima superba* as dominant tree species. The subtropical monsoon climate is characterized by a mean annual temperature of 15.3°C and a mean annual precipitation of about 2000 mm (Hu and Yu, 2008). Within the reserve, 27 study plots of 30 m x 30 m were established in 2008. The plots were selected to represent the range of woody plant species richness (25–69 tree and shrub species per plot) and successional stages (<20–>80 yr) found in the reserve (Bruehlheide *et al.*, 2011).

Herbivory was assessed on saplings (between 20 and 100 cm in height) of ten dominant tree and shrub species: *Ardisia*

*crenata* Sims, *Camellia fraterna* Hance, *Castanopsis eyrei* (Champ. ex Benth.) Tutch., *Cyclobalanopsis glauca* (Thunb.) Oerst., *Eurya muricata* Dunn, *Lithocarpus glaber* (Thunb.) Nakai, *Loropetalum chinense* (R. Br.) Oliv., *Machilus thunbergii* Sieb. et Zucc., *Neolitsea aurata* (Hayata) Koidz., and *Schima superba* Gardn. et Champ.). These ten evergreen species accounted for about 50% of the total biomass of the tree and shrub layers in the study plots (see Schuldt *et al.*, 2010). A maximum of ten saplings per species and plot were checked for herbivory. Herbivory was quantified as the overall leaf damage caused by chewing, mining, galling and (if visible) sucking insects on all leaves of the saplings (mean number of leaves per sapling =  $45.4 \pm 45.3$  SD). Assessments were conducted at the end of the rainy season in June/July 2008, which also marks the end of a major activity period for arthropods in these forests (Schuldt *et al.*, 2012). We used predefined percentage classes (estimated as 0%, <1%, 1–5%, >5–15%, >15–35%, and >35%; see e.g. Scherber *et al.*, 2010, Schuldt *et al.*, 2010, Ness *et al.*, 2011) to visually assess standing levels of leaf damage. The actual, mean amount of damage for each estimated percentage class was then checked in detail by analyzing samples of randomly collected leaves (20–30) for each class; these were digitally scanned to determine the exact amount of leaf damage as the ratio of removed to estimated total leaf area (Schuldt *et al.*, 2010, Schuldt *et al.*, 2012). For the statistical analyses, we then used the mean damage of the scanned leaves of each class to calculate mean damage levels for each sapling (i.e. to account for potential deviations in the visually estimated damage from the digitally verified mean damage levels; see Schuldt *et al.*, 2010 for details).

### Plant community data and general plot characteristics

For our analyses, we used a set of three morphological and four chemical leaf traits that are related to leaf quality and palatability and that might thus particularly strongly affect herbivory (Coley and Barone, 1996, Perez-Harguindeguy *et al.*, 2003, Poorter *et al.*, 2004): leaf area (LA), specific leaf area (SLA) and leaf dry matter content (LDMC), as well as leaf C content, leaf C:N ratio, leaf C:P ratio, and leaf

polyphenolics content. The traits were measured for about 80% of the 147 woody plant species recorded on the 27 study plots, and these species represented 95% of the total number of tree and shrub individuals at the study sites. As we used abundance-weighted indices to quantify functional community composition and diversity, these data should not be affected by the 5% of woody plant individuals for which trait values were missing. Data on leaf toughness, which has been shown in previous studies to potentially affect herbivory (e.g. Kitajima and Poorter, 2010), was only available for one third of all species and thus not included in the analysis. However, Schuldt *et al.*, (2012) showed that leaf toughness is probably not a limiting factor to herbivore damage in our study system. Details on trait measurements are provided in Kröber *et al.* (2012). In short, samples for trait measurements were taken from sun-exposed leaves of five to seven plant individuals in total, collected from up to seven plots per species in the summer of 2008. Trait measurements followed the standardized protocols of Cornelissen *et al.* (2003) and, for leaf polyphenolics, Hagermann (1987) (see Kröber *et al.*, 2012). Our analysis focused on interspecific variation in trait values that determine community-level trait diversity, as intraspecific trait variability within species was previously shown to have negligible effects on trait-environment relationships across our study plots (Kröber *et al.*, 2012). Moreover, we show below that plot-level characteristics that can be expected to particularly strongly affect intraspecific trait variation (stand age, elevation and other abiotic conditions) were not retained in our final explanatory model, which further indicates that, unlike community-level trait diversity, intraspecific trait variation within species only plays a minor role for species-level variation in herbivory across the 27 study plots.

Phylogenetic data was obtained from an ultrametric phylogenetic tree of all angiosperm woody species recorded in the 27 study plots (Michalski and Durka, 2013). Woody plant species richness was recorded at the time of plot establishment in 2008 and based on a complete inventory of all tree and

shrub individuals of a height  $> 1$  m (Bruehlheide *et al.*, 2011).

We also accounted for general plot characteristics such as stand age, tree density, canopy cover, herb cover, elevation and aspect (see Bruehlheide *et al.*, 2011), as they might potentially confound diversity-functioning relationships in observational studies. Many of these characteristics were strongly correlated with each other, and we used principal components analysis (PCA) on these variables to obtain orthogonal predictor axes (see Schuldt *et al.*, 2010 for details of this analysis). Only the first principal component axis ( $PC1_{\text{abio}}$ ), which represented stand age and age-dependent aspects of stand structure and biomass, was related to herbivore damage (Schuldt *et al.*, 2010), and therefore was included in our analyses to account for diversity-independent plot effects. Other plot characteristics, as well as sapling height and the total number of saplings sampled, were shown by Schuldt *et al.* (2010) to have no effect on herbivory patterns of the study species.

### Diversity metrics and statistical analysis

In many cases, it remains unclear whether ecological functions are more strongly affected by community-weighted mean trait values, the variability within single traits, or the diversity of multiple traits (Butterfield and Suding, 2013, Dias *et al.*, 2013), and to what extent phylogenetic diversity provides additional information (e.g. Cadotte *et al.*, 2009). To quantify functional and phylogenetic aspects of the woody plant communities, we thus used a three-fold approach calculating i) Rao's quadratic entropy  $Q$  (Rao, 1982) to assess plot-level trait and phylogenetic diversity, ii) community-weighted mean trait values to identify mass ratio effects of single traits, and iii) functional and phylogenetic relatedness between each of our focal species and all other species in the study plots to measure species-specific diversity effects.

Rao's  $Q$  is calculated as the variance in pairwise dissimilarities among all individuals in a community. It can be easily applied to both functional and phylogenetic data, calculated for single as well as for multiple traits, and

weighted by abundance data (Schleuter *et al.*, 2010, Pavoine and Bonsall, 2011). It thus enables a comparison between different facets of diversity using a consistent statistical framework (Pavoine and Bonsall, 2011). Moreover, as a measure of trait dispersion Rao's  $Q$  complements measures of community-weighted mean trait values (CWM) (Ricotta and Moretti, 2011). Whereas CWM quantifies a community's average functional trait value, weighted by the relative abundances of all individuals in this community, Rao's  $Q$  provides a measure of trait variation around this mean. We calculated both CWM values and Rao's  $Q$  for single traits ( $CWM_{\text{single.trait}}$ ,  $Q_{\text{single.trait}}$ ), as well as two multivariate versions of Rao's  $Q$  that assessed the overall diversity of morphological ( $Q_{\text{morph}}$ ) and chemical leaf traits ( $Q_{\text{chem}}$ ), respectively. We also tested for the effects of an overall Rao's  $Q$  measure that integrates both the leaf morphological and chemical traits, but as this measure was less strongly related to herbivory than  $Q_{\text{chem}}$ , we kept the distinction between morphological and chemical leaf trait diversity to allow for a better mechanistic interpretation of potential effects (while traits such as leaf dry matter content and C content might be related to some extent by both influencing leaf palatability (Poorter *et al.*, 2009), the former also includes a strong morphological component (Kitajima and Poorter, 2010), and distinguishing between these effects via morphological and chemical trait diversity yielded straightforward results). Calculations of Rao's  $Q$  were based on standardized trait values (mean=0,  $SD=1$ ) and a Euclidean species distance matrix. For the multivariate measures of Rao's  $Q$  based on the three morphological and four chemical traits, respectively, we used all axes of a PCA (as these axes are orthogonal to each other) on the standardized traits for the distance matrix to avoid collinearity effects (Böhnke *et al.*, 2013, Purschke *et al.*, 2013). For the phylogenetic data, we correspondingly calculated Rao's  $Q$  from a phylogenetic cophenetic distance matrix ( $Q_{\text{phylo}}$ ). All measures of functional and phylogenetic diversity were weighted by plot-level abundance data to account for the relative

impact of dominant versus rare species on community-level metrics.

In each plot, and for each of the ten focal species, we further calculated a species-specific phylogenetic distance measure ( $Q_{\text{phylo}}^{\text{spec}}$ ), based on the mean phylogenetic distance between an individual of a given focal species to all other woody plant individuals in a given study plot (Webb *et al.*, 2002, Webb *et al.*, 2006)—for consistency we again expressed this measure as Rao's  $Q$ , which in the abundance-weighted case is analogous to the MPD used in other studies (Vellend *et al.*, 2011). Recent studies have shown that not only overall phylogenetic diversity, but in particular the phylogenetic distance of a focal individual to all other individuals in a community can determine herbivore effects (Webb *et al.*, 2006, Paine *et al.*, 2012, Parker *et al.*, 2012). The species-specific measure of Rao's  $Q$  was also calculated for trait data, and we included both multivariate relatedness measures for our focal species based on morphological ( $Q_{\text{morph}}^{\text{spec}}$ ) and chemical leaf traits ( $Q_{\text{chem}}^{\text{spec}}$ ) and measures for each individual trait ( $Q_{\text{T}}^{\text{spec}}$ , where T is the respective trait) in our analysis. Species-specific indices were calculated from the same distance matrices used for the calculation of plot-level Rao's  $Q$ , but by contrasting individuals of the respective focal species to all other individuals in each of the communities. Again, all measures were weighted by plot-level abundance data.

We used generalized linear mixed models with a binomial error structure (as a recommended way to analyze proportion data; Zuur *et al.*, 2009), fit by Laplace approximation (Bolker *et al.*, 2009), to analyze the effects of functional and phylogenetic diversity metrics on the degree of herbivore damage of the ten study species across the 27 study plots, while accounting for the effects of woody plant species richness and general plot characteristics. To determine which functional and phylogenetic characteristics particularly affect herbivory, and to assess whether their effects were complementary to simple species richness effects and independent of plot characteristics, we constructed five sets of models. These contained i) all predictors, ii)  $PC1_{\text{abio}}$  and all functional metrics (functional

diversity sensu Diaz *et al.*, 2007), iii)  $PC1_{\text{abio}}$  and phylogenetic metrics, iv)  $PC1_{\text{abio}}$  and woody plant species richness, and v) only  $PC1_{\text{abio}}$ , respectively.  $PC1_{\text{abio}}$  was included in all model sets to account for potentially confounding plot characteristics. Species identity, with individuals nested within species, and plot identity were considered as crossed random effects. Using species identity as a random factor accounts for all interspecific differences in levels of herbivory, leaving individual-level differences as the only source of variation. We also included a random factor with the total number of observations as factor levels to account for potential overdispersion in the data (Bates *et al.*, 2013). Before the analysis, predictors were checked for collinearity and where there was strong correlation ( $>0.7$ ) among predictors, we excluded those that were less strongly related to herbivory (e.g.  $CWM_{\text{CN}}$  and  $CWM_{\text{C,P}}$ —which were strongly correlated with  $CWM_{\text{Phenol}}$ , but less strongly correlated with herbivory than  $CWM_{\text{Phenol}}$ , and several correlated species-specific  $Q^{\text{spec}}$  measures; see Supplementary Material Table S3.1 for a correlation matrix and a list of excluded variables). The final set of predictors included the general plot characteristics  $PC1_{\text{abio}}$ , woody plant species richness, the phylogenetic diversity measure  $Q_{\text{phylo}}$ , the multivariate chemical trait diversity  $Q_{\text{chem}}$ , the single trait dispersion variables  $Q_{\text{LDMC}}$ ,  $Q_{\text{C}}$ ,  $Q_{\text{C:N}}$ ,  $Q_{\text{Phenol}}$ , the community-weighted mean values  $CWM_{\text{LA}}$ ,  $CWM_{\text{LDMC}}$ ,  $CWM_{\text{C}}$ ,  $CWM_{\text{Phenol}}$ , and the species-specific measures  $Q^{\text{spec}}_{\text{phylo}}$ ,  $Q^{\text{spec}}_{\text{LA}}$ ,  $Q^{\text{spec}}_{\text{LDMC}}$ ,  $Q^{\text{spec}}_{\text{C}}$ ,  $Q^{\text{spec}}_{\text{C:N}}$ ,  $Q^{\text{spec}}_{\text{C,P}}$ , and  $Q^{\text{spec}}_{\text{Phenol}}$ . We also included the interaction between woody plant species richness and overall phylogenetic diversity  $Q_{\text{phylo}}$ , as this was recently shown to influence species richness effects in grasslands (Dinnage, 2013). All predictors were standardized to a mean of zero and a standard deviation of one before the analysis. Each model set was simplified by sequential deletion of predictors based on the reduction in AICc values to obtain the most parsimonious, minimal adequate model (which may potentially also contain variables that are not statistically significant at  $P < 0.05$  if deletion of these variables would have markedly decreased AICc fit; see Burnham

and Anderson, 2004). The five resulting minimal adequate models were compared on the basis of their AICc values ( $\Delta\text{AICc}$ ) and AICc weights, with particularly low AICc values and high AICc weights indicating the best model fit (Burnham and Anderson, 2004). Model residuals were checked to comply with modeling assumptions. All analyses were performed with R 3.0.0 (<http://www.R-project.org>) and the package lme4 (Bates *et al.*, 2013).

## Results

Mean leaf damage to the ten study species, averaged across all 27 study plots, ranged between 3% (*Camellia fraterna*) and 17% (*Cyclobalanopsis glauca*). Species-specific damage levels varied by 15% ( $\pm 9.5$  SD), on average, among the individual study plots. Species richness, functional characteristics, and phylogenetic diversity of the plant communities all added essential explanatory value to the individual-level herbivory data. The minimal models based on abiotic characteristics and only phylogenetic or functional plant characteristics had a higher explanatory power than the models including only species richness and abiotic characteristics, or abiotic characteristics alone (Table 3.1). By far the best minimal model with the highest empirical support (based on a  $\Delta\text{AICc} = 11.4$  to the second-best model and an AICc weight of 1) was the one derived from the full data set. This model included woody plant species richness as well as a combination of functional and phylogenetic characteristics of the woody plant communities that were also included in the more simple functional and phylogenetic models (Table 3.1). The multivariate Rao's  $Q$  measure of chemical trait diversity ( $Q_{\text{chem}}$ ) and the community-weighted mean leaf C content of the plant communities ( $CWM_{\text{C}}$ ) contributed most to the overall best model, followed by weaker effects of woody plant species richness, the dispersion of leaf C content ( $Q_{\text{C}}$ ), the species-specific mean phylogenetic distance ( $Q^{\text{spec}}_{\text{phylo}}$ ), the species-specific mean distance in leaf area ( $Q^{\text{spec}}_{\text{LA}}$ ), and the CWM of leaf dry matter content ( $CWM_{\text{LDMC}}$ ) within the plant communities. Note that the effects



**Table 3.1.** Results for the fixed effects of the minimal generalized mixed-effects models on herbivore damage based on the full set of predictors and selected sets of predictors, respectively. Models are ordered by AICc, predictors within models by the absolute size of their standardized effects

Model	Fixed effects	Std. Est.	SE	$\bar{z}$	<i>P</i>	AICc	ΔAICc	AICc <sub>weight</sub>
<i>All predictors</i>						996.6	0	1
	$Q_{\text{chem}}$	0.19	0.04	5.1	<0.0001			
	CWM <sub>C</sub>	-0.19	0.04	-4.9	<0.0001			
	Woody plant species richness	0.14	0.04	3.9	0.0001			
	$Q_C$	-0.14	0.04	-3.8	0.0002			
	$Q^{\text{spec}}_{\text{phylo}}$	0.14	0.04	3.0	0.0025			
	$Q^{\text{spec}}_{\text{LA}}$	-0.10	0.04	-2.4	0.0168			
	CWM <sub>LDMC</sub>	0.08	0.04	1.9	0.0529			
<i>Functional structure + abiotic characteristics</i>						1008.0	11.4	0
	$Q_{\text{chem}}$	0.23	0.04	5.8	<0.0001			
	$Q_C$	-0.15	0.04	-3.6	0.0003			
	CWM <sub>C</sub>	-0.14	0.04	-4.0	0.0001			
	$Q_{\text{LDMC}}$	0.07	0.04	1.9	0.0546			
<i>Phylogenetic diversity + abiotic characteristics</i>						1017.9	21.3	0
	PC1 <sub>abio</sub>	0.19	0.05	3.7	0.0002			
	$Q^{\text{spec}}_{\text{phylo}}$	0.11	0.05	2.3	0.0198			
<i>Species richness + abiotic characteristics</i>						1019.6	23.0	0
	PC1 <sub>abio</sub>	0.18	0.05	3.7	0.0002			
	Woody plant species richness	0.09	0.05	2.0	0.0492			
<i>Abiotic characteristics only</i>						1021.1	24.5	0
	PC1 <sub>abio</sub>	0.19	0.05	3.8	0.0001			

Std. Est = standardized slope, SE = standard error, AICc = corrected Akaike Information Criterion. Fixed effects in the minimal models are: Rao's  $Q$  measures of leaf chemical trait diversity ( $Q_{\text{chem}}$ ), leaf C content dispersion ( $Q_C$ ), leaf dry matter content dispersion ( $Q_{\text{LDMC}}$ ), species-specific mean of phylogenetic distance of individuals of the target species to all other plant individuals in a community ( $Q^{\text{spec}}_{\text{phylo}}$ ), and species-specific mean of leaf area trait dispersion ( $Q^{\text{spec}}_{\text{LA}}$ ); community-weighted mean values of leaf C content (CWM<sub>C</sub>) and leaf dry matter content (CWM<sub>LDMC</sub>); woody plant species richness of the study plots, and the first principal component of a PCA on general plot characteristics (PC1<sub>abio</sub>) that represents stand age and age-dependent aspects of stand structure and biomass

of most predictors were highly significant, so potential issues of testing on the boundary of parameter space do not affect our results (Zuur *et al.*, 2009). Herbivory decreased with increasing values of both CWM<sub>C</sub> and  $Q_C$  (Figs 1b, c) and also of  $Q^{\text{spec}}_{\text{LA}}$ , whereas it was positively related to  $Q_{\text{chem}}$  and  $Q^{\text{spec}}_{\text{phylo}}$  (Figs 1a, d) as well as to woody plant species richness and CWM<sub>LDMC</sub>. Abiotic plot

characteristics were not included in the best minimal model (Table 3.1), supporting our assumption that intraspecific trait variation promoted by these environmental characteristics was of little importance compared to community-level trait diversity. Single-regressions relationships between herbivory and the two strongest predictors,  $Q_{\text{chem}}$  and CWM<sub>C</sub>, for the individual species

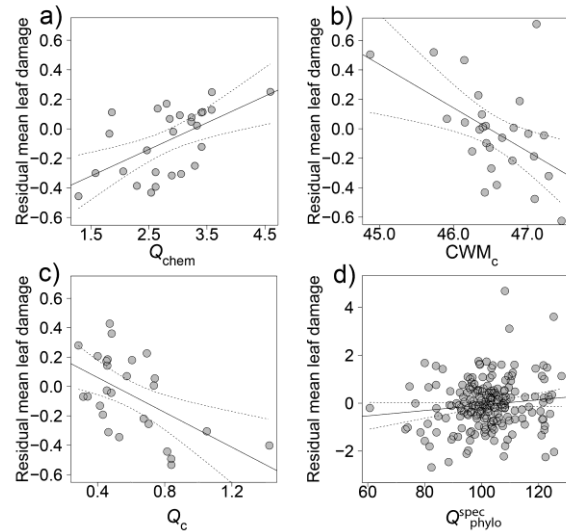
show that the generalized relationships of the mixed model approach (while not statistically significant for all single species, but with a higher number of significant relationships than the one out of 20 relationships expected by chance for  $\alpha = 0.05$ ) are well-reflected in most of the individual species (Fig. 3.2).

## Discussion

Our study shows that measures of both functional and phylogenetic community characteristics contribute to explaining variation in herbivory on tree recruits along a natural gradient in woody plant species richness—and that they clearly go beyond the explanatory power previously found for pure woody plant species richness in this respect (Schuldt *et al.*, 2010). Our results particularly highlight the importance of multivariate trait variability, in addition to the effects of single traits, in informing our understanding of herbivory patterns in the context of biodiversity and ecosystem function relationships. Moreover, the positive relationships between herbivory and diversity measures contrast with common expectations for such highly diverse forests and indicate that the way biodiversity affects the regulation of ecosystem functions requires a better understanding of the degree of food web specialization in such species-rich ecosystems.

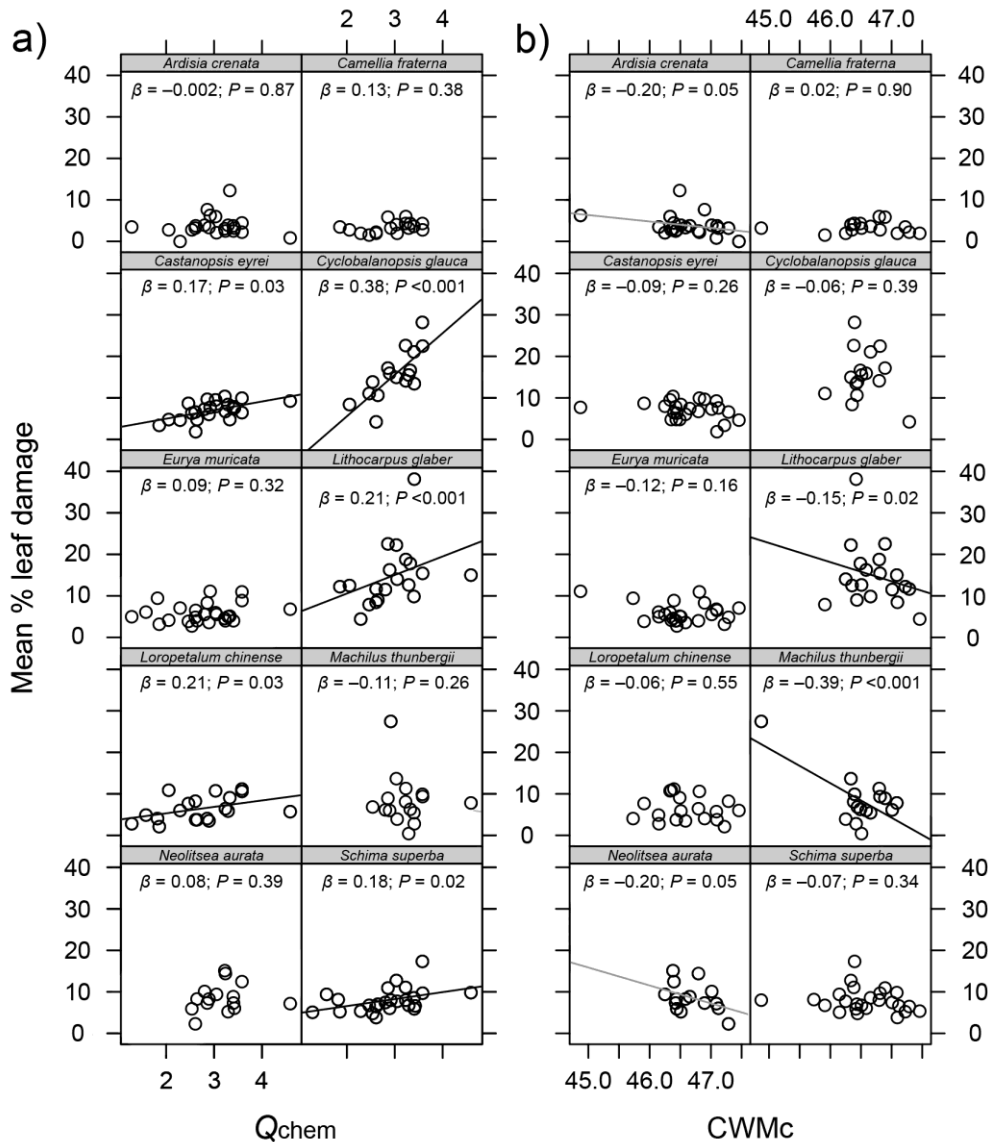
### Trait interactions strongly affect herbivory

The best predictor of individual-level variation in herbivory along the 27 plots of our study was the multivariate  $Q_{\text{chem}}$ , an integrative measure of the variation in leaf chemical traits (leaf C content, C:N and C:P ratios, leaf polyphenolics) that are considered to be of particular importance for the palatability of plants and their defense against herbivores (Coley and Barone, 1996, Perez-Harguindeguy *et al.*, 2003, Poorter *et al.*, 2004). Apparently, this multivariate index contains information that is not provided by single trait measures of community-weighted mean values and variability. Several studies have shown that multivariate functional diversity indices can reveal non-additive effects that arise from interactions among species and traits (e.g. Moullot *et al.*, 2011, Dias *et al.*, 2013). For herbivores, such interactions might



**Figure 3.1.** Independent effect on herbivore damage (partial residuals and 95% confidence bands) of a) chemical leaf trait diversity ( $Q_{\text{chem}}$ ), b) community-weighted mean leaf C values ( $\text{CWM}_C$ ), c) leaf C content dispersion within the plant communities ( $Q_C$ ), and d) species-specific mean phylogenetic distance of individuals of the target species to all other plant individuals in the plant communities; a-c) show mean values of community-level measures across the 27 study plots, d) shows mean values per study plot for each of the ten target species. Standardized slopes are provided in Table 3.1.

encompass palatability and defense traits that determine trade-offs in resource use. This can become particularly relevant when multi-species assemblages of herbivores affect damage patterns: recent studies have shown that under natural conditions herbivory patterns are often much better explained by a complex of multiple traits (Agrawal and Fishbein, 2006, Carmona *et al.*, 2011, Loranger *et al.*, 2012, Schuldt *et al.*, 2012). An interesting finding is that the traits represented in our  $Q_{\text{chem}}$  index appear to be less relevant in determining the general susceptibility of the studied plant species to herbivores than for instance morphological characteristics (Schuldt *et al.*, 2012; but note that the latter study showed a positive relationship between leaf C content and leaf dry matter content—one of the strongest predictors of general susceptibility patterns among species in that study—such that palatability effects of the latter might be represented to some extent by the strong effects of C content in the present study). These leaf chemical traits may



**Figure 3.2.** Relationships between herbivore damage of the single study species and a) chemical leaf trait diversity ( $Q_{chem}$ ), and b) community-weighted mean leaf C values ( $CWMc$ ) (with regression slopes  $\beta$  and their probabilities  $P$ ). Black lines indicate significant, grey lines close to significant relationships.

also often be of less relevance when only effects of trait variation within individual focal species are being considered (Carmona *et al.*, 2011), rather than the effects of community-level trait variability on individual-level herbivory patterns (the latter of which was done in the present study). A recent study in experimental grasslands highlighted the importance of such community effects by showing strong non-additive effects of species composition from monocultures to plant species mixtures on herbivore damage (Loranger *et al.*, 2013). Thus, while the general susceptibility to herbivory may be strongly

determined by a focal species' traits (e.g. Schuldt *et al.*, 2012), the trait composition (and in part other traits than those affecting mean herbivory susceptibility) of the surrounding plant community may become important in influencing the variation around these mean damage levels along environmental gradients (e.g. Barbosa *et al.*, 2009). Recent findings of functionally more diverse diets of generalist (see next) herbivores in more diverse plant communities support this conclusion (Ibanez *et al.*, 2013). Quantifying the relative impact of these effects is beyond the scope of our study and requires experimental manipulation (see

Loranger *et al.*, 2013). Yet, community-level trait metrics have also been identified as major drivers of ecosystem functions in many other studies (e.g. Butterfield and Suding, 2013, and references therein), indicating that they generally also affect species-specific patterns. In our case, the degree of herbivore damage of the study species among plots was positively related to the community-level diversity of leaf chemical traits—a pattern that does not necessarily match common predictions of general diversity-herbivory relationships (see Cardinale *et al.*, 2012). This can be explained by the fact that many of the dominant herbivores in our study system are probably generalists that are not restricted to single host plant genera or families (Schuldt *et al.*, 2010; M. Noack, A. Schuldt, T. Assmann unpublished data, showing that DNA-barcoded caterpillars of dominant Geometridae species were found on tree and shrub species belonging to more than one plant family). These herbivores can benefit from increased community-level variability of both palatability and defense traits, as this allows for complementary resource use and dietary mixing of host plants that differ in individual nutrient or defense characteristics (Pfisterer *et al.*, 2003, Jactel and Brockerhoff, 2007, Schuldt *et al.*, 2010).

#### Single-trait measures complement multivariate indices in explaining herbivory

Effects of dietary mixing could also underlie the negative relationship between herbivory and the community-weighted mean levels of leaf C content ( $CWM_C$ ). The study species belonged to the tree and shrub species with a relatively high leaf C content (mean C content of the ten study species was  $47.8\% \pm 2.5 SD$ , compared to a range between 35 and 51% for the remaining species in the communities and a maximum  $CWM_C$  observed for our study plots of 47.5%). Herbivore damage on these species might decline if increasing  $CWM_C$  decreases the probability of herbivores being able to use alternative host plants with lower leaf C content (which are more abundant in low  $CWM_C$  communities) to compensate for low nutrient quality in their preferred hosts (potentially a mix of different nutrients, as indicated by the strong  $Q_{chem}$  effect and the

absence of C:N or C:P metrics in the minimal models [or of phenolic content, with which these ratios were in part strongly correlated and thus not included directly in the models]). We might also potentially have expected an effect of the species-specific  $Q_C^{spec}$  in this case. However, the fact that this variable did not provide additional explanation could be due to nutrient quality effects being largely captured by the more integrative  $Q_{chem}$ , with additional variation already largely explained by the effects of  $CWM_C$  and  $Q_C$ .

Effects of the variability in leaf C content ( $Q_C$ ) on herbivory might be explained by interrelations with  $CWM_C$  (see also Ricotta and Moretti, 2011, Dias *et al.*, 2013 for interaction effects between CWM and trait variability). Low  $Q_C$  can apply to both communities with overall high but also those with overall low leaf C content of the constituent species. In our study the communities with low  $Q_C$  tended to have a lower rather than higher  $CWM_C$  (Pearson's  $r = 0.3$ ;  $P = 0.12$ , see Table S3.1), such that low community-level variability in leaf C content could indicate better nutrient conditions. However, such a relationship would only be moderate in our case, as adding an interaction term for  $Q_C$  and  $CWM_C$  did not improve model fit (which could be explained by the fact that low  $Q_C$  and  $CWM_C$  only coincide at low leaf C concentrations, whereas high  $CWM_C$  might display both high and low variation in leaf C contents).

#### Phylogenetic relatedness more important than overall phylogenetic diversity

In contrast to leaf chemical traits, phylogenetic diversity measures were of less importance in explaining variation in herbivory across the 27 study plots (and for our system we were unable to detect an interaction between phylogenetic diversity and plant species richness, as recently reported by Dinnage (2013) for grasslands). This was not due to potential phylogenetic clustering in functional traits masking actual phylogenetic effects, as model fit for phylogenetic data was low even when considered in isolation of functional traits ( $\Delta AICc = 9.9$  compared to the minimal model based on functional traits; Table 3.1). However, whereas the overall

phylogenetic diversity of the woody plant communities had little effect ( $Q_{\text{phylo}}$  was not included in the best overall model or in the minimal phylogenetic model), herbivory was positively related to the species-specific measure  $Q_{\text{phylo}}^{\text{spec}}$ . As also indicated by the results for  $\text{CWM}_C$ , this makes it clear that the position of a focal species within trait space (in the case of  $Q_{\text{phylo}}^{\text{spec}}$  approximated by a phylogenetic measure) can provide information that is not captured by, and not necessarily dependent on, overall community diversity (e.g. Butterfield and Suding, 2013). The positive effect of  $Q_{\text{phylo}}^{\text{spec}}$  is contrary to effects reported for similar measures from other species-rich forests, where phylogenetic diversity and relatedness have been observed to decrease species-specific levels of herbivory via mechanisms of negative density dependence (Webb *et al.*, 2006, Ness *et al.*, 2011, Paine *et al.*, 2012). Yet, the positive effect is congruent with our findings for overall leaf chemical diversity and the expected impact of generalist herbivores (see also Parker *et al.*, 2012, Castagneyrol *et al.*, 2013). It thus supports our expectation that feeding specialization strongly determines how consumers affect the relationship between biodiversity and ecosystem functions (Thebault and Loreau, 2003, Cavender-Bares *et al.*, 2009).

### Species richness provides additional information

Although functional trait and phylogenetic information outperformed pure woody plant species richness in explaining the variability in herbivore levels across the 27 study plots, species richness was nevertheless retained as a predictor in the best minimal model (for a detailed discussion of the relationship between species richness and herbivory in our study system, see Schuldt *et al.*, 2010). While mechanistically advancing our understanding of diversity effects on herbivory compared to the analysis considering only species richness (Schuldt *et al.*, 2010), our measures of trait diversity and also the inclusion of phylogenetic diversity apparently do not fully account for the information contained in the simple species richness measure. This might indicate the effects of unmeasured traits that

are not phylogenetically conserved, or interaction effects not captured by our multivariate diversity indices, and shows the limitations of phylogenetic measures as a surrogate measure of functional trait variation (Srivastava *et al.*, 2012).

### Community-level consequences

The patterns we observed are likely to result in negative effects on the growth of our study species, as even low levels of persistent herbivore damage can strongly decrease plant fitness (e.g. Zvereva *et al.*, 2012). Our study species belong to the dominant woody plants on our study system, and increasing damage with increasing plant diversity might potentially promote overall woody plant diversity (but note that we lack long-term data from our study system). As the growth of tree and shrub recruits determines woody plant diversity in the long term, we would expect negative effects on diversity if all woody plant species were equally affected by herbivory. Particularly the effects of  $Q_{\text{chem}}$  and  $Q_{\text{phylo}}$  could potentially promote clustering over time in the phylogenetic composition and the trait space occupied by the woody plant communities (see also Cavender-Bares *et al.*, 2009). However, these effects will be mediated by eco-evolutionary feedbacks between plant and herbivore communities, with changes in plant communities affecting herbivores and their impact on plants, plant trait composition and diversity (e.g. Johnson *et al.*, 2009, Carmona and Fornoni, 2013). Such feedbacks can result in dynamic processes that require longer-term data for a better understanding of the complex interactions between herbivores and their hosts. The observed high plant species and functional diversity in the natural forests of our study suggests either that benefits of increased functional diversity (e.g. better resource partitioning among plants; Cardinale *et al.*, 2012) outweigh negative effects of herbivory or that not all species show the positive diversity-herbivory relationship. Several studies have suggested that abundant and rare species can be affected by herbivory in contrasting ways, resulting in a community compensatory trend that stabilizes diversity (e.g. Queensborough *et al.*, 2007, Chen *et al.*, 2010). High functional diversity

could thus be maintained by less abundant species that profit from increased herbivory of abundant species—and a potentially lower fitness and reduced impact of these species on other species—under these conditions. The fact that abundant woody plant species at our study site were previously found to experience higher mean damage levels than less common species supports this assumption (see Schuldt *et al.*, 2012).

### Conclusions

Our study shows how a combined approach that incorporates different facets of functional and phylogenetic community composition and diversity can help in informing our mechanistic understanding of how biodiversity affects ecosystem functions along natural environmental gradients. It emphasizes the impact of community-level functional properties on a set of focal species, which deviates from previously reported effects of species-specific trait variation within and among these species. Considering that individual species usually form part of larger communities (see also Karban, 2010), these community effects can help to better predict biodiversity-ecosystem function relationships under changing environmental conditions. Species richness, while mechanistically less informative, can add to this framework by indicating effects of unmeasured traits that are not phylogenetically conserved or interactive effects of traits that are not captured by multivariate diversity indices. With increasing loss of species, but in particular with the concomitant loss of functional variability and phylogenetic information in a community, the impact of herbivores can be expected to change – with consequences for the herbivore-mediated regulation of ecosystem functions and properties. In this respect, the largely positive relationship between herbivory and different facets of diversity indicates that the degree of food web specialization within a community is of crucial significance for the way biodiversity loss will affect ecosystem functioning.

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### References

- Agrawal AA, Fishbein M (2006) Plant defense syndromes. *Ecology* 87: S132-S149
- Barbosa P, Hines J, Kaplan I, Martinson H, Szczepaniec A, Szendrei Z (2009). Associational resistance and associational susceptibility: Having right or wrong neighbors. *Annual Review of Ecology and Systematics* 40: 1-20
- Bates DM, Maechler M, Bolker B, Walker S (2013) Linear mixed-effects models using Eigen and S4. R package version 1.0-5. [WWW document] URL <http://CRAN.R-project.org/package=lme4>. [accessed November 2013]
- Böhnke M, Kröber W, Welk E, Wirth C, Bruelheide H. (2013) Maintenance of constant functional diversity during secondary succession of a subtropical forest in China. *Journal of Vegetation Science*: DOI 10.1111/jvs.12114
- Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White JSS (2009). Generalized linear mixed models: A practical guide for ecology and evolution. *Trends in Ecology and Evolution* 24: 127-135
- Bonan GB (2008) Forests and climate change: Forcings, feedbacks, and the climate benefits of forests. *Science* 320: 1444-1449
- Bruehlheide H, Böhnke M, Both S, Fang T, Assmann T, Baruffol M, Bauhus J, Buscot F, Chen XY, Bing DY, et al. (2011) Community assembly during secondary forest succession in a Chinese subtropical forest. *Ecological Monographs* 81: 25-41
- Burnham KP, Anderson DR (2004) Model selection and multimodel inference : A practical information-theoretic approach. New York: Springer
- Butterfield BJ, Suding KN (2013) Single-trait functional indices outperform multi-trait

- indices in linking environmental gradients and ecosystem services in a complex landscape. *Journal of Ecology* 101: 9-17
- Cadotte MW, Cavender-Bares J, Tilman D, Oakley TH (2009) Using phylogenetic, functional and trait diversity to understand patterns of plant community productivity. *PLoS ONE* 4: e5695
- Cardinale BJ, Duffy JE, Gonzalez A, Hooper DU, Perrings C, Venail P, Narwani A, Mace GM, Tilman D, Wardle DA, et al. (2012) Biodiversity loss and its impact on humanity. *Nature* 486: 59-67
- Carmona D, Fornoni J (2013) Herbivores can select for mixed defensive strategies in plants. *New Phytologist* 197: 576-585
- Carmona D, Lajeunesse MJ, Johnson MTJ (2011) Plant traits that predict resistance to herbivores. *Functional Ecology* 25: 358-367
- Castagneyrol B, Jactel H, Vacher C, Brockerhoff EG (2013) Effects of plant phylogenetic diversity on herbivory depend on herbivore specialization. *Journal of Applied Ecology*: DOI 10.1111/1365-2664.12175
- Cavender-Bares J, Kozak KH, Fine PVA, Kembel SW (2009) The merging of community ecology and phylogenetic biology. *Ecology Letters* 12: 693-715
- Chen L, Mi X, Comita LS, Zhang L, Ren H, Ma K (2010) Community-level consequences of density dependence and habitat association in a subtropical broad-leaved forest. *Ecology Letters* 13: 695-704
- Coley PD, Barone JA (1996) Herbivory and plant defenses in tropical forests. *Annual Review of Ecology and Systematics* 27: 305-335
- Cornelissen JHC, Lavorel S, Garnier E, Diaz S, Buchmann N, Gurvich DE, Reich PB, ter Steege H, Morgan HD, van der Heijden MGA, et al. (2003) A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* 51: 335-380
- Devictor V, Mouillot D, Meynard C, Jiguet F, Thuiller W, Mouquet N (2010) Spatial mismatch and congruence between taxonomic, phylogenetic and functional diversity: The need for integrative conservation strategies in a changing world. *Ecology Letters* 13: 1030-1040
- Dias ATC, Berg MP, De Bello F, Van Oosten AR, Bila K, Moretti M (2013) An experimental framework to identify community functional components driving ecosystem processes and services delivery. *Journal of Ecology* 101: 29-37
- Diaz S, Lavorel S, De Bello F, Quetier F, Grigulis K, Robson M (2007) Incorporating plant functional diversity effects in ecosystem service assessments. *Proceedings of the National Academy of Sciences (USA)* 104: 20684-20689
- Dinnage R (2013) Phylogenetic diversity of plants alters the effect of species richness on invertebrate herbivory. *PeerJ* 1: e93
- Hagermann AE (1987) Radial diffusion method for determining tannin in plant extracts. *Journal of Chemical Ecology* 13: 437-449
- Hillebrand H, Matthiessen B (2009) Biodiversity in a complex world: Consolidation and progress in functional biodiversity research. *Ecology Letters* 12: 1405-1419
- Hu Z, Yu M (2008) Study on successions sequence of evergreen broad-leaved forest in Gutian mountain of Zhejiang, eastern China: Species diversity. *Frontiers of Biology in China* 3: 45-49
- Ibanez S, Manneville O, Miquel C, Taberlet P, Valentini A, Aubert S, Coissac P, Colace MP, Duparc Q, Lavorel S, et al. (2013) Plant functional traits reveal the relative contribution of habitat and food preferences to the diet of grasshoppers. *Oecologia* 173: 1459-1470
- Jactel H, Brockerhoff EG (2007) Tree diversity reduces herbivory by forest insects. *Ecology Letters* 10: 835-848
- Johnson MTJ, Vellend M, Stinchcombe JR (2009) Evolution in plant populations as a driver of ecological changes in arthropod communities. *Philosophical Transactions of the Royal Society B-Biological Sciences* 364: 1593-1605
- Karban R (2010) Neighbors affect resistance to herbivory - a new mechanism. *New Phytologist* 186: 565-566
- Kitajima K, Poorter L (2010) Tissue-level leaf toughness, but not lamina thickness, predicts sapling leaf lifespan and shade tolerance of tropical tree species. *New Phytologist* 186: 708-721
- Kröber W, Böhnke M, Welk E, Wirth C, Bruelheide H (2012) Leaf trait-environment relationships in a subtropical broadleaved forest in south-east China. *PLoS ONE* 7: e35742
- Loranger J, Meyer ST, Shipley B, Kattge J, Loranger H, Roscher C, Weisser WW (2012) Predicting invertebrate herbivory from plant traits: Evidence from 51 grassland species in experimental monocultures. *Ecology* 93: 2674-2682
- Loranger J, Meyer ST, Shipley B, Kattge J, Loranger H, Roscher C, Wirth C, Weisser WW (2013) Predicting invertebrate herbivory from plant traits: Polycultures show strong nonadditive effects. *Ecology* 94: 1499-1509
- Mason NWH, Irz P, Lanoiselee C, Mouillot D, Argillier C (2008) Evidence that niche

- specialization explains species-energy relationships in lake fish communities. *Journal of Animal Ecology* 77: 285-296.
- Michalski S, Durka W (2013) Phylogenetic tree of the tree species found in the CSPs. [WWW document] URL <http://china.befdata.biow.uni-leipzig.de/datasets/240>. [accessed September 2013]
- Mouillot D, Villéger S, Scherer-Lorenzen M, Mason NWH (2011) Functional structure of biological communities predicts ecosystem multifunctionality. *PLoS ONE* 6
- Naem S, Duffy JE, Zavaleta E (2012) The functions of biological diversity in an age of extinction. *Science* 336: 1401-1406
- Ness JH, Rollinson EJ, Whitney KD (2011) Phylogenetic distance can predict susceptibility to attack by natural enemies. *Oikos* 120: 1327-1334
- Novotny V, Miller SE, Hrcek J, Baje L, Basset Y, Lewis OT, Stewart AJA, Weiblen GD (2012) Insects on plants: Explaining the paradox of low diversity within specialist herbivore guilds. *American Naturalist* 179: 351-362.
- Paine CET, Norden N, Chave J, Forget PM, Fortunel C, Dexter KG, Baraloto C (2012) Phylogenetic density dependence and environmental filtering predict seedling mortality in a tropical forest. *Ecology Letters* 15: 34-41
- Parker JD, Burkepille DE, Lajeunesse MJ, Lind EM (2012) Phylogenetic isolation increases plant success despite increasing susceptibility to generalist herbivores. *Diversity and Distributions* 18: 1-9
- Pavoine S, Bonsall MB (2011) Measuring biodiversity to explain community assembly: A unified approach. *Biological Reviews* 86: 792-812
- Perez-Harguindeguy N, Diaz S, Vendramini F, Cornelissen JHC, Gurvich DE, Cabido M (2003) Leaf traits and herbivore selection in the field and in cafeteria experiments. *Austral Ecology* 28: 642-650
- Pfisterer AB, Diemer M, Schmid B (2003) Dietary shift and lowered biomass gain of a generalist herbivore in species-poor experimental plant communities. *Oecologia* 135: 234-241
- Poorter L, De Plassche MV, Willems S, Boot RGA (2004) Leaf traits and herbivory rates of tropical tree species differing in successional status. *Plant Biology* 6: 746-754
- Poorter H, Niinemets Ü, Poorter L, Wright IJ, Villar R (2009) Causes and consequences of variation in leaf mass per area (LMA): A meta-analysis. *New Phytologist* 182: 565-588
- Purschke O, Schmid BC, Sykes MT, Poschlod P, Michalski SG, Durka W, Kühn I, Winter M, Prentice HC (2013) Contrasting changes in taxonomic, phylogenetic and functional diversity during a long-term succession: Insights into assembly processes. *Journal of Ecology* 101: 857-866
- Queensborough SA, Burslem DFRP, Garwood NC, Valencia R (2007) Neighborhood and community interactions determine the spatial pattern of tropical tree seedling survival. *Ecology* 88
- Rao CR (1982) Diversity and dissimilarity coefficients: A unified approach. *Theoretical Population Biology* 21: 24-43
- Reiss J, Bridle JR, Montoya JM, Woodward G (2009) Emerging horizons in biodiversity and ecosystem functioning research. *Trends in Ecology and Evolution* 24: 505-514
- Ricotta C, Moretti M. 2011. CWM and Rao's quadratic diversity: A unified framework for functional ecology. *Oecologia*: 181-188
- Schemske DW, Mittelbach GG, Cornell HV, Sobel JM, Roy K (2009) Is there a latitudinal gradient in the importance of biotic interactions? *Annual Review of Ecology Evolution and Systematics* 40: 245-269
- Scherber C, Eisenhauer N, Weisser WW, Schmid B, Voigt W, Fischer M, Schulze ED, Roscher C, Weigelt A, Allan E, et al. (2010) Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. *Nature* 468: 553-556
- Schleuter D, Daufresne M, Massol F, Argillier C (2010) A user's guide to functional diversity indices. *Ecological Monographs* 80: 469-484
- Schmitz OJ (2008) Herbivory from individuals to ecosystems. *Annual Review of Ecology Evolution and Systematics* 39: 133-152
- Schowalter TD (2012) Insect herbivore effects on forest ecosystem services. *Journal of Sustainable Forestry* 31: 518-536
- Schuldts A, Baruffol M, Böhnke M, Bruelheide H, Härdtle W, Lang AC, Nadrowski K, von Oheimb G, Voigt W, Zhou H, et al. (2010) Tree diversity promotes insect herbivory in subtropical forests of south-east China. *Journal of Ecology* 98: 917-926
- Schuldts A, Bruelheide H, Durka W, Eichenberg D, Fischer M, Kröber W, Härdtle W, Ma K, Michalski SG, Palm WU, et al. (2012) Plant traits affecting herbivory on tree recruits in highly diverse subtropical forests. *Ecology Letters* 15: 732-739
- Srivastava DS, Cadotte MW, Macdonald AaM, Marushia RG, Mirotnick N (2012)



- Phylogenetic diversity and the functioning of ecosystems. *Ecology Letters* 15: 637-648
- Terborgh J. 2012. Enemies maintain hyperdiverse tropical forests. *American Naturalist* 179: 303-314
- Thebault E, Loreau M (2003) Food-web constraints on biodiversity-ecosystem functioning relationships. *Proceedings of the National Academy of Sciences (USA)* 100: 14949-14954
- Vellend M, Cornwell WK, Magnuson-Ford K, Mooers AO (2011) Measuring phylogenetic biodiversity. In: Magurran AE, McGill BJ, eds. *Biological diversity: Frontiers in measurement and assessment*. New York: Oxford Univ. Press, 194-207
- Webb CO, Ackerly DD, McPeck MA, Donoghue MJ (2002) Phylogenies and community ecology. *Annual Review of Ecology and Systematics* 33: 475-505
- Webb CO, Gilbert GS, Donoghue MJ (2006) Phylodiversity-dependent seedling mortality, size structure, and disease in a Bornean rain forest. *Ecology* 87: S123-S131
- Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) *Mixed effects models and extensions in ecology with R*. New York: Springer
- Zvereva EL, Zverev V, Kozlov MV (2012) Little strokes fell great oaks: Minor but chronic herbivory substantially reduces birch growth. *Oikos* 121: 2036-2043

### Supplementary Material

Additional supporting information may be found in the online version of this article.

**Table S3.1** Correlation matrix of predictors  
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## Supplementary Material

Table S3.1. Correlation matrix for plot means of the response variable (herbivory) and the predictor variables considered in the study. Variables not included in the full model due to strong correlation (>0.7, printed in bold) with other predictors (the latter of which, in turn, are more strongly correlated with the response variable than the dropped predictors) are:  $Q_{\text{morph}}$ ,  $Q_{\text{LA}}$ ,  $Q_{\text{SLA}}$ ,  $Q_{\text{CP}}$ ,  $\text{CWM}_{\text{SLA}}$ ,  $\text{CWM}_{\text{CN}}$ ,  $\text{CWM}_{\text{CP}}$ ,  $Q^{\text{spec}}_{\text{chem}}$ ,  $Q^{\text{spec}}_{\text{morph}}$ ,  $Q^{\text{spec}}_{\text{SLA}}$

	Herbivory	Richness	PC1	$Q_{\text{phylo}}$	$Q_{\text{chem}}$	$Q_{\text{morph}}$	$\text{CWM}_{\text{LA}}$	$\text{CWM}_{\text{SLA}}$	$\text{CWM}_{\text{LDMC}}$	$\text{CWM}_{\text{C}}$	$\text{CWM}_{\text{CN}}$	$\text{CWM}_{\text{CP}}$	$\text{CWM}_{\text{Phenol}}$	$Q_{\text{LA}}$	$Q_{\text{SLA}}$	$Q_{\text{LDMC}}$	$Q_{\text{C}}$	$Q_{\text{C:N}}$	$Q_{\text{C:P}}$	$Q_{\text{phenol}}$	$Q^{\text{spec}}_{\text{morph}}$	$Q^{\text{spec}}_{\text{chem}}$	$Q^{\text{spec}}_{\text{LA}}$	$Q^{\text{spec}}_{\text{SLA}}$	$Q^{\text{spec}}_{\text{LDMC}}$	$Q^{\text{spec}}_{\text{C}}$	$Q^{\text{spec}}_{\text{C:N}}$	$Q^{\text{spec}}_{\text{C:P}}$	$Q^{\text{spec}}_{\text{Phenol}}$		
Richness	0.47																														
PC1	0.65	0.19																													
$Q_{\text{phylo}}$	0.36	0.48	0.42																												
$Q_{\text{chem}}$	0.57	0.35	0.63	0.64																											
$Q_{\text{morph}}$	-0.08	0.18	-0.29	-0.32	-0.30																										
$\text{CWM}_{\text{LA}}$	0.15	0.56	-0.05	-0.05	-0.10	0.73																									
$\text{CWM}_{\text{SLA}}$	-0.28	-0.25	-0.47	-0.45	-0.63	0.68	0.25																								
$\text{CWM}_{\text{LDMC}}$	-0.25	-0.07	0.11	0.07	0.11	-0.30	-0.22	-0.48																							
$\text{CWM}_{\text{C}}$	-0.35	0.09	-0.04	0.44	0.20	-0.16	-0.06	-0.30	0.58																						
$\text{CWM}_{\text{CN}}$	0.40	0.25	0.53	0.57	0.68	-0.68	-0.26	-0.93	0.25	0.26																					
$\text{CWM}_{\text{CP}}$	0.47	0.27	0.62	0.52	0.80	-0.47	-0.09	-0.80	0.16	0.31	0.88																				
$\text{CWM}_{\text{Phenol}}$	0.55	0.43	0.52	0.43	0.69	-0.40	0.10	-0.82	0.09	0.07	0.85	0.81																			
$Q_{\text{LA}}$	-0.05	0.18	-0.34	-0.23	-0.31	0.86	0.74	0.61	-0.42	-0.17	-0.56	-0.43	-0.28																		
$Q_{\text{SLA}}$	-0.12	-0.03	-0.28	-0.47	-0.43	0.83	0.48	0.81	-0.42	-0.23	-0.74	-0.49	-0.54	0.61																	
$Q_{\text{LDMC}}$	0.00	0.24	0.11	0.05	0.20	0.37	0.23	-0.08	0.38	0.12	-0.09	0.00	-0.02	-0.05	0.12																
$Q_{\text{C}}$	-0.14	0.07	0.11	0.24	0.50	-0.13	-0.25	-0.39	0.27	0.30	0.29	0.42	0.13	-0.37	-0.18	0.51															
$Q_{\text{C:N}}$	0.62	0.40	0.46	0.18	0.52	0.18	0.25	-0.17	-0.18	-0.18	0.30	0.43	0.38	0.11	0.20	0.10	0.11														
$Q_{\text{C:P}}$	0.33	0.02	0.54	0.48	0.71	-0.46	-0.26	-0.52	0.26	0.38	0.58	0.66	0.42	-0.28	-0.54	-0.20	0.18	0.24													
$Q_{\text{phenol}}$	0.55	0.45	0.32	0.44	0.55	-0.02	0.19	-0.27	-0.20	-0.19	0.31	0.32	0.59	-0.07	-0.16	0.24	0.04	0.24	-0.04												
$Q^{\text{spec}}_{\text{morph}}$	0.11	0.07	-0.10	-0.12	-0.13	0.52	0.33	0.45	-0.21	-0.06	-0.43	-0.23	-0.27	0.39	0.50	0.22	-0.01	0.09	-0.22	0.01											
$Q^{\text{spec}}_{\text{chem}}$	-0.09	0.07	0.10	0.03	0.15	0.01	0.05	-0.04	-0.03	-0.09	0.04	0.06	0.10	0.00	-0.02	0.07	0.01	0.12	0.11	0.09	0.17										
$Q^{\text{spec}}_{\text{phylo}}$	0.05	0.04	0.15	0.15	0.16	0.01	0.03	0.02	-0.04	0.02	0.01	0.09	-0.01	-0.02	0.02	0.07	0.08	0.12	0.13	0.03	0.39	0.35									
$Q^{\text{spec}}_{\text{LA}}$	0.10	0.32	-0.19	-0.01	-0.21	0.65	0.64	0.42	-0.20	0.00	-0.43	-0.29	-0.17	<b>0.72</b>	0.39	0.12	-0.26	-0.03	-0.23	0.07	0.23	-0.11	-0.08								
$Q^{\text{spec}}_{\text{SLA}}$	-0.09	-0.11	-0.32	-0.38	-0.42	0.62	0.25	<b>0.81</b>	-0.41	-0.21	<b>-0.75</b>	-0.53	-0.60	0.47	<b>0.76</b>	0.04	-0.20	0.05	-0.41	-0.14	0.46	0.03	0.08	0.41							
$Q^{\text{spec}}_{\text{LDMC}}$	0.22	0.07	0.11	0.09	0.13	0.09	0.07	-0.02	-0.01	0.04	0.02	0.10	0.05	0.01	0.07	0.18	0.16	0.09	0.01	0.09	<b>0.81</b>	0.14	0.41	-0.14	-0.10						
$Q^{\text{spec}}_{\text{C}}$	-0.13	0.00	-0.03	-0.08	0.02	0.01	0.01	-0.03	-0.05	-0.11	0.02	0.02	0.04	-0.03	0.02	0.06	0.08	0.07	-0.07	0.04	0.14	0.43	0.16	-0.19	0.01	0.14					
$Q^{\text{spec}}_{\text{C:N}}$	-0.11	-0.04	0.11	-0.23	-0.03	0.18	0.13	0.20	-0.09	-0.23	-0.18	-0.08	-0.13	0.12	0.25	0.01	-0.12	0.32	0.04	-0.17	0.16	0.40	0.26	-0.12	0.39	-0.07	0.43				
$Q^{\text{spec}}_{\text{C:P}}$	0.29	0.08	0.28	0.16	0.31	-0.11	-0.01	-0.18	0.05	0.05	0.22	0.30	0.20	-0.04	-0.14	-0.08	0.02	0.20	0.39	-0.03	-0.08	0.24	0.22	0.01	-0.06	-0.01	-0.28	0.13			
$Q^{\text{spec}}_{\text{Phenol}}$	-0.16	0.06	-0.09	0.02	-0.06	0.08	0.06	0.09	-0.04	-0.05	-0.12	-0.17	-0.04	0.06	0.04	0.10	-0.07	-0.11	-0.13	0.14	0.18	<b>0.76</b>	0.17	0.06	0.06	0.11	0.07	-0.02	-0.14		

Abbreviations: Richness = Woody plant species richness; PC1 = first principal component of a PCA on general plot characteristics;  $Q_{\text{phylo}}$ ,  $Q_{\text{chem}}$ ,  $Q_{\text{morph}}$  = dissimilarity in phylogenetic (phylo), chemical trait (chem), and morphological (morph) trait diversity, respectively, of the woody plant communities;  $\text{CWM}_{\text{T}}$  = community weighted mean values,  $Q_{\text{T}}$  = plot level dispersion,  $Q^{\text{spec}}_{\text{T}}$  = species-specific mean distance of individuals of the target species to all other plant individuals in a community for Trait T, where T = leaf area (LA), specific leaf area (SLA), leaf dry matter content (LDMC), leaf C content (C), leaf C:N ratio (C:N), leaf C:P ratio (C:P), and leaf phenolics content (Phenol).

# CHAPTER 4

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Schuldt A, Bruelheide H, Härdtle W, Li Y, Ma K, von Oheimb G, Zhang J, Assmann T: Early positive effects of herbivory in a large-scale forest biodiversity experiment



# Early positive effects of tree species richness on herbivory in the world's largest forest biodiversity experiment

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## Abstract

Despite the importance of herbivory for the structure and functioning of species-rich forests, little is known about how herbivory is affected by tree species richness, and more specifically by random versus nonrandom species loss. We assessed herbivore damage in the early stage of a large-scale forest biodiversity experiment in subtropical China that features random and nonrandom extinction scenarios of tree mixtures numbering between one and 24 species. In contrast to random species loss, the nonrandom extinction scenarios were based on the tree species' local rarity and specific leaf area. Herbivory increased with tree species richness across all scenarios and was unaffected by the different species compositions in the random and nonrandom extinction scenarios. These positive effects only 2.5 years after planting indicate that key trophic interactions were quick to become established. They also suggest a crucial role of herbivory in regulating ecosystem functions and the structural development of species-rich forests from the very start of secondary forest succession. The lack of significant differences between the extinction scenarios, however, contrasts with findings from natural forests of higher successional age, where rarity had negative effects on herbivory. This indicates that the effects of nonrandom species loss could change with forest succession.

**Key words:** BEF China, biodiversity and ecosystem functioning, extinction, functional traits, resource concentration, succession, trophic interactions

## Introduction

Forests cover one third of the Earth's land surface (Bonan 2008) and assume a central role in global biogeochemical cycles, the mitigation of climate change effects, and the preservation of terrestrial biodiversity (Kremen et al. 2000; Bonan 2008). However, high rates of deforestation and forest degradation worldwide increase rates of species extinctions and seriously threaten the functions and services provided by forests (Kremen et al. 2000; Bala et al. 2007).

Herbivory is a key process in many forest ecosystems, mediating species coexistence and ecosystem functions, such as productivity and nutrient cycling (Schowalter

2012; Bagchi et al. 2014; Metcalfe et al. 2014). However, beyond comparisons of monocultures and mixtures of, in most cases, two or three tree species, little is known about how the loss of tree species affects herbivory (see Scherer-Lorenzen 2014 for an overview). This applies particularly to species-rich subtropical and tropical forests, even though herbivory has a considerable effect on their structure and functioning (Terborgh 2012; Bagchi et al. 2014; Metcalfe et al. 2014). Specifically, we lack insights from direct manipulative experiments that would help to unambiguously identify the role of tree species richness for ecosystem processes such as herbivory (Nadrowski et al. 2010; Cardinale et al. 2011). Large-scale tree diversity

experiments have only relatively recently been established (see Bruelheide et al. 2014) and thus mostly represent early successional forest conditions. And yet, data from these experiments may be highly interesting particularly for (sub)tropical regions. Fast tree growth and conditions that promote strong trophic interactions (Schemske et al. 2009; Rodriguez-Castaneda 2013) might lead to a fast development of relationships between herbivory and plant species richness in these regions. Early data can thus provide insight into the degree to which herbivory at the very start of forest development contributes to structuring and influencing the further development of forest communities at different levels of tree species richness.

It is often assumed that specialized consumers drive herbivory effects in species-rich (sub)tropical forests (Coley and Barone 1996; Dyer et al. 2007), suggesting that decreasing resource availability for these consumers leads to a decline in total herbivore damage with increasing plant species richness (Root 1973). However, recent studies have indicated that the impact of generalist herbivores can outweigh the impact of specialists in species-rich systems (Schuldt et al. 2010; Loranger et al. 2014). This may lead to an overall positive effect of plant species richness on herbivory by enabling generalist herbivores to increase their performance through dietary mixing of different plant species (Pfisterer et al. 2003; Jactel and Brockerhoff 2007; Dinnage 2013). The strength of such an effect probably depends on the extent to which plant species richness affects the distribution and diversity of key palatability and defense traits in plant communities (Loranger et al. 2013; Schuldt et al. 2014a). Morphological leaf traits (such as leaf dry matter content or specific leaf area) and the local rarity of plant species were shown to strongly determine mean levels of herbivory among woody plant species in a species-rich subtropical forest (Schuldt et al. 2012). Therefore, whether plant species are lost in a random or nonrandom way may have strong effects on herbivory patterns, but this remains poorly studied.

Here, we analyze herbivory across a gradient of tree species richness—ranging from monocultures to mixtures of 24 species—in a large-scale forest biodiversity experiment in subtropical China. This biodiversity-ecosystem functioning experiment (henceforth referred to as BEF-China experiment) is currently the world's largest forest biodiversity experiment and, in contrast to most previous experiments, features gradients of tree species richness based on both random and nonrandom (trait-based) extinction scenarios (Bruelheide et al. 2014). The nonrandom scenarios are based on local rarity and specific leaf area (SLA) of the tree species, with the most common species and those with the lowest SLA considered most likely to persist in the least diverse species mixtures. Interestingly, similar trait combinations in nearby natural forests of higher successional age were found to strongly promote species-specific herbivore damage levels (Schuldt et al. 2012). Here, we present results from the initial stage of the experiment, 2.5 years after planting, which yield insight into herbivory patterns during the establishment of tree communities with different tree species richness. Assuming that generalist herbivores potentially play a dominant role in such an early-successional ecosystem (Brown 1985; Siemann et al. 1999), we hypothesize that (i) total herbivore damage increases along the gradient of tree species richness of our experimental sites. Moreover, we expect that (ii) these effects differ between the random and nonrandom extinction scenarios due to differences in the distribution of plant traits that may be particularly relevant to herbivores (Schuldt et al. 2012; Bruelheide et al. 2014). Effects of tree species richness on herbivory at such an early stage of our experiment would have important implications for our understanding of how herbivores contribute to the processes that drive the assembly and functioning of establishing tree communities in species-rich forests. This is particularly important when considering that early successional stages in forests constitute an important developmental phase in which the survival rates of tree individuals are often determined.

## Methods

### *Study sites and experimental design*

The subtropical BEF-China tree diversity experiment is located close to Xingangshan, Jiangxi Province, in South-East China (29°08'–29°11' N, 117°90'–117°93' E). Mean annual temperature is 16.7°C and mean annual precipitation around 1800 mm (Yang et al. 2013). The experiment consists of two experimental sites (Site A and Site B) of ca 20 ha each, located in sloping terrain between 100 and 300 m asl. Details of the experimental design are provided in Bruelheide et al. (2014). In short, each site consists of 271 plots of ca 25.8 x 25.8 m (= 1 mu in the traditional Chinese areal unit). Each of the experimental plots consists of 400 trees planted in a grid of 20 x 20 individuals at a horizontal planting distance of 1.29 m, with species randomly assigned to individual planting positions within the plots. Plots were planted in 2009 (Site A) and 2010 (Site B) with either monocultures or mixtures of 2, 4, 8, 16, or 24 tree species. In total, 40 native broadleaved tree species were planted in the experiment. The species pools of the two sites overlapped by eight species (planted in one of the random extinction scenario replicates of each site). The species composition of the mixtures at both sites followed either a random or one of two nonrandom (trait-oriented) extinction scenarios. In the random extinction scenario (replicated with three different species pools per site, each composed of 16 species), the tree species of the less diverse mixtures were selected by randomly partitioning the species composition of the 16-species plots into non-overlapping fractions by means of a bootstrapping procedure (see Bruelheide et al. 2014). This ensures that all species are equally represented at all diversity levels. Species compositions in the two nonrandom scenarios were based on local rarity and SLA of the tree species, respectively, with the rarest species or those with the highest SLA being sequentially eliminated with decreasing diversity of the species mixtures (such that only the most common species or those with the lowest SLA remained in the least diverse mixtures; Bruelheide et al. 2014).

### *Herbivory assessment*

Herbivore damage was assessed for the two experimental sites on a total of 296 plots: in the random extinction scenario 80, 64, 32, 16, 8, and 4 plots of the tree richness levels 1, 2, 4, 8, 16, and 24, respectively, and in each of the two nonrandom extinction scenarios 24 plots of 2, 4, 8, and 16 species each. Plots with additional manipulation of shrub species richness or of seed family richness were excluded (see Bruelheide et al. 2014). The assessments were conducted at the end of the main growing season in September and October 2011 (Site A) and 2012 (Site B), i.e. 2.5 years after the initial planting of seedlings at each site. In each plot, the central 6 x 6 (=36) tree individuals were monitored for herbivore damage. On each tree, seven leaves on three randomly selected branches from different parts of the canopy (= 21 leaves per tree) were visually inspected. Herbivory was quantified as the overall leaf damage caused by chewing, mining, galling and (if visible) sucking insects per leaf. We used predefined percentage classes (estimated as 0%, <5%, <25%, <50%, <75%, >75%, with mean values per class used in the statistical analyses; see, for example, Scherber et al. 2010; Schuldt et al. 2010; Ness et al. 2011; Schuldt et al. 2012) to visually assess standing levels of leaf damage. To ensure that the analysis was consistent among species, we only used young, fully expanded leaves produced in the current growing season.

### *Predictors of herbivore damage*

In addition to the planted species richness of the plots, the respective extinction scenario treatment and the experimental site, we included the height of the tree saplings and the elevation and degree of 'northness' (cosine-transformed radian values of aspect) of the plots in the analyses to account for differences in tree height and the topographic heterogeneity of the experimental sites. Elevation and aspect were obtained from a 5 m digital elevation model (DEM) that was established based on differential GPS measurements when the experiment was started. The height of each sapling was measured with a measuring pole as the length from stem base to the apical meristem. Height

**Table 4.1.** Minimal mixed-effects model (with standard errors, degrees of freedom, *t* and *P* values) for herbivore damage across the two sites of the large-scale tree diversity experiment in subtropical China

Fixed effects <sup>a</sup>	Std. Est.	Std. Error	df	<i>t</i>	<i>P</i>
(Intercept)	1.38	0.12	48	11.8	< 0.001
Site B	0.12	0.08	260	1.6	0.122
Day	-0.16	0.05	200	-3.1	0.002
Tree height	0.17	0.02	5237	9.0	< 0.001
Elevation	-0.07	0.03	192	-2.2	0.031
Tree species richness (log)	0.09	0.03	73	2.7	0.009
Site B : day	0.36	0.06	215	6.4	< 0.001

<sup>a</sup>Degree of northness, extinction scenario and its interactions, and the site : richness interaction were dropped during model simplification

measurements were conducted at the same time as the herbivory assessments. Due to the large number of plots and tree individuals, the herbivory assessments took place over several weeks and we recorded the day of assessment for each plot to include it as a covariable in the statistical analyses.

### Statistical analysis

Mean leaf damage per tree individual was modeled as the response variable in mixed effects models. Tree species identity ( $n = 40$ ), plot identity ( $n = 296$ ) and species composition of plots ( $n = 232$ ), as well as the interactions between plot and species composition and between species pool and species composition were used as random effects to account for the hierarchical structure of our herbivory data. We also tested for random slope effects of tree species richness depending on species identity, but this effect did not improve model fit. As fixed effects, we included experimental site (to account for potential differences between locations and years), day of the assessment, tree height, elevation, the degree of 'northness', extinction scenario (three replicates of the random scenario with three different species pools, two nonrandom scenarios), and tree species richness. To account for potential differences in effects among sites and extinction scenarios, we also included the two-way interactions between site and day, site and scenario, site and tree species richness, scenario and tree species richness, as

well as the three-way interaction among site, scenario and tree species richness. The response variable and tree species richness were log-transformed to improve modeling assumptions, and all continuous predictors were standardized (mean = 0; SD = 1) before analysis.

We tested for model simplification in two steps. As the experiment was in a very early stage and potential effects of the different extinction scenarios might not yet have had an effect on observed levels of herbivory, we first checked three model variants that reduced the three random extinction scenario replicates and the two nonrandom extinction scenario levels to (i) one overall random scenario versus the two nonrandom scenarios (i.e. three levels), (ii) a contrast between an overall random and an overall nonrandom scenario (i.e. two levels), or that assumed no differences among scenarios by (iii) completely disposing of the extinction scenario (and its interactions) as a predictor. The three model variants were compared to the initial model, and the one with the lowest AIC was used for further analysis (Crawley 2007). With this model, we then tested for uninformative predictors and in a stepwise procedure deleted those predictors whose removal resulted in a reduction in the AIC of the model (Burnham and Anderson 2004). The model with the smallest number of predictors and the lowest global AIC was chosen as the most parsimonious, best-fit model. Model residuals were checked for

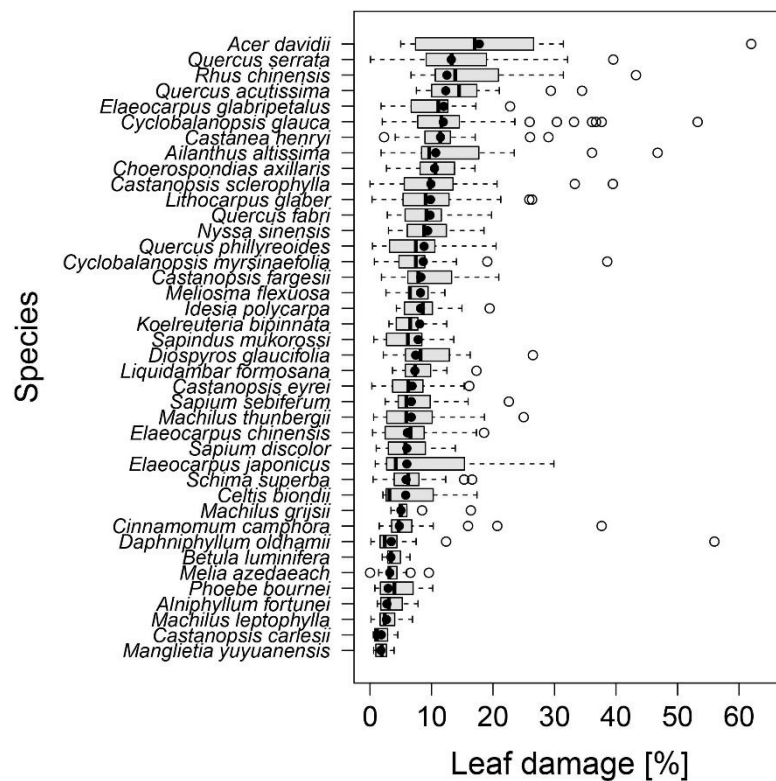


normality and homogeneity of variances. All analyses were conducted in R 3.1.0 (<http://www.R-project.org>) with the packages lme4 (Bates et al. 2014) and lmerTest (Kuznetsova et al. 2014).

## Results

The mean damage level across species and sites was  $8.3\% \pm 0.1$  SE. *Manglietia yuyuanensis* Y. W. Law and *Alniphyllum fortunei* (Hemsley) Makino exhibited the lowest mean damage levels ( $1.6\% \pm 0.1$  SE and  $2.8\% \pm 0.2$  SE, respectively), *Acer davidii* Franchet and *Quercus serrata* Murray showed the highest damage levels ( $17.8\% \pm 3.4$  SE and  $13.2\% \pm 0.7$  SE, respectively) (Fig. 1). Log-transformed tree species richness showed a significant positive relationship with log-transformed herbivory, with a predicted doubling in leaf damage from the monocultures (predicted mean = 5.7%) to the 24 tree species mixtures (predicted mean = 10.6%; Table 1, Fig. 2). This relationship and the mean herbivory levels did not differ

significantly between sites (Table 1) or among the different extinction scenarios, and the simplified model variant that did not differentiate among scenarios (AIC = 17571) was preferred to the variants that included all scenarios (AIC = 17591), an overall random versus the two nonrandom scenarios (AIC = 17580) or an overall random and an overall nonrandom scenario (AIC = 17573). This result was confirmed by separate tests of potential differences in herbivory between plots of the random and nonrandom extinction scenarios within the individual tree species richness levels, all of which were non-significant. In addition to the increase in herbivory with tree species richness, herbivory increased with individual tree height and decreased with the elevation of the plots (Table 1). The time at which the plots were checked for herbivory during the assessment campaigns also played a role, but the effect differed between the two experimental sites (Table 1).



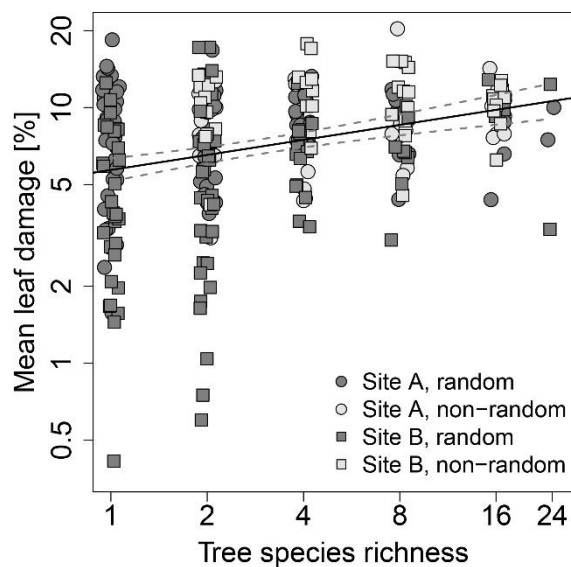
**Figure 4.1.** Leaf damage (%) on the 40 tree species planted in the experiment. Species are ordered by mean leaf damage levels (filled circles; black lines show medians) across all plots of the experiment.

## Discussion

Our study shows in the controlled setup of a large-scale forest biodiversity experiment that effects of tree species richness can strongly increase the degree of herbivore damage, irrespective of whether tree species richness levels were assembled randomly or were informed by rarity or SLA. The results of our study have important implications for our understanding of herbivory effects and their relationship with plant species richness in species-rich ecosystems. Moreover, our findings are relevant for the assessment of the conceivable impacts of herbivory on the recruitment of trees and the development success of tree plantations with different tree species richness.

The positive effect of tree species richness on herbivore damage is in line with other recent studies that found an increase in herbivory across gradients of plant species richness that included relatively high richness levels (e.g. Schuldt et al. 2010; Loranger et al. 2014). Early successional stages, such as our experimental sites, can be dominated by generalist herbivores (Brown 1985; Siemann et al. 1999) that benefit from the diversity of resources in species-rich plant communities (Pfisterer et al. 2003; Jactel and Brockerhoff 2007). Herbivory in our study plots was largely due to leaf chewers, with a particularly high abundance of grasshoppers and lepidopteran caterpillars (A. Schuldt, unpublished data). Many grasshoppers have a relatively broad host plant spectrum (Bernays and Chapman 2000), and the same probably applies to dominant caterpillars in our study region (see Schuldt et al. 2014a; Schuldt et al. 2014b). Increased performance of these herbivores by dietary mixing of different plant species, balancing nutrient and toxin intakes, is thus a probable explanation for the higher levels of herbivory in plots of higher tree species richness. This may also be one of the reasons for deviating results in other forest systems with potentially more specialized herbivore assemblages (and in most cases with relatively low levels of plant species richness; Jactel and Brockerhoff 2007; Vehviläinen et al. 2007; Sobek et al. 2009; Plath et al. 2011; Castagneyrol et al. 2013).

Interestingly, we observed the effects of tree species richness on herbivory at a very early stage of the experiment. In contrast, several studies in newly established plant communities documented a time lag in the response of important ecosystem processes to differences in plant species richness or an increase in the strength of this response over time (see Cardinale et al. 2012; Eisenhauer et al. 2012). Some of these effects were attributed to a lag in the establishment of biotic interactions with higher trophic levels (Eisenhauer et al. 2012). For our study system, this indicates that key trophic interactions became established quickly, possibly due to the fact that our study was conducted in a much more biodiverse region, where trophic interactions are often assumed to have a greater impact (Schemske et al. 2009), than most previous studies. Our results thus suggest that herbivory plays a crucial role in the regulation of ecosystem functions and the structural development of species-rich forests from the very start of secondary forest succession. Even the moderate levels of herbivory observed in our study, and thus the differences in herbivory along the tree species richness gradient, can have severe long-term effects on ecosystems (see e.g. Zvereva et al. 2012). In this context, it is interesting to note that Yang et al. (2013) found an unexpected increase with elevation in the survival rate of the seedlings planted in this experiment, and our finding that herbivory decreased with elevation (see also Rasmann et al. 2014) may potentially provide an explanation for this pattern. In addition, the differences in herbivore damage along the gradient of tree species richness may affect nutrient fluxes and primary productivity of the forest plots. Several studies have shown that herbivory can strongly increase the input of plant-available nitrogen and phosphorus (e.g. Belovsky and Slade 2000; Metcalfe et al. 2014), which may be of particular importance for nutrient-limited ecosystems such as (sub)tropical forests (Metcalfe et al. 2014). Increased herbivory at higher levels of species richness might change the environment in a way favorable for plant growth, and thus—at the community-level—cause a positive feedback loop between tree species richness and



**Figure 4.2.** Mean leaf damage (%) per plot due to insect herbivory across the gradient of tree species richness for the large-scale tree diversity experiment in subtropical China ( $\beta = 0.09$ ;  $P = 0.009$  for the log-log relationship).

herbivory that might outweigh the negative direct impact of herbivory on biomass loss. Indirect effects of herbivory via the regulation of nutrient fluxes and direct effects due to leaf damage may also affect plant species coexistence. Our results thus have important implications for our understanding of the processes that influence community assembly and interspecific competition of tree species in highly diverse regions. They highlight that the effects of herbivory as one of the potential drivers of plant community assembly (HilleRisLambers et al. 2012; Coley and Kursar 2014) can vary with, and thus potentially already have repercussions on, tree species richness patterns (see e.g. Schuldt et al. 2014a) in the early stages of the community assembly process.

Although the relationship between tree species richness and herbivory became established very quickly, there were no significant differences in this relationship among the random and nonrandom extinction scenarios of our experiment. Based on our findings from a nearby secondary forest (see Introduction; Schuldt et al. 2012), we might have expected the greatest herbivore damage at low levels of species richness for the plots of the nonrandom extinction scenarios.

However, the secondary forests in which the relationships between plant traits and herbivory were observed were much older in terms of successional age than our experimental setup (Schuldt et al. 2012; Schuldt et al. 2014a). It is conceivable that herbivores which dominate in the very early stages of our experiment show feeding preferences that do not necessarily represent those of herbivores associated with later successional forest stages. Thus, effects of specific plant traits on herbivory observed at later stages might not be detectable in the initial stages of forest succession and only develop over time with changes in the tree and herbivore assemblages (and potentially also shifts in species-specific trait values) and their interactions (see also Vehviläinen et al. 2007; Loranger et al. 2014). Considering the above-mentioned time-lag of biodiversity effects in newly established communities, this could mean that differences between random and nonrandom species loss on ecosystem processes such as herbivory can become stronger with time as well and, in our case, depend on forest age. However, continuous monitoring over longer time periods in an experimental context is required to evaluate this hypothesis.

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## References

- Bagchi R et al. (2014) Pathogens and insect herbivores drive rainforest plant diversity and composition. *Nature* 506:85-88
- Bala G et al. (2007) Combined climate and carbon-cycle effects of large-scale deforestation. *Proceedings of the National Academy of Sciences* 104:6550-6555

- Bates DM, Maechler M, Bolker B, Walker S (2014) lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-6. Available at <http://CRAN.R-project.org/package=lme4>. Last accessed 30 June 2014
- Belovsky G, Slade J (2000) Insect herbivory accelerates nutrient cycling and increases plant production. *Proceedings of the National Academy of Sciences* 97:14412-14417
- Bernays EA, Chapman RF (2000) Plant secondary compounds and grasshoppers: beyond plant defenses. *Journal of Chemical Ecology* 26:1773-1794
- Bonan GB (2008) Forests and climate change: forcings, feedbacks, and the climate benefits of forests. *Science* 320:1444-1449
- Brown VK (1985) Insect herbivores and plant succession. *Oikos*:17-22
- Bruehlheide H et al. (2014) Designing forest biodiversity experiments: general considerations illustrated by a new large experiment in subtropical China. *Methods in Ecology and Evolution* 5:74-89
- Burnham KP, Anderson DR (2004) Model selection and multimodel inference : a practical information-theoretic approach. Springer, New York
- Cardinale BJ et al. (2011) The functional role of producer diversity in ecosystems. *American Journal of Botany* 98:572-592
- Cardinale BJ et al. (2012) Biodiversity loss and its impact on humanity. *Nature* 486:59-67
- Castagneyrol B, Giffard B, Péré C, Jactel H (2013) Plant apparency, an overlooked driver of associational resistance to herbivory. *Journal of Ecology* 101:418-429
- Coley PD, Barone JA (1996) Herbivory and plant defenses in tropical forests. *Annual Review of Ecology and Systematics* 27:305-335
- Coley PD, Kursar TA (2014) On tropical forests and their pests. *Science* 343:35-36
- Crawley MJ (2007) *The R Book*. Wiley, Chichester
- Dinnage R (2013) Phylogenetic diversity of plants alters the effect of species richness on invertebrate herbivory. *PeerJ* 1:e93
- Dyer LA et al. (2007) Host specificity of Lepidoptera in tropical and temperate forests. *Nature* 448:696-U699
- Eisenhauer N, Reich PB, Scheu S (2012) Increasing plant diversity effects on productivity with time due to delayed soil biota effects on plants. *Basic and Applied Ecology* 13:571-578
- HilleRisLambers J, Adler P, Harpole W, Levine J, Mayfield M (2012) Rethinking community assembly through the lens of coexistence theory. *Annual Review of Ecology, Evolution, and Systematics* 43:227
- Jactel H, Brockerhoff EG (2007) Tree diversity reduces herbivory by forest insects. *Ecology Letters* 10:835-848
- Kremen C et al. (2000) Economic incentives for rain forest conservation across scales. *Science* 288:1828-1832
- Kuznetsova A, Brockhoff PB, Christensen RHB (2014) lmerTest: Tests for random and fixed effects for linear mixed effect models (lmer objects of lme4 package). R package version 2.0-6. Available at <http://CRAN.R-project.org/package=lmerTest>. Last accessed 30 June 2014.
- Loranger H et al. (2014) Invertebrate herbivory increases along an experimental gradient of grassland plant diversity. *Oecologia* 174:183-193
- Loranger J et al. (2013) Predicting invertebrate herbivory from plant traits: Polycultures show strong nonadditive effects. *Ecology* 94:1499-1509
- Metcalf DB et al. (2014) Herbivory makes major contributions to ecosystem carbon and nutrient cycling in tropical forests. *Ecology Letters* 17:324-332
- Nadrowski K, Wirth C, Scherer-Lorenzen M (2010) Is forest diversity driving ecosystem functioning and service? *Current Opinion in Environmental Sustainability* 2:75-79
- Ness JH, Rollinson EJ, Whitney KD (2011) Phylogenetic distance can predict susceptibility to attack by natural enemies. *Oikos* 120:1327-1334
- Pfisterer AB, Diemer M, Schmid B (2003) Dietary shift and lowered biomass gain of a generalist herbivore in species-poor experimental plant communities. *Oecologia* 135:234-241
- Plath M, Mody K, Potvin C, Dorn S (2011) Establishment of native tropical timber trees in monoculture and mixed-species plantations: Small-scale effects on tree performance and insect herbivory. *Forest Ecology and Management* 261:741-750
- Rasmann S, Pellissier L, Defosse E, Jactel H, Kunstler G (2014) Climate-driven change in plant-insect interactions along elevation gradients. *Functional Ecology* 28:46-54
- Rodriguez-Castaneda G (2013) The world and its shades of green: a meta-analysis on trophic cascades across temperature and precipitation gradients. *Global Ecology and Biogeography* 22:118-130
- Root RB (1973) Organization of a plant-arthropod association in simple and diverse habitats: the

- fauna of collards (*Brassica oleracea*). Ecological Monographs 43:95-124
- Schemske DW, Mittelbach GG, Cornell HV, Sobel JM, Roy K (2009) Is there a latitudinal gradient in the importance of biotic interactions? Annual Review of Ecology and Systematics 40:245-269
- Scherber C et al. (2010) Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. Nature 468:553-556
- Scherer-Lorenzen M (2014) The functional role of biodiversity in the context of global change. In: Burslem D, Coomes D, Simonson W (eds) Forests and Global Change. Cambridge University Press, Cambridge, pp 195-238
- Schowalter TD (2012) Insect herbivore effects on forest ecosystem services. Journal of Sustainable Forestry 31:518-536
- Schuldt A et al. (2010) Tree diversity promotes insect herbivory in subtropical forests of south-east China. Journal of Ecology 98:917-926
- Schuldt A et al. (2012) Plant traits affecting herbivory on tree recruits in highly diverse subtropical forests. Ecology Letters 15:732-739
- Schuldt A et al. (2014a) Functional and phylogenetic diversity of woody plants drive herbivory in a highly diverse forest. New Phytologist 202:864-873
- Schuldt A et al. (2014b) Woody plant phylogenetic diversity mediates bottom-up control of arthropod biomass in species-rich forests. Oecologia 176: 171-182
- Siemann E, Haarstad J, Tilman D (1999) Dynamics of plant and arthropod diversity during old field succession. Ecography 22:406-414
- Sobek S, Gossner MM, Scherber C, Steffan-Dewenter I, Tschamntke T (2009) Tree diversity drives abundance and spatiotemporal beta-diversity of true bugs (Heteroptera). Ecological Entomology 34:772-782
- Terborgh J (2012) Enemies maintain hyperdiverse tropical forests. American Naturalist 179:303-314
- Vehviläinen H, Koricheva J, Ruohomäki K (2007) Tree species diversity influences herbivore abundance and damage: meta-analysis of long-term forest experiments. Oecologia 152:287-298
- Yang X et al. (2013) Establishment success in a forest biodiversity and ecosystem functioning experiment in subtropical China (BEF-China). European Journal of Forest Research 132:593-606
- Zvereva EL, Zverev V, Kozlov MV (2012) Little strokes fell great oaks: minor but chronic herbivory substantially reduces birch growth. Oikos 121:2036-2043



# CHAPTER 5

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# Woody plant phylogenetic diversity mediates bottom-up control of arthropod biomass in species-rich forests

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## Abstract

Global change is predicted to cause nonrandom species loss in plant communities, with consequences for ecosystem functioning. However, beyond the simple effects of plant species richness, little is known about how plant diversity and its loss influence higher trophic levels, which are crucial to the functioning of many species-rich ecosystems. We analyzed to what extent woody plant phylogenetic diversity and species richness contribute to explaining the biomass and abundance of herbivorous and predatory arthropods in a species-rich forest in subtropical China. The biomass and abundance of leaf-chewing herbivores, and the biomass dispersion of herbivores within plots, increased with woody plant phylogenetic diversity. Woody plant species richness had much weaker effects on arthropods, but interacted with plant phylogenetic diversity to negatively affect the ratio of predator to herbivore biomass. Overall, our results point to a strong bottom-up control of functionally important herbivores mediated particularly by plant phylogenetic diversity, but do not support the general expectation that top-down predator effects increase with plant diversity. The observed effects appear to be driven primarily by increasing resource diversity rather than diversity-dependent primary productivity, as the latter did not affect arthropods. The strong effects of plant phylogenetic diversity and the overall weaker effects of plant species richness show that the diversity-dependence of ecosystem processes and interactions across trophic levels can depend fundamentally on nonrandom species associations. This has important implications for the regulation of ecosystem functions via trophic interaction pathways and for the way species loss may impact these pathways in species-rich forests.

**Key words:** BEF China; biodiversity; ecosystem function; herbivores; predators; species richness; trophic interactions

## Introduction

The diversity of life on earth strongly influences the dynamics and properties of ecosystems, and global change-induced biodiversity loss may thus significantly alter ecosystem functioning and service provisioning (Hooper et al. 2012; Naeem et al. 2012). Most notably, plant species loss has been shown to negatively affect a wide range

of ecosystem functions, such as biomass production and carbon sequestration (Cardinale et al. 2011; Cardinale et al. 2012). However, recent work has also indicated that plant species richness impacts on the abundance and diversity of higher trophic levels (e.g. Unsicker et al. 2006; Haddad et al. 2009; Sobek et al. 2009b; Scherber et al. 2010). This has important ecological consequences, as diversity-dependent effects on herbivores

and predators can feed back on the producer level and strongly mediate biodiversity-ecosystem function relationships under real-world conditions (Haddad et al. 2009; Schuldt et al. 2010).

However, we are far from having a general understanding of such diversity-dependent trophic interaction effects (see also Cardinale et al. 2011), as even basic relationships between plant diversity and the diversity or abundance of herbivores and predators often seem not to show a consistent pattern (Koricheva et al. 2000; Vehviläinen et al. 2007; Sobek et al. 2009a; Castagneyrol and Jactel 2012; Schuldt et al. 2014b). While such inconsistent patterns potentially indicate relevant biological differences among systems, their interpretation is complicated by two important aspects. First of all, many studies are biased toward analyzing relatively species-poor and often simplified plant communities, in which it may be difficult to distinguish the effects of community composition from diversity effects (Nadrowski et al. 2010). Extrapolating to more diverse systems is hardly possible. Yet, information on species-rich systems may be particularly crucial, as diversity-dependent interactions between plants and higher trophic levels can play a key role in the functioning of such systems (e.g. Terborgh 2012). Secondly, most studies have focused on the effects of plant species richness as a very basic measure of biodiversity. However, relationships with herbivores or predators might be more complex and not necessarily captured well by plant species richness alone. Plant species loss in natural communities often occurs, and may cascade to affect higher trophic levels, in a nonrandom way (Srivastava and Vellend 2005; Thebault et al. 2007; Cavender-Bares et al. 2009). Species may get lost in a phylogenetically structured manner that reflects phylogenetically conserved functional adaptations to their biotic and abiotic environments, such as the phylogenetically structured host selection of many consumers (e.g. Weiblen et al. 2006). This could explain why, even in plant species-rich systems, plant community composition was repeatedly found to be a better predictor of herbivore and predator assemblage structure than species

richness (Perner et al. 2005; Rzanny et al. 2013). Measures of diversity that incorporate the relatedness among species in terms of evolutionary and functional similarity may thus substantially improve our understanding of diversity relationships across trophic levels (Dinnage et al. 2012; Pellissier et al. 2013).

Plant phylogenetic diversity qualifies as a particularly comprehensive predictor in this respect, as it may not only account for complex functional trait interactions that affect higher trophic levels (if key functional traits are phylogenetically conserved; Cavender-Bares et al. 2009; Srivastava et al. 2012), but can also indicate the effects of shared evolutionary and biogeographic history among species (Futuyma and Agrawal 2009; Pellissier et al. 2013). Dinnage et al. (2012) recently showed in a grassland experiment that plant phylogenetic diversity strongly interacted with plant species richness to affect arthropod diversity, with effects of plant species richness becoming stronger at high levels of plant phylogenetic diversity. For natural systems, however, where processes of nonrandom community assembly may strongly affect the phylogenetic structure of plant and animal communities, the effects of phylogenetic diversity on arthropods remain poorly explored. This applies particularly to species-rich subtropical and tropical forests, where arthropods play an important role in maintaining the high tree diversity and may contribute to structuring plant phylogenetic community composition (Cavender-Bares et al. 2009; Paine et al. 2012; Terborgh 2012).

Here, we analyze to what extent the phylogenetic diversity and species richness of woody plants contribute to explaining the biomass and abundance of herbivorous and predatory arthropods along gradients of woody plant species richness and stand age in a highly diverse subtropical forest in China. Biomass, in particular, is directly related to the functional impact of consumers (Saint-Germain et al. 2007; Reiss et al. 2011), but its relationship with plant diversity in such highly diverse forests is poorly understood (and the same even applies to the more frequently studied abundance of arthropods; Whitfeld et al. 2012). We focus on the overall biomass and abundance of predators, leaf chewing

herbivores and sucking herbivores, which allows us to obtain insight into the net ecosystem effect of key functional groups in this system. In addition, we test for diversity effects on the variability in biomass distributions among individuals in each of our 27 study plots, which might be related to the degree of resource differentiation in arthropod assemblages (Rudolf 2012).

Plant diversity might have a direct effect on herbivore and predator assemblages via increased and more stable resource diversity, with positive effects on generalist herbivores and predators (the ‘dietary-mixing’ and ‘enemies’ hypotheses; Root 1973; Haddad et al. 2009; Dinnage 2013) and negative effects on specialized herbivores (the ‘resource-concentration’ hypothesis; Root 1973; but see Plath et al. 2012). It might also promote consumers indirectly via diversity-dependent effects of plant productivity on consumer biomass (the ‘more-individuals’ hypothesis; Srivastava and Lawton 1998). We hypothesize that (i) the biomass (and its variability within study plots) and abundances of both herbivores and predators increase with woody plant diversity in our study system. Specifically, we expect that (ii) changes in biomass and abundance are better predicted by plant phylogenetic diversity than plant species richness, as phylogenetic diversity better explains the complexity of evolutionary and functional characteristics that may underlie diversity effects. As woody plant diversity in our study plots has been found to increase primary productivity (Baruffol et al. 2013), we include alternative analyses that substitute productivity data for diversity metrics to test whether (iii) resource diversity or plant primary productivity underlie potential diversity effects. As support for both the resource diversity and productivity mechanism has been controversial, even for the much better studied grassland systems (Haddad et al. 2009; Borer et al. 2012), knowledge of these potential impacts of these mechanisms on herbivores and predators in highly diverse forests will advance our general understanding of the community-level consequences of changes in biodiversity.

## Methods

### Study site and plot design

The study was conducted in the Gutianshan National Nature Reserve (29°14′ N; 118°07′ E) in Zhejiang province, south-east China. The reserve covers 8000 ha of evergreen mixed broadleaved forest on a sloping terrain (300–1260 m a.s.l.). In the reserve, about 1430 seed plant species, 260 of them woody, have been recorded (Legendre et al. 2009; Bruelheide et al. 2011). The subtropical monsoon climate is characterized by a mean annual temperature of 15.3°C and a mean annual precipitation of about 2000 mm (Hu and Yu 2008), with most of the rainfall occurring in May and June (Geißler et al. 2012).

As part of the BEF (Biodiversity and Ecosystem Functioning) China project ([www.bef-china.de](http://www.bef-china.de)), 27 study plots of 30 x 30 m were established in 2008, which were randomly spread (as far as logistically feasible; distance among plots was on average 2.6 km  $\pm$  2.3 *SD* (range 0.1 - 8.6 km)) across the reserve. Plot selection followed a stratified sampling design based on woody plant species richness (25–69 species per plot) and stand age (with < 20 to > 80 years since the last logging events, or, in some cases, since agricultural activities). Details of plot selection and plot characteristics (including data on the plant species composition of all 27 plots) are given in Bruelheide et al. (2011).

### Arthropod sampling

Arthropods were sampled at three time periods to capture seasonal patterns in the herbivore assemblages, i.e. September/October 2011 (toward the end of the growing season), April 2012 (before the rainy season, after the start of the growing season) and June 2012 (at the end of the rainy season, peak of the growing season). We used a beating technique that allows for a direct assessment of arthropods at the level of individual trees (Ødegaard et al. 2005; Campos et al. 2006; Wardhaugh et al. 2012). Arthropods were knocked down from 25 tree and shrub saplings onto a beating sheet (70 cm diameter). Saplings were selected every two meters along a transect running diagonally

through the plot. The composition of these 25 randomly selected saplings very well mirrored the differences in the community composition among plots of the overall woody plant communities (Procrustes correlation = 0.90;  $P < 0.001$ ; see Methods in Electronic Supplementary Material (ESM)). Sapling species identity was determined with the help of local experts. The height of each sampled sapling was recorded in the field. Mean height was 1.77 m, with a SD of 0.48 m, indicating that a similar volume of plant structures was sampled from above the beating sheet for most individuals (see also Campos et al. 2006). However, to account for potential effects of tree height on arthropod samples, individual sapling height was included as a covariate in the statistical analyses. Transect lines varied between the fall and spring surveys, thus sampling a different set of tree and shrub individuals, but were identical between the spring and summer surveys for logistical reasons.

Arthropods were sorted to higher taxa (basically order level, but with further distinctions in orders such as Coleoptera, Hymenoptera, Hemiptera, to distinguish predators and different herbivore guilds; see Table S5.1 in ESM for details) and classified as (mainly) predators or herbivores (following the classification of Novotny et al. 2010 and using morphological characteristics such as mandible shapes where necessary). For the herbivores, we distinguished between leaf chewers and sap suckers; other herbivore guilds were too rare for separate analysis. As our main focus was on overall biomass and abundance patterns, we did not sort arthropods to (morpho)species, which can be challenging and error-prone for highly diverse taxa (e.g. many juvenile spiders and lepidopteran caterpillars; e.g. Strutzenberger et al. 2011). Biomass and abundance patterns are particularly important in determining the functional impact of primary and secondary consumers (Saint-Germain et al. 2007; Reiss et al. 2011), and many studies have shown that overall patterns at the level of important functional groups can be highly informative for our understanding of the regulation of ecosystem functions in light of changing plant diversity (Perner et al. 2005; Vehviläinen et al.

2007; Vehviläinen et al. 2008; Haddad et al. 2009; Borer et al. 2012; Whitfeld et al. 2012). For all predatory and herbivorous arthropods, body length (excluding body appendages such as ovipositors and antennae) was measured to the closest 0.1 mm under a stereomicroscope with a built-in micrometer gauge. Biomass for each sampled individual was estimated on the basis of taxon-specific body length-biomass equations of Hódar (1996) and Wardhaugh (2013).

### Environmental data

Woody plant species richness for each plot was based on a complete inventory of all tree and shrub individuals  $> 1$  m height, measured at the time of plot establishment in 2008. Data for the calculation of the phylogenetic diversity of the woody plant communities (see statistics) was obtained from an ultrametric phylogenetic tree of all angiosperm woody species recorded in the 27 study plots (Purschke et al. 2014). The tree was based on *rbcL* and *matK* sequences of the species (downloaded from NCBI Genbank; <http://www.ncbi.nlm.nih.gov>), which were aligned in Bioedit and processed in MEGA5 (Tamura et al. 2011) to obtain a phylogenetic tree based on maximum likelihood (ML). The ultrametric tree was computed from the ML topology using penalized likelihood, with branch lengths indicating divergence time.

Plot age was estimated from tree stem cores and diameter at breast height measurements (to the closest 0.1 mm) (Bruehlheide et al. 2011). Plot age was correlated with, and used as a comprehensive measure of, plot characteristics that change with succession, such as canopy cover (Pearson's  $r = 0.72$ ;  $P < 0.001$  for the correlation with plot age) and total basal area of woody plants ( $r = 0.76$ ;  $P < 0.001$ ) (see Schuldt et al. 2010). We also accounted for the topographic variability of our study site, which may further affect environmental plot conditions, by including the elevation (m) of the plots in our analyses.

Plot-level primary productivity over a two year period was inferred from tree growth data in 2008 and 2010. Basal area increments of all trees  $> 10$  cm diameter at breast height, assessed with permanent dendrometer bands

or with measuring tapes, were calculated and used as a proxy for relative tree growth (see Baruffol et al. 2013 for details). As a number of trees were destroyed in two plots due to illegal harvesting before measurements in 2010, productivity data was only available for 25 plots.

### Statistical analysis

Woody plant phylogenetic diversity ( $Q_{\text{phyl}}$ ) was calculated as the abundance-weighted version of Rao's quadratic entropy  $Q$  (Botta-Dukát 2005).  $Q_{\text{phyl}}$  was not completely independent of woody plant species richness ( $r = 0.48$ ;  $P = 0.011$ ) and plot age ( $r = 0.57$ ;  $P = 0.002$ ). As a metric of phylogenetic diversity that reflects the extent to which woody plant communities are phylogenetically more clustered or overdispersed than expected by chance, we thus calculated standardized effect sizes of  $Q_{\text{phyl}}$  ( $Q_{\text{phyl}}$  s.e.s.) based on the null model '1s' in Hardy et al. (2008). These s.e.s. values are independent of a given plant community's species richness ( $r = -0.26$ ;  $P = 0.186$  in our study). In our case, they were also unrelated to plot age ( $r = -0.01$ ;  $P = 0.959$ ). Standardized effect sizes were calculated as the observed phylogenetic diversity relative to expected values from the random communities:  $\text{ses} = (\text{observed phylogenetic diversity index score} - \text{mean expected index score}) / \text{standard deviation of the index}$  (Gotelli and Rohde 2002).

Based on Rao's  $Q$ , we also quantified the functional dispersion of the biomass of all leaf chewer, sap sucker or predator individuals per plot and sampling time ( $Q_{\text{Bio}}$ ). Higher values of  $Q_{\text{Bio}}$  indicate larger biomass dissimilarity of the individuals of a given group within a study plot, which may point to higher resource differentiation among individuals (Schleuter et al. 2010).  $Q_{\text{Bio}}$  was not dependent on the number of individuals in a given plot (chewers:  $r = -0.07$ ;  $P = 0.564$ ; suckers:  $r = -0.01$ ;  $P = 0.913$ ; predators:  $r = -0.19$ ;  $P = 0.084$ ). Calculations of Rao's  $Q$  were based on standardized variables (mean = 0, SD = 1) and a Euclidean species distance matrix. All continuous predictors (i.e. all variables except sampling time) were standardized prior to the analysis. Correlations among predictors (all with an  $r \leq 0.57$ )

indicated that none of the predictors were highly collinear. The mean biomass and abundances of leaf-chewing herbivores, sap-sucking herbivores, predatory arthropods, and the predator-herbivore biomass and abundance ratios per plot and sampling time—as well as the functional dispersion ( $Q_{\text{Bio}}$ ) of leaf chewer, sucker and predator biomass—were used as response variables. Arthropod biomass and abundance values were averaged for each of the three sampling times across the 25 saplings sampled per plot as different tree and shrub individuals were included in the three different sampling campaigns (see above). Linear mixed effects models were used to account for potential effects of temporal or spatial pseudoreplication. Plot identity was included as a random effect. We also tested for a random interaction effect of sampling time and plot identity, but likelihood ratio tests indicated that this term was not significant and could be dropped. As fixed effects, we included sampling time, elevation, sapling height, plot age, woody plant species richness, woody plant phylogenetic diversity (standardized effect sizes  $Q_{\text{phyl}}$  s.e.s.), as well as all two-way interactions between sampling time, plot age, species richness and phylogenetic diversity. The number of woody plant species sampled in a plot had no effect on any of the response variables and was not included in the models. The response variables and woody plant species richness were log-transformed to improve model fit. The full models with all predictors (i.e. in the form of:  $\text{response} \sim \text{sampling time} + \text{elevation} + \text{sapling height} + \text{plot age} + \text{woody plant species richness} + \text{woody plant phylogenetic diversity} (Q_{\text{phyl}} \text{ s.e.s.}) + \text{time:age} + \text{time:richness} + \text{time:phylo diversity} + \text{age:richness} + \text{age:phylo diversity} + \text{richness:phylo diversity}$ ,  $\text{random} \sim 1 | \text{plot}$ ) were simplified by excluding predictor variables in an automated stepwise procedure based on the AICc (Burnham and Anderson 2004) and maximum likelihood estimation. The models with the smallest number of predictors and the lowest global AICc were chosen as the most parsimonious, best-fit models for each response variable. Model residuals were checked for normality and

homogeneity of variances. To assess whether potential effects of tree diversity could be explained by plot-level primary productivity, we re-ran all analyses that indicated diversity effects in the minimal models, replacing the measures of diversity (woody plant species richness and phylogenetic diversity) by plot-level productivity data. Productivity in the study plots was previously found to be strongly related to woody plant species and phylogenetic diversity (Baruffol et al. 2013) and, to avoid statistical biases due to collinearity and to keep model complexity to an acceptable level, we did not directly include productivity in the models which tested for diversity effects. All analyses were conducted in R 3.1.0 (<http://www.R-project.org>) with the packages *picante* (Pinheiro et al. 2014) and *nlme* (Kembel et al. 2010).

## Results

In total, we recorded 6950 arthropods with a total biomass of 29,167 mg across the three sampling periods. Predators were most abundant (4737 individuals; 79% spiders), followed by leaf-chewing herbivores (1282 individuals; 41% lepidopteran caterpillars, 32% orthopterans) and sap-suckers (931 individuals; 74% Auchenorrhyncha). However, biomass was higher for leaf chewers (16,730 mg; 42% orthopterans, 37% lepidopteran caterpillars) than for predators (9387 mg; 66% spiders) and sap suckers (3050 mg; 82% Auchenorrhyncha). Biomass and abundance correlated particularly strongly for sap suckers (Pearson's  $r = 0.74$ ;  $P < 0.001$ ) but less so for predators ( $r = 0.38$ ;  $P < 0.001$ ) and leaf chewers ( $r = 0.37$ ;  $P < 0.001$ ). Predator and herbivore biomass were not significantly correlated ( $P > 0.80$  in all cases). In contrast, predator abundance was positively related to leaf chewer abundance ( $\beta = 0.26 \pm 0.09$  SE;  $t = 2.85$ ;  $P = 0.006$  for log-transformed abundance values in a mixed model including sampling time as a covariate) and tended to slightly increase with the abundance of sap suckers ( $\beta = 0.07 \pm 0.05$  SE;  $t = 1.37$ ;  $P = 0.175$ ).

In general, mixed models for both biomass and abundance pointed to similar variables affecting patterns within the predator and the two herbivore groups across the 27

study plots. However, diversity effects were always more pronounced for biomass as compared to mere abundance patterns (Table 5.1, Table S5.2). Thus, in the following we focus on biomass patterns (see Table S5.2 in ESM for abundance patterns). Leaf chewer biomass was particularly strongly affected by, and increased with, woody plant phylogenetic diversity ( $Q_{\text{phyl}}$  s.e.s.) (Table 5.1, Fig. 5.1a). Leaf chewer biomass further tended to increase with woody plant species richness, but this effect was not significant ( $P = 0.07$ ; Table 5.1). In contrast to leaf chewers, sap-sucking herbivores were not affected by plant phylogenetic diversity, showing only a response to sampling period (Table 5.1). Likewise, the biomass of predators was not related to plant phylogenetic diversity, but increased with plot age (Fig. 5.1b). In contrast, the ratio of predator to herbivore biomass was strongly affected by the interaction between woody plant phylogenetic diversity and plant species richness (a pattern that was not detectable with mere abundance data; Table S5.2). The ratio of predators to herbivores was highest in plant species-poor plots with lower than expected phylogenetic diversity and strongly decreased with increasing plant phylogenetic diversity and plant species richness (Fig. 5.1c).

The dissimilarity in biomass among leaf chewer individuals within plots—measured as biomass dispersion  $Q_{\text{Bio}}$ —was lowest in plant species-poor plots with lower than expected phylogenetic diversity and strongly increased with both woody plant phylogenetic diversity ( $Q_{\text{phyl}}$  s.e.s.) and plant species richness (Table 5.2, Fig. 5.2). Sap sucker biomass dispersion showed a response to plant phylogenetic diversity only during summer (Time 3; Table 5.2). Biomass dispersion among predators was not related to plant phylogenetic diversity, but decreased with woody plant species richness (only significant at Time 2; Table 5.2).

The effects of plant phylogenetic diversity on leaf chewing herbivores and the predator-herbivore ratio were also evident when observed plant phylogenetic diversity instead of standardized effect sizes were analyzed (however, with changes in the roles of plot age and plant species richness due to

**Table 5.1.** Mixed-effects models for the biomass of leaf-chewing herbivores, sap-sucking herbivores, predators, and the biomass ratio of predators to herbivores across 27 forest stands in subtropical China. Parameter estimates (with standard errors, degrees of freedom, t and *P* values) are shown for the variables retained in the minimal models

<i>Fixed effects</i> <sup>a,b</sup>	Herbivores: Leaf chewers					Herbivores: Suckers					Predators					Predator : Herbivore ratio				
	Est.	<i>SE</i>	<i>DF</i>	t	<i>P</i>	Est.	<i>SE</i>	<i>DF</i>	t	<i>P</i>	Est.	<i>SE</i>	<i>DF</i>	t	<i>P</i>	Est.	<i>SE</i>	<i>DF</i>	t	<i>P</i>
Intercept	1.53	0.14	52	10.6	<0.001	-0.64	0.23	52	-2.8	0.007	1.40	0.06	54	23.0	<0.001	-0.40	0.16	52	-2.5	0.016
Time 2-1 <sup>c</sup>	0.61	0.19	52	3.2	0.003	1.40	0.32	52	4.3	<0.001	-	-	-	-	-	-0.47	0.22	52	-2.2	0.035
Time 3-1 <sup>c</sup>	<i>0.26</i>	<i>0.19</i>	<i>52</i>	<i>1.3</i>	<i>0.183</i>	<i>-0.51</i>	<i>0.32</i>	<i>52</i>	<i>-1.6</i>	<i>0.122</i>	-	-	-	-	-	<i>-0.05</i>	<i>0.22</i>	<i>52</i>	<i>-0.2</i>	<i>0.825</i>
Plot age	-	-	-	-	-	-	-	-	-	-	0.17	0.06	25	2.8	0.009	-	-	-	-	-
Woody plant species richness (log)	<i>0.18</i>	<i>0.10</i>	<i>24</i>	<i>1.9</i>	<i>0.067</i>	-	-	-	-	-	-	-	-	-	-	<i>-0.18</i>	<i>0.10</i>	<i>23</i>	<i>-1.8</i>	<i>0.093</i>
<i>Qphyl</i> s.e.s. <sup>c</sup>	0.21	0.10	24	2.3	0.033	-	-	-	-	-	-	-	-	-	-	-0.28	0.12	23	-2.4	0.026
Woody plant richness : <i>Qphyl</i> s.e.s.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.30	0.13	23	2.4	0.025
AICc full model <sup>d</sup>	205.4					298.1					153.9					231.4				
AICc min. model <sup>d</sup>	192.4					266.0					127.5					206.9				

<sup>a</sup>Sapling height, elevation, and the interactions *Qphyl* s.e.s : plot age, richness : plot age, time : *Qphyl* s.e.s , time : plot age, and time : richness were included in the full models but not retained in any of the minimal models

<sup>b</sup>Italics denote data for non-significant terms retained in the minimal models

<sup>c</sup>*Qphyl* s.e.s. = standardized effect sizes of woody plant phylogenetic diversity (*Qphyl*)

<sup>d</sup>Akaike information criterion (corrected for small sample sizes) of the full model (containing all predictors) and the minimal adequate model (simplified model with lowest AICc)

**Table 5.2.** Mixed-effects models for the functional dispersion ( $Q_{Bio}$ ) of the biomass of leaf chewer, sap-sucker, and predator individuals per plot across 27 forest stands in subtropical China. Parameter estimates (with standard errors, degrees of freedom, t and  $P$  values) are shown for the variables retained in the minimal models

<i>Fixed effects<sup>a,b</sup></i>	Herbivores: Leaf choppers					Herbivores: Suckers					Predators				
	Est.	SE	DF	t	P	Est.	SE	DF	t	P	Est.	SE	DF	t	P
Intercept	-3.58	0.05	54	-75.4	<0.001	-4.25	0.21	50	-20.5	<0.001	-2.28	0.03	50	-72.2	<0.001
Time 2-1 <sup>c</sup>	-	-	-	-	-	0.73	0.29	50	2.5	0.016	<i>0.07</i>	<i>0.04</i>	<i>50</i>	<i>1.5</i>	<i>0.148</i>
Time 3-1 <sup>c</sup>	-	-	-	-	-	<i>0.43</i>	<i>0.29</i>	<i>50</i>	<i>1.5</i>	<i>0.149</i>	0.18	0.04	50	4.0	<0.001
Plot age	<i>0.09</i>	<i>0.05</i>	<i>22</i>	<i>2.0</i>	<i>0.058</i>	-	-	-	-	-	-	-	-	-	-
Woody plant species richness (log)	0.12	0.05	22	2.4	0.024	-	-	-	-	-	<i>0.05</i>	<i>0.03</i>	<i>25</i>	<i>1.4</i>	<i>0.166</i>
<i>Qphyl</i> s.e.s.	0.19	0.06	22	3.4	0.003	<i>-0.06</i>	<i>0.21</i>	<i>25</i>	<i>-0.3</i>	<i>0.759</i>	-	-	-	-	-
Woody plant richness : <i>Qphyl</i> s.e.s.	-0.15	0.06	22	-2.5	0.022	-	-	-	-	-	-	-	-	-	-
Time 2 : <i>Qphyl</i> s.e.s.	-	-	-	-	-	<i>-0.04</i>	<i>0.29</i>	<i>50</i>	<i>-0.1</i>	<i>0.890</i>	-	-	-	-	-
Time 3 : <i>Qphyl</i> s.e.s.	-	-	-	-	-	0.67	0.29	50	2.3	0.027	-	-	-	-	-
Time 2 : Woody plant richness	-	-	-	-	-	-	-	-	-	-	-0.11	0.04	50	-2.5	0.014
Time 3 : Woody plant richness	-	-	-	-	-	-	-	-	-	-	-0.07	0.04	50	-1.6	0.108
AICc full model	116.5					281.5					-24.4				
AICc min. model	88.4					253.1					-51.2				

<sup>a</sup>Sapling height, elevation, and the interactions *Qphyl* s.e.s. : plot age, richness : plot age, and time : plot age were included in the full models but not retained in any of the minimal models

<sup>b</sup>Italics denote data for non-significant terms retained in the minimal models

<sup>c</sup>*Qphyl* s.e.s. = standardized effect sizes of woody plant phylogenetic diversity (*Qphyl*)

<sup>d</sup>Contrasts between sampling time 1 (fall) and the successive sampling times 2 and 3 (spring and summer); the intercept is the overall mean

<sup>e</sup>Akaike information criterion (corrected for small sample sizes) of the full model (containing all predictors) and the minimal adequate model (simplified model with lowest AICc)



the correlation of these variables with observed phylogenetic diversity; Tables S5 and S6, Fig. S5.1).

Plot-level primary productivity did not underlie the effects of plant phylogenetic diversity on arthropods. Plant productivity was not retained in any of the minimal models when the analyses showing significant effects of  $Q_{\text{phyl}}$  s.e.s. were re-run with measures of woody plant diversity replaced by plant productivity (Tables S3 and S4).

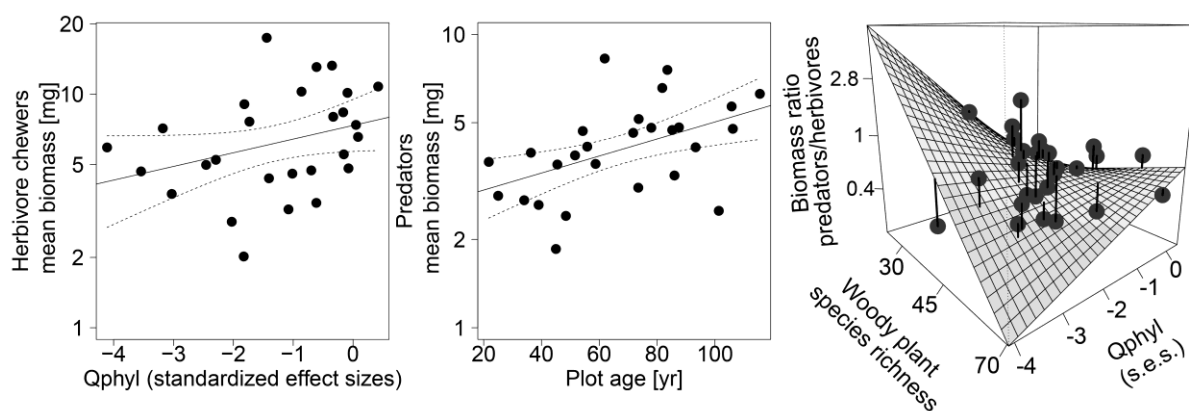
## Discussion

Our study highlights how effects of plant diversity that go beyond simple effects of increasing species numbers contribute to controlling consumer biomass across trophic levels in a highly diverse forest. Leaf chewer biomass and the biomass dispersion of herbivores strongly increased across forest stands with increasing plant phylogenetic diversity. In contrast, effects of woody plant species richness were less frequent and less pronounced, interacting with plant phylogenetic diversity to affect arthropods in some cases. Overall, our results indicate a strong bottom-up control of functionally important herbivores mediated by woody plant phylogenetic diversity, and they show no sign of the increase in top-down effects of predator biomass or abundance generally expected to occur with increasing plant diversity (Root 1973; Haddad et al. 2009). Our

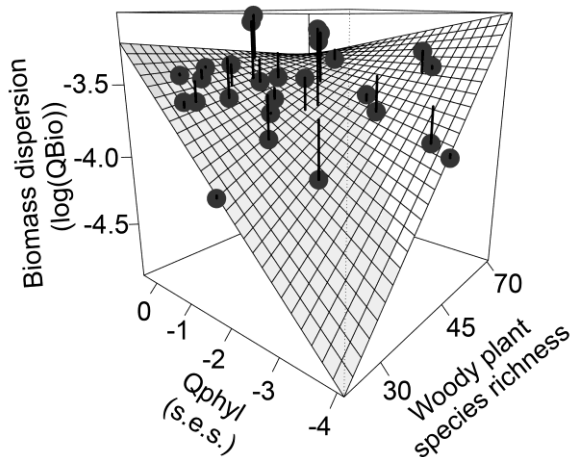
findings have important implications for the regulation of ecosystem functions via trophic interaction pathways in these species-rich forests.

## Plant species richness vs. phylogenetic diversity effects

While the comparatively weak direct influence of plant species richness on arthropod biomass and abundance in part contrasts with the findings from some other systems (mostly experimental grasslands; e.g. Haddad et al. 2009; Scherber et al. 2010), many other studies have likewise found no, or only weak and inconsistent, plant species richness effects (e.g. Koricheva et al. 2000; Perner et al. 2005; Vehviläinen et al. 2007; Vehviläinen et al. 2008). Interestingly, plant species richness effects are often considered to be mediated, and outperformed, by the influence of plant species composition (Perner et al. 2005; Zhang and Adams 2011; Rzanny et al. 2013). Metrics of plant diversity that account for the relatedness among species may thus help to reconcile contrasting findings by more effectively revealing the complexity of plant diversity effects beyond the mere impact of plant species richness (see Dinnage et al. 2012). This is demonstrated in our study, and for the first time for such species-rich forests, by the strong effects of woody plant phylogenetic diversity compared to overall weaker plant



**Figure 5.1.** Relationships between woody plant phylogenetic diversity ( $Q_{\text{phyl}}$  s.e.s.), woody plant species richness, plot age and the biomass of a) leaf chewers, b) predators, and c) the ratio of predators to herbivores across 27 forest plots in subtropical China. All relationships are significant at  $P < 0.05$  (see Table 5.1 for details).



**Figure 5.2.** Relationships between the dispersion of biomass per plot among individuals of leaf-chewing herbivores and woody plant phylogenetic diversity ( $Q_{\text{phyt}}$  s.e.s.) and woody plant species richness. All relationships are significant at  $P < 0.05$  (Table 5.1).

species richness effects. Many herbivores show phylogenetically structured host use (e.g. Weiblen et al. 2006), and phylodiversity-dependent patterns in herbivore assemblages might cascade to affect particularly specialized predators, whereas the response of generalist predators might be less pronounced. Thus, it is not surprising that the effect of woody plant phylogenetic diversity was particularly evident for herbivores and less so for predators, which in our case were largely generalist spiders. However, interactive effects of plant species richness and phylogenetic diversity on the predator to herbivore biomass ratio and on the biomass dispersion of leaf chewers indicate that species richness can contain information that is not fully captured by phylogenetic diversity, as can be the case when functionally important traits are not phylogenetically conserved (Srivastava et al. 2012; Schuldt et al. 2014b).

### Leaf-chewing vs. sap-sucking herbivores

Leaf-chewing herbivores are responsible for the majority of visible leaf damage in the studied forest (Schuldt et al. 2010; Schuldt et al. 2012), and they also represented the largest proportion of the arthropod biomass in our samples (ca. 57% of the total and 85% of the herbivore biomass). The increase in leaf chewer biomass and abundance with higher woody plant phylogenetic diversity corresponds well to the increase in herbivore damage with increasing woody plant diversity

found previously on the same study plots (Schuldt et al. 2014a). These patterns strongly suggest that the functional impact of herbivores increases with woody plant diversity. This contrasts with the general expectations of the resource-concentration hypothesis (Root 1973; Haddad et al. 2009) and also with commonly held assumptions that herbivores become increasingly specialized toward lower latitudes (Coley and Barone 1996; Dyer et al. 2007). However, our previous studies provided strong indications that the dominant herbivores in this system are generalists that may benefit from higher resource diversity in the more plant-diverse forest stands (Schuldt et al. 2014a). This mechanism, formulated by the ‘dietary-mixing’ hypothesis (Bernays et al. 1994; Dinnage 2013), and the probable dominance of generalist herbivores (which has also been suggested for other species-rich forests; e.g. Novotny et al. 2012), may explain the observed positive relationship between leaf chewer biomass and woody plant phylogenetic diversity. In particular, if the defense or palatability traits most relevant for herbivores show phylogenetic clustering, phylogenetically more diverse plant communities provide generalist herbivores with alternative hosts that help overcome dietary limitations on herbivore performance (Cavender-Bares et al. 2009; see Parker et al. 2012 for a real-world example). Leaf traits potentially important to herbivores that were found (among a set of 21 species) to show a phylogenetic signal at our study sites were e.g. dry matter content, toughness, polyphenols, tannins, and carbon and nitrogen contents (Schuldt et al. 2012; Eichenberg et al. 2014). Interactions among such traits and responses of individual herbivore species from the multidiverse set of herbivores potentially attacking a given plant species may make the functional response of plants highly complex, and our phylogenetic diversity metric might capture the overall response of herbivore assemblages by integrating over the evolutionary adaptations of these herbivores. Without doubt, however, plant functional traits need to be explicitly addressed to identify the mechanisms underlying the observed diversity effects, and traits might also provide additional

information on variation in the arthropod data not explained in our current models (see also Schuldt et al. 2014a). For instance, the fact that in some cases we observed effects of woody plant species richness beyond those of plant phylogenetic diversity might be a signal of functional trait information that is not phylogenetically conserved. The multitude of chemical, morphological and physiological traits that might potentially play a role in affecting arthropods, and the complexity of potential relationships among traits, however, require an extensive trait dataset for further testing that is often not available for many study regions. Yet, we hope that the results of our study will help to motivate efforts to unveil the complexity behind trophic interactions that might be key for ecosystem functioning in many species-rich systems.

The assumption that resource-diversity effects and not an increase in plant productivity were underlying reasons for the effects of plant phylogenetic diversity is supported by two additional findings of our study. First of all, even though primary productivity was previously found to increase with woody plant diversity (Baruffol et al. 2013), in our study it was not significantly related to any of the arthropod biomass and abundance patterns that showed a relationship with woody plant phylogenetic diversity. While the impact of plant diversity on arthropods operating through an increase in plant biomass may be common (e.g. Borer et al. 2012), the strength of these effects can vary and they may be overruled by resource diversity effects (Perner et al. 2005; Haddad et al. 2009; Dinnage et al. 2012). Secondly, the biomass distribution of leaf chewers within plots ( $Q_{\text{Bio}}$ ) became more diverse with increasing plant phylogenetic diversity and woody plant species richness, which might be indicative of increased niche separation among herbivores due to a more heterogeneous resource distribution (Mason et al. 2005). This higher biomass diversity, in turn, may contribute to strengthening the previously observed top-down effects of herbivores on the producer level with increasing plant diversity in the studied forest stands (see also Rudolf 2012).

The increase in herbivore biomass and

abundance which we found differs from recent studies in grasslands that reported no significant effects of plant phylogenetic diversity on herbivore abundance patterns (in contrast to stronger effects on herbivore species richness; Dinnage et al. 2012; Pellissier et al. 2013). However, these studies indicated either a strong top-down control of herbivore abundances by predators (Dinnage et al. 2012) or focused on specialized herbivore taxa (Pellissier et al. 2013). As our results show, predator top-down control seems to be, at best, weak for the arthropod assemblages of woody plant saplings at our study site, and the probable dominance of generalist herbivores may explain deviations from patterns for more specialized taxa.

Such deviations between herbivore taxa also became evident to some extent in our study, as we found no significant effect of plant phylogenetic diversity on the biomass of sap-sucking herbivores. Indeed, we did not find sap sucker biomass to be related to any of the plot characteristics. And while the biomass dispersion of sap suckers increased with plant phylogenetic diversity in summer (Time 3), this relationship was not evident in spring and fall, again suggesting an overall much weaker effect of plant diversity on sap suckers as compared to leaf chewers. Differences in feeding mode and in the degree of host specialization could have caused these feeding guild-specific results, but the ultimate drivers are difficult to elucidate with our study. Nevertheless, several studies that included sap suckers in their analyses likewise found no or only weak direct effects of plant diversity measures on these herbivores (e.g. Koricheva et al. 2000; Unsicker et al. 2006; Vehviläinen et al. 2007). As sap suckers pierce plants to consume assimilates from phloem, xylem, or individual cells, they trigger different signaling pathways in plants and are able to avoid many of the morphological and chemical defense mechanisms that deter leaf chewers (Howe and Jander 2008; Zvereva et al. 2010) and that may be related to the phylogenetic structure and diversity of plant communities (Baraloto et al. 2012). This may weaken potential relationships with plant phylogenetic diversity for sap-sucking herbivores and explain the patterns we found in our study, especially if a

dominance of leaf chewers shifts plant responses to a stronger defense against these dominant herbivores (see also Carmona and Fornoni 2013).

Analyses at the level of individual arthropod species might potentially provide further insight, but are beyond the scope of our study. Moreover, as most herbivores show at least some degree of lineage-specificity in their host use (Weiblen et al. 2006), and considering that we sampled a wide range of woody plant species in each of our plots and analyzed mean values for arthropods averaged across all woody plant individuals sampled per plot, it is unlikely that our results are driven by the response of only a few specific arthropod species from specific woody plant species. Rather, the overall changes in biomass point to more general effects across larger parts of the herbivore assemblages. This is supported by our finding that the biomass distribution ( $Q_{\text{Bio}}$ ) of leaf chewers increased with woody plant phylogenetic diversity, indicating that a wider range of species of different body size were promoted.

### Predators and the predator-herbivore ratio

In contrast to herbivores feeding directly on plants, organisms at higher trophic levels are less strongly related to the plant community. The impact of plant diversity may thus be expected to become weaker higher up in food webs (Scherber et al. 2010). However, several recent studies have shown that predator abundance can strongly increase with plant diversity and particularly also with plant phylogenetic diversity (e.g. Haddad et al. 2009; Dinnage et al. 2012). This may occur either through positive bottom-up effects of the quantity of available prey resources or via increased structural and non-trophic components of more diverse plant communities (Root 1973; Haddad et al. 2009). While our study indicates that predator abundance (but not biomass) was positively related to herbivore abundance, the strong effects of plant phylogenetic diversity on the latter did not translate to the predator level. The lack of plant phylogenetic diversity effects might be due to the fact that generalist predators (predominantly spiders), which may be less responsive to effects of plant

phylogeny on herbivore assemblage structure than specialized predators, made up the largest proportion of both total predator biomass and abundance. Moreover, considering that the diet of generalist predators is made up of various herbivore guilds, the lack of a plant phylogenetic diversity effect on sap suckers may have contributed to suppressing an overall plant diversity effect on predators.

Overall, these patterns indicate that predators exert weak top-down control on herbivore biomass and abundance in the undergrowth of the studied forest stands, and that bottom-up effects of the producer level prevail. This is also supported by the decreasing ratios of predator to herbivore biomass and abundance with increasing plant phylogenetic diversity and woody plant species richness. With regard to plant diversity-dependent regulation mechanisms of ecosystem functions, this suggests that the often hypothesized strong mediating role of higher trophic levels for such species-rich forests (Schemske et al. 2009; Terborgh 2012) in our case particularly applies to dominant herbivores and less so to predators or less abundant herbivores. As our study focused on tree and shrub recruits rather than on the established canopy tree community, these patterns may have strong effects on the long-term structuring of the woody plant communities. Our previous studies showed that saplings of abundant tree and shrub species experienced greater damage than less common species and that this damage increased with woody plant diversity (Schuldt et al. 2010; Schuldt et al. 2012). The higher biomass and abundance of herbivores in the more diverse forest stands may thus actually contribute to maintaining this high plant diversity, by decreasing the performance of common tree and shrub species, and thus promoting coexistence with less common species (see also Dyer et al. 2010).

### Conclusions

The strong effects of woody plant phylogenetic diversity, and the much less pronounced direct effects of plant species richness, on herbivore biomass and abundance show that the diversity-dependence of ecosystem processes and

interaction pathways across trophic levels can fundamentally depend on nonrandom associations among species. Scenarios of random species loss may thus underestimate the consequences for ecosystem functions if they do not reflect the driving forces of community assembly (see also Dinnage et al. 2012). Our study particularly highlights the impact of strong bottom-up effects of plant phylogenetic diversity, whereas top-down effects of predators, at least for the undergrowth of tree and shrub recruits studied here, are less responsive to plant diversity and in this context exert weak effects on herbivores. However, this means that herbivores may, in turn, strongly impact particular plant species, which may potentially lead to a positive feedback loop of bottom-up controlled herbivores on plant diversity maintenance. Moreover, considering that biomass is directly related to metabolic rates and the performance of individuals (Saint-Germain et al. 2007; Reiss et al. 2011), the more pronounced effects of plant diversity on arthropod biomass than on abundance found in our study suggest that abundance patterns alone (although more frequently analyzed than biomass patterns in ecological studies; Reiss et al. 2011) may be less effective in capturing the diversity-dependent impact of arthropods in such species-rich ecosystems.

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### References

- Baraloto C et al. (2012) Using functional traits and phylogenetic trees to examine the assembly of tropical tree communities. *J Ecol* 100:690-701
- Baruffol M et al. (2013) Biodiversity promotes tree growth during succession in subtropical forest. *PLoS ONE* 8:e81246
- Bernays EA, Bright KL, Gonzalez N, Angel J (1994) Dietary mixing in a generalist herbivore: tests of two hypotheses. *Ecology* 75:1997-2006
- Borer ET, Seabloom EW, Tilman D (2012) Plant diversity controls arthropod biomass and temporal stability. *Ecol Lett* 15:1457-1464
- Botta-Dukát Z (2005) Rao's quadratic entropy as a measure of functional diversity based on multiple traits. *J Veg Sci* 16:533-540
- Bruelheide H et al. (2011) Community assembly during secondary forest succession in a Chinese subtropical forest. *Ecol Monogr* 81:25-41
- Burnham KP, Anderson DR (2004) Model selection and multimodel inference : a practical information-theoretic approach. Springer, New York
- Campos RI, Vasconcelos HL, Ribeiro SP, Neves FS, Soares JP (2006) Relationship between tree size and insect assemblages associated with *Anadenanthera macrocarpa*. *Ecography* 29:442-450
- Cardinale BJ et al. (2012) Biodiversity loss and its impact on humanity. *Nature* 486:59-67
- Cardinale BJ et al. (2011) The functional role of producer diversity in ecosystems. *Am J Bot* 98:572-592
- Carmona D, Fornoni J (2013) Herbivores can select for mixed defensive strategies in plants. *New Phytol* 197:576-585
- Castagneyrol B, Jactel H (2012) Unraveling plant-animal diversity relationships: a meta-regression analysis. *Ecology* 93:2115-2124
- Cavender-Bares J, Kozak KH, Fine PVA, Kembel SW (2009) The merging of community ecology and phylogenetic biology. *Ecol Lett* 12:693-715
- Coley PD, Barone JA (1996) Herbivory and plant defenses in tropical forests. *Annu Rev Ecol Syst* 27:305-335
- Dinnage R (2013) Phylogenetic diversity of plants alters the effect of species richness on invertebrate herbivory. *PeerJ* 1:e93
- Dinnage R, Cadotte MW, Haddad NM, Crutsinger GM, Tilman D (2012) Diversity of plant evolutionary lineages promotes arthropod diversity. *Ecol Lett* 15:1308-1317
- Dyer LA, Letourneau DK, Chavarria GV, Amoretti DS (2010) Herbivores on a dominant understory shrub increase local plant diversity

- in rain forest communities. *Ecology* 91:3707-3718
- Dyer LA et al. (2007) Host specificity of Lepidoptera in tropical and temperate forests. *Nature* 448:696-U699
- Eichenberg D, Ristok C, Kröber W, Bruelheide H (2014) Plant polyphenols - implications of different sampling, storage and sample processing in biodiversity-ecosystem functioning experiments. *Chem Ecol*. DOI: 10.1080/02757540.2014.894987
- Futuyma DJ, Agrawal AA (2009) Macroevolution and the biological diversity of plants and herbivores. *Proc Natl Acad Sci USA* 106:18054-18061
- Geißler C, Kühn P, Böhnke M, Bruelheide H, Shi X, Scholten T (2012) Splash erosion potential under tree canopies in subtropical SE China. *Catena* 91:85-93
- Gotelli NJ, Rohde K (2002) Co-occurrence of ectoparasites of marine fishes: a null model analysis. *Ecol Lett* 5:86-94
- Haddad NM, Crutsinger GM, Gross K, Haarstad J, Knops JMH, Tilman D (2009) Plant species loss decreases arthropod diversity and shifts trophic structure. *Ecol Lett* 12:1029-1039
- Hardy OJ (2008) Testing the spatial phylogenetic structure of local communities: statistical performances of different null models and test statistics on a locally neutral community. *J Ecol* 96:914-926
- Hóðar JA (1996) The use of regression equations for estimation of arthropod biomass in ecological studies. *Acta Oecol* 17:421-433
- Hooper DU et al. (2012) A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature* 486:105-108
- Howe GA, Jander G (2008) Plant immunity to insect herbivores. *Annu Rev Plant Biol* 59:41-66
- Hu Z, Yu M (2008) Study on successions sequence of evergreen broad-leaved forest in Gutian Mountain of Zhejiang, Eastern China: species diversity. *Front Biol China* 3:45-49
- Kembel SW et al. (2010) Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* 26:1463-1464
- Koricheva J, Mulder CPH, Schmid B, Joshi J, Huss-Danell K (2000) Numerical responses of different trophic groups of invertebrates to manipulations of plant diversity in grasslands. *Oecologia* 125:271-282
- Legendre P et al. (2009) Partitioning beta diversity in a subtropical broad-leaved forest of China. *Ecology* 90:663-674
- Mason NWH, Mouillot D, Lee WG, Wilson JB (2005) Functional richness, functional evenness and functional divergence: the primary components of functional diversity. *Oikos* 111:112-118
- Nadrowski K, Wirth C, Scherer-Lorenzen M (2010) Is forest diversity driving ecosystem functioning and service? *Curr Opin Envir Sus* 2:75-79
- Naeem S, Duffy JE, Zavaleta E (2012) The functions of biological diversity in an age of extinction. *Science* 336:1401-1406
- Novotny V et al. (2010) Guild-specific patterns of species richness and host specialization in plant-herbivore food webs from a tropical forest. *J Anim Ecol* 79:1193-1203
- Novotny V et al. (2012) Insects on plants: explaining the paradox of low diversity within specialist herbivore guilds. *Am Nat* 179:351-362
- Ødegaard F, Diserud OH, Østbye K (2005) The importance of plant relatedness for host utilization among phytophagous insects. *Ecol Lett* 8:612-617
- Paine CET et al. (2012) Phylogenetic density dependence and environmental filtering predict seedling mortality in a tropical forest. *Ecol Lett* 15:34-41
- Parker JD, Burkepille DE, Lajeunesse MJ, Lind EM (2012) Phylogenetic isolation increases plant success despite increasing susceptibility to generalist herbivores. *Divers Distrib* 18:1-9
- Pellissier L et al. (2013) Turnover of plant lineages shapes herbivore phylogenetic beta diversity along ecological gradients. *Ecol Lett* 16:600-608
- Perner J et al. (2005) Effects of plant diversity, plant productivity and habitat parameters on arthropod abundance in montane European grasslands. *Ecography* 28:429-442
- Pinheiro J, Bates D, Debroy S, Sarkar D, R Core Team (2014) nlme: linear and nonlinear mixed effects models. R package version 3.1-117, available at <http://CRAN.R-project.org/package=nlme>. Last accessed 26 May 2014.
- Plath M, Dorn S, Riedel J, Barrios H, Mody K (2012) Associational resistance and associational susceptibility: specialist herbivores show contrasting responses to tree stand diversification. *Oecologia* 169:477-487
- Purschke O, Michalski SG, Bruelheide H, Durka W (2014) Spatial and temporal phylogenetic turnover during subtropical forest succession across ecological and phylogenetic scales. *J Ecol*:in review
- Reiss J, Bailey RA, Perkins DM, Pluchinotta A, Woodward G (2011) Testing effects of consumer richness, evenness and body size on

- ecosystem functioning. *J Anim Ecol* 80:1145-1154
- Root RB (1973) Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). *Ecol Monogr* 43:95-124
- Rudolf VHW (2012) Seasonal shifts in predator body size diversity and trophic interactions in size-structured predator-prey systems. *J Anim Ecol* 81:524-532
- Rzanny M, Kuu A, Voigt W (2013) Bottom-up and top-down forces structuring consumer communities in an experimental grassland. *Oikos* 122:967-976
- Saint-Germain M et al. (2007) Should biomass be considered more frequently as a currency in terrestrial arthropod community analyses? *J Appl Ecol* 44:330-339
- Schemske DW, Mittelbach GG, Cornell HV, Sobel JM, Roy K (2009) Is there a latitudinal gradient in the importance of biotic interactions? *Annu Rev Ecol Evol Syst* 40:245-269
- Scherber C et al. (2010) Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. *Nature* 468:553-556
- Schleuter D, Daufresne M, Massol F, Argillier C (2010) A user's guide to functional diversity indices. *Ecol Monogr* 80:469-484
- Schuldt A et al. (2014a) Functional and phylogenetic diversity of woody plants drive herbivory in a highly diverse forest. *New Phytol* 202:864-873
- Schuldt A et al. (2010) Tree diversity promotes insect herbivory in subtropical forests of south-east China. *J Ecol* 98:917-926
- Schuldt A et al. (2012) Plant traits affecting herbivory on tree recruits in highly diverse subtropical forests. *Ecol Lett* 15:732-739
- Schuldt A, Bruelheide H, Durka W, Michalski SG, Purschke O, Assmann T (2014b) Tree diversity promotes functional dissimilarity and maintains functional richness despite species loss in predator assemblages. *Oecologia* 174:533-543
- Sobek S, Scherber C, Steffan-Dewenter I, Tschamtker T (2009a) Sapling herbivory, invertebrate herbivores and predators across a natural tree diversity gradient in Germany's largest connected deciduous forest. *Oecologia* 160:279-288
- Sobek S, Steffan-Dewenter I, Scherber C, Tschamtker T (2009b) Spatiotemporal changes of beetle communities across a tree diversity gradient. *Divers Distrib* 15:660-670
- Srivastava DS, Cadotte MW, MacDonald AAM, Marushia RG, Mirotnick N (2012) Phylogenetic diversity and the functioning of ecosystems. *Ecol Lett* 15:637-648
- Srivastava DS, Lawton JH (1998) Why more productive sites have more species: An experimental test of theory using tree-hole communities. *Am Nat* 152:510-529
- Srivastava DS, Vellend M (2005) Biodiversity-ecosystem function research: Is it relevant to conservation? *Annu Rev Ecol Evol Syst* 36:267-294
- Strutzenberger P, Brehm G, Fiedler K (2011) DNA barcoding-based species delimitation increases species count of Eois (Geometridae) moths in a well-studied tropical mountain forest by up to 50%. *Insect Sci* 18:349-362
- Tamura K, Peterson D, Peterson N, Stecher G, Nei M, Kumar S (2011) MEGA5: Molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. *Mol Biol Evol* 28:2731-2739
- Terborgh J (2012) Enemies maintain hyperdiverse tropical forests. *Am Nat* 179:303-314
- Thebault E, Huber V, Loreau M (2007) Cascading extinctions and ecosystem functioning: contrasting effects of diversity depending on food web structure. *Oikos* 116:163-173
- Unsicker SB, Baer N, Kahmen A, Wagner M, Buchmann N, Weisser WW (2006) Invertebrate herbivory along a gradient of plant species diversity in extensively managed grasslands. *Oecologia* 150:233-246
- Vehviläinen H, Koricheva J, Ruohomäki K (2007) Tree species diversity influences herbivore abundance and damage: meta-analysis of long-term forest experiments. *Oecologia* 152:287-298
- Vehviläinen H, Koricheva J, Ruohomäki K (2008) Effects of stand tree species composition and diversity on abundance of predatory arthropods. *Oikos* 117:935-943
- Wardhaugh CW (2013) Estimation of biomass from body length and width for tropical rainforest canopy invertebrates. *Aust J Entomol* 52:291-298
- Wardhaugh CW, Stork NE, Edwards W (2012) Feeding guild structure of beetles on Australian tropical rainforest trees reflects microhabitat resource availability. *J Anim Ecol* 81:1086-1094
- Weiblen GD, Webb CO, Novotny V, Basset Y, Miller SE (2006) Phylogenetic dispersion of host use in a tropical insect herbivore community. *Ecology* 87:S62-S75
- Whitfield TJS, Novotny V, Miller SE, Hrcek J, Klimes P, Weiblen GD (2012) Predicting tropical insect herbivore abundance from host plant traits and phylogeny. *Ecology* 93:S211-S222

- Zhang Y, Adams J (2011) Top-down control of herbivores varies with ecosystem types. *J Ecol* 99:370-372
- Zvereva E, Lanta V, Kozlov M (2010) Effects of sap-feeding insect herbivores on growth and reproduction of woody plants: a meta-analysis of experimental studies. *Oecologia* 163:949-961

### **Electronic supplementary material**

The online version of this article (doi:10.1007/s00442-014-3006-7) contains supplementary material, which is available to authorized users.



## Supplementary Material

### Methods sampling design

A funnel-shaped beating sheet (70 cm diameter) was placed at the base of the sampled tree and arthropods were dislodged and knocked down from the tree onto the sheet by sharply hitting the tree seven times with a beating stick. In each study plot, 25 tree and shrub saplings were sampled along a transect running diagonally through the plot. Every two meters, the sapling growing closest to the transect line was selected, resulting in a random selection of tree and shrub species in each plot.

To assess the degree to which the 25 randomly selected tree and shrub saplings reflect the differences in the community composition among plots of the overall woody plant communities, we compared the sapling and overall plant communities with Procrustes analysis. For this analysis, we calculated community dissimilarities among plots for sampled saplings and overall woody plant data with nonmetric multidimensional scaling (NMDS) analysis. Abundance data in both species sets were square root transformed and the Morisita-Horn index was used as a dissimilarity metric. NMDS were based on two-dimensional analyses ( $k = 2$ ), with stress values  $< 0.2$  indicating appropriate fit. Procrustes analysis of the sapling and overall plant NMDS objects (symmetric Procrustes rotation) was conducted with the *protest* function in the *vegan* package in R (Oksanen et al. 2013), with P values estimated based on 999 permutations.

As with most sampling methods, a few of the arthropod individuals sampled with the beating method might belong to vagrant species not necessarily directly associated with

the plant individual they were collected from. However, as we focused on plot-level data (arthropod data were averaged across all individuals per plot, see ‘Statistical analysis’) rather than individual plants or plant species, and many of the abundant taxa such as lepidopteran caterpillars are not highly mobile, the potential occurrence of such vagrants can be assumed to have little effect on our analyses. Moreover, although interspecific differences in the precision of these equations necessarily include a certain extent of estimation error, the equations represent average estimates derived from a wide range of different species in a given taxon and have been shown to adequately capture taxon-specific biomass patterns of arthropod assemblages that are comparable in complexity to those of our study (Lampert and Tlustý 2013; Wardhaugh 2013).

Lampert A, Tlustý T (2013) Resonance-induced multimodal body-size distributions in ecosystems. *Proceedings of the National Academy of Sciences USA* 110:205-209

Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Henry M, Stevens H, Wagner H (2013). *vegan: Community Ecology Package*. R package version 2.0-10. <http://CRAN.R-project.org/package=vegan>. Last accessed 31 May 2014

Wardhaugh CW (2013) Estimation of biomass from body length and width for tropical rainforest canopy invertebrates. *Australian Journal of Entomology* 52:291-29

**Table S5.1.** Overview of the higher taxa sampled, their functional group identity, and total number of individuals and overall biomass per taxon for beating samples from 27 forest plots in subtropical China

Taxon	Functional group	Individuals	Total biomass [mg]
Araneae	Predator	3732	6191
Opiliones	Predator	205	1379
Coleoptera - Cantharidae	Predator	20	684
Coleoptera - Carabidae	Predator	10	215
Coleoptera - Chrysomeloidea	Leaf-chewing herbivore	131	783
Coleoptera - Coccinellidae	Predator	20	38
Coleoptera - Curculionidea	Leaf-chewing herbivore	111	723
Coleoptera - Scarabaeidae	Leaf-chewing herbivore	29	739
Coleoptera - Staphylinidae	Predator	9	12
Dermoptera	Predator	26	174
Hemiptera - Aphidina	Sap-sucking herbivore	94	13
Hemiptera - Auchenorrhyncha	Sap-sucking herbivore	693	2512
Hemiptera - Heteroptera	Sap-sucking herbivore	100	508
Hemiptera - Heteroptera - Reduviidae	Predator	12	273
Hemiptera - Sternorrhyncha - Other	Sap-sucking herbivore	25	16
Hymenoptera - Formicidae	Predator	686	399
Lepidoptera - larvae	Leaf-chewing herbivore	522	6226
Mantodea	Predator	8	5
Neuroptera	Predator	9	17
Orthoptera	Leaf-chewing herbivore	408	7065
Phasmatodea	Leaf-chewing herbivore	81	1194
Thysanoptera	Sap-sucking herbivore	19	1
<b>Total</b>		<b>6950</b>	<b>29167</b>

**Table S5.2.** Mixed-effects models for the **abundance** of leaf chewing herbivores, sap-sucking herbivores, predators, and the abundance ratio of predators to herbivores across 27 forest stands in subtropical China. Parameter estimates (with standard errors, degrees of freedom, t and *P* values) are shown for the variables retained in the minimal models

<i>Fixed effects</i> <sup>a,b</sup>	Herbivores: Leaf chewers					Herbivores: Suckers					Predators					Predator : Herbivore ratio				
	Est.	<i>SE</i>	<i>DF</i>	t	<i>P</i>	Est.	<i>SE</i>	<i>DF</i>	t	<i>P</i>	Est.	<i>SE</i>	<i>DF</i>	t	<i>P</i>	Est.	<i>SE</i>	<i>DF</i>	t	<i>P</i>
Intercept	-0.52	0.04	54	-13.5	<0.001	-0.94	0.13	52	-7.0	<0.001	1.05	0.06	52	17.8	<0.001	1.05	0.07	52	15.0	<0.001
Time 2-1 <sup>c</sup>	-	-	-	-	-	0.39	0.16	52	2.5	0.018	-0.21	0.07	52	-3.0	0.004	-0.43	0.09	52	-4.8	<0.001
Time 3-1 <sup>c</sup>	-	-	-	-	-	-0.87	0.16	52	-5.4	<0.001	-0.67	0.07	52	-9.4	<0.001	-0.51	0.09	52	-5.7	<0.001
Elevation	-	-	-	-	-	-	-	-	-	-	0.13	0.04	24	3.1	0.005	0.19	0.05	24	3.8	0.001
Plot age	-	-	-	-	-	-	-	-	-	-	0.11	0.04	24	2.6	0.015	0.12	0.05	24	2.5	0.019
<i>Q<sub>phyt</sub></i> s.e.s.	0.10	0.04	25	2.5	0.018	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
AICc full model <sup>d</sup>	83.4					201.8					73.9					97.5				
AICc min. model <sup>d</sup>	63.6					172.7					43.4					74.7				

<sup>a</sup>Sapling height, tree species richness and the interactions richness : *Q<sub>phyt</sub>* s.e.s. (standardized effect size of *Q<sub>phyt</sub>*), richness : plot age, time : *Q<sub>phyt</sub>* s.e.s., and time : richness were included in the full models but not retained in any of the minimal models

<sup>b</sup>Italics denote data for non-significant terms retained in the minimal models

<sup>c</sup>Contrasts between sampling time 1 (fall) and the successive sampling times 2 and 3 (spring and summer); the intercept is the overall mean

<sup>d</sup>Akaike information criterion (corrected for small sample sizes) of the full model (containing all predictors) and the minimal adequate model (simplified model with lowest AICc)

**Table S5.3.** Mixed-effects models for the biomass and abundance of leaf chewing herbivores and the biomass ratio of predators to herbivores across 27 forest stands in subtropical China. Parameter estimates (with standard errors, degrees of freedom, t and *P* values) are shown for the variables retained in the minimal models. Woody plant species richness and phylogenetic diversity ( $Q_{\text{phyl}}$  s.e.s.) in the initial, full models were **replaced by a plot-level primary productivity measure** to test whether observed plant diversity effects can be explained by plant productivity

<i>Fixed effects</i> <sup>a,b</sup>	Leaf chewers: Biomass					Leaf chewers: Abundance					Predator : Herbivore biomass ratio				
	Est.	<i>SE</i>	<i>DF</i>	t	<i>P</i>	Est.	<i>SE</i>	<i>DF</i>	t	<i>P</i>	Est.	<i>SE</i>	<i>DF</i>	t	<i>P</i>
Intercept	1.41	0.15	48	9.7	<0.001	-0.53	0.04	50	-13.7	<0.001	-0.40	0.17	48	-2.4	0.020
Time 2-1 <sup>c</sup>	0.77	0.19	48	4.0	<0.001	-	-	-	-	-	-0.52	0.23	48	-2.2	0.031
Time 3-1 <sup>c</sup>	0.36	0.19	48	1.9	0.064	-	-	-	-	-	-0.08	0.23	48	-0.3	0.736
Elevation	-	-	-	-	-	-0.09	0.04	23	-2.2	0.034	-	-	-	-	-
Plot age	0.21	0.10	23	2.2	0.038	-	-	-	-	-	-	-	-	-	-
AICc full model <sup>d</sup>	188.8					68.8					207.4				
AICc min. model <sup>d</sup>	173.3					55.5					192.7				

<sup>a</sup>Sapling height, primary productivity and the interactions productivity : plot age, time : plot age, and time : productivity were included in the full models but not retained in any of the minimal models

<sup>b-d</sup> see Table S5.2

**Table S5.4.** Mixed-effects models for the functional dispersion ( $Q_{\text{Bio}}$ ) of the biomass of leaf chewer, sap-sucker and predator individuals per plot across 27 forest stands in subtropical China. Parameter estimates (with standard errors, degrees of freedom, t and  $P$  values) are shown for the variables retained in the minimal models. Woody plant species richness and phylogenetic diversity ( $Q_{\text{phyl}}$ ) in the initial, full models were **replaced by a plot-level primary productivity measure** to test whether observed plant diversity effects can be explained by plant productivity

<i>Fixed effects<sup>a,b</sup></i>	Herbivores: Leaf chewers					Herbivores: Sap suckers					Predators				
	Est.	<i>SE</i>	<i>DF</i>	t	<i>P</i>	Est.	<i>SE</i>	<i>DF</i>	t	<i>P</i>	Est.	<i>SE</i>	<i>DF</i>	t	<i>P</i>
Intercept	-	-	-	-	-	-4.24	0.23	48	-18.5	<0.001	-3.72	0.06	48	-63.1	<0.001
Time 2-1 <sup>c</sup>	-	-	-	-	-	0.78	0.32	48	2.4	0.020	-0.18	0.08	48	-2.2	0.035
Time 3-1 <sup>c</sup>	-	-	-	-	-	0.40	0.32	48	1.2	0.218	0.20	0.08	48	2.4	0.021
AICc full model	114.7					257.0					52.5				
AICc min. model	91.9					240.8					37.5				

<sup>a-d</sup> see Table S5.3

**Table S5.5.** Mixed-effects models for the biomass of leaf-chewing herbivores, sap-sucking herbivores, predators, and the biomass ratio of predators to herbivores across 27 forest stands in subtropical China, **based on observed  $Q_{phyt}$  instead of standardized effect sizes of  $Q_{phyt}$ .** Parameter estimates (with standard errors, degrees of freedom, t and *P* values) are shown for the variables retained in the minimal models

<i>Fixed effects</i> <sup>a,b</sup>	Herbivores: leaf chewers					Herbivores: suckers					Predators					Predator—herbivore ratio				
	Est.	<i>SE</i>	<i>DF</i>	t	<i>P</i>	Est.	<i>SE</i>	<i>DF</i>	t	<i>P</i>	Est.	<i>SE</i>	<i>DF</i>	t	<i>P</i>	Est.	<i>SE</i>	<i>DF</i>	t	<i>P</i>
Intercept <sup>c</sup>	1.30	0.14	50	9.4	<0.001	-0.64	0.23	52	-2.8	0.007	1.40	0.06	54	23.0	<0.001	-0.27	0.16	52	-1.7	0.102
Time 2-1 <sup>c</sup>	0.61	0.18	50	3.3	0.002	1.40	0.32	52	4.3	<0.001	-	-	-	-	-	-0.47	0.21	52	-2.2	0.033
Time 3-1 <sup>c</sup>	<i>0.26</i>	<i>0.18</i>	<i>50</i>	<i>1.4</i>	<i>0.160</i>	<i>-0.51</i>	<i>0.32</i>	<i>52</i>	<i>-1.6</i>	<i>0.122</i>	-	-	-	-	-	<i>-0.05</i>	<i>0.21</i>	<i>52</i>	<i>-0.2</i>	<i>0.822</i>
Plot age	<i>0.17</i>	<i>0.09</i>	<i>23</i>	<i>1.8</i>	<i>0.079</i>	-	-	-	-	-	0.17	0.06	25	2.8	0.009	<i>0.05</i>	<i>0.11</i>	<i>23</i>	<i>0.4</i>	<i>0.661</i>
<i>Q<sub>phyt</sub></i>	<i>-0.09</i>	<i>0.14</i>	<i>23</i>	<i>-0.7</i>	<i>0.522</i>	-	-	-	-	-	-	-	-	-	-	<i>-0.22</i>	<i>0.11</i>	<i>23</i>	<i>-2.0</i>	<i>0.061</i>
Plot age : <i>Q<sub>phyt</sub></i>	0.41	0.09	23	4.6	<0.001	-	-	-	-	-	-	-	-	-	-	-0.38	0.10	23	-3.7	0.001
Time 2 : <i>Q<sub>phyt</sub></i>	<i>0.29</i>	<i>0.18</i>	<i>50</i>	<i>1.6</i>	<i>0.117</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Time 3 : <i>Q<sub>phyt</sub></i>	0.46	0.18	50	2.5	0.015	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
AICc full model <sup>d</sup>	200.1					300.3					153.1					224.5				
AICc min. model <sup>d</sup>	180.3					266.0					127.5					201.3				

<sup>a</sup>Sapling height, elevation, tree species richness and the interactions richness : *Q<sub>phyt</sub>*, richness : plot age, time : plot age, and time : richness were included in the full models but not retained in any of the minimal models

<sup>b</sup>Italics denote data for non-significant terms retained in the minimal models

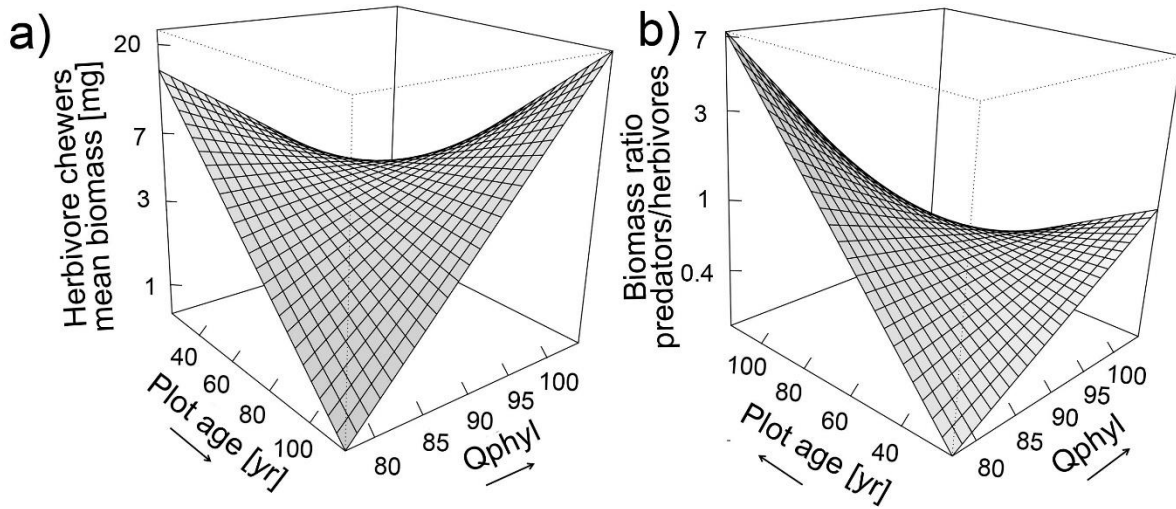
<sup>c</sup>Contrasts between sampling time 1 (fall) and the successive sampling times 2 and 3 (spring and summer); if time included in the minimal model, the intercept is the overall mean

<sup>d</sup>Akaike information criterion (corrected for small sample sizes) of the full model (containing all predictors) and the minimal adequate model (simplified model with lowest AICc)

**Table S5.6.** Mixed-effects models for the functional dispersion ( $Q_{\text{Bio}}$ ) of the biomass of leaf chewer, sap-sucker, and predator individuals per plot across 27 forest stands in subtropical China, **based on observed  $Q_{\text{phyl}}$  instead of standardized effect sizes of  $Q_{\text{phyl}}$ .** Parameter estimates (with standard errors, degrees of freedom, t and  $P$  values) are shown for the variables retained in the minimal models

<i>Fixed effects</i> <sup>a,b</sup>	Herbivores: Leaf chowers					Herbivores: Suckers					Predators				
	Est.	<i>SE</i>	<i>DF</i>	t	<i>P</i>	Est.	<i>SE</i>	<i>DF</i>	t	<i>P</i>	Est.	<i>SE</i>	<i>DF</i>	t	<i>P</i>
Intercept <sup>c</sup>	-3.61	0.06	54	-63.0	<0.001	-4.25	0.21	52	-19.8	<0.001	-3.72	0.05	50	-67.9	<0.001
Time 2-1 <sup>c</sup>	-	-	-	-	-	0.73	0.30	52	2.4	0.019	-0.16	0.08	50	-2.1	0.038
Time 3-1 <sup>c</sup>	-	-	-	-	-	<i>0.43</i>	<i>0.30</i>	<i>52</i>	<i>1.4</i>	<i>0.163</i>	0.19	0.08	50	2.5	0.016
Plot age	0.06	0.06	23	1.0	0.330	-	-	-	-	-	-	-	-	-	-
Qphyl	0.14	0.06	23	2.2	0.040	-	-	-	-	-	<i>0.05</i>	<i>0.06</i>	<i>25</i>	<i>1.0</i>	<i>0.331</i>
Plot age : Qphyl	0.13	0.06	23	2.4	0.027	-	-	-	-	-	-	-	-	-	-
Time 2 : Qphyl	-	-	-	-	-	-	-	-	-	-	-0.18	0.08	50	-2.3	0.028
Time 3 : Qphyl	-	-	-	-	-	-	-	-	-	-	<i>-0.04</i>	<i>0.08</i>	<i>50</i>	<i>-0.5</i>	<i>0.641</i>
AICc full model <sup>d</sup>	114.7					289.5					63.5				
AICc min. model <sup>d</sup>	91.0					254.9					38.1				

<sup>a-d</sup> see Table S5.5



**Figure S5.1.** Relationships between plot age, **observed woody plant phylogenetic diversity** ( $Q_{\text{phyl}}$ ) and the biomass of a) leaf chewers, and b) the ratio of predators to herbivores across 27 forest plots in subtropical China. Note the inverted orientation of the x-axis (plot age) in b) for better visual representation. All relationships are significant at  $P < 0.05$  (see Table 1 for details). All relationships significant at  $P < 0.05$  (see Table S2 for details).



# CHAPTER 6

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# Predator Diversity and Abundance Provide Little Support for the Enemies Hypothesis in Forests of High Tree Diversity

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## Abstract

Predatory arthropods can exert strong top-down control on ecosystem functions. However, despite extensive theory and experimental manipulations of predator diversity, our knowledge about relationships between plant and predator diversity—and thus information on the relevance of experimental findings—for species-rich, natural ecosystems is limited. We studied activity abundance and species richness of epigeic spiders in a highly diverse forest ecosystem in subtropical China across 27 forest stands which formed a gradient in tree diversity of 25–69 species per plot. The enemies hypothesis predicts higher predator abundance and diversity, and concomitantly more effective top-down control of food webs, with increasing plant diversity. However, in our study, activity abundance and observed species richness of spiders decreased with increasing tree species richness. There was only a weak, non-significant relationship with tree richness when spider richness was rarefied, i.e. corrected for different total abundances of spiders. Only foraging guild richness (i.e. the diversity of hunting modes) of spiders was positively related to tree species richness. Plant species richness in the herb layer had no significant effects on spiders. Our results thus provide little support for the enemies hypothesis—derived from studies in less diverse ecosystems—of a positive relationship between predator and plant diversity. Our findings for an important group of generalist predators question whether stronger top-down control of food webs can be expected in the more plant diverse stands of our forest ecosystem. Biotic interactions could play important roles in mediating the observed relationships between spider and plant diversity, but further testing is required for a more detailed mechanistic understanding. Our findings have implications for evaluating the way in which theoretical predictions and experimental findings of functional predator effects apply to species-rich forest ecosystems, in which trophic interactions are often considered to be of crucial importance for the maintenance of high plant diversity.

## Introduction

The presence, abundance and biodiversity of predatory arthropods have significant impacts on the functioning of ecosystems (Snyder et al. 2006; Schmitz 2007; Bruno and Cardinale 2008; Letourneau et al. 2009). Predator-mediated changes in herbivore feeding preferences or intensity can alter plant community structure and diversity (e.g. Schmitz 2009). Interactions between predators and detritivores affect decomposition dynamics (Lawrence and Wise 2004). While the importance of these trophic interactions in

influencing and modifying ecosystem processes such as biomass production and nutrient cycling is increasingly recognized, and trophic complexity is increasingly being implemented in ecosystem functioning experiments (Bruno and Cardinale 2008; Griffiths et al. 2008; Hillebrand and Matthiessen 2009), our basic knowledge on how the diversity and abundance of secondary consumers relates to plant diversity in natural ecosystems is still limited (Balvanera et al. 2006; Vehviläinen et al. 2008; Haddad et al. 2009). More information on the relationship between the biodiversity at different trophic

levels is required to understand how natural ecosystems and their functioning are influenced by the potentially diversity-dependent effects of trophic interactions reported from experiments or theory (Duffy et al. 2007; Hillebrand and Matthiessen 2009). This knowledge is also of crucial importance in biodiversity conservation (e.g. Voigt et al. 2003).

Generally, predator abundance and diversity are expected to increase with increasing plant diversity, as diverse plant communities are hypothesized to offer a greater amount of resources (in terms of biomass production and resource heterogeneity; (Hutchinson 1959; Strong et al. 1984; Srivastava and Lawton 1998)) to consumers. A popular hypothesis concerned with trophic interactions in relation to species diversity is the ‘enemies hypothesis’ (Root 1973), which predicts that predators are more abundant and more diverse (and can thus more effectively regulate lower trophic levels such as herbivores) in species-rich plant communities because these communities offer a greater variety of habitats as well as a broader spectrum and temporally more stable availability of prey (Jactel et al. 2005). Many of the studies which analyzed predator diversity and abundance in relation to plant diversity so far, however, only compared monocultures to mixtures of few plant species (e.g. Andow 1991; Vehviläinen et al. 2008; Sobek et al. 2009). Results of these studies were ambiguous and often depended on the plant species studied, with strong effects of plant species identity making it difficult to assess the effect of plant species richness *per se* (Riihimäki et al. 2005; Schuldt et al. 2008; Nadrowski et al. 2010). Several studies in grassland ecosystems have also analyzed the relationship between plant diversity and predators over larger gradients of plant diversity, but here again results were mixed (Siemann et al. 1998; Koricheva et al. 2000; Perner et al. 2005; Haddad et al. 2009; Eisenhauer et al. 2011). For more complex ecosystems such as forests, however, which are characterized by long-lived plant individuals and which provide critically important ecosystem services (Scherer-Lorenzen et al. 2005), comparable studies

including high diversity levels are lacking (Vehviläinen et al. 2008). Yet, species-rich forests are of particular interest in this respect, as trophic interactions might play an important role in maintaining the high levels of tree diversity in these ecosystems (Givnish 1999; Hubbell 2006; Wills et al. 2006).

Here, we analyze activity abundance and species richness of an important group of predatory forest arthropods, epigeic spiders, across 27 differentially diverse forest stands (between 25 and 69 tree and shrub species per 900 m<sup>2</sup>; (Bruehlheide et al. 2011)) of different ages in subtropical China. Epigeic arthropods make up a large part of the overall faunal diversity in plant species-rich forests (Stork and Grimbacher 2006) and can play an indirect role in the long-term maintenance of tree diversity: ground-active predators can particularly affect densities of insect herbivores feeding on recruits (seedlings and saplings) growing close to the forest floor (e.g. Garcia-Gunman and Benitez-Malvido 2003), i.e., on plant individuals which will determine tree diversity in the long run. These predators might even affect herbivores of higher vegetation strata, as many of these herbivores develop or take shelter during inactivity periods on the forest floor (Tanhuanpää et al. 1999; Riihimäki et al. 2005; Pringle and Fox-Dobbs 2008; Vehviläinen et al. 2008). Moreover, the diversity and abundance of epigeic predators can strongly affect decomposer assemblages and thus influence ecosystem functions such as nutrient cycling (Lawrence and Wise 2004). Tree species diversity, in turn, can directly or indirectly feed back on epigeic arthropods by affecting abiotic and biotic characteristics (e.g., litter depth and structure, microclimate, pH, prey availability and vegetation structure) of the forest floor (Hättenschwiler and Gasser 2005; Scheu 2005). We tested to which degree predator assemblages at plant diversity levels beyond the scope of most previous biodiversity studies respond to differences in plant diversity. Whether relationships observed at lower levels of plant diversity reach an asymptote at higher diversity or not is still unclear (Hooper et al. 2005; Schmid et al. 2009). Epigeic spiders might respond positively to higher structural heterogeneity

(e.g., via a more diverse litter layer or a potentially higher herb layer diversity) and potentially increased prey availability in forest stands of high tree diversity, which would be in accordance with the enemies hypothesis (Strong et al. 1984; Jactel et al. 2005). Interestingly, in a previous study we found that insect herbivory on saplings (i.e., tree individuals with a strong connection to the forest floor) in these 27 study plots was higher in the more diverse plant stands (Schuldt et al. 2010): this is in contrast to the predictions of the enemies hypothesis and more consistent with a positive bottom-up effect of plant diversity on herbivore diversity (Scherber et al. 2010). Our present study provides information needed for a better understanding of the role of trophic interactions in the long-term maintenance of high plant diversity and the functioning of such phytodiverse ecosystems (Coley and Barone 1996; Givnish 1999; Haddad et al. 2009) by testing one of the major assumptions of the enemies hypothesis (increasing abundance and richness of predators with higher plant species richness) for an important group of generalist predators.

## Methods

### Study site and plot selection

The study was conducted in the Gutianshan National Nature Reserve (GNNR; 29°14' N, 118°07' E), Zhejiang Province, in South-East China. The GNNR is located in a mountain range at an elevation of 300–1260 m a.s.l. It was established as a National Forest Reserve in 1975 and is characterized by 8000 ha of semi-evergreen, broad-leaved forests in a subtropical monsoon climate. The mean annual temperature is 15.3°C; mean annual precipitation amounts to ca. 2000 mm. The parent rock of the mountain range is granite, with pH ranging from 5.5–6.5 (Hu and Yu 2008; Legendre et al. 2009).

Within the framework of the 'BEF China' project (Bruehlheide et al. 2011), we established 27 study plots of 30 x 30 m in the GNNR. The original intention was to select plots according to a factorial design of three richness levels of woody species and three successional stages. However, it was not

possible to find young stages with high richness. Thus, the plots, which represented a deliberately large range of woody species richness (25–69 tree and shrub species per plot), were stratified a posteriori according to stand age (between < 20 and ≥ 80 years, (Bruehlheide et al. 2011)) into five classes reflecting different successional stages and woody species richness. Plots were randomly distributed throughout the reserve, with limitations due to inaccessibility or inclinations > 55°. Typical tree species of this subtropical forest are the evergreen *Castanopsis eyrei* (Champ. ex Benth.) Tutch and *Schima superba* Gardn. et Champ. Mean height of the upper tree layer varies from 13–25 m along the successional gradient. Further details on plot establishment and plot characteristics are provided in (Bruehlheide et al. 2011).

### Spider data

In each of the 27 study plots, four pitfall traps (i.e. a total of 108 traps) were installed for standardized trapping of epigeic arthropods. The traps were set up at the corners of a 10 x 10 m square around the center of each plot and consisted of a plastic cup (diameter 8.5 cm, depth 15 cm, capacity 550 ml) sunk into the ground and filled with 150 ml of preserving solution (40% ethanol, 30% water, 20% glycerol, 10% acetic acid, with a few drops of detergent to reduce surface tension) for continuous trapping. Sampling was conducted in 2009 for five months (30 March–2 September) and covered the main growing season. The traps were emptied and refilled at 14 day intervals. As composite measures of activity and abundance of the species caught (Topping and Sunderland 1992), pitfall traps record 'activity abundances'. These can be interpreted as longer-term (over the trapping interval) patterns in the locomotory activity and the densities of individual species (Southwood and Henderson 2000). In the following, we use 'activity abundance' to characterize the trap catches.

Spiders were sorted and determined to species or morphospecies level. Classification of spiders by morphospecies (within families or genera) can be easily and reliably achieved on the basis of their genitalia (e.g. Kapoor

2008). For our analyses we further assigned spiders to foraging guilds. The functional effects of spiders depend on their foraging mode, and foraging guild diversity can thus be a functionally important characteristic of spider assemblages (Schmitz 2008; Schmitz 2009). Guild classification was based on the primary hunting mode of the respective family (Uetz et al. 1999, and own observations; Jocqué and Dippenaar-Schoeman 2007) and comprised the following nine guilds: orb-web weavers (Araneidae, Tetragnathidae), space-web weavers (Dictynidae, Theridiidae), sheet-web weavers (Hahniidae, Linyphidae), ground-funnel-web weavers (Agelenidae, Amaurobiidae), ground-space-web weavers (Leptonetidae), ground-tube-web or burrow weavers (Atypidae, Ctenizidae, Hexathelidae, Nemesidae), trip-line-retreat builders (Segestriidae), foliage hunters (Clubionidae, Ctenidae, Mimetidae, Philodromidae, Pisauridae, Salticidae, Sparassidae, Thomisidae) and ground hunters (Corinnidae, Gnaphosidae, Liocranidae, Lycosidae, Oonopidae, Zodariidae, Zodidae).

While scales of perception of plant diversity by epigeic spiders might vary between species, this does not affect our results: first, our plots represent subsections of larger forest expanses for which they could be considered typical; second, many predatory arthropods can establish viable populations already in areas as small as our study plots (e.g. Matern et al. 2008); third, woody plant species richness at the plot level was also highly correlated with plant species richness at subplot levels (Pearson's  $r$  between 0.88 and 0.72 for correlations between total and rarefied richness for 200–20 tree individuals (Schuldt et al. 2010)).

### Environmental predictors

Observational studies allow for the analysis of ecological patterns and processes under near-natural conditions (e.g. fully established animal and plant communities) in complex, real-world ecosystems (Leuschner et al. 2009). However, adequate interpretation of species richness effects in such studies requires that potentially confounding environmental factors, which might be correlated with plant species richness and might directly or

indirectly affect spiders, are taken into consideration (Vilà et al. 2005). We thus included a set of environmental variables in the analyses to account for potential effects of important abiotic (e.g. soil pH, vegetation-mediated light availability) and biotic (e.g. plant biomass, which might, for instance affect prey densities) characteristics of the plots and the immediate surroundings of the traps: besides successional stage and species richness of woody plants (see above), canopy and herb cover, altitude, tree density (all tree and shrub individuals > 1 m height—constituting the bulk of plant biomass and production in the plots) were assessed for all plots during plot establishment in 2008. Total basal area of trees and shrubs as a measure of plot biomass was calculated from diameter at breast height (dbh) measurements of all trees > 10 cm dbh in the whole plot and for all individuals > 3 cm dbh in a central subplot of 10 x 10 m. The pH of the topsoil (0–5 cm) was determined from nine dried and sieved soil samples per plot, taken in the summer of 2009. These were pooled and measured potentiometrically in a water-soil solution (Bruehlheide et al. 2011). To take into account differences in the surrounding matrix of the pitfall traps, which can affect spider movement and catch efficiency (Topping and Sunderland 1992; Southwood and Henderson 2000), we further recorded litter depth, percentage cover of litter and of plants in the (in many cases relatively sparsely developed) herb layer, and vegetation height of the herb layer in a 1 x 1 m grid around each trap in the summer of 2009. We also included the richness of plant species in the herb layer (all plant individuals < 1 m height, measured in the 10 x 10 m central subplot) to distinguish between effects of the tree (e.g. via tree litter heterogeneity) and the herb layer (i.e., horizontal plant structure within the realm of ground-active spiders).

### Statistical analysis

All analyses were performed using R 2.8.1 (R Development Core Team 2008). Activity abundance was square-root transformed to meet assumptions of normality and homogeneity of variances. Spider species richness in our samples was found to be

correlated with spider activity abundance (Pearson's  $r = 0.63$ ;  $P < 0.001$ ). We thus used two different measures of spider species richness, observed and individual-based rarefied, to analyze relationships between the richness of woody plant species and spider species. Rarefaction calculates species numbers for a standardized number of individuals across all samples and yields species richness data which are independent of the number of individuals in a particular sample, as the latter is potentially affected by differences in sampling efficiency. However, differences in the number of individuals sampled may also reflect real and biologically meaningful patterns (Gotelli and Colwell 2001). Thus, the two measures allow for a simultaneous assessment of pure (rarefied richness) and abundance-mediated (observed richness) responses of spider species richness to differences in woody plant species richness. We also checked for the completeness of our trap catches with nonparametric first-order jackknife estimation (Brose and Martinez 2004). Rarefaction and species estimations were performed using the package VEGAN (Oksanen et al. 2008). Species richness of woody plants was not affected by potential sampling bias and thus not corrected for differences in the total number of individuals per plot (density). Furthermore, observed and rarefied (for  $n = 200$  individual plants) species richness of woody plants were highly correlated ( $r = 0.88$ ;  $P < 0.001$ ) because observed species richness was not correlated with density of woody plants ( $r = -0.07$ ;  $P = 0.737$ ). The species richness of woody plants was also not correlated with the abundance of any of the dominant tree or shrub species (Pearson correlations with the eight most abundant species, which accounted for  $> 55\%$  of all tree individuals in the 27 study plots, were all non-significant; not shown), i.e., relationships between woody plant species richness and spiders are independent of and not affected by the species identity of the dominant tree and shrub species in the individual study plots.

The relationships between a) activity abundance, b) observed spider species richness, c) rarefied spider species richness and d) foraging guild richness of spiders as

response variables and species richness of woody plants as an explanatory variable were analyzed with linear mixed-effects models, using the package NLME in R (Pinheiro et al. 2009). Mixed-effects models take into account hierarchical structures and potential non-independence of data by the inclusion of a random effects structure (Pinheiro and Bates 2000). In our case, the hierarchical structure was given by the traps nested within plots; thus, plot identity was fitted as random effect. We checked for significant nonlinear relationships between the response variables and the predictors by analyzing second- and third-order polynomials of the predictors. Before fitting the full model, the environmental predictors were checked for collinearity. Tree density (Pearson's  $r = -0.77$ ;  $P < 0.001$ ) and total basal area ( $r = 0.82$ ;  $P < 0.001$ ) were strongly related to successional stage and primarily reflected stand age-related differences in plot characteristics [see also 41]. Likewise, vegetation height of the herb layer was strongly correlated with vegetation cover around the traps ( $r = 0.73$ ;  $P < 0.001$ ). To avoid potential effects of multicollinearity, we did not include tree density, total basal area or vegetation height in the models. The full models were thus fitted with successional stage, canopy and herb cover, altitude, soil pH, woody plant species richness of the shrub and tree layers, and the richness of plant species in the herb layer as covariates representing plot characteristics, and with litter cover, litter depth and vegetation cover as covariates representing characteristics of the microhabitat around the traps within plots. We also fitted the interaction between woody plant species richness and stand age to check whether potential species richness effects depended on the successional age of the forest stands.

We used model simplification with an information-theoretic approach to obtain the most parsimonious explanatory models. Model simplification was based on the Akaike Information Criterion, corrected for small sample sizes (AIC<sub>c</sub> (Burnham and Anderson 2004)). Predictors whose exclusion improved model fit by reducing the AIC<sub>c</sub> of the resulting model were eliminated in an automated stepwise procedure (a modified

version of the stepAIC procedure in R; (Scherber et al. 2010)) until a minimal, best-fit model with the lowest global AICc was obtained. The model with the smallest number of predictors was chosen as being the most parsimonious in case differences in AICc ( $\Delta\text{AICc}$ ) of  $\leq 2$  between two candidate models indicated that both models are almost equally likely (Burnham and Anderson 2004). Model residuals were checked for assumptions of normality and homoscedasticity. Further, we calculated Moran's I coefficients to test for spatial autocorrelation in the model residuals, using the R package NCF (Bjornstad 2009).

## Results

### Species numbers, activity abundance and foraging guild richness

In total, 7952 spiders (of which 6166 were adults), belonging to 195 (morpho-) species of 29 families, were captured in pitfall traps. The most species-rich families in the forest stands were Salticidae (35 species) and Linyphiidae (30), while the most abundant families were Lycosidae (2125 individuals belonging to 6 species) and Liocranidae (1485 individuals of 12 species). First-order jackknife estimation (with traps as samples) showed that all plots were equally sampled, with 66–78% of the estimated species numbers for each plot. In total, 268 ( $\pm 19$  SE) epigeic spider species can be expected to occur on the forest floor of the 27 study sites.

The mean number of spider individuals per trap decreased strongly from more than 100 in the plots with the lowest woody plant species richness to about 50 individuals in the plots with the highest woody plant species richness (Fig. 6.1A), and a minimal model with negative effects of woody plant species richness ( $t = -3.8$ ;  $P < 0.001$ ) and positive effects of soil pH ( $t = 3.0$ ;  $P = 0.007$ ) best explained the observed patterns in activity abundance (Table 6.1). There was a strong positive relationship between activity abundance and the species richness of spiders in the study plots (see Methods section), and, like abundance, mean spider richness per plot (trap means ranging from 12.8 to 23.0) decreased significantly with increasing woody plant species richness (Fig. 6.1B). Woody plant species richness ( $t = -2.6$ ;  $P = 0.015$ ),

together with a negative effect of altitude ( $t = -3.2$ ;  $P = 0.004$ ), was also retained in the minimal mixed-effects model for spider richness when potentially confounding plot characteristics were accounted for (Table 6.1). Species richness and activity abundance of spiders were neither affected by plant species richness of the herb layer, nor by litter cover, litter depth or vegetation cover in the immediate surroundings of the traps, and none of these variables were retained in any of the minimal mixed-effects models (Table 6.1).

Rarefied species richness of spiders tended to increase slightly across the gradient of woody plant species richness (Fig. 6.1C). However, this effect was not significant, and thus woody plant species richness was not retained in the minimal mixed-effects model for rarefied spider richness, which only included successional age as an explanatory variable (Table 6.1). Rarefied spider species richness was high in plots  $> 20$  yr and lowest in the youngest forest stands (Fig. 6.2). In contrast, there was a significant increase in rarefied feeding-guild richness of spiders with increasing species richness of trees and shrubs (Fig. 6.1D). The minimal mixed-effects model pointed out positive effects of both woody plant species richness ( $t = 2.6$ ;  $P = 0.015$ ) and herb cover ( $t = 3.0$ ;  $P = 0.006$ ) in the forest stands (Table 6.1). The results of our study were not affected by the sequence in which woody plant species richness and stand age were fitted in the analyses (i.e., results did not differ between models with plant richness fitted before or after stand age; not shown). There was no significant spatial autocorrelation in the residuals of the minimal mixed models, with Moran's I values all close to zero and  $P > 0.05$  (not shown).

## Discussion

The results of our study provide insight into the relationship between predator and plant diversity for complex forest ecosystems, extending our knowledge from observational and experimental studies of relatively species-poor to highly diverse forest ecosystems. Our findings for spider activity and species richness only partially reflect patterns reported from studies of species-poor forests or other ecosystems and do not unambiguously



**Table 6.1.** Mixed-effects models for spider species richness and activity abundance

<i>Fixed effects<sup>d</sup></i>	Activity abundance <sup>b</sup>				Spider species richness				Rarefied richness				Foraging guilds (rarefied)			
	<i>DF<sub>n</sub></i>	<i>DF<sub>d</sub></i>	<i>F<sup>c</sup></i>	<i>P</i>	<i>DF<sub>n</sub></i>	<i>DF<sub>d</sub></i>	<i>F<sup>c</sup></i>	<i>P</i>	<i>DF<sub>n</sub></i>	<i>DF<sub>d</sub></i>	<i>F<sup>c</sup></i>	<i>P</i>	<i>DF<sub>n</sub></i>	<i>DF<sub>d</sub></i>	<i>F<sup>c</sup></i>	<i>P</i>
Successional stage	-	-	-	-	-	-	-	-	4	22	2.9	0.045	-	-	-	-
Herb cover	-	-	-	-	-	-	-	-	-	-	-	-	1	24	7.9 (+)	0.009
Altitude	-	-	-	-	1	24	10.9 (-)	0.003	-	-	-	-	-	-	-	-
Soil pH	1	24	8.7 (+)	0.007	-	-	-	-	-	-	-	-	-	-	-	-
Woody plant species richness	1	24	14.5 (-)	<0.001	1	24	6.9 (-)	0.015	-	-	-	-	1	24	6.8 (+)	0.015
<i>AIC<sub>c</sub> full model<sup>d</sup></i>	396.1				598.5				371.1				199.9			
<i>AIC<sub>c</sub> minimal model</i>	373.5				578.5				349.4				179.9			

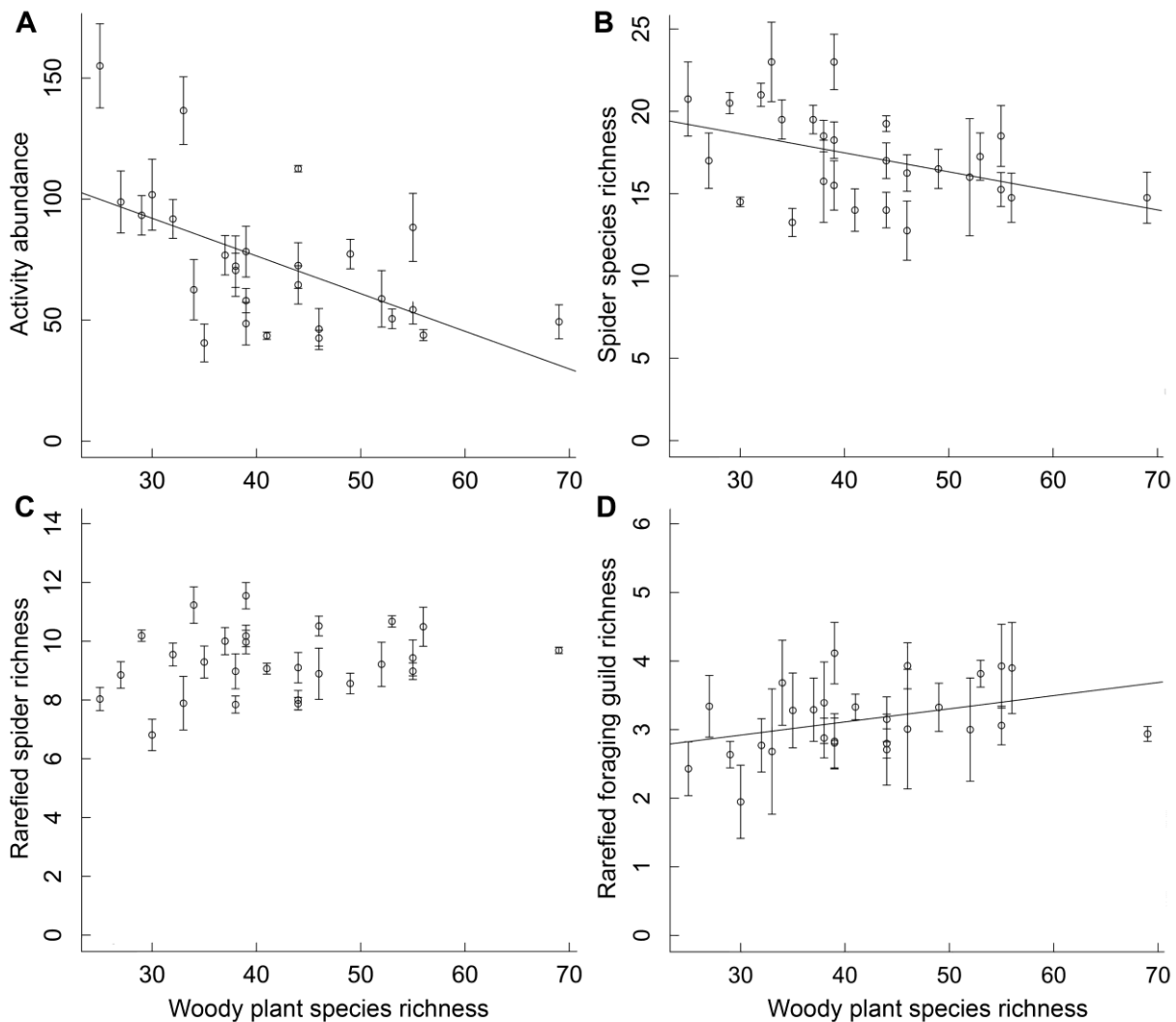
Results for the fixed effects of the minimal mixed-effects models (numerator and denominator degrees of freedom  $DF_n$  and  $DF_d$ ;  $F$ -value and probabilities  $P$ ; terms dropped during model simplification are marked “-”) for activity abundance, original and rarefied species richness, and rarefied foraging guild richness of spiders as response variables.

<sup>a</sup> Canopy cover, litter cover (trap surroundings), litter depth (trap surroundings), vegetation cover of the herb layer (trap surroundings) and interaction successional age:woody plant species richness (non-significant and excluded in all cases during model simplification) not shown

<sup>b</sup> Square root-transformed

<sup>c</sup> (+) and (-) indicate positive and negative relationship, respectively

<sup>d</sup> Full model: fitted with the full set of fixed effects; minimal model: simplified model with lowest  $AIC_c$



**Figure 6.1.** Relationships between species richness of woody plants and spiders. (A) activity abundance, (B) original species richness, (C) rarefied species richness, and (D) rarefied foraging guild richness of epigeic spiders (trap means  $\pm$  SE for each plot) across a plant species diversity gradient of 27 study plots in subtropical China. Regression lines show significant relationships at  $P < 0.05$ .

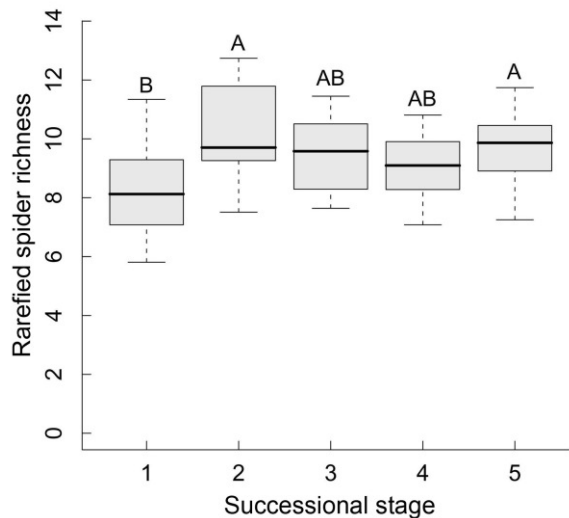
support common hypotheses on diversity-dependent relationships between predators and other trophic levels.

#### *Spider activity abundance*

Contrary to what might have been expected, we observed a decrease in activity abundance of spiders in forest stands of high woody plant diversity. Considering the commonly stated positive plant productivity–diversity relationship (cf. Hooper et al. 2005) and the predictions made by the enemies hypothesis (Root 1973), we would have expected to find the opposite pattern of higher predator activity abundance (and higher species richness, see below) in more diverse forest stands. This pattern was observed for predator

activity and abundance in several previous studies, mainly of non-forest ecosystems (e.g. Andow 1991; Johnson et al. 2006, and references therein; Haddad et al. 2009). In contrast, results from the few studies conducted in forests were ambiguous and, due to comparisons of relatively species-poor stands, often strongly affected by tree species identity (Schuldt et al. 2008; Vehviläinen et al. 2008; Sobek et al. 2009).

A negative relationship between the activity of predators and plant diversity across a gradient from low to relatively high plant species richness was also found by Koricheva et al. (2000) in an experimental grassland study. They attributed this negative relationship primarily to indirect effects of



**Figure 6.2.** Rarefied spider species richness in relation to plot age. Mean values per trap are shown in relation to the successional stage (1 – 5: < 20, < 40, < 60, < 80 and  $\geq 80$  years old) of the 27 subtropical forest stands in south-east China. Different letters indicate significant differences between successional stages at  $P < 0.05$ .

plant diversity on predator activity through diversity-dependent changes in microclimate and prey availability. This probably does not apply in the same way to our study, as characteristics of the plots and the immediate trap surroundings which are often considered to influence the activity of ground-dwelling arthropods, such as vegetation density or litter depth (which, in turn, affect habitat structure and microclimatic conditions; (Pearce et al. 2004; Sayer 2006)), had no effect on spider activity abundance. The only abiotic variable which significantly covaried with spider activity abundance in our study was soil pH (which ranged between 4.1 and 5.1), which was not related to plant diversity. However, woody plant species richness had a stronger effect than pH and was retained in the minimal mixed-effects model. Our results thus indicate a negative effect of plant diversity on spider activity abundance independent of covarying plot characteristics. This effect is due to changes in tree- and shrub-layer, rather than herb-layer plant diversity, as the latter was not related to our spider data. This suggests that in the studied forest stands, the horizontal plant structure of the herb layer has little impact on epigeic spiders compared to the effects of the tree and shrub layers. Forming the dominant vegetation strata of the studied forests in terms of biomass, the latter

layers and their plant diversity can be expected to have strong effects on abiotic (e.g. litter diversity) or biotic (e.g., faunal assemblage structure) characteristics at the forest floor. Missing effects of important abiotic parameters, in particular of litter depth and cover, on spider activity abundance, indicate that biotic characteristics mediated by tree diversity might play an important role in determining the observed patterns.

While a higher prey abundance in the more diverse forest stands could potentially reduce foraging time and thus spider activity, the opposite pattern of higher spider activity in forest stands with higher prey availability has also been reported (Schuldt et al. 2008), which shows that prey availability cannot be used consistently as a predictor of predator activity. It will be intriguing to further explore the potential causes of the unexpected negative relationship between spider activity abundance (and observed species richness) and tree diversity. For instance, patterns in richness and abundance of spiders could be affected by the abundance or diversity of their enemies (e.g. pompilid wasps, birds, vertebrates) or competing predatory taxa (e.g. ants) (see e.g. Mooney et al. 2010; Pinol et al. 2010). Elucidating the mechanisms underlying the observed patterns requires further investigation. Yet, the facts that in our study plots herbivore damage levels of saplings increased with increasing species richness of woody plants (Schuldt et al. 2010) and that these damage levels are negatively correlated with spider activity abundance (Pearson's  $r = -0.48$ ;  $P = 0.012$ ) indicate that the influence of important predator groups on herbivores is not necessarily higher in the forest stands with higher tree and shrub diversity. With seedlings and saplings growing close to the forest floor, interactions between epigeic predators and herbivores (see Introduction) can be important for these tree recruits, which play a key role in the long-term maintenance of tree diversity. The absence of positive predator effects with increasing plant species richness would be in contradiction to predictions of the enemies hypothesis (see e.g. Root 1973; Jactel et al. 2005) and to suggestions from a recent grassland study (Haddad et al. 2009); however, studies of less diverse forest

ecosystems (Riihimäki et al. 2005; Vehviläinen et al. 2008) also found no evidence of the effects predicted by the enemies hypothesis, as can also be deduced from a further study on grassland systems (Knop et al. 2006).

### Species richness and foraging guilds

In contrast to predator activity and abundance, little information is available on patterns of predator species richness across gradients of high plant diversity, and this information is basically limited to non-forest ecosystems. In a long-term grassland experiment Haddad et al. (2009) found that species richness of predators was positively related to plant diversity (see also Siemann et al. 1998). However, species numbers depended on predator abundance, and rarefied species richness actually declined with increasing plant diversity. The positive effect of plant diversity on the observed species richness was attributed to higher numbers of individuals in more productive plots, in accordance with the more individuals hypothesis, which assumes that more productive sites (in terms of biomass) support larger populations of a greater number of consumer species than less productive sites (Haddad et al. 2009). We also found a strong dependence of species richness patterns of spiders on activity abundance, however, with the opposite effect of decreasing activity and richness with increasing tree species richness. Our activity abundance data do not directly allow for quantification of actual abundance patterns per unit area (cf. Topping and Sunderland 1992). An evaluation of the productivity–abundance relationship as implied by the more individuals hypothesis (Srivastava and Lawton 1998) is thus not directly possible in our case, as we cannot completely exclude effects of prey availability on activity patterns. However, even with richness patterns potentially influenced by effects of prey availability on spider activity in the study plots, these patterns mean that the activity-dependent species density of spiders is lower in plots with higher tree diversity. Reduced species density can affect prey organisms such as herbivores or detritivores, as the behavior of different predator species (regarding, for instance, foraging mode and

foraging intensity) influences prey behavior and performance (Schmitz 2008; Schmitz 2009). Lower species densities due to lower predator activity (see above) might thus also contribute to less strong top-down control and to effects such as higher herbivory in forest stands with high tree diversity (see also Griffiths et al. 2008). In our case, this might primarily apply to effects on seedlings and saplings, which grow close to the forest floor. However, long-term maintenance of tree diversity essentially depends on these tree recruits and thus on trophic interactions influencing tree recruitment (Coley and Barone 1996; Wills et al. 2006). Moreover, changes in the strength of top-down control can also have effects on other important ecosystem functions, such as nutrient cycling, via predator impacts on decomposer food webs (Lawrence and Wise 2004).

Even for rarefied species richness of spiders, which is independent of the observed spider activity abundance, our results are not supportive of the assumed positive effects of plant diversity and of the concomitant higher structural heterogeneity on the species richness of predators, as proposed by the enemies hypothesis and other related hypotheses (Strong et al. 1984; Jactel et al. 2005; Haddad et al. 2009). Removing the effect of activity abundance on species richness of spiders resulted in the elimination of woody plant species richness as a predictor of spider species richness in the mixed model analysis. Even though a tendency towards increasing rarefied spider richness with increasing plant diversity might be discernible, this relationship was of low explanatory power and not significant for rarefied spider species richness. Instead, effects of forest stand age became important for rarefied richness. Forest age can have strong impacts on animal communities because not only biotic conditions such as plant diversity but also abiotic conditions change considerably during the course of forest succession (Vilà et al. 2005; Leuschner et al. 2009). The results of our study were independent of the sequence in which woody plant richness and stand age were fitted in the analyses. When effects of the number of spider individuals are factored out, successional age thus seems to overrule

effects of tree diversity on species richness of epigeic spiders in our subtropical study system.

Interestingly, woody plant species richness positively affected the rarefied number of spider foraging guilds. Higher structural heterogeneity, as also shown by a positive relationship with herb layer cover, probably promotes the coexistence of species with different foraging behavior in plots with high plant diversity (cf. Uetz et al. 1999). In contrast to mere species numbers, results for foraging guilds as an aspect of functional diversity are in accordance with predictions of the enemies hypothesis. In general, such higher functional diversity of predators has been shown to affect ecosystem processes, as different hunting modes of spiders can strongly impact herbivore behavior (e.g. Schmitz 2008). However, in view of our findings for spider activity and the herbivory patterns observed for the study sites (Schuldt et al. 2010), further research is needed to evaluate the significance of this increase in feeding-guild richness for trophic interactions such as herbivory, and to assess how this affects ecosystem processes in these forests (cf. Letourneau et al. 2009).

## Conclusions

Ground-dwelling arthropods make up a large part of the invertebrate biodiversity in forests of high tree diversity (Stork and Grimbacher 2006) and can have strong effects on food webs also of higher vegetation strata (Tanhuanpää et al. 1999; Riihimäki et al. 2005; Pringle and Fox-Dobbs 2008; Vehviläinen et al. 2008). Knowledge of the diversity of these invertebrates and of their interactions across trophic levels is essential for our understanding of the functioning of these ecosystems (Coley and Barone 1996). Our study provides information on predator diversity across a gradient of tree diversity far beyond the range of previous studies in forest ecosystems. For dominant epigeic predators, our results contradict common hypotheses of predator–plant diversity relationships, such as the enemies hypothesis, which were derived from studies in less diverse ecosystems. In view of previous findings of increased herbivory in the more diverse forest stands of

our study sites it is questionable whether effects predicted from this hypothesis, for which support is also already mixed for less diverse ecosystems, have a strong impact on ecosystem processes also in higher vegetation strata of our subtropical forest ecosystem. Our study supports findings from previous studies of species-rich ecosystems which state that predator diversity is not necessarily a positive or simple function of plant diversity in such highly diverse plant communities (Koricheva et al. 2000; Perner et al. 2005). As our diversity gradient started at medium diversity levels it might be possible that positive effects often observed at lower plant diversity levels have leveled off (e.g. due to redundancy effects) in our forest stands (cf. Hooper et al. 2005). Our results have implications for evaluating the way in which theoretical predictions and experimental findings of functional effects of predators apply to such ecosystems of high tree diversity, in which trophic interactions are often considered to be of crucial importance for the maintenance of high plant diversity (Givnish 1999; Hubbell 2006; Wills et al. 2006). Further exploration under experimentally controlled conditions, such as in the new tree plantations of the BEF China project, will help to shed light on the ecosystem consequences of the observed patterns.

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## Author contributions

Conceived and designed the experiments: AS HB WH BS HZ TA.  
 Performed the experiments: AS  
 Analyzed the data: AS  
 Contributed reagents/materials/analysis tools: SB HB WH BS  
 Wrote the paper: AS  
 Commented on previous versions of the manuscript: SB HB WH BS HZ TA

## References

- Andow DA (1991) Vegetational diversity and arthropod population response. *Annual Review of Entomology* 36:561-586
- Balvanera P et al. (2006) Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecology Letters* 9:1146-1156
- Bjornstad ON (2009) ncf: spatial nonparametric covariance functions. R package version 1.1-3. Available from: <http://cran.r-project.org>.
- Brose U, Martinez ND (2004) Estimating the richness of species with variable mobility. *Oikos* 105:292-300
- Bruelheide H et al. (2011) Community assembly during secondary forest succession in a Chinese subtropical forest. *Ecological Monographs* 81:25-41
- Bruno JF, Cardinale BJ (2008) Cascading effects of predator richness. *Frontiers in Ecology and the Environment* 6:539-546
- Burnham KP, Anderson DR (2004) Model selection and multimodel inference : a practical information-theoretic approach. Springer, New York
- Coley PD, Barone JA (1996) Herbivory and plant defenses in tropical forests. *Annual Review of Ecology and Systematics* 27:305-335
- Duffy JE, Cardinale BJ, France KE, McIntyre PB, Thebault E, Loreau M (2007) The functional role of biodiversity in ecosystems: incorporating trophic complexity. *Ecology Letters* 10:522-538
- Eisenhauer N et al. (2011) Plant diversity surpasses plant functional groups and plant productivity as driver of soil biota in the long term. *PLoS ONE* 6:e16055
- Garcia-Gunman G, Benitez-Malvido J (2003) Effect of litter on the incidence of leaf-fungal pathogens and herbivory in seedlings of the tropical tree *Nectandra ambigens*. *Journal of Tropical Ecology* 19:171-177
- Givnish TJ (1999) On the causes of gradients in tropical tree diversity. *Journal of Ecology* 87:193-210
- Gotelli NJ, Colwell RK (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters* 4:379-391
- Griffiths GJK, Wilby A, Crawley MJ, Thomas MB (2008) Density-Dependent Effects of Predator Species-Richness in Diversity-Function Studies. *Ecology* 89:2986-2993
- Haddad NM, Crutsinger GM, Gross K, Haarstad J, Knops JMH, Tilman D (2009) Plant species loss decreases arthropod diversity and shifts trophic structure. *Ecology Letters* 12:1029-1039
- Hättenschwiler S, Gasser P (2005) Soil animals alter plant litter diversity effects on decomposition. *Proceedings of the National Academy of Sciences (USA)* 102:1519-1524
- Hillebrand H, Matthiessen B (2009) Biodiversity in a complex world: consolidation and progress in functional biodiversity research. *Ecology Letters* 12:1405-1419
- Hooper DU et al. (2005) Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecological Monographs* 75:3-35
- Hu Z, Yu M (2008) Study on successions sequence of evergreen broad-leaved forest in Gutian Mountain of Zhejiang, Eastern China: species diversity. *Frontiers of Biology in China* 3:45-49
- Hubbell SP (2006) Neutral theory and the evolution of ecological equivalence. *Ecology* 87:1387-1398
- Hutchinson G (1959) Homage to Santa Rosalia, or why are there so many kinds of animals? *American Naturalist* 93:145-159
- Jactel H, Brockerhoff EG, Duelli P (2005) A test of the biodiversity-stability theory: meta-analysis of tree species diversity effects in insect pest infestations, and re-examination of responsible factors. In: Scherer-Lorenzen M, Körner C, Schulze E-D (eds) *Forest diversity and function: temperate and boreal systems*. Springer, Berlin, Heidelberg, pp 235-261
- Jocqué R, Dippenaar-Schoeman AS (2007) Spider families of the world. Royal Museum for Central Africa, Tervuren
- Johnson MTJ, Lajeunesse MJ, Agrawal AA (2006) Additive and interactive effects of plant genotypic diversity on arthropod communities and plant fitness. *Ecology Letters* 9:24-34
- Kapoor V (2008) Effects of rainforest fragmentation and shade-coffee plantations on spider communities in the Western Ghats, India. *Journal of Insect Conservation* 12:53-68
- Knop E, Kleijn D, Herzog F, Schmid B (2006) Effectiveness of the Swiss agri-environment scheme in promoting biodiversity. *Journal of Applied Ecology* 43:120-127
- Koricheva J, Mulder CPH, Schmid B, Joshi J, Huss-Danell K (2000) Numerical responses of different trophic groups of invertebrates to manipulations of plant diversity in grasslands. *Oecologia* 125:271-282
- Lawrence KL, Wise DH (2004) Unexpected indirect effect of spiders on the rate of litter

- disappearance in a deciduous forest. *Pedobiologia* 48:149-157
- Legendre P et al. (2009) Partitioning beta diversity in a subtropical broad-leaved forest of China. *Ecology* 90:663-674
- Letourneau DK, Jedlicka JA, Bothwell SG, Moreno CR (2009) Effects of Natural Enemy Biodiversity on the Suppression of Arthropod Herbivores in Terrestrial Ecosystems. *Annual Review of Ecology Evolution and Systematics* 40:573-592
- Leuschner C, Jungkunst HF, Fleck S (2009) Functional role of forest diversity: Pros and cons of synthetic stands and across-site comparisons in established forests. *Basic and Applied Ecology* 10:1-9
- Matern A, Drees C, Meyer H, Assmann T (2008) Population ecology of the rare carabid beetle *Carabus variolosus* (Coleoptera : Carabidae) in North-west Germany. *Journal of Insect Conservation* 12:591-601
- Mooney KA, Gruner DS, Barber NA, Van Bael SA, Philpott SM, Greenberg R (2010) Interactions among predators and the cascading effects of vertebrate insectivores on arthropod communities and plants. *Proceedings of the National Academy of Sciences (USA)* 107:7335-7340
- Nadrowski K, Wirth C, Scherer-Lorenzen M (2010) Is forest diversity driving ecosystem functioning and service? *Current Opinion in Environmental Sustainability* 2:75-79
- Oksanen E et al. (2008) *vegan: Community Ecology Package*. R package version 1.15-1. Available from <http://cran.r-project.org>.
- Pearce JL, Venier LA, Eccles G, Pedlar J, McKenney D (2004) Influence of habitat and microhabitat on epigeal spider (Araneae) assemblages in four stand types. *Biodiversity and Conservation* 13:1305-1334
- Perner J et al. (2005) Effects of plant diversity, plant productivity and habitat parameters on arthropod abundance in montane European grasslands. *Ecography* 28:429-442
- Pinheiro JC, Bates DM (2000) *Mixed-effects models in S and S-Plus*. Springer, New York
- Pinheiro JC, Bates DM, DebRoy S, Sarkar D, the R Core team (2009) *nlme: linear and nonlinear mixed effects models*. R package version 3.1-93. Available from: <http://cran.r-project.org>.
- Pinol J, Espadaler X, Canellas N, Martínez-Vilalta J, Barrientos JA, Sol D (2010) Ant versus bird exclusion effects on the arthropod assemblage of an organic citrus grove. *Ecological Entomology* 35:367-376
- Pringle RM, Fox-Dobbs K (2008) Coupling of canopy and understory food webs by ground-dwelling predators. *Ecology Letters* 11:1328-1337
- R Development Core Team (2008) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Available from <http://www.R-project.org>
- Riihimäki J, Kaitaniemi P, Koricheva J, Vehviläinen H (2005) Testing the enemies hypothesis in forest stands: the important role of tree species composition. *Oecologia* 142:90-97
- Root RB (1973) Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). *Ecological Monographs* 43:95-124
- Sayer EJ (2006) Using experimental manipulation to assess the roles of leaf litter in the functioning of forest ecosystems. *Biological Reviews* 81:1-31
- Scherber C et al. (2010) Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. *Nature* 468:553-556
- Scherer-Lorenzen M, Körner C, Schulze ED (2005) The functional significance of forest diversity: a synthesis. In: Scherer-Lorenzen M, Körner C, Schulze ED (eds) *Forest diversity and function: temperate and boreal systems*. Springer, Berlin, Heidelberg, pp 377-389
- Scheu S (2005) Linkages between tree diversity, soil fauna and ecosystem processes. In: Scherer-Lorenzen M, Körner C, Schulze ED (eds) *Forest diversity and function: Temperate and boreal systems*. Springer, Berlin, Heidelberg, pp 211-233
- Schmid B et al. (2009) Consequences of species loss for ecosystem functioning: meta-analyses of data from biodiversity experiments. In: Naeem S, Bunker DE, Hector A, Loreau M, Perrings C (eds) *Biodiversity, ecosystem functioning, and human wellbeing. An ecological and economic perspective*. Oxford Univ. Press, Oxford, pp 14-29
- Schmitz OJ (2007) Predator diversity and trophic interactions. *Ecology* 88:2415-2426
- Schmitz OJ (2008) Effects of predator hunting mode on grassland ecosystem function. *Science* 319:952-954
- Schmitz OJ (2009) Effects of predator functional diversity on grassland ecosystem function. *Ecology* 90:2339-2345
- Schuldt A et al. (2010) Tree diversity promotes insect herbivory in subtropical forests of south-east China. *Journal of Ecology* 98:917-926
- Schuldt A, Fahrenholz N, Brauns M, Migge-Kleian S, Platner C, Schaefer M (2008) Communities of ground-living spiders in deciduous forests:

- Does tree species diversity matter? *Biodiversity and Conservation* 17:1267-1284
- Siemann E, Tilman D, Haarstad J, Ritchie M (1998) Experimental tests of the dependence of arthropod diversity on plant diversity. *American Naturalist* 152:738-750
- Snyder WE, Snyder GB, Finke DL, Straub CS (2006) Predator biodiversity strengthens herbivore suppression. *Ecology Letters* 9:789-796
- Sobek S, Scherber C, Steffan-Dewenter I, Tscharntke T (2009) Sapling herbivory, invertebrate herbivores and predators across a natural tree diversity gradient in Germany's largest connected deciduous forest. *Oecologia* 160:279-288
- Southwood TRE, Henderson PA (2000) *Ecological Methods*. Third Edition. Blackwell Science, Oxford
- Srivastava DS, Lawton JH (1998) Why more productive sites have more species: An experimental test of theory using tree-hole communities. *American Naturalist* 152:510-529
- Stork NE, Grimbacher PS (2006) Beetle assemblages from an Australian tropical rainforest show that the canopy and the ground strata contribute equally to biodiversity. *Proceedings of the Royal Society B* 273:1969-1975
- Strong DR, Lawton JH, Southwood TRE (1984) *Insects on plants: community patterns and mechanisms*. Blackwell, Oxford
- Tanhuanpää M, Ruohomäki K, Kaitaniemi P, Klemola T (1999) Different impact of pupal predation on populations of *Epirrita autumnata* (Lepidoptera; Geometridae) within and outside the outbreak range. *Journal of Animal Ecology* 68:562-570
- Topping CJ, Sunderland KD (1992) Limitations to the use of pitfall traps in ecological studies exemplified by a study of spiders in a field of winter wheat. *Journal of Applied Ecology* 29:485-491
- Uetz GW, Halaj J, Cady AB (1999) Guild structure of spiders in major crops. *Journal of Arachnology* 27:270-280
- Vehviläinen H, Koricheva J, Ruohomäki K (2008) Effects of stand tree species composition and diversity on abundance of predatory arthropods. *Oikos* 117:935-943
- Vilà M et al. (2005) Confounding factors in the observational productivity-diversity relationship in forests. In: Scherer-Lorenzen M, Körner C, Schulze ED (eds) *Forest diversity and function: temperate and boreal systems*. Springer, Heidelberg, pp 65-85
- Voigt W et al. (2003) Trophic levels are differentially sensitive to climate. *Ecology* 84:2444-2453
- Wills C et al. (2006) Nonrandom processes maintain diversity in tropical forests. *Science* 311:527-531



# CHAPTER 7

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# Predator assemblage structure and temporal variability of species richness and abundance in forests of high tree diversity

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## Abstract

Predators significantly affect ecosystem functions, but our understanding of to what extent findings can be transferred from experiments and low-diversity systems to highly diverse, natural ecosystems is limited. With a particular threat of biodiversity loss at higher trophic levels, however, knowledge of spatial and temporal patterns in predator assemblages and their interrelations with lower trophic levels is essential for assessing effects of trophic interactions and advancing biodiversity conservation in these ecosystems. We analyzed spatial and temporal variability of spider assemblages in tree species-rich subtropical forests in China, across 27 study plots varying in woody plant diversity and stand age. Despite effects of woody plant richness on spider assemblage structure, neither habitat specificity nor temporal variability of spider richness and abundance were influenced. Rather, variability increased with forest age, probably related to successional changes in spider assemblages. Our results indicate that woody plant richness and theory predicting increasing predator diversity with increasing plant diversity do not necessarily play a major role for spatial and temporal dynamics of predator assemblages in such plant species-rich forests. Diversity effects on biotic or abiotic habitat conditions might be less pronounced across our gradient from medium to high plant diversity than in previously studied less diverse systems, and bottom-up effects might level out at high plant diversity. Instead, our study highlights the importance of overall (diversity-independent) environmental heterogeneity in shaping spider assemblages and, as indicated by a high species turnover between plots, as a crucial factor for biodiversity conservation at a regional scale in these subtropical forests.

**Key words:** BEF China; ecosystem functioning; enemies hypothesis; Gutianshan; invertebrates; spiders; trophic interactions.

## Introduction

Trophic interactions play important roles in the functioning of ecosystems (McCann 2000, Thebault and Loreau 2005, Duffy et al. 2007). This applies particularly to highly diverse ecosystems, such as (sub)tropical forests, where herbivores and top-down effects of predators can have a large impact on the producer level and might even be drivers for the maintenance of high tree diversity (Givnish 1999, Schemske et al. 2009, Dyer et al. 2010). In light of increasing global biodiversity loss, knowledge of these issues is also highly relevant for biodiversity conservation, as extinctions can cascade

through food webs and particularly affect higher trophic levels (Duffy 2003, Srivastava and Bell 2009). Ecological theory often predicts a positive effect of plant diversity—via a higher and temporally more stable availability of habitats and prey—on predators and thus, for instance, a more effective top-down control of food webs in more plant diverse communities (summarized, for example, in the ‘enemies hypothesis’, Root 1973, Jactel et al. 2005; but see Letourneau et al. 2009 for potential effects of intraguild interactions). Whether these predictions can be transferred to complex and highly diverse natural ecosystems, however, is unclear (Tylianakis et al. 2008, Zhang and Adams

2011). For example, results from a highly plant-diverse subtropical forest ecosystem in China showed little support for the hypothesized positive relationship between plant diversity and the overall abundance and richness of predators: across a gradient in tree diversity and successional age, the abundance of a major predator group, epigeic spiders, actually declined with, and rarefied spider richness was not related to, increasing species richness of woody plants (Schuldt et al. 2011). Rarefied spider richness was, however, strongly related to forest age, as predicted by successional theory (Odum 1969, Anderson 2007).

Here, we focus on fine-scale patterns in the spatial and temporal dynamics of the assemblage structure of generalist predators during the main growing season in a highly diverse forest ecosystem, taking the above-mentioned subtropical forests in China as an example. We analyzed spatial patterns of species composition (turnover and habitat specificity) and temporal changes in richness and abundance of epigeic spiders in relation to woody plant diversity and stand age across 27 forest stands. Both factors might modify the general structure of predator assemblages, for instance by promoting species with specific habitat requirements, and, via effects on species composition, influence the functional impact of these assemblages (Straub and Snyder 2006, Woodcock and Heard 2011). Differences in species composition could affect the temporal stability of predator assemblages and their potential for top-down control, as individual species respond differently to variability in environmental conditions and can show pronounced differences in functional characteristics (*e.g.*, hunting mode, Niemelä et al. 1996; Schmitz 2009, Woodcock and Heard 2011). Moreover, differences in the habitat specificity of spider species in relation to woody plant diversity and stand age might also provide insight into processes driving the assembly of predator communities. We thus tested whether woody plant species richness, stand age, and other plot characteristics (such as tree density, herb cover or litter depth) influence species assemblage structure of spiders. We also explored the degree to which species are

specific to the individual forest stands (henceforth *habitat specificity*), and whether temporal variability in species richness and abundance is related to plot characteristics.

Epigeic arthropods make up a large proportion of the faunal diversity in species-rich forests (Stork and Grimbacher 2006). Ground-dwelling spiders have an important functional role as generalist predators and can, for instance, be strongly linked to plant–herbivore food webs (Garcia-Gunman and Benitez-Malvido 2003, Riihimäki et al. 2005, Pringle and Fox-Dobbs 2008). Epigeic spiders are also sensitive to variations in environmental conditions caused by tree and shrub diversity (*e.g.*, via effects on litter structure, microclimate or prey availability) and forest succession (Niemelä et al. 1996, Hättenschwiler et al. 2005, Oxbrough et al. 2010). We thus hypothesize that: (1) spider assemblage structure changes with increasing diversity of woody plants and with stand age (Sobek et al. 2009, Oxbrough et al. 2010); (2) woody plant diversity and stand age increase the number of spiders specific to the individual forest stands (Oxbrough et al. 2010, Proulx et al. 2010); and at the same time (3) temporal variability in both spider richness and abundance decreases with increasing plant species richness (Haddad et al. 2010, Proulx et al. 2010) and stand age (Anderson 2007, Dovciak and Halpern 2010).

## Methods

### Study site and sampling design

Twenty-seven study plots were established in the Gutianshan National Nature Reserve (29°14' N, 118°07' E), Zhejiang Province, southeast China. The reserve is located in a low mountain range (300–1260 m asl) and comprises 81 km<sup>2</sup> of semi-evergreen broad-leaved forest. It is characterized by a subtropical monsoon climate, with a mean annual temperature of 15.3°C and mean annual precipitation of about 2000 mm (Hu and Yu 2008, Legendre et al. 2009). Plots were 30 × 30 m and selected based on the species richness of woody plants (ranging from 25–69 species per plot) and the successional age (between < 20 and > 80 years) of the forest stands (Bruelheide et al. 2011). They were randomly distributed across the whole reserve,

with limitations to site selection due to inaccessibility or steep slopes ( $> 55^\circ$ ). For details on plot establishment and plot characteristics see Bruelheide et al. (2011).

In the center of each plot, four pitfall traps for continuous trapping of epigeic spiders were installed in the corners of a  $10 \times 10$  m square. Traps consisted of 550 ml plastic jars (diameter 8.5 cm) filled with 150 ml of a trapping solution (40% ethanol, 30% water, 20% glycerol, 10% acetic acid, with a few drops of detergent to reduce surface tension). Traps were emptied at fortnightly intervals during the main growing season, from 30 March to 2 September 2009. As pitfall traps can provide information on abundances, but record activity patterns in particular, we refer to 'activity abundance' to characterize trap catches (Southwood and Henderson 2000). Adult spiders (accounting for 78% of all individuals caught) were determined to species (Song and Zhu 1999) or, in most cases, morphospecies (within families or genera) on the basis of their genitalia.

The study plots represent subsections of larger forest expanses for which they can be considered typical, and many arthropod predators can establish viable populations in areas comparable to the size of our plots (e.g., Matern et al. 2008). Moreover, species richness of woody plants at the plot level was strongly correlated with richness at subplot levels (Schuldt et al. 2011). Plot size can thus be considered to have had little effect on the general results of our study.

### Habitat characteristics

While an advantage of observational studies is that they can be conducted in natural systems with established plant and animal communities, potentially confounding factors need to be taken into account when studying the effects of selected environmental factors (Vilà et al. 2005). We therefore recorded biotic and abiotic habitat characteristics that potentially influence spider assemblages (e.g., via habitat structure, microclimate or prey availability). Species richness of woody plants in the 27 study plots was based on the assessment of all tree and shrub individuals  $> 1$  m height. Plots were assigned to one of five successional stages ( $< 20$ ,  $< 40$ ,  $< 60$ ,  $< 80$

and  $\geq 80$  years old). Stand age was verified from stem core analyses and diameter at breast height (dbh) measurements, and for consistency across plots standardized to the age of the fifth largest tree (as single old trees were retained during harvesting in some of the young plots) in each plot, which was shown to be representative of the overall stand age (Bruelheide et al. 2011). Measures of tree density and total basal area in each plot were strongly related to stand age and, to avoid multicollinearity, were not included in the analyses (see Schuldt et al. 2011). Altitude, canopy cover and herb cover (%) were measured during plot establishment in 2008 and included as further plot characteristics. Soil pH (0–5 cm) was determined from dried and sieved samples taken in the summer of 2009 (Bruelheide et al. 2011). In addition, we recorded litter depth and vegetation cover (%) in the herb layer in a  $1 \times 1$  m area around each trap, as the surrounding matrix of the traps can affect movement and catch efficiency (Southwood and Henderson 2000).

### Statistical analysis

We used additive partitioning of spider species richness based on Lande (1996) to determine  $\alpha$ - (mean richness per plot over the trapping period) and spatial  $\beta_{\text{between}}$ - (turnover in species richness between plots) components of overall  $\gamma$ -diversity across all plots, with  $\gamma = \alpha + \beta$ . Likewise, we extracted a measure of spatial turnover ( $\beta_{\text{within}}$ ) between the traps in each plot, calculated as the spatial  $\beta$ -component of the total number of species recorded in each plot, to quantify the spatial heterogeneity of the spider assemblages within plots. We used Mantel tests to check whether patterns in species turnover between traps within plots, and the species richness between plots, were dependent on the spatial location of the plots. Species turnover and similarity in spider assemblages between the 27 plots was further analyzed using non-metric multidimensional scaling (NMDS) based on the Morisita-Horn index. This index, based on relative abundances of species, is density-invariant and resistant to potential undersampling (Jost et al. 2011). Data were square root-transformed, and the minimal number of required dimensions was determined based on the

reduction in stress for solutions with one to six dimensions. A stable solution was computed from multiple random starting configurations. Results were centered, and principal components rotation was used to obtain maximum variance of points on the first dimension (Quinn and Keough 2002). To evaluate the potential impact of environmental factors on spider assemblage structure, habitat parameters were standardized and fitted to the ordination plot on the basis of a regression analysis with the NMDS axes scores (Quinn and Keough 2002). Significance of the correlations was assessed with permutation tests ( $N = 1000$ ).

We used a specificity index that compares the observed and expected abundance of each spider species for each forest stand, to test whether the degree of habitat specificity of spiders was related to the species richness of woody plants, stand age or other habitat parameters of the plots (see next section). We followed the approach of Tylianakis et al. (2005), where the number of individuals of species  $i$  in plot  $j$  that would be expected ( $E_{ij}$ ) from a random distribution of the species across all plots was calculated as  $E_{ij} = N_i \times P_j$ , where  $N_i$  is the total number of individuals of species  $i$  across all plots, and  $P_j$  the proportion of the total number of individuals of all species caught in plot  $j$ . Specificity was then defined as the deviation in abundance patterns of species  $i$  from this random distribution. It was calculated as  $\log_{10}([O_{ij}/E_{ij}] + 1)$ , where  $O_{ij}$  is the actual number of species  $i$  observed in plot  $j$  (Tylianakis et al. 2005). Specificity for each plot was expressed as the mean specificity index across all species (with a total of  $\geq 4$  individuals to reduce the influence of accidental occurrences.) found in the given plot. We also tested for a more general successional pattern in the species composition of the spider assemblages by analyzing whether spider species were significantly associated with one of the five successional stages. We used the group-equalized phi coefficient ( $r_{\phi}^g$ ), based on the frequencies of all spider species (excluding species with a total number of  $< 4$  individuals) across the plots of the five successional stages (De Cáceres and Legendre 2009).

Temporal variability in species richness and activity abundance were calculated as the coefficients of variation (CV = standard deviation divided by the mean) of richness and abundance (mean of all traps per plot), respectively, among sampling intervals. We used linear regression models to assess the impact of woody plant species richness, forest stand age and other habitat characteristics on spider specificity and temporal variability in species richness and activity abundance. Significant non-linear relationships were accounted for by including second-order polynomials. Potential effects of the number of individuals caught on the CV of species richness were controlled for by including activity abundance as a covariate in the regression of richness CV. We also checked for multicollinearity among the predictors included in our analyses, but correlations were  $< 0.6$  (Pearson's  $r$ ) in all cases. The full models were simplified in a stepwise procedure based on the reduction in AICc (Burnham and Anderson 2004). Models with the lowest AICc (and with the smallest number of predictors in the case of  $\Delta AICc < 2$  between two candidate models) were selected as minimal, best-fit models (Burnham and Anderson 2004). Model residuals were checked for normality and homoscedasticity.

All analyses were performed in R 2.12.0 (R Development Core Team 2010).

## Results

In the total catch of 6166 adult spiders of 195 (morpho-) species from 28 families, Lycosidae (34% of all individuals) and Liocranidae (24%) were the most abundant. Salticidae (18% of all species) and Linyphiidae (15%) were the most species-rich.

### Spatial variation and specificity in assemblage structure

Additive partitioning of species richness revealed a strong spatial turnover in species between plots, with a mean  $\alpha$ -richness of 34.9 ( $\pm 1.04$  SE) species (17.9% of  $\gamma = 195$ ), compared to a  $\beta_{between}$ -component of 160.1 species (82.1%). This pattern remained constant even when rare species (which might potentially comprise species that were recorded in a limited number of plots due to

**Table 7.1.** Correlation coefficients, explained variation ( $R^2$ ) and probabilities (based on 1000 permutations) for the relationships between environmental variables (ordered by  $R^2$ ) and the NMDS axes scores

Factor	NMDS 1	NMDS 2	$R^2$	$P$
Altitude	-0.01	-1.00	0.74	0.001
Location (Longitude)	0.79	-0.62	0.51	0.001
Location (Latitude)	-0.42	-0.91	0.30	0.015
Stand age <sup>a</sup>	0.94	-0.33	0.28	0.019
Litter depth	0.23	0.97	0.25	0.028
Woody plant species richness	0.99	0.14	0.20	0.058
Herb cover	0.12	0.99	0.17	0.110
Soil pH	-0.63	0.77	0.16	0.114
Vegetation cover	-0.69	0.73	0.13	0.188
Canopy cover	-0.21	0.98	0.04	0.664

<sup>a</sup>Based on the age of the 5th largest tree individual, cf. Bruelheide et al. (2011)

insufficient sampling) were excluded from the analysis ( $a = 13.0\%$  vs.  $\beta_{between} = 87.0\%$  for all species with  $\geq 4$  individuals). There was also a high spatial turnover between traps within the individual plots (mean  $\beta_{within} = 17.58 (\pm 0.64$  SE) species, accounting on average for 50.3 percent of the mean richness of 34.9 species per plot). This turnover tended to decrease with increasing stand age (Pearson’s  $r = -0.32$ ;  $P = 0.099$ ), but was not related to woody plant species richness ( $r = 0.04$ ;  $P = 0.824$ ). Neither the spatial turnover within plots nor the change in species richness across plots was affected by spatial autocorrelation (Mantel tests:  $r = 0.02$ ;  $P = 0.404$ , and  $r = 0.12$ ;  $P = 0.141$ , respectively).

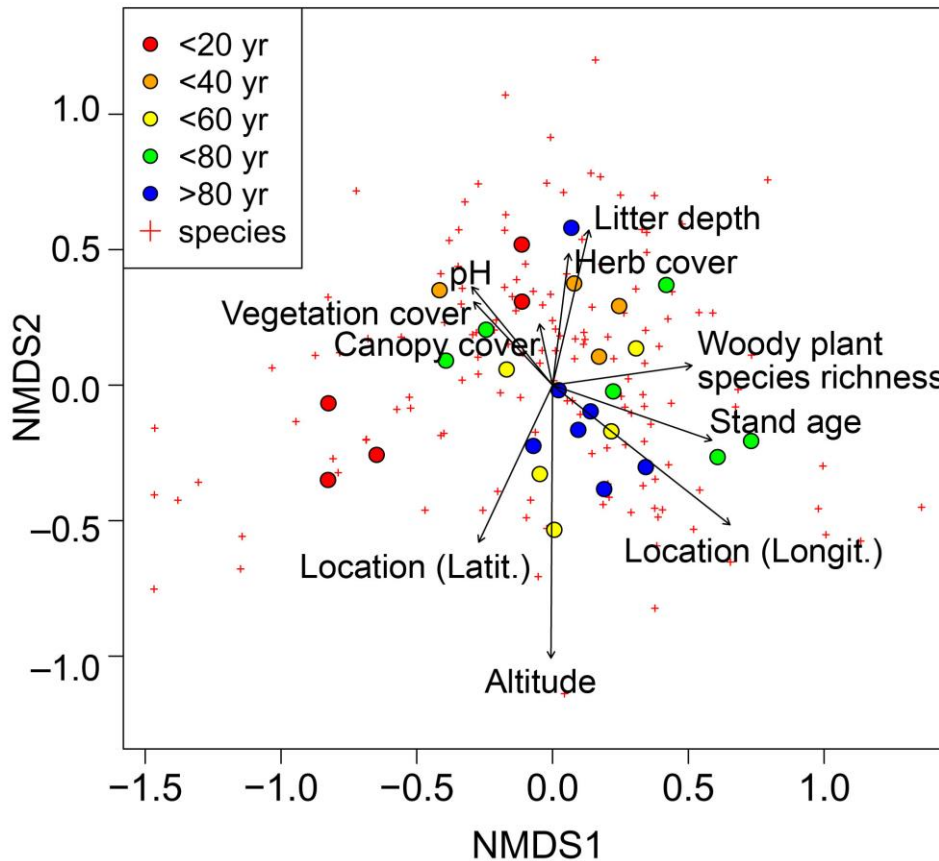
The spatial turnover in spider assemblages between plots is also shown by the NMDS ordination plot (Fig. 7.1). The largest reduction in stress was achieved by a two-dimensional solution after three random starts (minimum stress value = 13.16). The clear differentiation of the 27 plots was particularly strongly correlated with altitude, spatial location of the plots, and stand age (Table 7.1). Species richness of woody plants had a marginally significant effect on spider assemblage structure (Fig. 7.1; Table 7.1).

In contrast, neither woody plant species richness nor stand age had an effect on the degree of specificity of spider species for individual forest stands (Pearson’s  $r = 0.05$ ,  $P = 0.80$  and  $r = -0.29$ ,  $P = 0.15$ , respectively), and they were not included in

the minimal regression model (Table 7.2). The specificity index was only related to percentage cover of the herb layer around the traps and showed a linear increase with increasing herb cover ( $0.001 \pm 0.0003$  SE) (Fig. 7.2A, Table 7.2). Likewise, the majority of spider species were not associated with a specific successional stage.

**Table 7.2.** Linear model results for the specificity of spider species ( $F_{1, 25}$ ;  $R^2_{adj.} = 0.32$ ) and for temporal variability (CV) in species richness ( $F_{3, 23} = 16.6$ ;  $R^2_{adj.} = 0.64$  for the overall model) and activity abundance ( $F_{1, 25} = 8.6$ ;  $R^2_{adj.} = 0.23$ ) across the 27 forest plots in subtropical China. Significant non-linear relationships were accounted for by including second-order polynomial

Factor	Response	df	$F$	$P$
<i>Specificity</i>				
Herb cover	+	1, 25	13.29	0.001
<i>CV species richness</i>				
Activity abundance	-	1, 23	24.93	<0.001
Stand age	+	1, 23	18.32	<0.001
Stand age <sup>2</sup>	-	1, 23	6.61	0.017
<i>CV activity abundance</i>				
Stand age	+	1, 25	8.60	0.007



**Figure 7.1.** NMDS ordination plot (based on Morisita-Horn index of square root-transformed relative abundance data) of the assemblages of epigeic spider species in the 27 forest stands. Stress = 13.16. Environmental variables were standardized and fitted in a post-hoc correlation procedure with the axes scores. See Table 7.1 for significance of correlations.

Only three species showed a significant association with the youngest successional stage, five with plots of an age between 20 and 40 yr, and one with the oldest successional stage (Table S7.1).

### Temporal variability in species richness and abundance

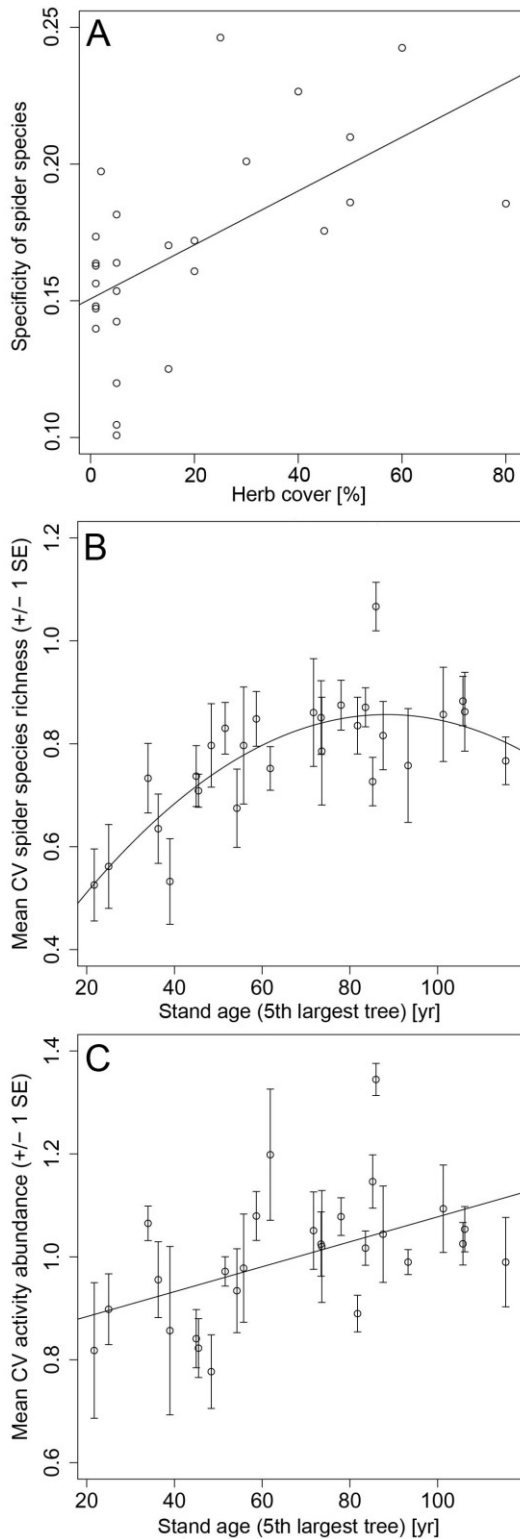
Temporal variability in species richness of spiders per plot decreased with increasing  $\alpha$ -richness per sampling interval (Pearson's  $r = -0.49$ ,  $P = 0.01$ ), whereas temporal variability in activity abundance was not significantly related to mean activity abundance per sampling interval (Pearson's  $r = -0.23$ ,  $P = 0.25$ ). Species richness of woody plants did not affect the temporal variability of spider species richness or activity abundance in the 27 forest stands. Rather, stand age explained notable parts of the patterns in the CV for richness (when controlling for activity abundance, which had a strong negative effect

on the richness CV; Table 7.2) and abundance of spiders (Table 7.2, Fig. 7.2B,C). Temporal variability in spider species richness increased with stand age ( $0.069 \pm 0.015$  SE) and levelled out at the oldest plots ( $-0.039 \pm 0.015$  SE) (Fig. 7.2B). Stand age was also positively related to the temporal variability of activity abundance of spiders (Fig. 7.2C). The latter increased linearly with stand age ( $0.002 \pm 0.001$  SE). The temporal variability measures of richness and activity abundance were also correlated with the scores of the first axis of the NMDS for spider assemblage structure (Pearson's  $r = 0.61$ ;  $P < 0.001$  for the CV of species richness, and  $r = 0.48$ ;  $P = 0.01$  for the CV of activity abundance).

### Discussion

A better understanding of the role of trophic interactions in the functioning of ecosystems and the development of appropriate strategies for biodiversity conservation requires testing





**Figure 7.2.** Relationships between (A) specificity of spider species and percent herb cover, (B) temporal variability (among sampling intervals) in spider species richness and stand age (standardized by the age of the 5<sup>th</sup> oldest tree individual), and between (C) temporal variability in spider activity abundance and stand age across the 27 study plots. All relationships were significant with  $P < 0.05$ .

whether patterns derived from simplified experimental and often low-diversity systems

can be transferred to species-rich and complex natural ecosystems (*cf.* Tylianakis et al. 2008, Hillebrand and Matthiessen 2009). Our results provide insight into spatial patterns of species composition and temporal variability in epigeic spider assemblages, complementing previous findings from our study system on overall richness and abundance patterns (Schuldt et al. 2011). They are only in part in accordance with our expectations and suggest that the relevance of common hypotheses on the relationship between plants and higher trophic levels is not necessarily supported for such real-world ecosystems (see also Zhang and Adams 2011).

### Spatial variation in spider assemblage structure

In line with our expectations we found a clear turnover in species composition between plots. As expected for the topographically heterogeneous study region, the assemblage structure of epigeic spiders was notably affected by altitude and spatial location. These two factors represent general changes in environmental conditions (*e.g.*, temperature) important for the structuring of assemblages (*e.g.*, Novotny and Weiblen 2005, Axmacher et al. 2009). Yet, variables showing the highest correlation with the first NMDS axis were stand age and woody plant species richness. Both variables can modify environmental conditions on the forest floor (Hättenschwiler et al. 2005, Leuschner et al. 2009) and might thus influence spider assemblage composition and the occurrence of individual species, which are sensitive to such changes in habitat conditions (Niemelä et al. 1996, Oxbrough et al. 2010).

The impact of woody plant species richness and its modifying effect on habitat characteristics, however, was less strong than that of stand age and topography. While generalist predators such as spiders might not directly depend on plant species and plant diversity, spider species differ in their habitat requirements, foraging strategies and food requirements, which in turn can be influenced by plant species diversity and composition (Zhang and Adams 2011). An impact of plant species composition on spider assemblage structure even across such highly plant-diverse

forest stands is indicated by strong correlations between the NMDS axes scores for spiders and scores from an NMDS on woody plant species composition of the study plots (Bruehlheide et al. 2011) (Pearson's  $r = 0.79$  and  $-0.70$  for correlations between scores of the first and the second axes, respectively;  $P < 0.001$ ). These correlations only reflect to a limited degree similar response of spiders and plants to common environmental drivers such as stand age and altitude (*cf.* Bruehlheide et al. 2011), but instead point rather to a structuring role of tree and shrub species identity in the assembly of epigeic spider communities (Schuldt et al. 2008, Zhang and Adams 2011).

### Specificity of spider species

Despite the general effects of woody plant species richness and stand age on spider assemblage structure, these variables did not influence the specificity (*i.e.*, the degree to which species are specific to the individual forest stands) of spiders across the 27 study plots. The only variable significantly related to specificity was the percentage herb cover, which is important to web-builders and species foraging in the vegetation close to the forest floor (Oxbrough et al. 2005, Schuldt et al. 2008). Herb cover, in turn, was not significantly related to woody plant richness or plot age (see also Both et al. 2011). The number of rare species and habitat specialists has previously been found to increase during succession (Anderson 2007, Dovciak and Halpern 2010, Oxbrough et al. 2010) and with increasing plant species richness, which is expected to provide a higher variation of habitat types or higher prey diversity (Oxbrough et al. 2010, Proulx et al. 2010).

One reason for our failure to find these patterns could be that, while differences in diversity-mediated habitat conditions are important for the general structuring of spider assemblages, actual increases in habitat heterogeneity (*e.g.*, litter diversity and structure) that benefit habitat specialists are not as pronounced across our plant diversity gradient as might be the case in less diverse plant communities investigated by previous studies (*e.g.*, Schuldt et al. 2008, Haddad et al. 2010). The same might be true for differences between young and old stands, as younger

plots in these species-rich forests already show a high degree of habitat heterogeneity. Moreover, many spiders have a high power of dispersal (Niemelä et al. 1996), such that many forest specialists may have colonized younger stands relatively quickly from the surrounding forest (Niemelä et al. 1996, Oxbrough et al. 2010). This is supported by our phi coefficient analysis of general successional patterns: the majority of spider species did not show a significant association with a particular successional stage. While the relative abundance of spider species might change with successional age, as shown by the NMDS, the process of species assembly does not seem to be strongly affected by succession. Rather, many species occurring in older forest stands can also be frequently found in young stands (see also Mallis and Hurd 2005).

### Temporal variability in species richness and activity abundance

While we previously found a negative effect of woody plant species richness on overall patterns of spider activity abundance and no effect on spider species richness for the total sampling period (Schuldt et al. 2011), woody plant species richness might still have the potential to stabilize spider assemblages. As different spider species respond in different ways to changes in environmental conditions over time, stands richer in plant species (with a potentially higher habitat variability) might be expected to exhibit lower temporal variability (CV) in richness or abundance of spiders over the sampling period (see also Root 1973, Haddad et al. 2010, Proulx et al. 2010). In fact, temporal variability of spider richness and abundance was correlated with the first axis of the spider NMDS, which, in turn, was related to stand age and woody plant species richness. Our regression analyses, however, did not show a direct relationship between woody plant species richness and the temporal variability of spider richness and abundance. While this is in contrast to findings of significant bottom-up effects of plant diversity on the temporal stability of predator assemblages in other ecosystems (Haddad et al. 2010, Proulx et al. 2010), our findings for temporal variability are supported

by results for overall diversity patterns of spiders in these forests (Schuldt et al. 2011). Effects of plant species richness on higher trophic levels could decrease with increasing trophic distance (Scherber et al. 2010) and might also be less pronounced (*i.e.*, level out) at high levels of plant species richness (Hooper et al. 2005), which could explain the patterns we found. Similarly, for instance, Veddeler et al. (2010) found no effect of tree diversity on the species richness of parasitoids and the temporal variability in parasitism, respectively, in a complex tropical agroforest system.

In contrast, and against expectations, our measures of temporal variability were higher in older than in younger forest stands. We are unable to directly elucidate the underlying mechanisms in our study, but as discussed above, correlations between the variability measures and spider NMDS scores indicate that spider species composition might have an effect on variability patterns. For instance, younger stands might be characterized by spider assemblages featuring a broader range of life strategies (*e.g.*, including more species from open habitats; *cf.* Oxbrough et al. 2010) than more mature stands, and larger differences in the main activity periods of the species could increase the temporal stability of overall activity abundance and species richness. Younger stands might also show a higher degree of small-scale heterogeneity in environmental conditions and thus higher compositional heterogeneity in spider species than more mature stands (Niemelä et al. 1996). This compositional heterogeneity might cause less similar responses of individual species to temporal changes in environmental conditions, which would also reduce overall temporal variability in abundances and species richness. In fact, the spatial  $\beta$ -richness component ( $\beta_{within}$ ) within plots showed that the spatial heterogeneity in spider species composition tended to decrease with increasing plot age. One reason for this could be that the proportion of deciduous trees decreased with increasing stand age (Bruehlheide et al. 2011), which might cause higher variability in habitat conditions for spiders in younger compared to older stands

over the growing season. Likewise, trait dissimilarity between woody plant species decreased with increasing stand age (M. Böhnke *et al.*, unpubl. data), which might also add to greater habitat heterogeneity in younger plots. Moreover, prey availability might play a role, in that for instance some of the herbivorous prey becomes scarcer near the forest floor as trees grow higher, such that prey availability or the diversity of prey might be higher and more stable for epigeic spiders in young stands with smaller trees (Hurd and Fagan 1992). Of course, our results only reflect temporal patterns of one growing season and considering interannual patterns is likely to yield further insights.

## Conclusions

Our study shows that while spider assemblage structure is, to a certain extent, related to plant community composition and woody plant species richness, these bottom-up effects do not result in increases in species specificity or a decrease in temporal variability of species richness and activity abundance of spiders. These findings argue against a strong impact of woody plant species richness on this important predatory taxon in our plant species-rich forest ecosystem (see also Schuldt et al. 2011). Results from studies of less diverse forests, however, are also not unambiguously supportive of the general assumptions of a positive effect of plant diversity on predators, as implied, for instance, by the enemies hypothesis (Schuldt et al. 2008, Vehviläinen et al. 2008). Rather, environmental variation which is independent of plant species richness, as caused by forest stand age and herb cover, seems to be important for epigeic spiders. Environmental heterogeneity has been shown in previous studies to modify biodiversity-function relationships in natural ecosystems (Cardinale et al. 2000, Tylianakis et al. 2008). The differences in assemblage structure and the large contribution of the spatial  $\beta$ -richness components to overall spider species richness show that spatial variation and the variety of forest stands, in terms of overall environmental heterogeneity, are also important factors for the conservation of the biodiversity of predator assemblages at a

regional scale in these forests.

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## References

- Anderson, K. J. 2007. Temporal patterns in rates of community change during succession. *Am. Nat.* 169: 780-793.
- Axmacher, J. C., G. Brehm, A. Hemp, H. Tunte, H. V. M. Lyaruu, K. Muller-Hohenstein, and K. Fiedler. 2009. Determinants of diversity in afro-tropical herbivorous insects (Lepidoptera: Geometridae): plant diversity, vegetation structure or abiotic factors? *J. Biogeogr.* 36: 337-349.
- Both, S., T. Fang, M. Böhnke, H. Bruelheide, C. Geißler, P. Kühn, T. Scholten, S. Trogisch, and A. Erfmeier. 2011. Lack of tree layer control on herb layer characteristics in a subtropical forest, China. *J. Veg. Sci.* 22: 1120-1131.
- Bruelheide, H., M. Böhnke, S. Both, T. Fang, T. Assmann, M. Baruffol, J. Bauhus, F. Buscot, X. Y. Chen, B. Y. Ding, W. Durka, A. Erfmeier, M. Fischer, C. Geißler, D. Guo, L. D. Guo, W. Härdtle, J. S. He, A. Hector, W. Kröber, P. Kühn, A. C. Lang, K. Nadrowski, K. Pei, M. Scherer-Lorenzen, X. Shi, T. Scholten, A. Schuldt, S. Trogisch, G. von Oheimb, E. Welk, C. Wirth, Y. T. Y. Wu, X. X. Zeng, S. Zhang, H. Zhou, K. Ma, and B. Schmid. 2011. Community assembly during secondary forest succession in a Chinese subtropical forest. *Ecol. Monogr.* 81: 25-41.
- Burnham, K. P., and D. R. Anderson. 2004. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York.
- Cardinale, B. J., K. Nelson, and M. A. Palmer. 2000. Linking species diversity to the functioning of ecosystems: on the importance of environmental context. *Oikos* 91: 175-183.
- De Cáceres, M., and P. Legendre. 2009. Associations between species and groups of sites: indices and statistical inference. *Ecology* 90: 3566-3574.
- Dovciak, M., and C. B. Halpern. 2010. Positive diversity-stability relationships in forest herb populations during four decades of community assembly. *Ecol. Lett.* 13: 1300-1309.
- Duffy, J. E. 2003. Biodiversity loss, trophic skew and ecosystem functioning. *Ecol. Lett.* 6: 680-687.
- Duffy, J. E., B. J. Cardinale, K. E. France, P. B. McIntyre, E. Thebault, and M. Loreau. 2007. The functional role of biodiversity in ecosystems: incorporating trophic complexity. *Ecol. Lett.* 10: 522-538.
- Dyer, L. A., T. R. Walla, H. F. Greeney, J. O. Stireman III, and R. F. Hazen. 2010. Diversity of interactions: a metric for studies of biodiversity. *Biotropica* 42:281-289.
- Eisenhauer, N., A. Milcu, A. C. W. Sabais, H. Bessler, J. Brenner, C. Engels, B. Klärner, M. Maraun, S. Partsch, C. Roscher, F. Schonert, V. M. Temperton, K. Thomisch, A. Weigelt, W. W. Weisser, and S. Scheu. 2011. Plant diversity surpasses plant functional groups and plant productivity as driver of soil biota in the long term. *PLoS ONE* 6: e16055.
- Garcia-Gunman, G., and J. Benitez-Malvido. 2003. Effect of litter on the incidence of leaf-fungal pathogens and herbivory in seedlings of the tropical tree *Nectandra ambigens*. *J. Trop. Ecol.* 19: 171-177.
- Givnish, T. J. 1999. On the causes of gradients in tropical tree diversity. *J. Ecol.* 87: 193-210.
- Haddad, N. M., G. M. Crutsinger, K. Gross, J. Haarstad, and D. Tilman. 2010. Plant diversity and the stability of foodwebs. *Ecol. Lett.* 14: 42-46.
- Hättenschwiler, S., A. V. Tiunov, and S. Scheu. 2005. Biodiversity and litter decomposition in terrestrial ecosystems. *Annu. Rev. Ecol. Evol. Syst.* 36: 191-218.
- Hillebrand, H., and B. Matthiessen. 2009. Biodiversity in a complex world: consolidation and progress in functional biodiversity research. *Ecol. Lett.* 12: 1405-1419.
- Hooper, D. U., F. S. Chapin, J. J. Ewel, A. Hector, P. Inchausti, S. Lavorel, J. H. Lawton, D. M. Lodge, M. Loreau, S. Naeem, B. Schmid, H. Setälä, A. J. Symstad, J. Vandermeer, and D. A. Wardle. 2005. Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecol. Monogr.* 75: 3-35.
- Hu, Z., and M. Yu. 2008. Study on successions sequence of evergreen broad-leaved forest in Gutian Mountain of Zhejiang, Eastern China:

- species diversity. *Front. Biol. China* 3: 45-49.
- Hurd, L. E., and W. F. Fagan. 1992. Cursorial spiders and succession: age or habitat structure? *Oecologia* 92: 215-221.
- Jactel, H., E. G. Brockerhoff, and P. Duelli. 2005. A test of the biodiversity-stability theory: meta-analysis of tree species diversity effects in insect pest infestations, and re-examination of responsible factors. *In* M. Scherer-Lorenzen, C. Körner, and E.-D. Schulze [Eds.], *Forest diversity and function: temperate and boreal systems*, 235-261. Springer, Berlin, Heidelberg.
- Jost, L., A. Chao, and R. L. Chazdon. 2011. Compositional similarity and  $\beta$  (beta) diversity. *In* A. E. Magurran and B. J. McGill [Eds.], *Biological diversity: frontiers in measurement and assessment*, 66-84. Oxford Univ. Press, New York.
- Lande, R. 1996. Statistics and partitioning of species diversity, and similarity among multiple communities. *Oikos* 76: 5-13.
- Legendre, P., X. C. Mi, H. B. Ren, K. P. Ma, M. J. Yu, I. F. Sun, and F. L. He. 2009. Partitioning beta diversity in a subtropical broad-leaved forest of China. *Ecology* 90: 663-674.
- Letourneau, D.K., J.A. Jedlicka, S.G. Bothwell, and C.R. Moreno 2009. Effects of natural enemy biodiversity on the suppression of arthropod herbivores in terrestrial ecosystems. *Annu. Rev. Ecol. Evol. Syst.* 40: 573-592.
- Leuschner, C., H. F. Jungkunst, and S. Fleck. 2009. Functional role of forest diversity: Pros and cons of synthetic stands and across-site comparisons in established forests. *Basic Appl. Ecol.* 10: 1-9.
- Mallis, R. E., and L. E. Hurd. 2005. Diversity among ground-dwelling spider assemblages: habitat generalists and specialists. *J. Arachnol.* 33: 101-109.
- Matern, A., C. Drees, H. Meyer, and T. Assmann 2008. Population ecology of the rare carabid beetle *Carabus variolosus* (Coleoptera: Carabidae) in North-west Germany. *J. Insect Conserv.* 12: 591-601.
- McCann, K. S. 2000. The diversity-stability debate. *Nature* 405: 228-233.
- Niemelä, J., Y. Haila, and P. Punttila. 1996. The importance of small-scale heterogeneity in boreal forests: Variation in diversity in forest-floor invertebrates across the succession gradient. *Ecography* 19: 352-368.
- Novotny, V., and G. D. Weiblen. 2005. From communities to continents: beta diversity of herbivorous insects. *Ann. Zool. Fenn.* 42: 463-475.
- Odum, E. P. 1969. The strategy of ecosystem development. *Science* 164: 262-270.
- Oxbrough, A., S. Irwin, T. C. Kelly, and J. O'Halloran. 2010. Ground-dwelling invertebrates in reforested conifer plantations. *For. Ecol. Manage.* 259: 2111-2121.
- Oxbrough, A. G., T. Gittings, J. O'Halloran, P. S. Giller, and G. F. Smith. 2005. Structural indicators of spider communities across the forest plantation cycle. *For. Ecol. Manage.* 212: 171-183.
- Pringle, R. M., and K. Fox-Dobbs. 2008. Coupling of canopy and understory food webs by ground-dwelling predators. *Ecol. Lett.* 11: 1328-1337.
- Proulx, R., C. Wirth, W. Voigt, A. Weigelt, C. Roscher, S. Attinger, J. Baade, R. L. Barnard, N. Buchmann, F. Buscot, N. Eisenhauer, M. Fischer, G. Gleixner, S. Halle, A. Hildebrandt, E. Kowalski, A. Kuu, M. Lange, A. Milcu, P. A. Niklaus, Y. Oelmann, S. Rosenkranz, A. Sabais, C. Scherber, M. Scherer-Lorenzen, S. Scheu, E. D. Schulze, J. Schumacher, G. Schwichtenberg, J. F. Soussana, V. M. Temperton, W. W. Weisser, W. Wilcke, and B. Schmid. 2010. Diversity Promotes Temporal Stability across Levels of Ecosystem Organization in Experimental Grasslands. *PLoS One* 5: e13382.
- Quinn, G. P., and M. J. Keough. 2002. *Experimental design and data analysis for biologists*. University Press, Cambridge.
- R Development Core Team. 2010. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, R Foundation for Statistical Computing, Vienna, Austria. Available from <http://www.R-project.org>.
- Riihimäki, J., P. Kaitaniemi, J. Koricheva, and H. Vehviläinen. 2005. Testing the enemies hypothesis in forest stands: the important role of tree species composition. *Oecologia* 142: 90-97.
- Root, R. B. 1973. Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). *Ecol. Monogr.* 43: 95-124.
- Schemske, D. W., G. G. Mittelbach, H. V. Cornell, J. M. Sobel, and K. Roy. 2009. Is there a latitudinal gradient in the importance of biotic interactions? *Annu. Rev. Ecol. Evol. Syst.* 40: 245-269.
- Scherber, C., N. Eisenhauer, W. W. Weisser, B. Schmid, W. Voigt, M. Fischer, E. D. Schulze, C. Roscher, A. Weigelt, E. Allan, H. Bessler, M. Bonkowski, N. Buchmann, F. Buscot, L. W. Clement, A. Ebeling, C. Engels, S. Halle, I. Kertscher, A. M. Klein, R. Koller, S. König, E. Kowalski, V. Kummer, A. Kuu, M. Lange, D.

- Lauterbach, C. Middelhoff, V. D. Migunova, A. Milcu, R. Müller, S. Partsch, J. S. Petermann, C. Renker, T. Rottstock, A. Sabais, S. Scheu, J. Schumacher, V. M. Temperton, and T. Tschamntke. 2010. Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. *Nature* 468: 553-556.
- Schmitz, O. J. 2009. Effects of predator functional diversity on grassland ecosystem function. *Ecology* 90: 2339-2345.
- Schuldt, A., N. Fahrenholz, M. Brauns, S. Migge-Kleian, C. Platner, and M. Schaefer. 2008. Communities of ground-living spiders in deciduous forests: Does tree species diversity matter? *Biodivers. Conserv.* 17: 1267-1284.
- Schuldt, A., S. Both, H. Bruelheide, W. Härdtle, B. Schmid, H. Zhou, and T. Assmann. 2011. Predator diversity and abundance provide little support for the enemies hypothesis in forests of high tree diversity. *PLoS ONE* 6: e22905; doi: 22910.21371/journal.pone.0022905.
- Sobek, S., I. Steffan-Dewenter, C. Scherber, and T. Tschamntke. 2009. Spatiotemporal changes of beetle communities across a tree diversity gradient. *Divers. Distrib.* 15: 660-670.
- Song, D., and Zhu, M. 1999. *The spiders of China*. Hebei Science and Technology Publ. House, Shijiazhuang.
- Southwood, T. R. E., and P. A. Henderson. 2000. *Ecological Methods*. Third Edition. Blackwell Science, Oxford.
- Srivastava, D. S., and T. Bell. 2009. Reducing horizontal and vertical diversity in a foodweb triggers extinctions and impacts functions. *Ecol. Lett.* 12: 1016-1028.
- Stork, N. E., and P. S. Grimbacher. 2006. Beetle assemblages from an Australian tropical rainforest show that the canopy and the ground strata contribute equally to biodiversity. *Proc. R. Soc. B* 273: 1969-1975.
- Straub, C. S., and W. E. Snyder. 2006. Species identity dominates the relationship between predator biodiversity and herbivore suppression. *Ecology* 87: 277-282.
- Thebault, E., and M. Loreau. 2005. Trophic interactions and the relationship between species diversity and ecosystem stability. *Am. Nat.* 166: E95-E114.
- Tylianakis, J. M., A. M. Klein, and T. Tschamntke. 2005. Spatiotemporal variation in the diversity of hymenoptera across a tropical habitat gradient. *Ecology* 86: 3296-3302.
- Tylianakis, J. M., T. A. Rand, A. Kahmen, A. M. Klein, N. Buchmann, J. Perner, and T. Tschamntke. 2008. Resource heterogeneity moderates the biodiversity-function relationship in real world ecosystems. *PLoS Biology* 6: 947-956.
- Veddeler, D., J. Tylianakis, T. Tschamntke, and A.-M. Klein. 2010. Natural enemy diversity reduces temporal variability in wasp but not bee parasitism. *Oecologia* 162: 755-762.
- Vehviläinen, H., J. Koricheva, and K. Ruohomaki. 2008. Effects of stand tree species composition and diversity on abundance of predatory arthropods. *Oikos* 117: 935-943.
- Vilà, M., P. Inchausti, J. Vayreda, O. Barrantes, C. Gracia, J. J. Ibáñez, and T. Mata. 2005. Confounding factors in the observational productivity-diversity relationship in forests. *In* M. Scherer-Lorenzen, C. Körner, and E. D. Schulze [Eds.], *Forest diversity and function: temperate and boreal systems*, 65-85. Springer, Heidelberg.
- Woodcock, B. A., and M. S. Heard. 2011. Disentangling the effects of predator hunting mode and habitat domain on the top-down control of insect herbivores. *J. Anim. Ecol.* 80: 495-503.
- Zhang, Y. A., and J. Adams. 2011. Top-down control of herbivores varies with ecosystem types. *J. Ecol.* 99: 370-372.

### Supplementary Material

Additional Supporting Information may be found in the online version of this article.

Table S7.1. *Spider species significantly associated with one of five successional stages, based on the group-equalized phi coefficient  $r_{\phi}^g$ .*

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**Supplementary Material**

**Table S7.1.** Spider (morpho-) species significantly associated with one of the five successional stages (1-5: < 20, < 40, < 60, < 80 and  $\geq$  80 years old), based on the group-equalized phi coefficient  $r_{\phi}^g$

Species	Family	Successional stage	$r_{\phi}^g$	<i>P</i>
<i>Pardosa procurva</i> Yu and Song 1988	Lycosidae	1	0.63	0.006
<i>Xysticus kurilensis</i> Strand 1907	Thomisidae	1	0.63	0.005
<i>Pardosa laura</i> Karsch 1879	Lycosidae	1	0.52	0.050
<i>Zelotes</i> spec_3	Gnaphosidae	2	0.60	0.012
<i>Agelenidae</i> spec_6	Agelenidae	2	0.59	0.024
<i>Linyphiinae</i> spec_5	Linyphiidae	2	0.57	0.038
<i>Phintella</i> spec_1	Salticidae	2	0.56	0.015
<i>Gamasomorpha</i> spec_1	Oonopidae	2	0.56	0.026
<i>Xysticus</i> spec_1	Thomisidae	5	0.64	0.010

Nomenclature after Platnick NI (2011) The world spider catalog, version 12.0. American Museum of Natural History, online at <http://research.amnh.org/iz/spiders/catalog>. Accessed July 2011. DOI: 10.5531/db.iz.0001





# CHAPTER 8

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# Tree diversity promotes functional dissimilarity and maintains functional richness despite species loss in predator assemblages

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## Abstract

The effects of species loss on ecosystems depend on the community's functional diversity. However, how functional diversity responds to environmental changes is poorly understood. This applies particularly to higher trophic levels, which regulate many ecosystem processes and are strongly affected by human-induced environmental changes. We analyzed how functional richness, evenness, and divergence of important generalist predators—epigeic spiders—are affected by changes in woody plant species richness, plant phylogenetic diversity, and stand age in highly diverse subtropical forests in China. Functional evenness and divergence of spiders increased with plant richness and stand age. Functional richness remained on a constant level despite decreasing spider species richness with increasing plant species richness. Plant phylogenetic diversity had no consistent effect on spider functional diversity. The results contrast with the negative diversity effect on spider species richness and suggest that functional redundancy among spiders decreased with increasing plant richness through nonrandom species loss. Moreover, increasing functional dissimilarity within spider assemblages with increasing plant richness indicates that the abundance distribution of predators in functional trait space affects ecological functions independent of predator species richness or the available trait space. While plant diversity is generally hypothesized to positively affect predators, our results only support this hypothesis for functional diversity—and here particularly for trait distributions within the overall functional trait space—and not for patterns in species richness. Understanding the way predator assemblages affect ecosystem functions in such highly diverse, natural ecosystems thus requires explicit consideration of functional diversity and its relationship with species richness.

**Key words:** BEF China; biodiversity; ecosystem function; invertebrate; trophic interaction

## Introduction

Increasing awareness that major human activities negatively affect species and ecosystems has focused much attention on disentangling the relationship between biodiversity and the functioning of ecosystems (Hooper et al. 2005; Naeem et al. 2012). While many studies have demonstrated positive effects of species richness on ecosystem functioning and stability (Cardinale et al. 2012; Hooper et al. 2012), much of our current

knowledge is based on relatively species-poor plant communities and experiments from grassland ecosystems (Schmid et al. 2009). However, species-rich ecosystems such as tropical and subtropical forests are particularly affected by habitat degeneration and alteration, and the consequences of species loss for ecological processes and the resulting ecosystem services are of high ecological and economic importance (Kremen et al. 2000; Lopez-Pujol et al. 2006).

Most importantly, however, it has

become clear that in many cases the effects of species richness depend on the diversity of the respective species' functional traits (Hooper et al. 2005). Yet, this functional trait diversity is not necessarily a linear function of species richness (e.g. Mason et al. 2008), and contrasting patterns of species and functional diversity indicate that species diversity may not always be a consistent predictor of the diversity and strength of functional effects of species assemblages (Böhnke et al. 2013; Devictor et al. 2010; Villéger et al. 2010). Recent studies have shown that functional diversity might better explain biodiversity effects on ecosystem functions than species richness measures (e.g. Cadotte et al. 2009). Yet, our knowledge of how functional diversity, and consequently the functional effects, of species assemblages are affected by environmental changes—whether of anthropogenic or natural cause—still lags behind our understanding of general patterns in species richness (Feld et al. 2009). This applies particularly to higher trophic levels such as predators, which affect ecosystem functions through their interactions with primary consumers and producers (Haddad et al. 2009; Schmitz 2006). Trophic interactions play a crucial role in species-rich subtropical and tropical forests (Terborgh 2012), but little attention has been paid to how tree diversity or forest age affect predator functional diversity. Knowledge of such relations is also particularly relevant for conservation strategies concerned with the question of whether secondary (and potentially less species-rich) forests can preserve the functional diversity of higher trophic levels in the face of increasing loss of natural forests (Bihn et al. 2010).

Here, we analyze key features of the functional diversity of epigeic spiders across gradients in woody plant species richness and stand age in a highly diverse forest ecosystem in subtropical China. The forest floor compartment contributes a substantial part of the overall arthropod diversity of species-rich forests (Stork and Grimbacher 2006), and epigeic spiders can have an important impact on ecosystem functions in these forests by affecting decomposers (e.g. Wise 2004) and herbivores (which often spend part of their life cycle on the forest floor or are affected by

epigeic predators when feeding on tree seedlings; e.g. Riihimäki et al. 2005; Visser et al. 2011). A previous study in these forests indicated that the functional effects of these predators might be opposed to species richness effects (Schuldt et al. 2011). However, these indications were based on a coarse assignment of spiders to functional groups that excluded variation in functional traits within groups and did not account for abundance patterns or body size distributions. Here, we incorporate a variety of traits related to the resource use of spiders into complementary measures of functional diversity which allow for a thorough assessment of the richness, evenness and divergence of functional traits within species assemblages (Mouchet et al. 2010; Villéger et al. 2008). In short, functional richness measures the volume of trait space occupied by an assemblage, whereas functional evenness and divergence characterize how regular and dissimilar, respectively, the species are distributed in this functional trait space (Pavoine and Bonsall 2011; Villéger et al. 2008). Higher functional richness, but also higher evenness or divergence, would indicate a broader resource use within the spider assemblages and might, in consequence, lead to stronger prey control.

Besides testing for the effects of woody plant species richness (as the most general and widely used measure of diversity) and forest age, we included phylogenetic diversity of the forest stands as a predictor of the functional diversity of spiders. Phylogenetic diversity of plant communities might be used as a proxy for unmeasured functional plant traits (see Cadotte et al. 2009; Purschke et al. 2013) and has recently been shown to affect the abundance of predators in a grassland experiment (Dinnage et al. 2012). However, comparative data from other ecosystems are lacking so far. We hypothesize that (i) depending on how strongly functional richness is related to spider species richness, it either decreases (strong relationship with the likewise decreasing spider richness observed in the studied forests; Schuldt et al. 2011) or increases (weak relationship due to functional redundancy; stronger effects of potentially available niches or resources; Root 1973,

Haddad et al. 2009) with woody plant species richness, phylogenetic diversity and plot age. Moreover, we expect (ii) the evenness and divergence of abundances of spiders within the available trait space to increase with plant diversity and plot age, independent of patterns in functional richness. Older and more plant species-rich plots might promote resource diversity and allow abundant and more specialized species to effectively separate within the available niche space (Mason et al. 2008).

## Methods

### Study site and sampling design

The study was conducted in the Gutianshan National Nature Reserve (9°14' N, 118°07' E), Zhejiang Province, southeast China. The reserve covers 81 km<sup>2</sup> of mountainous, semi-evergreen broad-leaved forest (at 300 – 1260 m a.s.l.) and is characterized by a subtropical monsoon climate (mean annual temperature ca. 15°C, mean annual precipitation ca. 2000 mm) (Legendre et al. 2009). Dominant tree species are *Castanopsis eyrei* (Champ. ex Benth.) Tutch. and *Schima superba* Gardn. et Champ. A total of 27 study plots (30 x 30 m) were established in 2008. The plots were selected based on stand age (ranging between < 20 and > 80 yr) and species richness of woody plants (25–69 species) (see Bruelheide et al. 2011 for details).

Four pitfall traps were installed in the corners of the central 10 x 10 m square of each plot in 2009. Traps (550 ml plastic cups with an upper diameter of 8.5 cm) were filled with an ethanol-glycerol-acetic acid solution as a trapping fluid and emptied fortnightly during the main growing season from 30 March to 2 September 2009 (Schuldt et al. 2011).

### Functional traits

Adult spiders, which accounted for almost 80% of the total catch, were determined to species or morphospecies (within families or genera) on the basis of their genitalia. For our analyses of functional diversity, we selected five traits that are considered to have a major effect on the foraging characteristics of spiders (Cardoso et al. 2011) and thus strongly determine the functional impact of spider assemblages on their prey. Specifically, these

were body size, phenology, hunting type, vegetational stratification and prey range. Body size was measured as the total length from the front of the carapace to the end of the abdomen. Body size influences a wide range of ecological and physiological characteristics of a species (e.g. locomotion, space use, life history) and, in particular, strongly affects resource use (Brose et al. 2006). Up to six individuals per species were measured, and mean body size (averaged across male and female data) was used as a continuous variable. Phenology was based on the main activity periods of each species over the trapping season. The three categories (early, late, or whole season) were reclassified as two binary variables (early and late, where whole-season species have positive values in both cases) for the analyses, and each of the two variables was assigned a weight = 0.5 in the calculation of the functional diversity indices to ensure overall equal weights for each trait (Laliberté and Legendre 2010). Differences in species phenology determine temporal patterns of predator pressure within species assemblages and can promote the coexistence of otherwise ecologically similar species (Uetz 1977). Spiders can further be separated in terms of their hunting type into web-building and cursorial species, and this classification can be refined by the vegetation stratum that is primarily used and the range of prey organisms consumed. These characteristics contribute to resource partitioning among species and thus to defining the functional effects of predators on prey communities. Hunting type, vegetation stratum and prey range were coded as binary variables depending on whether species were web-builders or cursorial hunters, preferred forest floor habitats or higher vegetational strata, and whether they were generalists or prey specialists (e.g. many Mimetidae and Zodariidae are specialized spider and ant hunters, respectively; Jocqué and Dippenaar-Schoeman 2007). Data on hunting type, stratum and prey range is mostly available at a family or genus level only. However, these traits have been shown to be largely conserved within families and are sufficient to enable adequate classification of species in most cases (Cardoso et al. 2011). We used data from

Jocqué and Dippenaar-Schoeman (2007), Cardoso et al. (2011), and our own observations to assign species to the respective hunting type, preferred stratum and prey range.

### Environmental variables

Woody plant species richness was based on all tree and shrub individuals > 1 m height. Plot age was estimated from stem cores and diameter at breast height (dbh) measurements (Bruehlheide et al. 2011). We also calculated Shannon diversity and evenness of the woody plant communities based on the total basal area of each species in the plots. Shannon diversity was highly correlated with woody plant species richness ( $r = 0.81$ ;  $P < 0.001$ ), and we only included evenness (less strongly correlated,  $r = 0.57$ ;  $P < 0.001$ ) as an additional measure of woody plant diversity in our analyses. We also included the species richness of the herb layer, measured as the species richness of all plant individuals < 1 m in the central 10 x 10 m of each plot (Both et al. 2011). To assess the potential impacts of the phylogenetic composition of the woody plant communities on spiders, we calculated several measures of phylogenetic diversity (see Statistical analysis). As functional measures of plant diversity based on traits that can be meaningfully related to spider diversity were difficult to obtain for our study, phylogenetic diversity might help to quantify functional differences among woody plant species in the studied forests stands (e.g. Cadotte et al. 2009).

Observational studies in natural ecosystems have the advantage of testing ecological hypotheses under real world conditions with established plant and animal communities; however, plot characteristics that might potentially confound the results need to be taken into account. We therefore included altitude (m), soil pH, canopy cover (%) and cover of the herb layer (%) at the plot level, and litter cover (%), litter depth (cm) and vegetation cover (%) at the trap level as covariables in our analyses. These variables can influence spiders via effects on microclimate or habitat structure (Southwood and Henderson 2000). Altitude, canopy and herb layer cover were assessed during plot

establishment in 2008. Soil pH (0-5 cm) was measured from dried and sieved samples in the summer of 2009 (Bruehlheide et al. 2011). At the same time, trap-level data were measured in a 1 x 1 m square around each pitfall trap. Measures of tree density and basal area were not included in the analyses due to strong collinearity with plot age (see Schuldt et al. 2011). While none of these variables were strongly correlated with, and their effects thus independent of, woody plant species richness (maximum correlation was  $r = 0.24$ ), not accounting for this environmental variability might obscure potential effects of woody plant species richness on spider functional diversity.

### Statistical analysis

Functional diversity (FD), like all measures of diversity, can be split into independent components that characterize distinct aspects of this diversity, namely richness, regularity or evenness, and divergence of functional diversity within species assemblages (Mouchet et al. 2010; Pavoine and Bonsall 2011; Schleuter et al. 2010). For our study, we used the multidimensional functional richness (FRic), functional evenness (FEve) and functional divergence (FDiv) indices proposed by Villéger et al. (2008). These indices have been shown to be adequate and complementary measures of FD, which allow for incorporation of different data types and (in the case of FEve and FDiv) species abundances (Laliberté and Legendre 2010; Mouchet et al. 2010; Schleuter et al. 2010). FRic usually increases with the number of species in an assemblage, whereas FEve and FDiv are less affected by species richness (Pavoine and Bonsall 2011; Schleuter et al. 2010). FRic estimates the amount of functional space occupied by a given species assemblage by calculating the convex hull volume that comprises the entire trait space filled by all species of this assemblage (Villéger et al. 2008). It can thus be used as a proxy of the range of functional traits represented in an assemblage, but does not take into account (in contrast to FEve and FDiv) differences in species abundance. Whereas FRic can increase with the overall range of trait values in an assemblage, FEve and FDiv are relative

measures of the evenness and divergence, respectively, of trait distributions within the convex hull of functional richness and are thus independent of the overall range of functional traits. FEve increases with increasing regularity of species' abundances within the trait space. Functional evenness is highest when the spacing among species with different trait values is identical and all species are equally abundant. FDiv complements this measure by quantifying how species abundances are distributed in trait space. It is low when species with high abundances have trait values that are close to the center of functional trait space of an assemblage, and high when abundant species strongly deviate from these central trait values (Villéger et al. 2008).

The functional diversity indices were calculated on the basis of the above spider traits (log-transformed body size, phenology, hunting type, vegetational stratification and prey range) with the R package FD (Laliberté and Legendre 2010). We used dimensionality reduction (using both binary and continuous variables increased the number of dimensions) in the principal coordinates analysis required for the calculation of FRic (Laliberté and Legendre 2010), and the five axes retained accounted for 89% of the overall trait information. The principal coordinates analysis was calculated from a Gower dissimilarity matrix and based on standardized trait values as implemented in the FD package. It is difficult to know whether species recorded with very few individuals are biologically associated to a habitat, as in many cases they only represent accidental occurrences of vagrant species. For a meaningful analysis we thus focused on species that were recorded with more than four individuals in the total catch. On average, the species excluded made up 3.6% ( $\pm 1.4$  SD) of spider individuals recorded per plot and were smaller than the species analyzed, indicating that their functional impact is low (see also Bihn et al. 2010). Species richness patterns were not affected by this procedure (cf. Schuldt et al. 2011). We also tested the extent to which each of the five traits contributed to the effects of the multivariate diversity indices. For this, we recalculated the

indices for each combination of only four of the five traits by downweighting each trait in turn (by a factor of 10,000) and reanalyzed effects on plant diversity measures with these modified functional diversity indices. This approach produces five different versions of the indices, where each version basically excludes the impact of one of the five traits, but it avoids numerical problems in the calculation of the indices that can arise from complete exclusion of a trait. To assess whether observed values of functional diversity were simply a reflection of the species richness at a particular site, observed values of FRic, FEve and FDiv were compared to those obtained from 999 random communities. The latter were generated using null model '1s' in Hardy (2008), shuffling the species' abundances in the species x plot matrix across species and sites. This null model keeps constant (i) species richness within a plot, (ii) species abundance distributions among plots, and (iii) levels of spatial clustering (e.g. caused by dispersal limitation). For each plot and each of the three FD indices, standardized effect sizes (FRic.ses, FEve.ses, FDiv.ses; according to Gotelli and Rohde 2002) were calculated as the observed functional diversity relative to expected values from the random communities:  $ses = (\text{observed functional diversity index score} - \text{mean expected index score}) / \text{standard deviation of the index across the 999 randomizations}$ .

As a measure of phylogenetic diversity of the woody plant communities that is independent of species richness (in our study:  $r = -0.24$ ;  $P = 0.221$ ; Fig. S2a in ESM1), we calculated the mean pairwise phylogenetic distance (MPD). In comparison to woody species, herb species contributed relatively little to overall plant diversity (Both et al. 2011) and were not considered. Plant diversity effects on epigeic spiders (via litter structure, prey availability) are probably driven primarily by the tree and shrub layers (see Schuldt et al. 2011), which contribute most to overall plant biomass. MPD quantifies the mean divergence between species (non-abundance-weighted MPD) or individuals (abundance-weighted MPD) within a community (Webb et al. 2002). Phylogenetic diversity measures were

calculated based on an ultrametric phylogenetic tree of all woody species of the 27 study plots (Fig. S8.1 in Electronic Supplementary Material (ESM) 1; O. Purschke, S. G. Michalski, H. Bruelheide and W. Durka *unpublished*). Of the two measures of phylogenetic diversity, only the unweighted MPD index showed a significant relationship with the functional diversity of spiders. Thus, we only included this index in the analysis.

Patterns in functional diversity were analyzed with linear mixed effects models and FRic, FEve, and FDiv, and their corresponding standardized effect sizes (FRic.ses, FEve.ses, FDiv.ses) as response variables. As fixed effects, we included plot characteristics (canopy cover, herb layer cover, altitude, soil pH) and characteristics of the trap surroundings (litter depth, litter cover, vegetation cover) as covariables in addition to woody plant species richness, evenness of woody plant diversity, herb layer species richness, MPD, and plot age. We also included the interactions between plot age and woody plant species richness or MPD, respectively, in the full models. Woody plant species richness, MPD, and vegetation cover were log-transformed to increase normality and homoscedasticity of the models. For the minimal model on FRic.ses, we included an exponential variance structure of the predictors as a weighting factor to achieve homogeneous variances of the model residuals (Zuur et al. 2009). We also checked for non-linear relationships between the FD indices and the predictor variables by analyzing second-order polynomials of the variables. Predictors were checked for multicollinearity ( $r > 0.7$ ) before being included in the full

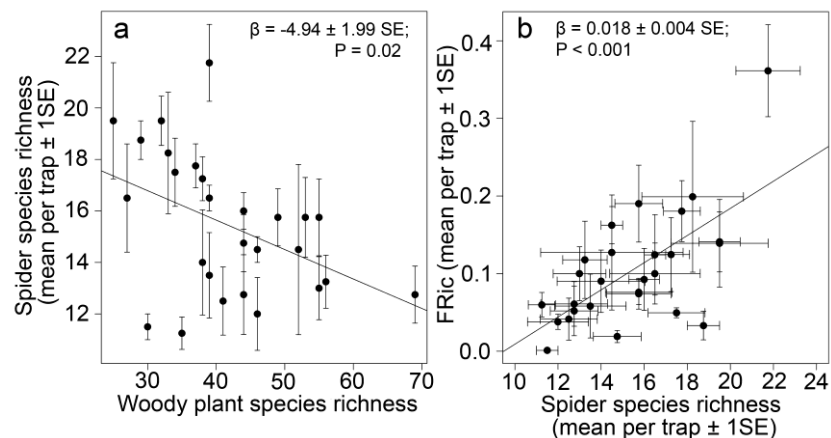
models. Due to the hierarchical structure of our data, we included plot identity as a random effect. We used model simplification by excluding predictor variables in an automated stepwise procedure based on the AICc (Burnham and Anderson 2004). The models with the smallest number of predictors and the lowest global AICc were chosen as the most parsimonious, best-fit models for each FD index. Model residuals were checked for normality and homogeneity of variances. All analyses were conducted in R 2.15.1 (<http://www.R-project.org>).

## Results

The analysis comprised 5967 individuals of 80 spider species, with five species (*Pardosa laura* Karsch, *Pirata* Morph.Spec.1, *Liocranidae* Morph.Spec.2, *Pardosa wuyiensis* Yu and Song, *Itatsina praticola* (Bösenberg and Strand)) accounting for 55% of all individuals. Mean species richness of spiders per trap strongly declined with increasing species richness of woody plants across the 27 study plots (Fig. 8.1a), but was not significantly related to plot age ( $t = -0.59$ ;  $P = 0.561$ ; Fig. S8.2b in ESM1). As expected, mean functional richness (FRic) of the spider assemblages increased with spider species richness across the plots (Fig. 8.1b). All other measures of functional diversity were not related to spider species richness or FRic ( $P > 0.2$  in all cases), indicating that functional richness, divergence and evenness indeed represented distinct and independent aspects of spider functional diversity.

**Figure 8.1.**

Relationships between mean spider species richness per trap and (a) woody plant species richness and (b) functional richness (FRic) of the spider assemblages across a diversity gradient of 27 study plots in subtropical China.





**Table 8.1.** Fixed factors retained in the minimal mixed-effects models for a) functional richness (FRic), evenness (FEve), and divergence (FDiv), and b) their standardized effect sizes from null model comparisons (FRic.ses, FEve.ses, FDiv.ses)

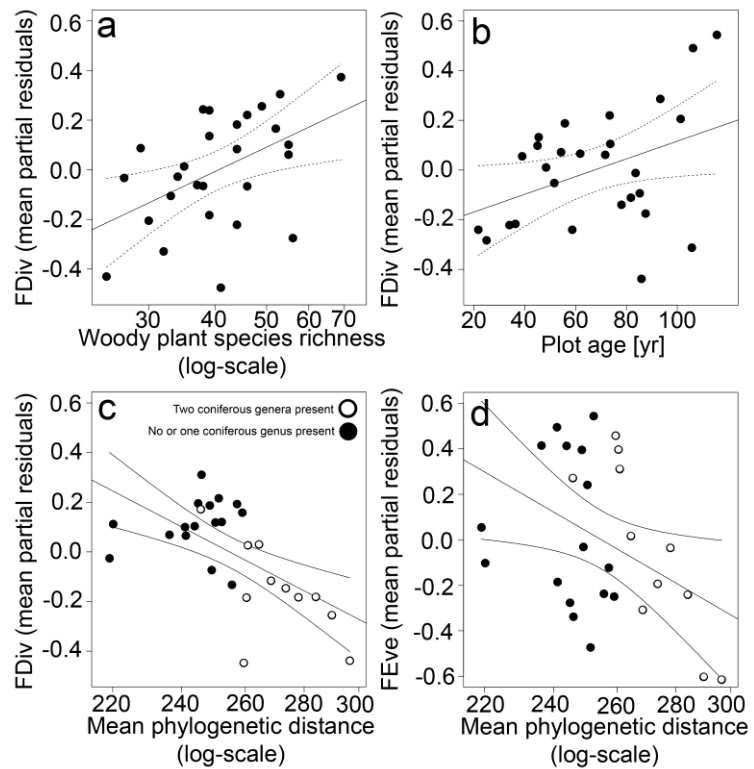
<i>Response</i>	<i>Fixed effects</i>	Stand. Est. ( $\pm$ SE)	df	<i>t</i>	<i>P</i>
<b>a) observed values</b>					
<b>Functional richness (FRic)</b>					
- - - - -					
AICc full/minimal model: -168.8/-194.4					
<b>Functional evenness (FEve)</b>					
	Mean phylogenetic distance <sup>1</sup>	-0.249 ( $\pm$ 0.109)	25	-2.29	0.031
AICc full/minimal model: -251.1/-265.7					
<b>Functional divergence (FDiv)</b>					
	Elevation (plot)	-0.322 ( $\pm$ 0.089)	22	-3.59	0.002
	Woody plant species richness (plot) <sup>1</sup>	0.258 ( $\pm$ 0.092)	22	2.28	0.011
	Plot age	0.211 ( $\pm$ 0.095)	22	2.22	0.037
	Mean phylogenetic distance <sup>1</sup>	-0.392 ( $\pm$ 0.094)	22	-4.16	<0.001
AICc full/minimal model: -266.2/-279.4					
<b>b) standardized effect sizes</b>					
<b>Functional richness (FRic.ses)</b>					
	Vegetation cover (trap) <sup>1</sup>	0.182 ( $\pm$ 0.071)	80	2.55	0.012
	Woody plant species richness (plot) <sup>1</sup>	0.275 ( $\pm$ 0.128)	25	2.15	0.041
AICc full/minimal model: 252.6/232.3					
<b>Functional evenness (FEve.ses)</b>					
	Litter cover (trap)	0.228 ( $\pm$ 0.093)	80	2.45	0.017
	Herb layer plant species richness	0.224 ( $\pm$ 0.094)	25	2.38	0.025
AICc full/minimal model: 315.4/294.0					
<b>Functional divergence (Fdiv.ses)</b>					
	Canopy cover (plot)	0.357 ( $\pm$ 0.097)	21	3.68	0.001
	Elevation (plot)	-0.238 ( $\pm$ 0.091)	21	-2.61	0.016
	Herb layer plant species richness	-0.296 ( $\pm$ 0.097)	21	-3.05	0.006
	Woody plant species richness (plot) <sup>1</sup>	0.436 ( $\pm$ 0.093)	21	4.70	<0.001
	Plot age	0.207 ( $\pm$ 0.098)	21	2.13	0.460
AICc full/minimal model: 309.6/291.5					

<sup>1</sup>log-transformed

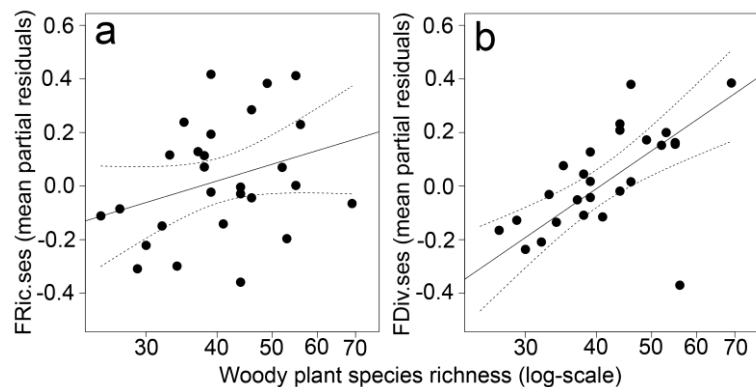
Despite the correlation with spider richness, FRic was not significantly related to woody plant species richness or plot age ( $t = -0.23$ ;  $P = 0.822$ , and  $t = -0.65$ ;  $P = 0.521$ , respectively, Fig. S8.2c-d in ESM1). None of the explanatory variables were retained in the minimal model of FRic (Table 8.1). In contrast to FRic, however, functional divergence (FDiv) significantly increased with woody plant species richness (Table 8.1; Fig. 8.2a), indicating that in particular the spread of

abundances within the convex hull of the assemblages' functional traits increased with plant species richness. At the same time, FDiv and also functional evenness (FEve) decreased with increasing mean phylogenetic distance (MPD) of the woody plant communities (Table 8.1, Fig. 8.2c-d). However, this was primarily an effect of the presence or absence of conifers (Fig. 8.2c). Excluding conifers and basing MPD calculations only on angiosperms removed any effect of MPD on FDiv and

**Figure 8.2.** Independent effects on functional diversity indices of a) woody plant species richness, b) plot age, and c-d) mean phylogenetic distance of woody plant species across the 27 study plots (partial residuals and 95% confidence bands). FEve: functional evenness, FDiv: functional divergence. All relationships are significant at  $P < 0.05$  (see Table 1).



**Figure 8.3.** Independent effects of woody plant species richness on a) standardized effect sizes of FRic, and b) standardized effect sizes of FDiv (partial residuals and 95% confidence bands). Both relationships are significant at  $P < 0.05$  (see Table 8.1).



FEve, and instead revealed a positive effect of woody plant species richness also on FEve (Table S8.1 in ESM1). Plot age was only included in the minimal model of FDiv, where it had a positive effect (Table 8.1, Fig. 8.2b). There were no significant effects of quadratic plant species richness or plot age terms on the relationships between woody plant species richness and functional diversity in any of the models. The evenness of woody plant diversity was not included in the minimal models of any of the functional diversity measures. Downweighting the impact of each of the five traits in turn showed that while the relationship between spider FDiv and woody plant species richness (and similarly MPD)

was particularly strongly affected by spider phenology, the other traits as well contributed to the strength of this relationship (i.e. standardized slopes became weaker when the impact of any of the traits, except for vegetational stratum, was downweighted; Table S8.2 in ESM1). Variability in FEve was particularly strongly affected by the spider assemblages' phenological, hunting type (for the relationship with woody plant species richness), and body size characteristics (for the relationship with MPD; Table S8.2 in ESM1).

The standardized effect sizes of spider functional richness (FRic.ses), divergence (FDiv.ses) and evenness (FEve.ses), generated from the null model randomizations, were

independent of spider species richness ( $P > 0.75$  in all cases). The minimal model for FRic.ses showed a marginally significant, positive effect of woody plant species richness (Table 8.1), i.e. spider functional richness tended to be on a higher level than expected, given the levels of spider species richness, in the more plant species-rich plots (Fig. 8.3a). In contrast, the minimal adequate model for FDiv.ses was qualitatively similar to the results for FDiv (Table 8.1, Fig. 8.3b). Likewise, results for FEve.ses showed a significant positive effect of plant species richness (Table 8.1; in this case an effect of herb layer plant species richness) that was similar to the effects observed for FEve when MPD was based on angiosperm community structure (see above).

## Discussion

Our study shows that patterns in the functional diversity of predators can deviate from those based solely on species richness. Accounting for differences in the functional characteristics of species can thus help to better understand the potential effects, and the change in effects along environmental gradients, of predator assemblages on ecosystem functions.

### Functional richness: decreasing redundancy of spiders with increasing tree diversity

Despite a strong decline in the species richness of spiders with increasing woody plant species richness, their functional richness (FRic) did not change. Similarly, plot age had no effect on spider functional richness. The latter finding may be due to the high dispersal power of many spiders, which promotes relatively rapid immigration from surrounding forest sites (Niemelä et al. 1996; Oxbrough et al. 2010). This could also explain deviating results for taxa such as ants, which were shown to continuously increase in functional richness with stand age in tropical forests (Bihn et al. 2010). Regarding the gradient in woody plant species richness, contrasting patterns in the functional and species richness of spiders indicate that functional redundancy within spider assemblages decreased with increasing plant richness. Similar levels of functional richness

were based on far fewer spider species in the more plant-species rich stands than in the less plant species-rich ones. Likewise, the weakly increasing standardized effect sizes of spider functional richness (FRic.ses) with woody plant species richness, together with the fact that FRic.ses was independent of spider species richness, indicate that the maintenance of constant functional richness (FRic) observed across the woody plant diversity gradient was due to the nonrandom assembly and nonrandom loss of spider species in the more plant species-rich plots. This means that woody plant species richness tended to keep spider functional richness on a higher level than expected by chance, despite decreasing spider species richness.

Possible explanations for these patterns could be higher resource quality or decreased intraguild interactions in the more plant species-rich plots, and we discuss these in more detail below (patterns in FDiv). In any case, the results suggest that despite a higher than expected functional richness in the more plant species-rich plots, the effect of woody plant species richness at our study site is apparently not strong enough to increase overall niche space to a level that might reflect the positive predator-plant diversity effects reported from less species-rich or less complex ecosystems (e.g. Haddad et al. 2009). Previous studies have suggested that the impact of plant diversity on higher trophic levels is attenuated at high levels of plant diversity (e.g. Scherber et al. 2010), such that effects observed at low diversity levels might be less relevant for our study system with medium to high plant diversity. At high levels of plant diversity, even negative diversity effects might be conceivable via increased spatial heterogeneity leading to tradeoffs with the area available to individual species (Allouche et al. 2012)—and we in fact observed a negative relationship between the species richness of spiders and woody plants in our study. However, such an effect would only be likely for highly specialized taxa and should have led to functionally less rich and less divergent spider communities in the more plant species-rich plots (as only more generalized species would be able to cope with such high environmental heterogeneity;

Allouche et al. 2012), a pattern that does not match our findings for FRic and particularly for FDiv (see Schuldt et al. 2011 for a discussion on species richness patterns).

However, decreasing redundancy of spider species with increasing plant species richness and a nonrandom spider assemblage structure could indicate that the functional impact of these assemblages is sensitive to the loss of individual spider species and thus to disturbances caused, for instance, by human activities—at least on a larger, landscape scale where species loss will not be as easily compensated for by immigration of new species. Previous results for these assemblages suggest that woody plant species richness does not affect the stability of patterns in the species richness of spiders (Schuldt et al. 2012); however, it might still affect the stability of their functional effects if functional richness is only moderately related to species richness (see also Finke and Snyder 2010). These relationships have not as yet been tested rigorously in natural systems, and more research is needed to address their functional consequences.

### Functional divergence and evenness: plant species richness promotes complementary resource use

While the functional richness of spiders and thus the overall niche space used remained on a constant level along the woody plant richness gradient, functional divergence (FDiv)—and to a lesser extent functional evenness (FEve)—within the available niche space increased with plant species richness (and FDiv also with plot age). Low functional divergence and evenness values in the less plant species-rich (and younger) plots indicate that the dominant spider species were functionally similar and characterized by trait values close to the center of the assemblages' overall functional trait space. In the more plant species-rich (and older) plots, in contrast, trait values showed a more regular and diverging pattern, meaning that abundance distributions in these plots were functionally more differentiated, with a higher dominance of functionally dissimilar species. In fact, the relative abundance of *Pardosa laura*, the species with the highest overall number of

individuals, strongly decreased from 32% in the least diverse to 3% in the most diverse forest stand. Several other of the most abundant species showed similar trends (not shown), indicating that a decrease in these highly abundant species caused a more even and less centered distribution of spider abundances within the functional trait space. Böhnke et al. (2013) described a similar pattern for functional evenness of the community of woody species along the same succession series. While functional richness decreased with age, the trait values became more evenly distributed among the resident species.

These shifts might cause differences in the functional effects of the spider assemblages along the woody plant richness and plot age gradients, despite similar functional richness. These effects would be in a direction opposite to those expected from mere spider richness patterns (see also Schuldt et al. 2011). Despite lower spider species richness, spider assemblages in the more plant species-rich (and in older) forest plots could have a strong impact on prey because the most abundant spider species display more dissimilar and complementary resource use (high FDiv) than the assemblages in the less plant species-rich (and younger) plots. The latter might have more spider species, but a more centered resource use (low FDiv) by abundant species (see also Mouillot et al. 2011; Villéger et al. 2010). Even among largely generalist predators such as spiders, differences in body size, phenology and microhabitat use may lead to differences in resource use and the partitioning of prey (Schmitz 2007; Uetz 1977).

FDiv and FEve were unaffected by both spider species richness and FRic, and the observed effects were supported by the models for the standardized effect sizes FDiv.ses and FEve.ses. The fact that the standardized effect sizes increased with plant species richness (in the case of FEve.ses with a stronger impact of herb layer rather than tree and shrub layer species richness) indicates that, similar to functional richness, the increase with plant species richness in the abundance-based spread and regularity of trait values of the spider assemblages was higher

than expected from the number of spider species; i.e. nonrandom assembly processes became more evident with increasing niche differentiation of the spider assemblages. Again, these patterns point to lower redundancy among dominant species in the more plant species-rich plots, as already discussed above. Contrasting patterns between species and functional richness on the one hand and functional divergence and evenness on the other were also shown in other studies (Gerisch et al. 2012; Mouillot et al. 2011; Villéger et al. 2010). These findings indicate that the relative distribution of abundant species in functional trait space strongly affects ecological functions, independent of potentially contrasting patterns in species richness or the overall available functional trait space (Mouillot et al. 2011).

The mechanisms responsible for causing the observed trait divergence are difficult to elucidate in an observational study. Increasing productivity and higher resource availability, as often occurs with increasing plant diversity (e.g. Haddad et al. 2009), are an unlikely explanation, as we would have expected a simultaneous increase in the number of spider species. Rather than the amount of available resources, however, the quality of these resources may be part of the explanation. Higher plant species richness is likely to increase the diversity of herbivores (Lewinsohn and Roslin 2008). This, in turn, results in higher prey diversity and alternative prey resources for predators, which may allow for, and promote adaptations in, resource use and thus increase functional divergence among the dominant predator species (and it might also promote higher-than-expected functional richness). Intraguild predation and competition might also have an effect (Finke and Snyder 2010). Lycosids are well known for their strong impact on other spiders, and the dominance of *Pardosa* species in the low-diversity and young forest plots (which might be due to particularly suitable conditions and a competitive advantage of these relatively large cursorial species in these environments; Hurd and Fagan 1992; Mallis and Hurd 2005) could negatively affect the relative abundances of many other species (Schmidt-Entling and Siegenthaler 2009). Moreover, competitive

pressure due to the generally high spider species richness in the less plant species-rich forest plots could lead to further trait convergence if dissimilar species are systematically excluded as weaker competitors (de Bello et al. 2012). Research into the mechanisms of community assembly patterns may yield further insight in this respect, but is beyond the focus of our study.

#### Mean pairwise phylogenetic distance: phylogenetic diversity does not consistently explain predator functional diversity

Dinnage et al. (2012) recently showed that the phylogenetic diversity of grassland plant communities can have effects on higher trophic level diversity that are in part complementary to the effects of plant species richness. For predators, they explained these patterns by positive effects of increasing productivity with potentially decreasing niche overlap in more distantly related plant species. In our study, effects of plant phylogenetic diversity were basically due to the absence or presence of conifers in the study plots. The negative influence of conifers on FDiv and FEve might have been caused by increased shading or a homogenization of the litter layer that promoted the abundances of spiders with very general resource use characteristics (again, Lycosids were particularly abundant in these plots). When the three coniferous species occurring at the study site were excluded from the calculation of MPD, the phylogenetic distance among woody plant species was no longer included in any of the minimal models. This might underline our assumption that functional diversity patterns of spiders in the forests we studied are not primarily affected by plant productivity (but more research is needed to directly test for productivity relationships). Our study comprised forest stands from medium to high woody plant species richness, and the effects of productivity might not be as limiting as in comparisons including monocultures (see also Scherber et al. 2010).

#### Conclusions

Our study shows that functional diversity patterns provide insights into the assemblage

structure of predatory arthropods that go beyond, and in part contrast with, the information provided by mere species richness patterns. In contrast to other studies (e.g. Haddad et al. 2009), our results for epigeic spiders are supportive of the promoting effects that plant diversity is generally hypothesized to have on predators, only in the context of functional diversity (and here particularly in terms of the divergence of trait distributions within the overall functional space, and less evident in terms of the size of this functional space; (see also Villéger et al. 2010) and not for patterns of species richness (see also Zhang and Adams 2011). As for the strength of predator functional effects, carefully designed experiments are required to test whether a higher total abundance of very generalist predators (as in the less plant species-rich forest stands of our study) or a broader divergence in resource use (but lower total abundances, as in our plant species-rich plots) can achieve, for instance, a more effective top-down control. Several studies have demonstrated that abundance distributions of predators strongly mediate the impact of species richness on predator functional effects (Finke and Snyder 2010; Griffiths et al. 2008). While these studies were limited to small-scale manipulations of just a small number of predator species, they highlight that hypotheses of the relationship between plant diversity and predators need to incorporate functional aspects more explicitly. The contrasting findings of our study regarding the species richness and functional diversity of spiders show the need for a more rigorous assessment of these aspects in complex, highly diverse natural systems.

### Acknowledgments

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### Author Contributions

AS, TA and HB conceived and designed the study. AS conducted fieldwork and performed statistical analyses, WD and SGM provided phylogenetic data, OP provided analytical methods, AS wrote the manuscript, with input from all coauthors

### References

- Allouche O, Kalyuzhny M, Moreno-Rueda G, Pizarro M, Kadmon R (2012) Area-heterogeneity tradeoff and the diversity of ecological communities. *Proceedings of the National Academy of Sciences* 109:17495-17500
- Bihn JH, Gebauer G, Brandl R (2010) Loss of functional diversity of ant assemblages in secondary tropical forests. *Ecology* 91:782-792
- Böhnke M, Kröber W, Welk E, Wirth C, Bruelheide H (2013) Maintenance of constant functional diversity during secondary succession of a subtropical forest in China. *Journal of Vegetation Science*:under review
- Both S et al. (2011) Lack of tree layer control on herb layer characteristics in a subtropical forest, China. *Journal of Vegetation Science* 22:1120-1131
- Brose U et al. (2006) Consumer-resource body-size relationships in natural food webs. *Ecology* 87:2411-2417
- Bruehlheide H et al. (2011) Community assembly during secondary forest succession in a Chinese subtropical forest. *Ecological Monographs* 81:25-41
- Burnham KP, Anderson DR (2004) Model selection and multimodel inference : a practical information-theoretic approach. Springer, New York
- Cadotte MW, Cavender-Bares J, Tilman D, TH O (2009) Using phylogenetic, functional and trait diversity to understand patterns of plant community productivity. *PLoS ONE* 4:e5695
- Cardinale BJ et al. (2012) Biodiversity loss and its impact on humanity. *Nature* 486:59-67
- Cardoso P, Pekar S, Jocque R, Coddington JA (2011) Global patterns of guild composition and functional diversity of spiders. *Plos One*

- 6:e21710
- de Bello F et al. (2012) Functional species pool framework to test for biotic effects on community assembly. *Ecology* 93:2263–2273
- Devictor V, Mouillot D, Meynard C, Jiguet F, Thuiller W, Mouquet N (2010) Spatial mismatch and congruence between taxonomic, phylogenetic and functional diversity: the need for integrative conservation strategies in a changing world. *Ecology Letters* 13:1030–1040
- Dinnage R, Cadotte MW, Haddad NM, Crutsinger GM, Tilman D (2012) Diversity of plant evolutionary lineages promotes arthropod diversity. *Ecology Letters* 15:1308–1317
- Feld CK et al. (2009) Indicators of biodiversity and ecosystem services: a synthesis across ecosystems and spatial scales. *Oikos* 118:1862–1871
- Finke DL, Snyder WE (2010) Conserving the benefits of predator biodiversity. *Biological Conservation* 143:2260–2269
- Gerisch M, Agostinelli V, Henle K, Dziöck F (2012) More species, but all do the same: contrasting effects of flood disturbance on ground beetle functional and species diversity. *Oikos* 121:508–515
- Gotelli NJ, Rohde K (2002) Co-occurrence of ectoparasites of marine fishes: a null model analysis. *Ecology Letters* 5:86–94
- Griffiths GJK, Wilby A, Crawley MJ, Thomas MB (2008) Density-Dependent Effects of Predator Species-Richness in Diversity-Function Studies. *Ecology* 89:2986–2993
- Haddad NM, Crutsinger GM, Gross K, Haarstad J, Knops JMH, Tilman D (2009) Plant species loss decreases arthropod diversity and shifts trophic structure. *Ecology Letters* 12:1029–1039
- Hardy OJ (2008) Testing the spatial phylogenetic structure of local communities: statistical performances of different null models and test statistics on a locally neutral community. *Journal of Ecology* 96:914–926
- Hooper DU et al. (2012) A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature* 486:105–108
- Hooper DU et al. (2005) Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecological Monographs* 75:3–35
- Hurd LE, Fagan WF (1992) Cursorial spiders and succession: age or habitat structure? *Oecologia* 92:215–221
- Jocqué R, Dippenaar-Schoeman AS (2007) Spider families of the world. Royal Museum for Central Africa, Tervuren
- Kremen C et al. (2000) Economic incentives for rain forest conservation across scales. *Science* 288:1828–1832
- Laliberté E, Legendre P (2010) A distance-based framework for measuring functional diversity from multiple traits. *Ecology* 91:299–305
- Legendre P et al. (2009) Partitioning beta diversity in a subtropical broad-leaved forest of China. *Ecology* 90:663–674
- Lewinsohn TM, Roslin T (2008) Four ways towards tropical herbivore megadiversity. *Ecology Letters* 11:398–416
- Lopez-Pujol J, Zhang F-M, Ge S (2006) Plant biodiversity in China: richly varied, endangered, and in need of conservation. *Biodiversity and Conservation* 15:3983–4026
- Mallis RE, Hurd LE (2005) Diversity among ground-dwelling spider assemblages: habitat generalists and specialists. *Journal of Arachnology* 33:101–109
- Mason NWH, Irz P, Lanoiselee C, Mouillot D, Argillier C (2008) Evidence that niche specialization explains species-energy relationships in lake fish communities. *Journal of Animal Ecology* 77:285–296
- Mouchet MA, Villéger S, Mason NWH, Mouillot D (2010) Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. *Functional Ecology* 24:867–876
- Mouillot D, Villéger S, Scherer-Lorenzen M, Mason NWH (2011) Functional structure of biological communities predicts ecosystem multifunctionality. *PLoS ONE* 6
- Naeem S, Duffy JE, Zavaleta E (2012) The functions of biological diversity in an age of extinction. *Science* 336:1401–1406
- Niemelä J, Haila Y, Punttila P (1996) The importance of small-scale heterogeneity in boreal forests: Variation in diversity in forest-floor invertebrates across the succession gradient. *Ecography* 19:352–368
- Oxbrough A, Irwin S, Kelly TC, O'Halloran J (2010) Ground-dwelling invertebrates in reforested conifer plantations. *Forest Ecology and Management* 259:2111–2121
- Pavoine S, Bonsall MB (2011) Measuring biodiversity to explain community assembly: a unified approach. *Biological Reviews* 86:792–812
- Purschke O et al. (2013) Contrasting changes in taxonomic, phylogenetic and functional diversity during a long-term succession: insights into assembly processes. *Journal of Ecology* 101:857–866
- Riihimäki J, Kaitaniemi P, Koricheva J, Vehviläinen H (2005) Testing the enemies hypothesis in forest stands: the important role of tree species composition. *Oecologia* 142:90–

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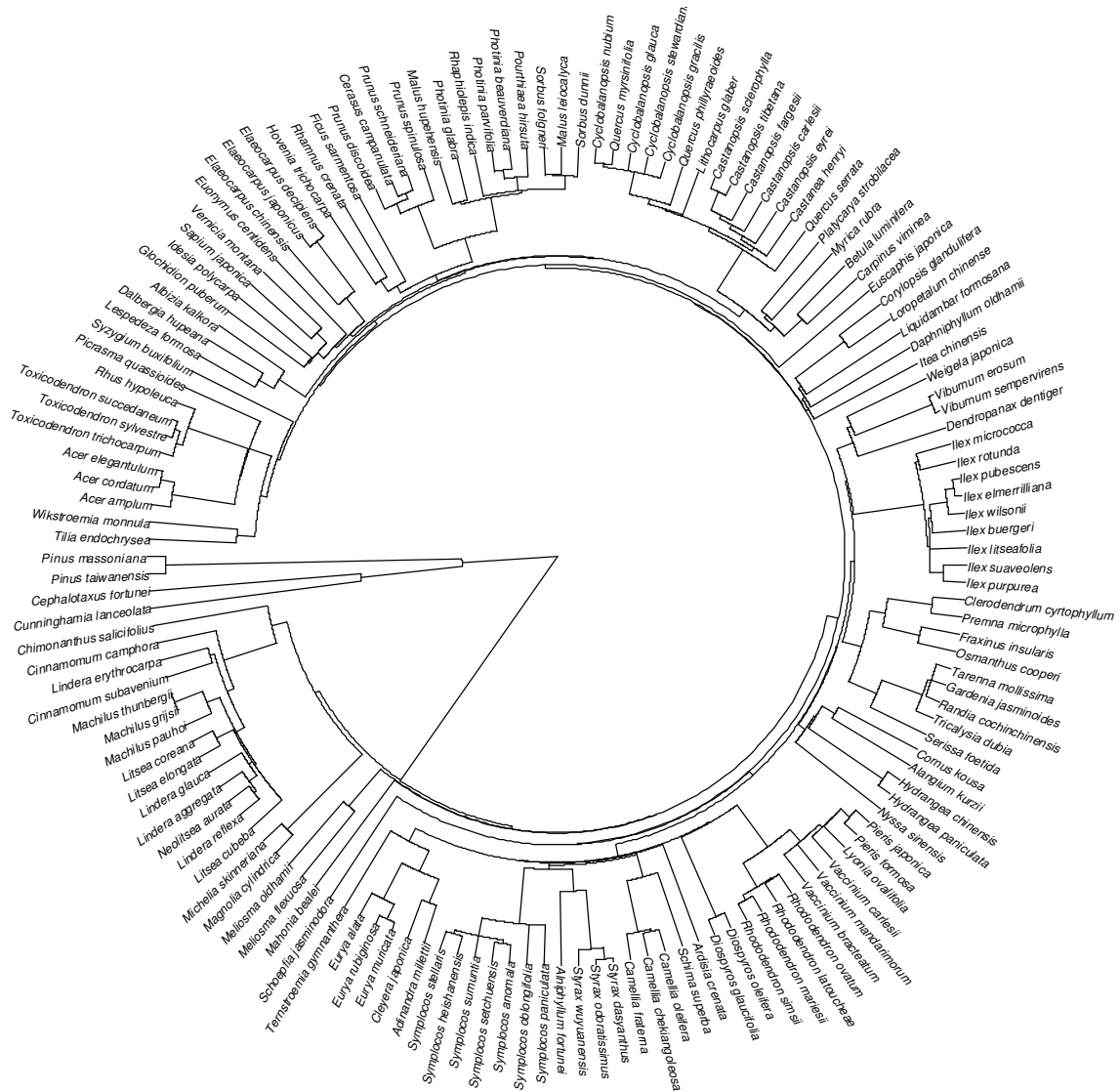
- Scherber C et al. (2010) Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. *Nature* 468:553-556
- Schleuter D, Daufresne M, Massol F, Argillier C (2010) A user's guide to functional diversity indices. *Ecological Monographs* 80:469-484
- Schmid B et al. (2009) Consequences of species loss for ecosystem functioning: meta-analyses of data from biodiversity experiments. In: Naeem S, Bunker DE, Hector A, Loreau M, Perrings C (eds) *Biodiversity, ecosystem functioning, and human wellbeing. An ecological and economic perspective*. Oxford Univ. Press, Oxford, pp 14-29
- Schmidt-Entling MH, Siegenthaler E (2009) Herbivore release through cascading risk effects. *Biology Letters* 5:773-776
- Schmitz OJ (2006) Predators have large effects on ecosystem properties by changing plant diversity, not plant biomass. *Ecology* 87:1432-1437
- Schmitz OJ (2007) Predator diversity and trophic interactions. *Ecology* 88:2415-2426
- Schuldt A et al. (2011) Predator diversity and abundance provide little support for the enemies hypothesis in forests of high tree diversity. *PLoS ONE* 6:e22905
- Schuldt A, Bruelheide H, Härdtle W, Assmann T (2012) Predator assemblage structure and temporal variability of species richness and abundance in forests of high tree diversity. *Biotropica* 44:793-800
- Southwood TRE, Henderson PA (2000) *Ecological Methods*. Third Edition. Blackwell Science, Oxford
- Stork NE, Grimbacher PS (2006) Beetle assemblages from an Australian tropical rainforest show that the canopy and the ground strata contribute equally to biodiversity. *Proceedings of the Royal Society B* 273:1969-1975
- Terborgh J (2012) Enemies Maintain Hyperdiverse Tropical Forests. *American Naturalist* 179:303-314
- Uetz GW (1977) Coexistence in a guild of wandering spiders. *Journal of Animal Ecology* 46:531-541
- Villéger S, Mason NWH, Mouillot D (2008) New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* 89:2290-2301
- Villéger S, Ramos Miranda J, Flores Hernandez D, Mouillot D (2010) Contrasting changes in taxonomic vs. functional diversity of tropical fish communities after habitat degradation. *Ecological Applications* 20:1512-1522
- Visser MD, Muller-Landau HC, Wright SJ, Rutten G, Jansen PA (2011) Tri-trophic interactions affect density dependence of seed fate in a tropical forest palm. *Ecology Letters* 14:1093-1100
- Webb CO, Ackerly DD, McPeck MA, Donoghue MJ (2002) Phylogenies and community ecology. *Annual Review of Ecology and Systematics* 33:475-505
- Wise DH (2004) Wandering spiders limit densities of a major microbi-detritivore in the forest-floor food web. *Pedobiologia* 48:181-188
- Zhang YA, Adams J (2011) Top-down control of herbivores varies with ecosystem types. *Journal of Ecology* 99:370-372
- Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) *Mixed effects models and extensions in ecology with R*. Springer, New York

### Electronic supplementary material

The online version of this article (doi:10.1007/s00442-013-2790-9) contains supplementary material, which is available to authorized users.



Supplementary Material

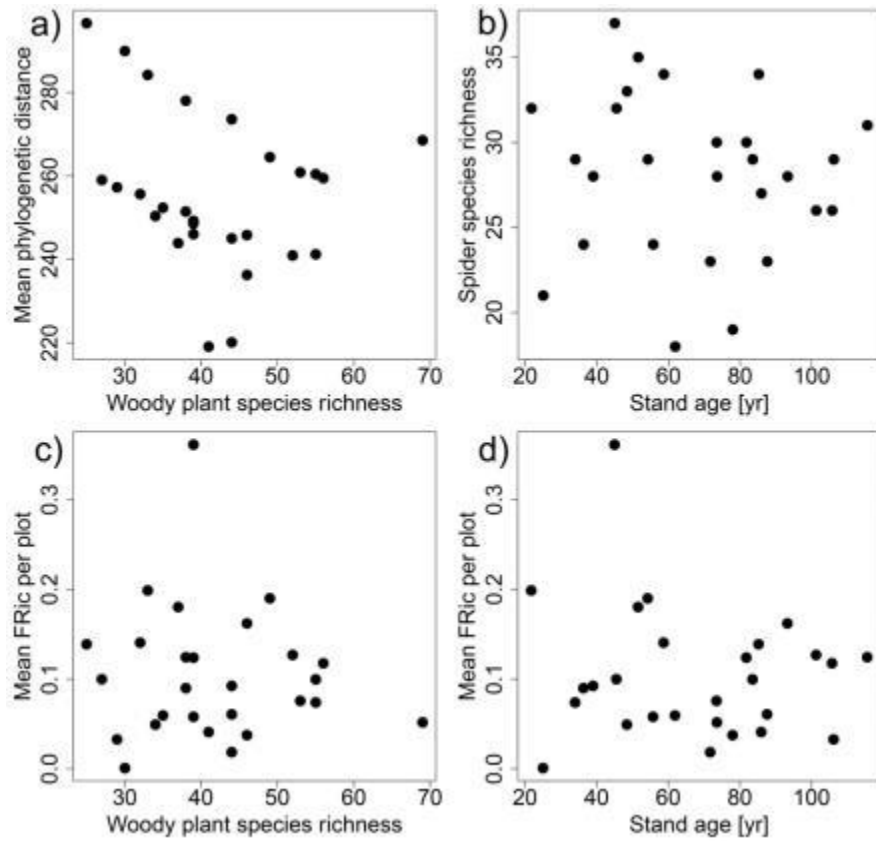


**Figure S8.1.** Phylogeny of 147 woody plant species in the 27 study plots extracted from a larger phylogeny of 440 woody species in the Gutianshan National Nature Reserve (O. Purschke, S. G. Michalski, B. Bruelheide and W. Durka *unpublished*). The phylogeny is based on public and new sequence data (*matK*, *rbcL* ITS, GenBank), Maximum Likelihood tree inference using PhyML (Guindon and Gascuel 2003) applying the GTR+I+G model, and calculation of an ultrametric tree by non-parametric rate smoothing (Sanderson 1997) using 28 fossil calibration points.

References

Guindon S, Gascuel O (2003) A simple, fast, and accurate algorithm to estimate large phylogenies by Maximum Likelihood. *Systematic Biology*, 52, 696-704.

Sanderson MJ, 1997, A nonparametric approach to estimating divergence times in the absence of rate constancy, *Molecular Biology and Evolution* 14: 1218-1231.



**Figure S8.2.** Relationships between a) mean phylogenetic distance and species richness of woody plants, b) spider species richness and stand age, c) spider functional richness (FRic) and woody plant species richness, and d) spider functional richness (FRic) and stand age. Relationships were non-significant with  $P > 0.2$  in all cases. For further details see main text.

**Table S8.1.** Fixed factors retained in the minimal mixed-effects models for functional richness (FRic), evenness (FEve), and divergence (FDiv) when MPD was included into the full model as the mean pairwise phylogenetic distance among angiosperms (i.e. excluding conifers; for results with conifers included see Table 1 in the main text)

<i>Response</i>	<i>Fixed effects</i>	Stand. Est. ( $\pm$ SE)	df	<i>t</i>	<i>P</i>
<b>Functional richness (FRic)</b>					
AICc full/minimal model: -169.7/-194.4					
<b>Functional evenness (FEve)</b>					
	Herb cover (plot)	0.209 ( $\pm$ 0.104)	24	2.02	0.055
	Woody plant species richness (plot) <sup>1</sup>	0.259 ( $\pm$ 0.104)	24	2.50	0.020
AICc full/minimal model: -246.6/-267.31					
<b>Functional divergence (FDiv)</b>					
	Canopy cover (plot)	0.324 ( $\pm$ 0.102)	21	3.19	0.004
	Elevation (plot)	-0.327 ( $\pm$ 0.095)	21	-3.42	0.003
	Herb species richness (plot)	-0.299 ( $\pm$ 0.102)	21	-2.94	0.008
	Woody plant species richness (plot) <sup>1</sup>	0.446 ( $\pm$ 0.097)	21	4.58	<0.001
	Plot age	0.317 ( $\pm$ 0.102)	21	3.10	0.005
AICc full/minimal model: -266.6/-275.9					

<sup>1</sup>log-transformed

**Table S8.2.** Standardized effects sizes ( $\pm$  SE) and probabilities for the relationships between the three metrics of spider functional diversity (FRic, FDiv, FEve) and the species richness and the mean pairwise phylogenetic distance (MPD, including all woody plant species), respectively, of woody plants in the 27 study plots. Each of the five spider traits used in the analyses was downweighted in turn (by a factor of 10,000) to show the impact of each trait on the observed relationships (completely excluding traits was not possible due to numerical problems, see main text)

<i>Response</i>	<i>Trait data downweighted</i>	<i>Woody plant species richness</i>		<i>MPD</i>	
		Std. Est. ( $\pm$ SE)	<i>P</i>	Std. Est. ( $\pm$ SE)	<i>P</i>
<b>Functional richness (FRic)</b>					
	Stratum downweighted	-0.021 ( $\pm$ 0.140)	0.882	-0.022 ( $\pm$ 0.140)	0.877
	Hunting type downweighted	-0.094 ( $\pm$ 0.139)	0.504	0.027 ( $\pm$ 0.140)	0.850
	Prey range downweighted	0.003 ( $\pm$ 0.134)	0.983	-0.029 ( $\pm$ 0.133)	0.832
	Body size downweighted	0.006 ( $\pm$ 0.134)	0.963	-0.009 ( $\pm$ 0.134)	0.949
	Phenology downweighted	-0.083 ( $\pm$ 0.136)	0.546	0.037 ( $\pm$ 0.136)	0.791
	No trait downweighted	-0.032 ( $\pm$ 0.141)	0.822	0.034 ( $\pm$ 0.141)	0.814
<b>Functional divergence (FDiv)</b>					
	Stratum downweighted	0.424 ( $\pm$ 0.137)	0.005	-0.503 ( $\pm$ 0.126)	<0.001
	Hunting type downweighted	0.373 ( $\pm$ 0.148)	0.018	-0.529 ( $\pm$ 0.127)	<0.001
	Prey range downweighted	0.349 ( $\pm$ 0.151)	0.029	-0.498 ( $\pm$ 0.133)	0.001
	Body size downweighted	0.352 ( $\pm$ 0.151)	0.028	-0.515 ( $\pm$ 0.131)	<0.001
	Phenology downweighted	0.237 ( $\pm$ 0.138)	0.099	-0.260 ( $\pm$ 0.137)	0.068
	No trait downweighted	0.414 ( $\pm$ 0.135)	0.005	-0.531 ( $\pm$ 0.118)	<0.001
<b>Functional evenness (FEve)</b>					
	Stratum downweighted	0.301 ( $\pm$ 0.106)	0.009	-0.249 ( $\pm$ 0.112)	0.035
	Hunting type downweighted	0.206 ( $\pm$ 0.119)	0.097	-0.240 ( $\pm$ 0.117)	0.051
	Prey range downweighted	0.283 ( $\pm$ 0.103)	0.011	-0.268 ( $\pm$ 0.104)	0.017
	Body size downweighted	0.368 ( $\pm$ 0.123)	0.006	-0.166 ( $\pm$ 0.139)	0.246
	Phenology downweighted	0.187 ( $\pm$ 0.130)	0.164	-0.210 ( $\pm$ 0.129)	0.117
	No trait downweighted	0.241 ( $\pm$ 0.110)	0.037	-0.249 ( $\pm$ 0.109)	0.031

# CHAPTER 9

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# Tree diversity promotes predator but not omnivore ants in a subtropical Chinese forest

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## Abstract

Epigeic ants are functionally important arthropods in tropical and subtropical forests, particularly by acting as predators. High predation pressure has been hypothesized to be a mechanism facilitating high diversity across trophic levels. In this study standardized pitfall traps were used in a highly diverse subtropical forest to test if and how ant species richness is related to tree species richness and a comprehensive set of other environmental variables such as successional age, soil properties or elevation. 13,441 ant individuals belonging to 3839 species occurrences and 71 species were collected, of which 26 species were exclusive predators and 45 species were omnivores. Occurrence and species richness of total and omnivore ants were positively related to soil pH. Predator ant occurrence was unrelated to all environmental variables tested. The species richness of predator ants increased with tree species richness but decreased with leaf functional diversity and shrub cover. Elevation negatively influenced only total ant species richness. The evenness of predators increased with tree species richness, whilst the evenness of all ants decreased with shrub cover. Omnivore ant evenness decreased with tree evenness while increasing with successional age. The results highlight the value of diverse forests in maintaining species richness and community evenness of a functionally important predator group. Moreover, the results stress the importance of analyzing trophic groups separately when investigating biodiversity effects.

**Key words:** BEF-China; biodiversity effects; Formicidae; Gutianshan National Nature Reserve; soil properties; species diversity; trophic guilds; vegetation structure

## Introduction

Tropical and subtropical forests are the most diverse terrestrial habitats (e.g. Kier et al. 2005; Basset et al. 2012). In a warm and wet climate mediated by low latitude diverse plant communities have evolved (Kier et al. 2005) that facilitate high diversity of other trophic levels (Hillebrand 2004). In the last decades, these species-rich forests have been exploited worldwide by a growing human population (Gibbs et al. 2010; Miettinen et al. 2011). Forest use, such as logging or agroforestry, reduce the diversity of trees and other forest organisms (Barlow et al. 2007; Gibson et al. 2011). However, it has widely been recognized that biodiversity loss is strongly related to ecosystem change (Cardinale et al. 2011;

Hooper et al. 2012) and that high biodiversity enhances ecosystem functioning and services (Duffy 2009; Gamfeldt et al. 2013) e.g. by stabilizing trophic cascades (Scherber et al. 2010).

Ants (Hymenoptera: Formicidae) are the dominant arthropods in terms of biomass and abundance in tropical and subtropical forest ecosystems (Hölldobler and Wilson 1990). They are important keystone organisms contributing to mutualisms, seed dispersal, and soil fertilization (Hölldobler and Wilson 1990; Folgarait 1998; Del-Toro et al. 2012). Moreover, ants are successful and effective predators that influence the populations and community composition of almost all other co-occurring arthropods (e.g. Floren et al. 2002; Berghoff et al. 2003; Philpott and

Armbrecht 2006; Cerda and Dejean 2011). Being ubiquitous but moderately diverse and sensitive to changing habitat conditions, ants are well established as indicator organisms for biodiversity studies (Alonso 2000; Majer et al. 2007).

By exerting a high predation pressure, ants can have cascading effects across trophic levels and structure the diversity, abundance, and community composition of other arthropods in the lower levels of a food web (Bruno and Cardinale 2008; Letourneau et al. 2009; Finke and Snyder 2010). Several studies have reported a positive relationship between plant diversity and arthropod diversity across trophic guilds including predators (e.g. Haddad et al. 2009; Scherber et al. 2010; Dinnage et al. 2012). These patterns are mainly attributed to higher habitat heterogeneity in more diverse ecosystems leading to a higher availability of more heterogeneous prey objects caused by more heterogeneous plant resources. In forests, higher tree diversity can also influence the properties and conditions of vegetation structure and leaf litter, thus increasing habitat heterogeneity and the number of available niches such as for nesting sites (e.g. Burghouts et al. 1992; Kaspari 1996, dos Santos Bastos and Harada 2011).

However, to date only a few studies have examined the relationship between the plant diversity and the diversity of epigeic ants in natural and diverse forests. With the exception of Basset et al. (2012) and Gunawardene et al. (2012), which both address plant-ant-diversity correlates in tropical forests, existing studies have either been conducted in agricultural landscapes comparing different land-use types with natural forests (e.g. Belshaw and Bolton 1993; Kone et al. 2012) or addressed arboreal ants (e.g. Floren and Linsenmair 2005; Klimes et al. 2012). None of these studies explicitly focused on the functionally important predator part of the ant community.

This study tests if tree species richness or other biotic and abiotic variables such as elevation, soil and leaf litter properties or vegetation structure influence occurrence, species richness, and evenness of epigeic ants in a highly diverse subtropical forest in South-

East China (Bruelheide et al. 2011). To gain deeper insight into the extent to which ant trophic groups are influenced differently by the environmental variables tested, the total ant community was divided into omnivores and exclusive predators and both groups tested separately. Specifically, this study tests the hypothesis that epigeic predator ants are positively influenced by tree species richness as there are probably more heterogeneous prey objects available in forests with higher tree species richness (sensu Haddad et al. 2009; Dinnage et al. 2012). It is also hypothesized that epigeic omnivore ants are less influenced by tree species richness as they do not exclusively depend on prey organisms and feed on a broad variety of food resources that are readily available in the forest studied.

## Material and methods

### Study site

The study was conducted in the Gutianshan National Nature Reserve (GNNR, 29°14' N/118°07' E), Zhejiang Province, in South-East China. The GNNR covers 8000 ha of highly-diverse mixed evergreen broad-leaved forest along an elevation gradient from 250-1260 m a.s.l. Most of the area has been used for agriculture or forestry in the past. Today the reserve consists of a mosaic of secondary forests, ranging from about 20 years to >100 years recovery time since abandonment. About half of the naturally occurring tree species are deciduous, but evergreen species dominate tree individual numbers. Common canopy tree species are the evergreen *Castanopsis eyrei* (Champion ex Benth.) Hutch. (Fagaceae), *Cyclobalanopsis glauca* (Thunberg) Oers. (Fagaceae) and *Schima superba* Gardn. et Champion (Theaceae) (Bruelheide et al. 2011). The area is located in a typical seasonal subtropical monsoon climate. Mean annual temperature is 15.3 °C and mean annual precipitation 1964 mm (Geißler et al. 2012). Leaf fall phenology has a peak in October and November when deciduous and semi-deciduous tree species shed leaves. For the rest of the year, leaf shed of evergreen species is continuous.

In 2008, the 'Biodiversity-Ecosystem Functioning China' project selected 27 plots with a size of 30 m x 30 m in the GNNR



(Bruelheide et al. 2011). Plots were selected based on tree species richness (ranging from 25-69 species per plot) and successional age (ranging from < 20yrs - > 100yrs) and were distributed over the entire reserve with the exception of areas that were inaccessible due to very steep slopes. In total 147 species of woody plants with a height > 1 m (from here on termed “trees” for simplicity) were identified in the secondary forest within the study plots. Patterns of tree species richness are not driven by rare species and are independent of abiotic variables such as elevation or soil properties (Bruelheide et al. 2011). For more details on site characteristics, a list of tree species, and a map of the study area are given in Bruelheide et al. (2011).

### Environmental variables

In order to test for the influences of abiotic (e.g. elevation, soil pH) and biotic (e.g. tree species richness, successional age) habitat characteristics on epigeic ant species richness, a comprehensive set of environmental variables was recorded during plot establishment in 2008. Tree species richness per plot was defined as the species richness of all tree and shrub individuals > 1 m height. The age of the secondary forest growing within a plot was determined by counting growth rings from stem core drillings of the tree with the fifth largest diameter at breast height within the respective plot. This approach was chosen as single large trees were commonly kept in local cropping systems to provide shading and multiple regression analysis revealed that the diameter of the fifth largest tree corresponds with local knowledge on former land use (Bruelheide et al. 2011).

In addition to tree species richness and successional age, canopy cover (%), shrub cover (%), tree abundance, tree basal area, herb layer cover (%), herb layer species richness, and elevation were also measured. To include the effect of soil on epigeic ants, total organic C, total organic N, C/N ratio, soil moisture and pH of the mineral soil were measured per plot. The proportion of deciduous tree species and the Shannon-based evenness of the tree community were calculated. As further measures of functional aspects of the tree community tree

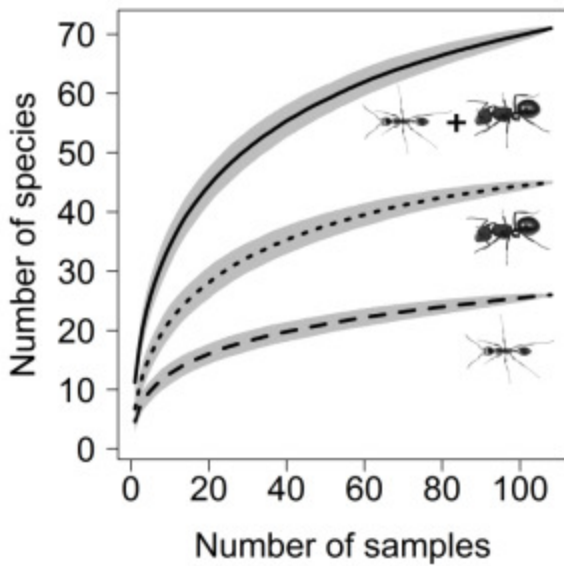
phylogenetic diversity based on abundance weighted genera and family occurrences was calculated using Rao's Q in the R-package `ade4` (<http://CRAN.R-project.org/package=ade4>). Mean leaf functional diversity was also calculated using Rao's Q with the morphological and chemical leaf traits measured by Kröber et al. (2012) considering the weighted abundances of tree species.

To account for trap-specific microhabitat conditions, mean litter depth, litter cover (%), vegetation cover of the herb layer (%), and vegetation height of the herb layer in a square of 1 m<sup>2</sup> centered on each trap was recorded in summer 2009. Mean annual temperature on the plot level was measured continuously with data loggers (HOBO U23 Pro v2, Onset Computer Corporation, Cape Cod, Massachusetts, U.S.A.) from June 2011 to June 2012. Detailed descriptions of the environmental variables used in this study can be found in Bruelheide et al. (2011) and Schuldt et al. (2011). A list of all 23 environmental variables measured is given in Table S9.1.

### Ant sampling

Epigeic foraging ants were sampled with standardized plastic pitfall traps. Four pitfall traps (diameter 8.5 cm, height 15 cm) were placed at the corners of a central 10 m x 10 m square in each of the 27 plots (summing up to 108 traps in total). Traps were filled with approximately 150 ml preserving solution (40% ethanol, 30% water, 20% glycerol, 10% acetic acid, few drops of dishwashing detergent). Sampling was conducted from 30-Mar-2009 to 02-Sep-2009 and covered the main vegetation period. Traps were emptied and the preserving solution was replaced every second week, giving ten samples per trap and 1080 samples in total.

Ants were sorted to genera following Bolton (1994) and identified to the species or morphospecies level. Voucher specimens have been deposited at the Institute of Earth and Environmental Sciences, University of Freiburg. The functional role of ants is closely linked to their trophic niche (Blüthgen et al. 2003; Gibb and Cunningham 2011; Pfeiffer et al. 2014) and it has been shown that the



**Figure 9.1** Sample-based species accumulation curves based on 1000 permutations for total ants (solid line), omnivore ants (dotted line), and predator ants (dashed line). Grey shaded areas mark 95% CI. In total, 71 species were collected that belong to 45 omnivore and to 26 predator species. All three groups have been sampled equally, as indicated by the similar shape of each species accumulation curve. Embedded pictures from [www.alexanderwild.com](http://www.alexanderwild.com), ©Alex Wild, used with permission.

trophic position of ant genera is relatively stable across habitats (Gibb and Cunningham 2011). Based on published literature about their feeding ecology (reviewed in Hölldobler and Wilson 1990; Brown 2000), a recent study on the trophic position of oriental ant genera (Pfeiffer et al. 2014), and personal field observations (M. Staab, unpubl. data), all ant genera were classified as either “predators” or “omnivores”. While predators such as *Aenictus* or *Odontomachus* rely exclusively on active hunting for arthropod prey, omnivores such as *Camponotus* or *Pheidole* can hunt as well but do not solely depend on prey arthropods as they also commonly scavenge and feed on a wide range of plant-based food objects such as honeydew, extra-floral nectar or seeds (Hölldobler and Wilson 1990; Brown 2000; Blüthgen and Feldhaar 2010; Cerda and Dejean 2011).

All genera of the subfamilies Aenictinae, Cerapachyinae, Ponerinae, and

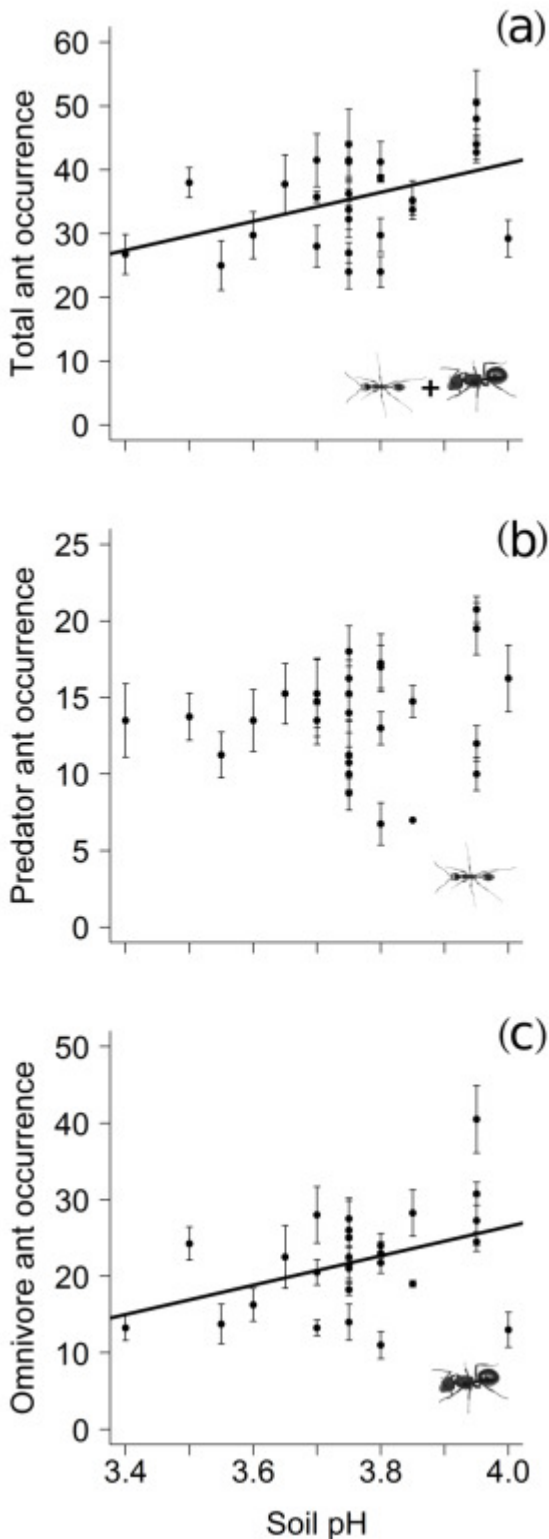
Proceratiinae were classified as predators. Ectatomminae were also classified as predators because in China none of the extra-floral nectary visiting genera of this subfamily occur (Guénard and Dunn 2012). All Myrmicinae genera listed to be predacious or cryptic litter species in Brown (2000) were also treated as predators. The remaining Myrmicinae, all Formicinae, Dolichoderinae, and Pseudomyrmicinae were classified as omnivores.

### Statistical analyses

All analyses were conducted with R 2.15.1 (<http://www.r-project.org>). Prior to analyses, the ten samples per trap were pooled, resulting in four samples per plot. For every sample the total number of species and the number of species occurrences was recorded, i.e. the sum of all species occurrences for the ten original samples taken together. The effectiveness of the sampling was tested with species accumulation curves based on 1000 permutations of individual samples without replacement. First-order jackknife (jack1) estimators were calculated for total ants, predators, and omnivores. Pooled traps were taken as sample units and calculations were performed with the R-package “vegan” (<http://CRAN.R-project.org/package=vegan>). Evenness was calculated based on the Shannon-index of occurrences for each group. To analyze the relationship between a) ant occurrence, b) ant species richness and c) ant evenness as response variables and environmental variables as explanatory variables linear mixed-effects models were computed using the R-package “nlme” (<http://CRAN.R-project.org/package=nlme>). Mixed-effect models account for a possible non-independence of the data and for hierarchical data structures by inclusion of random effects (Zuur et al. 2009). In this study, the four pitfall traps were nested inside the respective plot; thus plot identity was treated as random effect to account for plot-specific biotic and abiotic effects. Before fitting the initial full models, all environmental variables were analyzed for collinearity. If two variables were correlated with  $r_s > 0.7$  (Dormann et al. 2013), only one of the correlated variables was used. In total, nine

**Table 9.1.** Ant genera collected in pitfall traps within the 27 study plots in the GNNR. Shown are the number of occurrences and the number of species per genus. The overall ant community is split into exclusive predators (P) and omnivores with broad dietary niches (O) based on the reviews of Hölldobler and Wilson (1990), Brown (2000) and own observations

Subfamily	Genus	Occurrence	Species	Group
Aenictinae	<i>Aenictus</i>	51	5	P
Cerapachyinae	<i>Cerapachys</i>	1	1	P
Dolichoderinae	<i>Dolichoderus</i>	2	1	O
	<i>Liometopum</i>	2	1	O
	<i>Technomyrmex</i>	191	2	O
Ectatomminae	<i>Gnamptogenys</i>	26	1	P
Formicinae	<i>Camponotus</i>	880	6	O
	<i>Formica</i>	41	1	O
	<i>Lasius</i>	7	1	O
	<i>Nylanderia</i>	34	4	O
	<i>Polyrbachis</i>	272	7	O
	<i>Prenolepis</i>	48	2	O
Myrmicinae	<i>Aphaenogaster</i>	485	3	O
	<i>Carebara</i>	3	2	P
	<i>Crematogaster</i>	50	4	O
	<i>Dilobocondyla</i>	2	1	O
	<i>Kartidris</i>	7	1	P
	<i>Myrmecina</i>	4	2	P
	<i>Pheidole</i>	175	2	O
	<i>Pheidologeton</i>	17	1	P
	<i>Pristomyrmex</i>	1	1	O
	<i>Rhoptromyrmex</i>	8	1	O
	<i>Rotstruma</i>	2	1	O
	<i>Temnothorax</i>	2	1	O
	<i>Tetramorium</i>	151	4	O
	Ponerinae	<i>Anochetus</i>	8	1
<i>Cryptopone</i>		1	1	P
<i>Leptogenys</i>		238	2	P
<i>Odontomachus</i>		138	2	P
<i>Pachycondyla</i>		979	6	P
Proceratiinae	<i>Discothyrea</i>	4	1	P
Pseudomyrmicinae	<i>Tetraoponera</i>	7	2	O



**Figure 9.2** Relationship between soil pH and occurrence of (a) total ants, (b) predator ants, and (c) omnivore ants in the 27 study plots in the GNNR. Shown are means per plot  $\pm$  1 SE. Regression lines show significant relationships at  $P < 0.05$  (see Table 2). Embedded pictures from [www.alexanderwild.com](http://www.alexanderwild.com), ©Alex Wild, used with permission.

of the 23 variables were excluded. Spearman's  $r_s$  was taken as a measure of correlation as not all variables (e.g. canopy cover, vegetation cover around traps) were normally distributed. Correlation coefficients for all pairwise Spearman correlations between environmental variables are shown in Table S9.1.

Accordingly, the initial full models were fitted with elevation, herb layer cover, herb layer species richness, leaf functional diversity, shrub cover, soil C/N ratio, soil pH, successional age, proportion of deciduous tree species, tree evenness and tree species richness as variables describing plot characteristics. To account for the microhabitat around a trap inside a plot, litter cover, litter depth and vegetation cover were used. Finally, the interaction between tree species richness and successional age was included to test for possible interdependence of tree species richness and successional age.

The initial full models were simplified to obtain the most parsimonious explanatory models containing a minimum number of variables. Model simplification was based on Akaike Information Criterion, corrected for small sample sizes (AICc). Using a modified version of the stepAIC function in R (Scherber et al. 2010) all variables whose exclusion improved the model fit by reducing AICc were removed until a minimal best fitting model with the lowest AICc was obtained. If two models were almost equally likely ( $\Delta AICc \leq 2$ ) the model with the smaller number of variables was chosen as it was more parsimonious. Residuals of all models were analyzed for normality and homoscedasticity.

## Results

A total of 13,441 ant individuals and 3839 ant occurrences belonging to nine subfamilies, 32 genera, and 71 species were sampled. In total, five species were collected with 300 or more occurrences (out of 1080 possible total occurrences) accounting for 53% of all occurrences. Twelve species (17%) occurred as singletons and six species (8%) as doubletons. All species found are native to China (Guénard and Dunn 2012), no invasive ant species occurred. The species

**Table 9.2.** Results of minimal most parsimonious mixed-effects models for ant occurrence, ant species richness, and ant evenness separated for total ants, predator ants, and omnivore ants. Shown are standardized model estimates  $\pm$  SE which enables a direct comparison of explanatory variables, t-value, and probabilities *P* of the t-statistics. Variables dropped during model simplification are marked by a dash

Variable <sup>a</sup>	Total ants			Predator ants			Omnivore ants		
	Estimate $\pm$ SE	t	<i>P</i>	Estimate $\pm$ SE	t	<i>P</i>	Estimate $\pm$ SE	t	<i>P</i>
<i>Occurrence</i>									
Soil pH	3.15 $\pm$ 1.29	2.45	0.02	-	-	-	2.66 $\pm$ 1.16	2.3	0.03
AICc full <sup>b</sup> /minimal <sup>c</sup>	778.1 / 748.6			623.9 / 607.8			732.8 / 708.7		
<i>Richness</i>									
Elevation	-0.64 $\pm$ 0.29	-2.23	0.04	-	-	-	-	-	-
Leaf functional diversity	-	-	-	-0.45 $\pm$ 0.16	-2.88	0.01	-	-	-
Shrub cover	-	-	-	-0.47 $\pm$ 0.15	-3.14	0.01	-	-	-
Soil pH	0.60 $\pm$ 0.29	2.1	0.05	-	-	-	0.59 $\pm$ 0.23	2.6	0.02
Tree species richness	-	-	-	0.41 $\pm$ 0.15	2.69	0.01	-	-	-
AICc full <sup>b</sup> /minimal <sup>c</sup>	517.8 / 495.6			415.5 / 392.7			461.9 / 440.8		
<i>Evenness</i>									
Herb layer cover	-	-	-	0.021 $\pm$ 0.011	1.91	0.07	-	-	-
Shrub cover	-0.008 $\pm$ 0.003	-2.49	0.02	-	-	-	-	-	-
Successional age	-	-	-	-	-	-	-0.018 $\pm$ 0.008	-2.23	0.04
Tree evenness	-	-	-	-	-	-	0.022 $\pm$ 0.008	2.7	0.01
Tree species richness	-	-	-	0.029 $\pm$ 0.011	2.64	0.01	-	-	-
AICc full <sup>b</sup> /minimal <sup>c</sup>	-450.6 / -471.8			-184.3 / -201.7			-308.8 / -329.3		

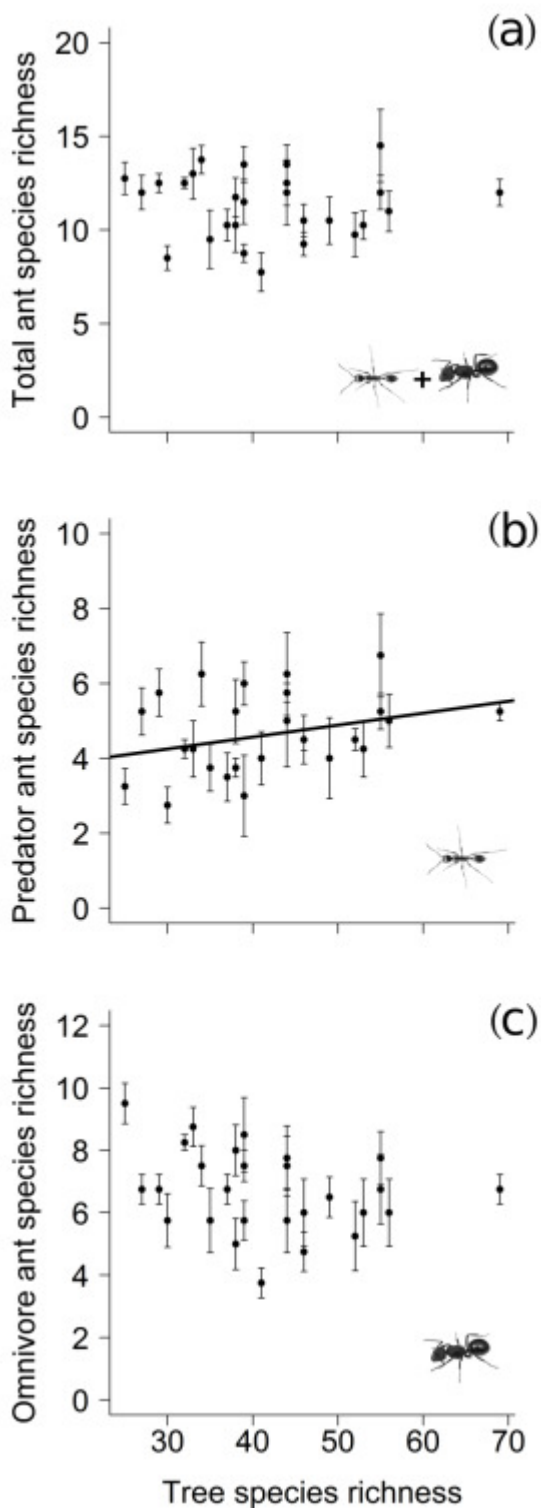
<sup>a</sup> herb layer species richness, litter cover, litter depth, soil C/N ratio, proportion of deciduous trees, vegetation cover, and the interaction tree species richness:successional age were dropped during model simplification in all cases and are not shown.

<sup>b</sup> initial mixed-effects model containing the entire set of variables.

<sup>c</sup> reduced minimal most parsimonious mixed-effects model.

accumulation curve indicates that the total epigeic ant community was adequately sampled (Fig. 9.1). Jack1 indicates that 86 ( $\pm$  4 SE) species are expected to occur, of which 83% were collected. Twenty-six species (37%) were considered to be exclusive predators and 45 species to be omnivores (see Table 9.1 for a list of genera and their trophic group). Predator species accounted for 5847 individuals (44%) and 1447 occurrences (38%). Community structure of both groups resembled the structure of the total

community: two (three) species of predators (omnivores) accounted for 56% (52%) of occurrences, five (seven) species as singletons and two (four) species as doubletons. Sampling efficiency for predators and omnivores was high. Species accumulation curves were shaped similarly and started to converge to an asymptote (Fig. 9.1). Based on jack1, 79% of the expected predator ant species (expected richness  $\pm$  SE: 33  $\pm$  3) and 85% of the expected omnivore ant species (53  $\pm$  3) were collected.



**Figure 9.3** Relationship between tree species richness and species richness of (a) total ants, (b) predatory ants, and (c) omnivore ants along a tree diversity gradient of 27 study plots in the GNNR. Shown are means per plot  $\pm$  1 SE. Regression line shows significant relationship at  $P < 0.05$  (see Table 2). Embedded pictures from [www.alexanderwild.com](http://www.alexanderwild.com), ©Alex Wild, used with permission.

Soil pH was the most important environmental variable explaining occurrence and richness of total and omnivore ants. The minimal model for the occurrences of these two groups contained only soil pH as a significant and positive explanatory variable (Fig. 9.2a,c; see Table 9.2 for statistical information). Increasing soil pH also increased the species richness of both groups. In addition, the minimal model for total ant species richness indicated a negative influence of increasing elevation (Table 9.2). Predator occurrence was not related to soil pH (Fig. 9.2b) or any other environmental variable.

In contrast, species richness and evenness of predator ants were best explained by tree species richness and environmental variables related to vegetation structure. Predator species richness and evenness increased significantly with increasing tree species richness (Fig. 9.3b; Fig. 9.4b; Table 9.2). The model for predator species richness also contained negative effects of leaf functional diversity and shrub cover (Fig. S9.1; Fig. S9.2; Table 9.2). Likewise, the model for predator evenness indicated a positive influence of herb layer species richness (Table 9.2) that was, however, not significant. Tree species richness neither influenced occurrence nor species richness nor evenness of total (Fig. 9.3a; Fig. 9.4a) and omnivore ants (Fig. 9.3c; Fig. 9.4c). Total ant evenness was explained by a minimal mixed-effects model containing only a negative influence of shrub cover, while omnivore ant evenness increased with increasing tree evenness but decreased with increasing successional age (Table 9.2).

## Discussion

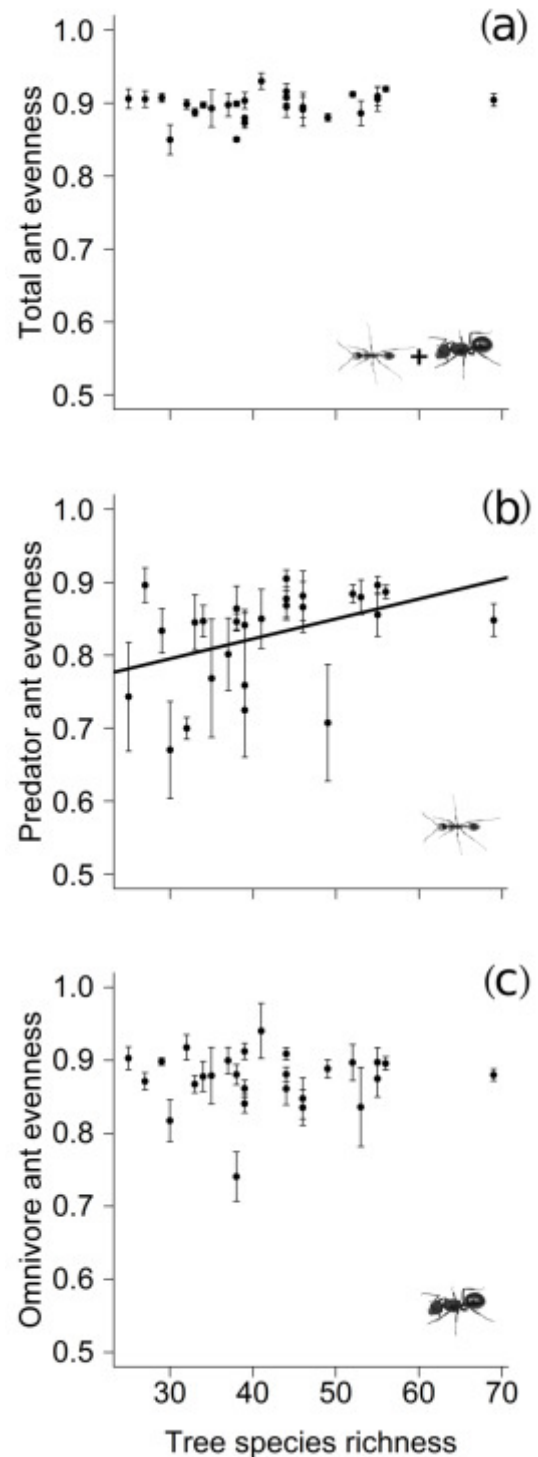
This study provides novel insights into the influence of tree species richness and other abiotic and biotic environmental variables on a epigeic ant community. This is the first ant study conducted in the highly diverse subtropical forests of South-East China and, in particular, it was shown that species richness and evenness of predator, but not of omnivore ants, increased with tree species richness. So far, most studies showing an increase of predator species richness with increasing plant species richness have been conducted in experimental or low diversity

systems and largely neglected species-rich natural habitats (Duffy et al. 2007; Hillebrand and Matthiessen 2009).

### The influence of abiotic environmental variables

Elevation strongly influences the abiotic characteristic of a habitat, most prominently due to the decrease in mean annual temperature with increasing elevation. Ant species richness usually declines with increasing elevation (e.g. Brühl et al. 1999; Sanders et al. 2007), a pattern that is supported by a weak but significant decline of total ant species richness found in this study.

Soil properties directly shape plant communities by having far reaching consequences on nutrient availability and cycling (Ashman and Puri 2008). Epigeic ants, in particular ground-nesting species, are in direct contact with the soil and are thus strongly influenced by soil properties. While the ant community was not influenced by soil nutrients, it was strongly influenced by soil pH. Under normal properties (at pH values between 4 and 9), soil acidity has only a marginal influence on epigeic ants (Boulton et al. 2005, Jacquemin et al. 2012). This general pattern might change under extreme properties that can seriously interfere with the physiology of the ants or even be toxic. Soils in the GNNR are derived from granite bedrock which is covered by a weathered and highly eroded saprolite (Geißler et al. 2012). The pH of the top-soil is highly acidic, ranging from pH 3.4 to 4.0. The local plant community mostly consists of genera that are well adapted to low pH e.g. by having a high tolerance to free Aluminum ions (reviewed in Jansen et al. 2002) that reach high concentrations in acidic soils. Under such harsh acidic properties, a low pH can have a strong negative influence on arthropods (Lavelle et al. 1995; van Straalen and Verhoef 1997), as reflected by the significantly higher occurrence and species richness of total and omnivore ants on plots with less acidic soil. It is suspected that these results may partly be explained by the nesting habits of epigeic ants. In the study site, most predator ant genera nest in the leaf litter (Brown 2000; M. Staab, unpubl. data) where they are less prone to the



**Figure 9.4** Relationship between tree species richness and evenness based on the Shannon-index of occurrences for (a) total ants, (b) predator ants, and (c) omnivore ants along a tree diversity gradient of 27 study plots in the GNNR. Shown are means per plot  $\pm$  1 SE. Regression line shows significant relationship at  $P < 0.05$  (see Table 2). Embedded pictures from www.alexanderwild.com, ©Alex Wild, used with permission.

negative effects of soil acidity as are several litter-nesting omnivores, such as *Pheidole*. While other omnivore genera dwell in dead-wood or build arboreal nests, several genera excavate soil nests, making them susceptible to harsh soil properties such as low pH.

### The influence of tree species richness and biotic variables

While the sign of the effect of abiotic environmental variables on epigeic ants matches with general expectations and with patterns reported from other ecosystems, the influences of biotic variables are often interwoven and less clear. On a large scale there is a close association between plant and arthropod species richness in tropical forests across taxonomic groups and trophic levels (Basset et al. 2012). However, there is little information available on how ant species richness, and in particular the richness of predator ants, changes across gradients of tree species richness at more local scales. Usually, primary forests have a more species-rich ant community than disturbed forests (e.g. Olson 1991; Floren and Linsenmair 2005; Klimes et al. 2012), but most of these studies have focused on arboreal ants and did not specifically analyze tree species richness gradients. Arboreal ant communities are profoundly different from epigeic ant communities (e.g. Floren et al. 2014) by comprising mostly omnivore canopy specialists that are more likely to benefit from higher structural heterogeneity caused by higher tree species richness (Ribas et al. 2003; Klimes et al. 2012). In contrast, for epigeic ants even degraded forests have been shown to maintain high species richness (e.g. Belshaw et al. 1993; Woodcock et al. 2011).

However, for epigeic predator ants the ‘enemies hypothesis’ (Root 1973) suggests an increase of predator species richness with increasing plant species richness. It is predicted that higher plant richness will provide more heterogeneous resources for herbivores and decomposers, both in space and time, and thus support a more diverse community of prey arthropods that would promote a more diverse and more even set of predators. Most evidence for this hypothesis so far comes either from low diversity forest

ecosystems (e.g. Vehviläinen et al. 2008) or from grassland experiments (e.g. Haddad et al. 2009, 2011; Dinnage et al. 2012). Root’s hypothesis also implies an increase of omnivore ant species richness, and thus also of total ant species richness with increasing tree species richness, which was not found. Omnivore ants have broad trophic niches and do not depend exclusively on prey organisms (Blüthgen and Feldhaar 2010).

Trees have a direct influence on the leaf-litter matrix (Burghouts et al. 1992). Higher leaf-litter cover (e.g. McGlynn et al.; 2009b), leaf-litter quantity (e.g. dos Santos Bastos and Harada 2011), moisture (e.g. Levings and Windsor 1984), and litter leaf morphology (Silva et al. 2011) are known to positively influence ants by increasing nesting resources. The availability of diverse nest sites is a prime factor explaining ant species richness (Benson and Harada 1988; Kaspari 1996; Blüthgen and Feldhaar 2010). As discussed above, predator ants are mainly nesting in leaf litter and are therefore more likely than omnivore ants to benefit from increased leaf-litter heterogeneity and quantity (dos Santos Bastos and Harada 2011). Whilst measures of litter attributes such as cover and depth had no influence on predator ants, tree species richness increased the species richness and evenness of this group, suggesting a direct positive effect of trees on predators only. This effect was invariant of the community evenness of trees that had a positive influence only on omnivore species that are more dependent on plant-based resources (Blüthgen and Feldhaar 2010). In contrast to the findings of Silva et al. (2011), functional attributes of leaves had a negative influence on predator ant richness. The leaf traits used for calculating leaf functional diversity were, in addition to morphological leaf traits, predominately leaf nutrients and other chemical leaf traits that were measured on freshly collected, living young leaves (Kröber et al. 2012). Thus the environmental variable leaf functional diversity reflects the functional diversity of the living tree community and is not surprisingly positively correlated with tree species richness (see Table S9.1). However, before litter fall during leaf senescence the majority of leaf nutrients are resorbed into the



woody tissue of the trees (Aerts 1996), making the dead and decaying leaves in the leaf litter matrix on the forest floor much more homogenous than the foliage this litter originates from. Consequently, the unexpected negative correlation between leaf functional diversity and predator ant richness found in this study should be interpreted with caution. To obtain a better understanding of the effect of leaf functional diversity on epigeic ants, it is desirable to assess functional attributes of leaf litter in future studies.

The positive influence of tree species richness on predator ants was independent of successional age, and thus not driven by forest succession. Usually, successional age and tree species richness are directly positively correlated which was not the case in this study. Nevertheless, successional age strongly influences habitat properties in regenerating forests (Guariguata and Ostertag 2001), and has cascading effects on arthropod communities, such as shifting the foraging preferences of the ant community (Bihn et al. 2008). Successional age only had a negative influence on omnivore ant evenness. However, the successional age of a plot had direct consequences for a variety of environmental variables that relate to the structure of the vegetation such as tree abundance or the cover of different vegetation layers.

Shrub cover was the variable with the strongest negative influence on predator species richness, and the evenness of the total ant community also decreased with shrub cover. Shading levels of the forest floor relate closely to the cover of the shrub and canopy layers. A dense shrub layer might be particularly effective in shading as it is, unlike the canopy, not steadily moved by wind. The cover of lower vegetation strata is known to influence epigeic ant species richness (e.g. Gunawardene et al. 2012) probably by mediating changes in microclimatic conditions on the forest floor. Increased shading has been shown to have an impact on ant colonies, both positively in a tropical forest (Armbrecht et al. 2005) and negatively in a temperate forest (Higgins and Lindgren 2012). While shade decreases the amount of sunlight reaching the ground and thus the energy

availability, shading also lowers desiccation risk due to higher moisture availability. Ants are sensitive to both effects (e.g. Levings and Windsor 1984; McGlynn et al. 2013). In the GNNR the hottest time of the year coincides with the period of highest precipitation (Geißler et al. 2012) making desiccation risk less likely to have negative effects on ants. Consequently, following the species-energy hypothesis (Wright 1983), a dense shrub layer might reduce energy availability with effects especially visible on organisms in higher trophic levels such as predator ants.

### Consequences for trophic interactions

The prime ecosystem function of predator ants, exhibiting a high predation pressure on other arthropods (e.g. Floren et al. 2002; Berghoff et al. 2003; Cerda and Dejean 2011) may be enhanced in more tree species-rich forests. Interestingly, Schuldt et al. (2011) found within the same plots that the diversity of epigeic spiders was negatively related to trees species richness. Spiders are prevalent generalist predators that frequently exhibit intraguild competition with ants (Sanders and Platner 2007; Sanders et al. 2011), and in the present study likely biotic interactions between predator ants and spiders causes the divergent correlations with tree species richness. However, it is largely unknown how interactions between different predator taxa relate to overall predation albeit such biotic interactions might be crucial for maintaining a high diversity. For example, in the GNNR, herbivore damage on tree saplings increased with tree species richness (Schuldt et al. 2010), which supports the pattern found for spiders but not for predator ants. In a different study, ants and spiders had a positive interactive effect on herbivore control (Nahas et al. 2012) and were thus complementing the ecosystem service predation. These results highlight the complexity of trophic interactions in species-rich forests and, ideally, future approaches studies on predators and predation should also address the complex biotic interactions between different predator groups.

### Limitations and conclusions

Pitfall traps were used to collect epigeic ants with a high number of replicates in a

subtropical forest. This collection method has been claimed to bias arthropod sampling towards mobile and large species, and to systematically underrepresent smaller, less mobile species (e.g. Olson 1991; Ivanov and Keiper 2009). Various studies have shown that Winkler extraction can be more effective to collect leaf-litter ants than pitfall traps (e.g. Bestelmeyer et al. 2000; Parr and Chown 2001). For future studies on predator ants the use of a broad set of collection methods, including pitfall traps and Winkler extraction is recommended, to rule out the particular biases of single collection methods. In the present study, pitfall traps have probably resulted in an underrepresentation of small cryptic litter-dwelling ants such as *Hypoponera* which are mostly predators. Due to their small body size these species might react sensitively to changes in environmental conditions and could be positively influenced by tree species richness, strengthening the main result of the study.

It should be noted that our genus-based separation approach cannot rule out that single species with wide trophic ranges may change their trophic position depending on forest type (Pfeiffer et al. 2014) or soil biogeochemistry (McGlynn et al. 2009a). In some cases, large-scale habitat disturbance might at least initially change the trophic position of the entire ant community (Woodcock et al. 2013). Despite this, there are few studies available to date that compare epigeic ant communities across habitats using isotope signatures (Gibb and Cunningham 2011; Pfeiffer et al. 2014; Woodcock et al. 2013) and conclusive results have yet to be obtained. The present study was only carried out in regenerating secondary forests of a single forest type. Even the youngest plots had not been disturbed for around 20 years. Hence a major bias of habitat disturbance and forest type on the trophic position of ant species is not expected.

Epigeic predatory arthropods influence the entire ground-living arthropod community and can even influence food webs in other strata (Pringle and Fox-Dobbs 2008). The present study revealed effects of tree species richness on predator but not on omnivore ant species. The results therefore

highlight the importance of considering functional and trophic groups separately when analyzing biodiversity. Only by disentangling the influence of tree diversity on the two main functional groups of the epigeic ant community it was shown that diverse forests maintain species-rich predator ant communities and thus the ecosystem functions dependent on predation (see Bruno and Cardinale 2008; Finke and Snyder 2010).

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## Contribution of authors

Designed the project: Michael Staab, Andreas Schuldt, Thorsten Assmann and Alexandra-Maria Klein

Collected the data: Michael Staab and Andreas Schuldt

Analyzed the data and wrote the first manuscript: Michael Staab

Revised the manuscript: Michael Staab, Andreas Schuldt, Thorsten Assmann and Alexandra-Maria Klein

## References

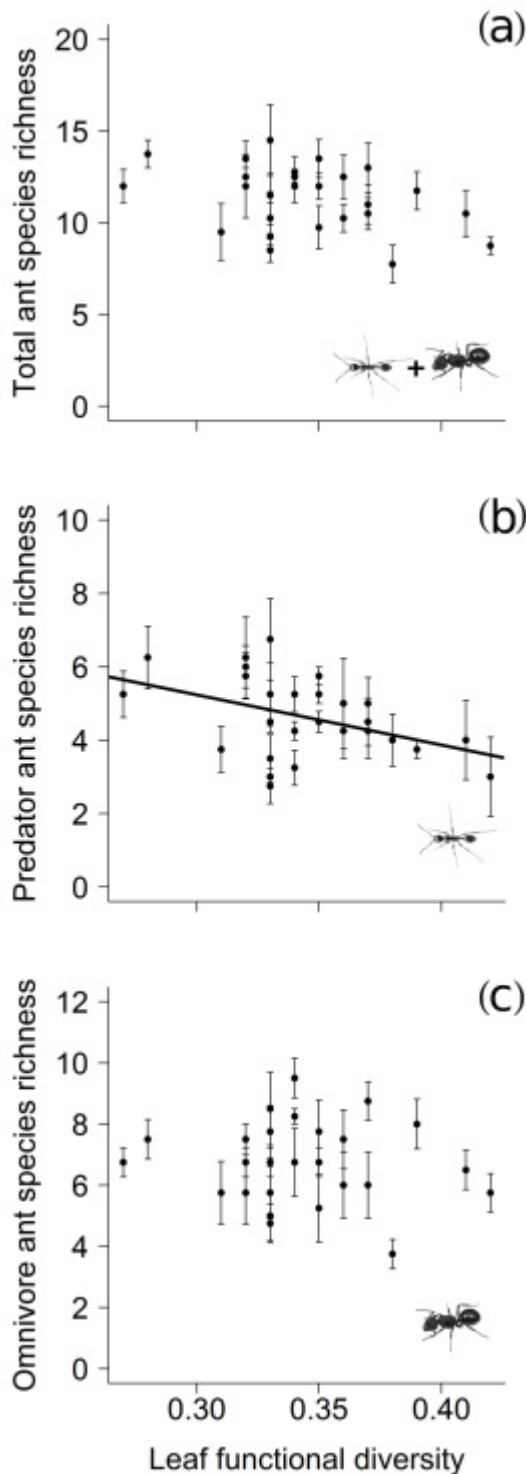
- Aerts R (1996) Nutrient resorption from senescing leaves of perennials: Are there general patterns? *Journal of Ecology* 84: 597-608
- Alonso LE (2000) Ants as indicators of diversity. In *Ants: standard methods for measuring and monitoring biodiversity* (ed. by Agosti D, Majer JD, Alonso LE, Schultz TR), pp. 80-88. Smithsonian Institution Press, Washington
- Armbrecht I, Rivera L, Perfecto I (2005) Reduced diversity and complexity in the leaf-litter ant assemblage of Colombian coffee plantations. *Conservation Biology* 19: 897-907
- Ashman M, Puri G (2008) *Essential soil science: a clear and concise introduction to soil science*. Wiley-Blackwell, New York
- Barlow J, Gardner TA, Araujo IS, Avila-Pires TC, Bonaldo AB, Costa JE, et al. (2007) Quantifying the biodiversity value of tropical primary, secondary, plantation forests. *Proceedings of the National Academy of Sciences of the United States of America* 104: 18555-18560
- Basset Y, Cizek L, Cuenoud P, Didham RK, Guilhaumon F, Missa O, et al. (2012) Arthropod diversity in a tropical forest. *Science* 338: 1481-1484
- Belshaw R, Bolton B (1993) The effect of forest disturbance on the leaf-litter ant fauna in Ghana. *Biodiversity and Conservation* 2: 656-666
- Berghoff SM, Maschwitz U, Linsenmair KE (2003) Influence of the hypogaecic army ant *Dorylus (Dichthadia) laevigatus* on tropical arthropod communities. *Oecologia* 135: 149-157
- Bestelmeyer BT, Agosti D, Alonso LE, Brandao CRF, Brown WL, Delabie JHC, Silvestre R (2000) Field techniques for the study of ground-dwelling ants: an overview, description, and evaluation. In *Ants: standard methods for measuring and monitoring biodiversity* (ed. by Agosti D, Majer JD, Alonso LE, Schultz TR), pp. 122-144. Smithsonian Institution Press, Washington
- Bihn JH, Verhaagh M, Brand R (2008) Ecological stoichiometry along a gradient of forest succession: Bait preferences of litter ants. *Biotropica* 40: 597-599
- Blüthgen N, Feldhaar H (2010) Food and shelter: how resources influence ant ecology. In *Ant ecology* (ed. by Lach L, Parr CL, Abbott KL), pp. 115-136. Oxford University Press, Oxford
- Blüthgen N, Gebauer G, Fiedler K (2003) Disentangling a rainforest food web using stable isotopes: dietary diversity in a species-rich ant community. *Oecologia* 137: 426-435
- Bolton B (1994) *Identification guide to the ant genera of the world*. Harvard University Press, Cambridge
- Boulton AM, Davies KF, Ward PS (2005) Species richness, abundance, and composition of ground-dwelling ants in northern California grasslands: Role of plants, soil, and grazing. *Environmental Entomology* 34: 96-104
- Brown WL (2000). Diversity of ants. In *Ants: standard methods for measuring and monitoring biodiversity* (ed. by Agosti D, Majer JD, Alonso LE, Schultz TR), pp. 45-79. Smithsonian Institution Press, Washington
- Bruehlheide H, Böhnke M, Both S, Fang T, Assmann T, Baruffol M, et al. (2011) Community assembly during secondary forest succession in a Chinese subtropical forest. *Ecological Monographs* 81: 25-41
- Bühl CA, Mohamed V, Linsenmair KE (1999) Altitudinal distribution of leaf litter ants along a transect in primary forests on Mount Kinabalu, Sabah, Malaysia. *Journal of Tropical Ecology* 15: 265-277
- Bruno JF, Cardinale BJ (2008) Cascading effects of predator richness. *Frontiers in Ecology and the Environment* 6: 539-546
- Burghouts T, Ernsting G, Korthals G, Devries T (1992) Litterfall, leaf litter decomposition and litter invertebrates in primary and selectively logged dipterocarp forest in Sabah, Malaysia. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* 335: 407-416
- Cardinale BJ, Matulich KL, Hooper DU, Byrnes JE, Duffy E, Gamfeldt L, et al. (2011) The functional role of producer diversity in ecosystems. *American Journal of Botany* 98: 572-592
- Cerda X, Dejean A (2011). Predation by ants on arthropods and other animals. In *Predation in the Hymenoptera: an evolutionary perspective* (ed. by Polidori C), pp. 39-78. TransWorld Research Network, Kerala
- Del Toro I, Ribbons RR, Peline SL (2012) The little things that run the world revisited: a review of ant-mediated ecosystem services and disservices (Hymenoptera: Formicidae). *Myrmecological News* 17: 133-146
- Dinnage R, Cadotte MW, Haddad NM, Crutsinger GM, Tilman D (2012) Diversity of plant evolutionary lineages promotes arthropod diversity. *Ecology Letters* 15: 1308-1317
- Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carre G, et al. (2013) Collinearity: a review of methods to deal with it and a

- simulation study evaluating their performance. *Ecography* 36: 27-46
- dos Santos Bastos AH, Harada AY (2011) Leaf-litter amount as a factor in the structure of a ponerine ants community (Hymenoptera, Formicidae, Ponerinae) in an eastern Amazonian rainforest, Brazil. *Revista Brasileira De Entomologia* 55: 589-596
- Duffy JE (2009) Why biodiversity is important to the functioning of real-world ecosystems. *Frontiers in Ecology and the Environment* 7: 437-444
- Duffy JE, Cardinale BJ, France KE, McIntyre PB, Thebault E, Loreau M (2007) The functional role of biodiversity in ecosystems: incorporating trophic complexity. *Ecology Letters* 10: 522-538
- Finke DL, Snyder WE (2010) Conserving the benefits of predator biodiversity. *Biological Conservation* 143: 2260-2269
- Floren A, Biun A, Linsenmair KE (2002) Arboreal ants as key predators in tropical lowland rainforest trees. *Oecologia* 131: 137-144
- Floren A, Linsenmair KE (2005) The importance of primary tropical rain forest for species diversity: An investigation using arboreal ants as an example. *Ecosystems* 8: 559-567
- Floren A, Wetzell W, Staab M (2014) The contribution of canopy species to overall ant diversity (Hymenoptera: Formicidae) in temperate and tropical ecosystems. *Myrmecological News* 19: 65-74
- Folgarait PJ (1998) Ant biodiversity and its relationship to ecosystem functioning: a review. *Biodiversity and Conservation* 7: 1221-1244
- Gamfeldt L, Snäll T, Bagchi R, Jonsson M, Gustafsson L, Kjellander P, et al. (2013) Higher levels of multiple ecosystem services are found in forests with more tree species. *Nature Communications* 4: 1340
- Geißler C, Kühn P, Böhnke M, Bruelheide H, Shi X, Scholten T (2012) Splash erosion potential under tree canopies in subtropical SE China. *Catena* 91: 85-93
- Gibb H, Cunningham SA (2011) Habitat contrasts reveal a shift in the trophic position of ant assemblages. *Journal of Animal Ecology* 80: 119-127
- Gibbs HK, Ruesch AS, Achard F, Clayton MK, Holmgren P, Ramankutty N, Foley JA (2010) Tropical forests were the primary sources of new agricultural land in the 1980s and 1990s. *Proceedings of the National Academy of Sciences of the United States of America* 107: 16732-16737
- Gibson L, Lee TM, Koh LP, Brook BW, Gardner TA, Barlow J, et al. (2011) Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature* 478: 378-381
- Guariguata MR, Ostertag R (2001) Neotropical secondary forest succession: changes in structural and functional characteristics. *Forest Ecology and Management* 148: 185-206
- Guénard B, Dunn RR (2012) A checklist of the ants of China. *Zootaxa*, 3558, 1-77
- Gunawardene NR, Majer JD, Edirisinghe JP (2012) Correlates of ant (Hymenoptera: Formicidae) and tree species diversity in Sri Lanka. *Myrmecological News* 17: 81-90
- Haddad NM, Crutsinger GM, Gross K, Haarstad J, Knops JMH, Tilman D (2009) Plant species loss decreases arthropod diversity and shifts trophic structure. *Ecology Letters* 12: 1029-1039
- Haddad, N.M., Crutsinger, G.M., Gross, K., Haarstad, J., Tilman, D. (2011) Plant diversity and the stability of foodwebs. *Ecology Letters* 14: 42-46.
- Higgins RJ, Lindgren BS (2012) The effect of manipulated shading on the colony abundance of two species of ants, *Formica aserva* and *Leptothorax muscorum*, in dead wood. *Entomologia Experimentalis et Applicata* 143: 292-300
- Hillebrand H (2004) On the generality of the latitudinal diversity gradient. *American Naturalist* 163: 192-211
- Hillebrand H, Matthiessen B (2009) Biodiversity in a complex world: consolidation and progress in functional biodiversity research. *Ecology Letters* 12: 1405-1419
- Hölldobler B, Wilson EO (1990) *The ants*. Belknap Press of Harvard University Press, Cambridge
- Hooper DU, Adair EC, Cardinale BJ, Byrnes JEK, Hungate BA, Matulich KL, et al. (2012) A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature* 486: 105-U129
- Ivanov K, Keiper . (2009) Effectiveness and biases of winker litter extraction and pitfall trapping for collecting ground-dwelling ants in northern temperate forests. *Environmental Entomology* 38: 1724-1736
- Jacquemin J, Drouet T, Delsinne T, Roisin Y, Leponce M (2012) Soil properties only weakly affect subterranean ant distribution at small spatial scales. *Applied Soil Ecology* 62: 163-169
- Jansen S, Broadley MR, Robbrecht E, Smets E (2002) Aluminum hyperaccumulation in angiosperms: A review of its phylogenetic significance. *Botanical Review* 68: 235-269

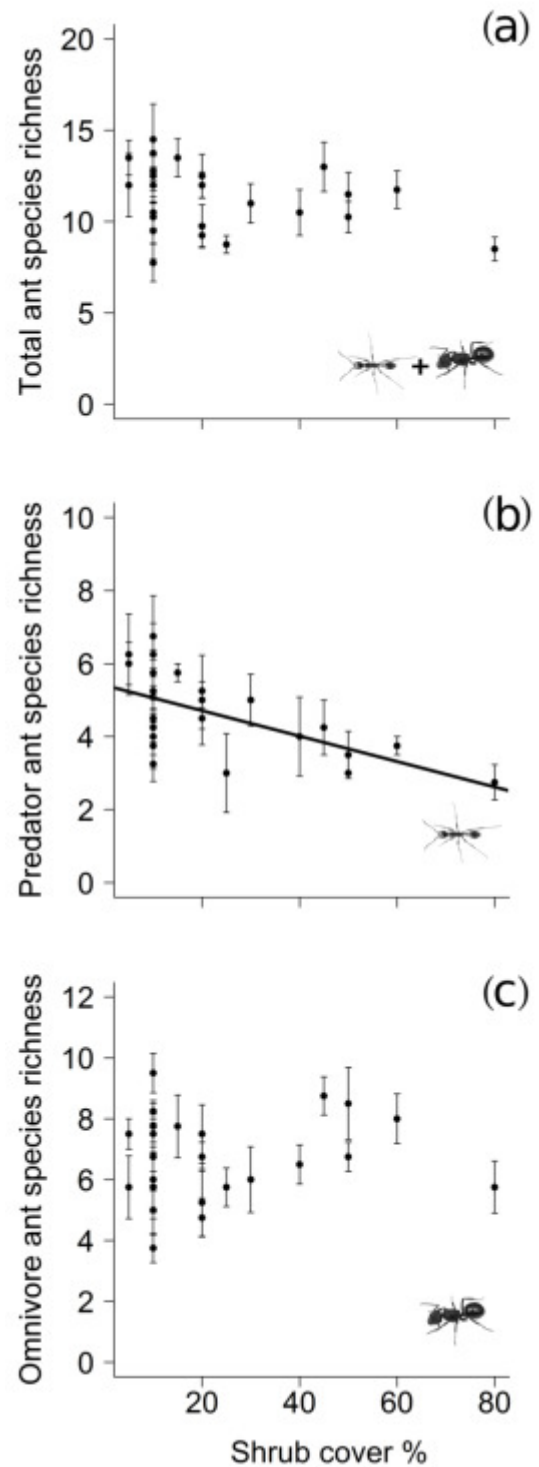
- Kaspari M (1996) Testing resource-based models of patchiness in four Neotropical litter ant assemblages. *Oikos* 76: 443-454
- Kier G, Mutke J, Dinerstein E, Ricketts TH, Küper W, Kreft H, Barthlott W (2005) Global patterns of plant diversity and floristic knowledge. *Journal of Biogeography* 32: 1107-1116
- Klimes P, Idigel C, Rimandai M, Fayle TM, Janda M, Weiblen GD, Novotny V (2012) Why are there more arboreal ant species in primary than in secondary tropical forests? *Journal of Animal Ecology* 81: 1103-1112
- Kone M, Konate S, Yeo K, Kouassi PK, Linsenmair KE (2012) Changes in ant communities along an age gradient of cocoa cultivation in the Oume region, central Cote d'Ivoire. *Entomological Science* 15: 324-339
- Kröber W, Böhnke M, Welk E, Wirth C, Bruelheide H (2012) Leaf trait-environment relationships in a subtropical broadleaved forest in South-East China. *PLoS One* 7: e35742
- Lavelle P, Chauvel A, Fragoso C (1995). Faunal activity in acid soils. In *Plant soil interactions at low pH: principles and management* (ed. by RDate RA, Grundon NJ, Payment GE, Probert ME), pp. 201-201. Kluwer Academic Publishers, Dordrecht, Netherlands
- Letourneau DK, Jedlicka JA, Bothwell SG, Moreno CR (2009). Effects of natural enemy biodiversity on the suppression of arthropod herbivores in terrestrial ecosystems. *Annual Review of Ecology Evolution and Systematics* 40: 573-592
- Levings SC, Windsor DM (1984) Litter moisture-content as a determinant of litter arthropod distribution and abundance during the dry season on Barro-Colorado Island, Panama. *Biotropica* 16: 125-131
- Majer JD, Orabi G, Bisevac L (2007) Ant (Hymenoptera: Formicidae) pass the bioindicator scorecard. *Myrmecological News* 10: 69-76
- McGlynn TP, Choi HK, Mattingly ST, Upshaw A, Poirson EK, Betzelberger J (2009a) Spurious and functional correlates of the isotopic composition of a generalist across a tropical rainforest landscape. *BMC Ecology* 9: 23
- McGlynn TP, Fawcett RM, Clark DA (2009b) Litter biomass and nutrient determinants of ant density, nest size, growth in a Costa Rican tropical wet forest. *Biotropica* 41: 234-240
- McGlynn TP, Alonso-Rodriguez AM, Weaver M (2013) A test of species-energy theory: patch occupancy and colony size in tropical rainforest litter-nesting ants. *Oikos* 122: 1357-1361
- Miettinen J, Shi C, Liew SC (2011) Deforestation rates in insular Southeast Asia between 2000 and 2010. *Global Change Biology* 17: 2261-2270
- Nahas L, Gonzaga MO, Del-Claro K (2012) Emergent Impacts of ant and spider interactions: Herbivory reduction in a tropical savanna tree. *Biotropica* 44: 498-505
- Olson DM (1991) A comparison of litter sifting and pitfall traps for sampling leaf litter ants (Hymenoptera, Formicidae) in a tropical wet forest, Costa Rica. *Biotropica* 23: 166-172.
- Parr CL, Chown SL (2001) Inventory and bioindicator sampling: testing pitfall and Winkler methods with ants in a South African savanna. *Journal of Insect Conservation* 5: 27-36
- Pfeiffer M, Mezger D, Dyckmans J (2014) Trophic ecology of tropical leaf litter ants (Hymenoptera: Formicidae) – a stable isotope study in four types of Bornean rain forest. *Myrmecological News* 19: 31-41
- Philpott SM, Armbrrecht I (2006) Biodiversity in tropical agroforests and the ecological role of ants and ant diversity in predatory function. *Ecological Entomology* 31: 369-377
- Pringle RM, Fox-Dobbs K (2008) Coupling of canopy and understory food webs by ground-dwelling predators. *Ecology Letters* 11: 1328-1337
- Ribas CR, Schoereder JH, Pic M, Soares SM (2003) Tree heterogeneity, resource availability, and larger scale processes regulating arboreal ant species richness. *Austral Ecology* 28: 305-314
- Root RB (1973) Organization of a plant-arthropod association in simple and diverse habitats: The fauna of collards (*Brassica oleracea*). *Ecological Monographs* 43: 95-120
- Sanders D, Platner C (2007) Intraguild interactions between spiders and ants and top-down control in a grassland food web. *Oecologia* 150: 611-624
- Sanders D, Schaefer M, Platner C, Griffith GJK (2011) Intraguild interactions among generalist predator functional groups drive impact on herbivore and decomposer prey. *Oikos* 120: 418-426
- Sanders NJ, Lessard JP, Fitzpatrick MC, Dunn RR (2007) Temperature, but not productivity or geometry, predicts elevational diversity gradients in ants across spatial grains. *Global Ecology and Biogeography* 16: 640-649
- Scherber C, Eisenhauer N, Weisser WW, Schmid B, Voigt W, Fischer M, et al. (2010) Bottom-up

- effects of plant diversity on multitrophic interactions in a biodiversity experiment. *Nature* 468: 553-556
- Schuldt A, Baruffol M, Böhnke M, Bruelheide H, Härdtle W, Lang AC, et al. (2010) Tree diversity promotes insect herbivory in subtropical forests of south-east China. *Journal of Ecology* 98: 917-926
- Schuldt A, Both S, Bruelheide H, Härdtle W, Schmid B, Zhou H, Assmann T (2011) Predator diversity and abundance provide little support for the enemies hypothesis in forests of high tree diversity. *PLoS One* 6: e22905.
- Silva PSD, Bieber AGD, Correa MM, Leal IR (2011) Do leaf-litter attributes affect the richness of leaf-litter ants? *Neotropical Entomology* 40: 542-547
- van Straalen NM, Verhoef HA (1997) The development of a bioindicator system for soil acidity based on arthropod pH preferences. *Journal of Applied Ecology* 34: 217-232
- Vehviläinen H, Koricheva J, Ruohomäki K (2008) Effects of stand tree species composition and diversity on abundance of predatory arthropods. *Oikos* 117: 935-943
- Woodcock P, Edwards DP, Fayle TM, Newton RJ, Khen CV, Bottrell SH, Hamer KC (2011) The conservation value of South East Asia's highly degraded forests: evidence from leaf-litter ants. *Philosophical Transactions of the Royal Society B-Biological Sciences* 366: 3256-3264
- Woodcock P, Edwards DP, Newton RJ, Khen CV, Bottrell SH, Hamer KC (2013) Impacts of intensive logging on the trophic organisation of ant communities in a biodiversity hotspot. *PLoS One* 8: e60756
- Wright DH (1983) Species-energy theory - An extension of species-area theory. *Oikos* 41: 496-506
- Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) *Mixed effects models and extensions in ecology with R* Springer, Berlin

Supplementary Material



**Figure S9.1** Relationship between leaf functional diversity and species richness of (a) total ants, (b) predatory ants, and (c) omnivore ants in the 27 study plots of the GNNR. Shown are means per plot  $\pm$  1 SE. Regression line shows significant relationship at  $P < 0.05$  (see Table 9.2). Embedded pictures from [www.alexanderwild.com](http://www.alexanderwild.com), ©Alex Wild, used with permission.



**Figure S9.2** Relationship between shrub cover and species richness of (a) total ants, (b) predatory ants, and (c) omnivore ants in the 27 study plots of the GNNR. Shown are means per plot  $\pm$  1 SE. Regression line shows significant relationship at  $P < 0.05$  (see Table 9.2). Embedded pictures from [www.alexanderwild.com](http://www.alexanderwild.com), ©Alex Wild, used with permission.

**Table S9.1.** Spearman correlation coefficients (rs) for all pairwise comparisons of all environmental variables measured. Bold numbers indicated when two variables were correlated with  $r_s > 0.70$  and hence one of the variables was excluded from all following analyses. Units of all variable measurements are shown in brackets

	Vegetation height <sup>a,b</sup> (cm)	Vegetation cover <sup>b</sup> (%)	Tree species richness	Tree phylogenetic diversity*	Tree evenness	Trees deciduous (%)	Tree basal area <sup>a</sup> (m <sup>2</sup> )	Tree abundance*	Successional age (yrs)	Soil pH	Soil N* (%)	Soil moisture* (%)	Soil C/N	Soil C* (%)	Shrub cover (%)	Mean temperature* (°C)	Litter depth <sup>b</sup> (cm)	Litter cover <sup>b</sup> (%)	Leaf functional diversity	Herb species richness <sup>a</sup>	Herb cover <sup>b</sup> (%)	Elevation (m)	Canopy cover* (%)
Canopy cover* (%)	-0.17	-0.13	0.15	0.3	0.43	-0.4	0.81	-0.61	0.76	0.21	-0.03	0.33	0.14	0.35	-0.39	-0.07	-0.1	-0.16	0.09	-0.25	-0.19	0.25	1
Elevation (m)	-0.18	-0.17	0.05	-0.13	-0.23	0.36	0.22	0.13	0.22	0.74	-0.38	0.46	-0.03	0.48	0.25	-0.85	-0.33	-0.22	0.45	-0.22	-0.37		1
Herb cover <sup>b</sup> (%)	0.44	0.47	0.14	0.21	0.11	-0.06	-0.13	0	-0.08	-0.17	-0.18	0.03	0.33	0.09	0.06	0.33	-0.01	-0.02	-0.05	0.09		1	
Herb species richness <sup>a</sup>	0.06	0.09	0.28	-0.07	-0.05	0.17	-0.3	0.28	-0.22	-0.04	0.28	-0.06	-0.4	-0.16	0.26	-0.06	-0.02	0.11	-0.09		1		
Leaf functional diversity	0.16	0.14	0.41	0.38	0.22	0.1	0.04	0.04	0.12	0.36	-0.43	0.17	0	0.18	0.45	-0.38	0.06	-0.15		1			
Litter cover <sup>b</sup> (%)	-0.09	-0.14	0.07	-0.16	-0.15	0.05	-0.19	0.26	-0.17	-0.17	0.18	-0.28	-0.13	-0.32	-0.04	0.05	0.19			1			
Litter depth <sup>b</sup> (cm)	0.04	-0.03	0.05	0.19	0.16	-0.27	-0.01	-0.06	-0.06	-0.21	0.06	-0.13	0.01	-0.12	-0.01	0.29			1				
Mean temperature* (°C)	0.15	0.1	-0.22	0.24	0.36	-0.49	0.03	-0.39	-0.04	-0.76	0.46	-0.46	0.3	-0.42	-0.41		1						
Shrub cover (%)	0.23	0.23	0.03	-0.21	-0.47	0.54	-0.54	0.6	-0.33	0.1	-0.14	-0.13	-0.39	-0.16	1								
Soil C* (%)	-0.15	-0.12	0.36	0.22	0.26	0.01	0.47	-0.26	0.51	0.8	-0.58	0.98	0.03	1									
Soil C/N	0.09	0.1	-0.17	0.24	0.31	-0.31	0.38	-0.41	0.31	-0.27	0.03	-0.11	1										
Soil moisture* (%)	-0.17	-0.13	0.41	0.2	0.24	0.04	0.41	-0.2	0.46	0.82	-0.6	1											
Soil N* (%)	-0.09	-0.12	-0.33	-0.04	0.06	-0.16	-0.04	-0.09	-0.11	-0.6	1												
Soil pH	-0.16	-0.13	0.25	-0.05	-0.06	0.31	0.19	0.02	0.24	1													
Successional age (yrs)	-0.2	-0.18	0.25	0.48	0.55	-0.36	0.91	-0.66	1														
Tree abundance*	0.11	0.11	0.05	-0.49	-0.64	0.6	-0.74	1															
Tree basal area <sup>a</sup> (m <sup>2</sup> )	-0.21	-0.21	0.16	0.42	0.52	-0.49	1																
Trees deciduous (%)	0.07	0.07	-0.05	-0.53	-0.6	1																	
Tree evenness	0.05	0.05	0.42	0.86	1																		
Tree phylogenetic diversity*	0.13	0.09	0.56	1																			
Tree species richness	0.01	0	1																				
Vegetation cover <sup>b</sup> (%)	0.86	1																					
Vegetation height <sup>a,b</sup> (cm)	1																						

\*variables showing collinearity with other variables that were excluded from statistical analyses

<sup>a</sup>variables measured in the central 10 x 10 m area of every plot

<sup>b</sup>variables measured on a 1m<sup>2</sup> square around each pitfall-trap



# CHAPTER 10

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Submitted as:

Staab M, Schuldt A, Assmann T, Bruelheide H, Klein AM (2014) Ant community structure during forest succession in a subtropical forest in South-East China.



# Ant community structure during forest succession in a subtropical forest in South-East China

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## Abstract

Understanding how communities respond to environmental gradients is critical to predict responses of species to changing habitat conditions such as in regenerating secondary habitats after human land use. In this study, ground-living ants were sampled with pitfall traps in 27 plots in a heterogeneous and diverse subtropical forest to test if and how a broad set of environmental variables including elevation, successional age and tree species richness influence ant diversity and community composition. In total, 13,441 ant individuals belonging to 71 species were found. Ant abundance was unrelated to all environmental variables. Ant species richness was negatively related to elevation, and Shannon diversity decreased with shrub cover. There was a considerable variation in ant species amongst plots associated to elevation, successional age and variables related to succession such as shrub cover. It is shown that already younger secondary forests may support a species-rich and diverse community of ants in subtropical forests even though the species composition between younger and older forests is markedly different. These findings confirm the conservation value of secondary subtropical forests, which is critical because subtropical forests have been heavily exploited by human activities globally. However, they also confirm that old-growth forest should have priority in conservation as it supports a distinct ant community. Our study identifies a set of ant species which are associated with successional age and may thus potentially assist local conservation planning.

**Key words:** BEF-China; biodiversity; conservation; ecosystem functioning; Formicidae; Gutianshan National Nature Reserve

## Introduction

Across taxa and trophic levels, tropical and subtropical forests support the highest species diversity on Earth (e.g. Basset et al. 2012; Gaston 2000; Primack and Corlett 2005). However, a steadily increasing human population, together with new agricultural practices, has caused large-scale exploitation and habitat conversion of these forests (e.g. Gibbs et al. 2010; Hansen et al. 2013). Human disturbance results in a change of species composition, and in general, in declining

diversity of forest organisms (Barlow et al. 2007; Gibson et al. 2011).

As land-use pressure on primary forest is predicted to persist (e.g. Hansen et al. 2013; Miettinen et al. 2011), secondary forests that regenerate from logging or abandoned agriculture will become even more important as habitats for forest organisms. Thus it is critical to assess if such secondary forests can conserve native forest organisms (Dunn et al. 2004), and which environmental conditions explain the diversity and community composition of organisms in secondary

forests, particularly in areas like subtropical South-East China where virtually none of the original species-rich primary forests remained after the 1950s Great Leap Forward (López-Pujol et al. 2006).

Ants (Hymenoptera: Formicidae) are ideal target organisms for these questions. As a taxonomic group they have a long history as biological indicators (Alonso 2000; Andersen and Majer 2004), because they are reliably and easily sampled and show ecologically interpretable responses to disturbance (Gerlach et al. 2013; Hoffmann and Andersen 2003). By being key-stone organisms as e.g. predators, seed dispersers and partners in countless mutualisms they directly relate to ecosystem processes (reviewed in Del-Toro et al. 2012; Folgarait 1998), especially in tropical and subtropical forests where they are dominant arthropods contributing greatly to total animal abundance and biomass.

Many studies have investigated the responses of ant communities to land use in tropical forests but there are less studies in subtropical forests. As a general trend, ongoing forest recovery and succession tended to increase ant species richness and diversity, and over time ant communities became more similar to old-growth forest communities (e.g. Bihn et al. 2008; Floren and Linsenmair 2005; Vasconcelos 1999).

Ground ant communities in forests are also known to be responsive to a wide range of environmental variables such as elevation (e.g. Brühl et al. 1999), soil moisture (e.g. Kaspari and Weiser 2000), litter cover (e.g. McGlynn et al. 2009) or understory vegetation cover (e.g. Gunawardene et al. 2012). It is therefore crucial to include a wide range of potentially confounding biotic and abiotic variables when studying ground ant communities in diverse and heterogeneous forest ecosystems, particularly when habitats change along environmental gradients such as forest succession. Understanding how individual species and entire communities respond to such gradients will help to better predict responses to future conditions, e.g. along elevation gradients in the light of likely up-slope shifts of species with ongoing global

warming (Lenoir et al. 2008).

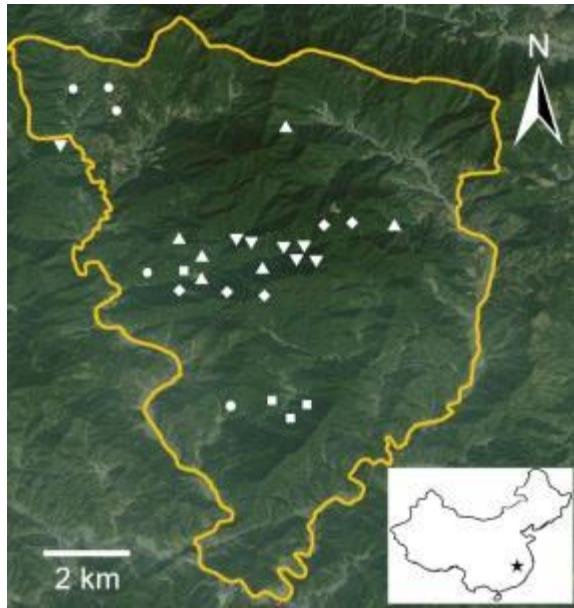
A further so-far unresolved question is whether producer diversity has an impact on ant diversity, as there is usually a direct relationship between plant and arthropod species (sensu Haddad et al. 2009; Scherber et al. 2010). However, studies correlating tree diversity with ground-living ant diversity are scarce. The few studies conducted so far found no influence of tree diversity on ground-living ants (Donoso et al. 2010; Gunawardene et al. 2012), but are not representative to reject cross-group diversity relationships between trees and ants.

We tested if and how the abundance, species richness, diversity (Shannon index) and community composition of ground-living ants are influenced by forest succession and a comprehensive set of environmental variables, including tree species richness and elevation, in a diverse subtropical forest in South-East China. In particular, we hypothesized (1) that the richness and diversity of the overall ground-living ant community is, as indicated for example by Gunawardene et al. (2012), not or only marginally influenced by tree species richness but instead driven by forest succession or environmental variables; (2) that there is pronounced species variation along environmental gradients and during forest succession. Finally, we aimed at identifying ant species that are associated to a certain successional age and might potentially support the diagnosis of successional age.

## Methods

### Study site

Our study was conducted in the Gutianshan National Nature Reserve (GNNR, 29°08'-29°17' N, 118°27'-118°11' E), Zhejiang Province, in South-East China. Along an elevation gradient of 250-1260 m asl, the GNNR protects 8000 ha of a diverse mixed evergreen broad-leaved forest. About half of the naturally occurring tree species are deciduous, but evergreen species numerically dominate in old-growth forest. Common canopy tree species are *Castanopsis eyrei* (Fagaceae), *Cyclobalanopsis glauca* (Fagaceae)



**Figure 10.1.** The Gutianshan National Nature Reserve (GNNR) in subtropical South-East China. Overview map (based on Google™ Earth) of the GNNR showing the boundary of the reserve, the location of study plots, and the location inside the P.R. China (embedded picture). Circles refer to successional stage 1, squares to stage 2, diamonds to stage 3, up-facing triangles to stage 4, and down-facing triangles to stage 5.

and *Schima superba* (Theaceae) (Bruehlheide et al. 2011; Legendre et al. 2009).

As almost everywhere in South-East China (López-Pujol et al. 2006), most of the area in and around the GNNR has been heavily logged or converted to agricultural land. However, slopes steeper than 30° were often left relatively undisturbed because they were inappropriate for agriculture. The GNNR is now one of the most prominent semi-natural forest remnants in South-East China. The reserve consists of a mosaic of secondary forests in different successional stages, ranging from <20 years to >80 years recovery time since the last clear-cut logging activities or the abandonment of former agriculture. Outside the protected areas, forests are dominated by two commercial coniferous plantation species, *Cunninghamia lanceolata* (Cupressaceae) and *Pinus massoniana* (Pinaceae). Apart from anthropogenic disturbance, occasional heavy ice storms are the main drivers of succession (Du et al. 2012). The area is located in a typical

subtropical summer monsoon climate. Mean annual precipitation is 1964 mm, with the strongest rainfalls from May to July and a short dry period from October to December (Geissler et al. 2012).

In 2008, 27 plots (30 m x 30 m) were established in the GNNR as part of the newly founded ‘Biodiversity-Ecosystem Functioning (BEF) China’ project (Bruehlheide et al. 2011, 2014) (Fig. 10.1). Plots were selected along gradients of tree species richness and successional age, and were randomly distributed over the entire reserve excluding areas that were inaccessible or had steep slopes >50°. The minimum distance between two neighboring plots was at least 200 m. In total, 147 species of trees were recorded, ranging from 25-69 species per plot (Table 10.1). Plots were classified into five successional stages (numbered 1-5) based on local knowledge on former agriculture and forestry: < 20 yrs (5 plots), < 40 yrs (4), < 60 yrs (5), < 80 yrs (6) and > 80 yrs (7) post disturbance (Fig. 10.1). To accurately measure the age of the secondary forest on a plot and to verify the successional stage, diameter at breast height (dbh) was measured on all trees with dbh > 10 cm and year rings were counted on stem core drillings from a subset. As single large trees are commonly kept in local agricultural and forestry systems after clear-cutting to provide shade to crops or to tree saplings, and these trees are still present in our plots, successional age was defined as the age of the tree with the fifth largest dbh. This measure corresponded well with successional stages (Bruehlheide et al. 2011), except that plots of the youngest successional stage (< 20 yrs), usually had more than five large trees, resulting in an estimated successional age slightly above 20 years. For more details on the study site, including tree species lists per successional stage and more exhaustive botanical information see Bruehlheide et al. (2011).

### Ant sampling

Ground-living ants were collected with pitfall traps. In each plot, we placed four plastic pitfall traps (diameter 8.5 cm, height 15 cm) filled with about 150 ml preserving solution (40% ethanol, 30% water, 20% glycerol, 10%

**Table 10.1.** Environmental variables of the 27 study plots in the GNNR. For details on measurements see methods section and Bruelheide et al. (2011)

Variable	Range	Median	Mean $\pm$ SD
Basal area <sup>a,b</sup> (m <sup>2</sup> )	0.2-4.9	2.1	2.2 $\pm$ 1.3
Canopy cover <sup>a</sup> (%)	5-50	20	21 $\pm$ 12
Elevation (m)	251-903	569	547 $\pm$ 168
Herb cover <sup>b</sup> (%)	1-80	5	18 $\pm$ 22
Herb species richness <sup>b</sup>	25-71	42	43 $\pm$ 10
Litter cover <sup>c</sup> (%)	21-92	70	66 $\pm$ 15
Litter depth <sup>c</sup> (cm)	0.6 – 3.0	1.6	1.6 $\pm$ 0.5
Mean temperature <sup>a</sup> (°C)	15.1-18.0	17.3	17.0 $\pm$ 0.8
Shrub cover (%)	5-80	10	22 $\pm$ 19
Soil pH	3.4-4.5	3.8	3.9 $\pm$ 0.3
Soil moisture <sup>a</sup> (%)	21-55	32	33 $\pm$ 7
Successional age (yrs)	21-116	72	67 $\pm$ 26
Tree abundance <sup>a</sup>	207-1233	513	597 $\pm$ 290
Tree species richness	25-69	39	42 $\pm$ 10
Vegetation cover <sup>c</sup> (%)	2-55	15	17 $\pm$ 12
Vegetation height <sup>a,c</sup> (cm)	4-55	24	25 $\pm$ 13

<sup>a</sup> variables showing collinearity with other variables that were excluded from statistical analyses.

<sup>b</sup> measured in the central 10 x 10 m area of every plot.

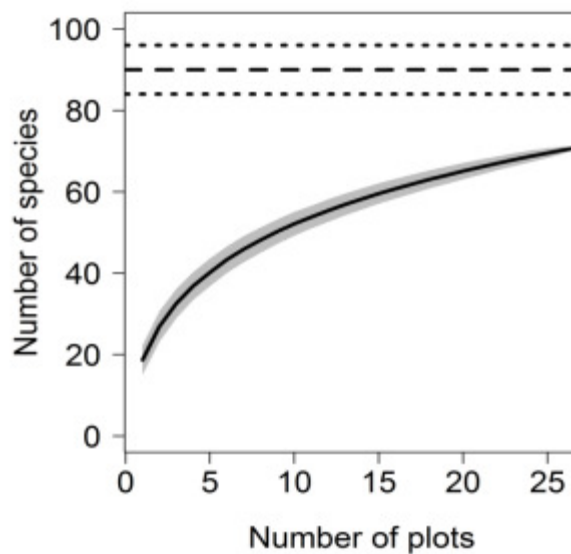
<sup>c</sup> measured on a 1m<sup>2</sup> square around each pitfall-trap

acetic acid and few drops of dishwashing detergent) at the corners of the central 10 m x 10 m square. We sampled consecutively from 30 March to 2 September 2009 to cover the main growing season. The traps were replaced every second week resulting in ten samples per trap, 40 samples per plot and 1080 samples in total. Ant specimens were identified to genera using Bolton (1994) and, whenever possible, identified to species level with the resources listed in Appendix A. Voucher specimens were deposited at the Institute of Earth and Environmental Sciences, University of Freiburg, Germany.

### Environmental variables

During plot setup in 2008 we recorded a comprehensive set of environmental variables (Table 10.1). This allowed us to test which biotic (e.g. tree species richness) and abiotic (e.g. elevation) environmental variables influence ground-living ant communities. Detailed technical descriptions of data collection methodologies are described in Bruelheide et al. (2011) and Schuldt et al. (2011). Tree species richness per 30 x 30 m

plot was defined as the number of species of all woody plants > 1 m height (from here on termed “trees” for simplicity) and tree abundance as the number of those individuals. Canopy cover was measured as the percentage of the plot area covered by the upper tree layer. Shrub cover was measured as the percentage area covered by low woody vegetation > 1 m high. Within the central 10 x 10 m of each plot we measured basal area (m<sup>2</sup>), based on all trees > 3 cm diameter, herb species richness, which included all herbs and woody recruit species < 1 m high and herb cover, being the percentage area covered by these plants. Soil moisture was measured gravimetrically as the mean percentage of water in three samples of the top-soil (0-50 cm) from each plot. Soil pH was averaged from nine independent top-soil samples measured in 1 M KCl solution. Temperature per plot was measured continuously every 30 minutes with HOBO data loggers over a year from July 2011 to June 2012 and the mean temperature was calculated.



**Figure 10.2.** Sample-based species accumulation curve of ant species collected on 27 study plots in subtropical South-East China. Grey shaded area marks 95% CI of the species accumulation curve; dashed line marks the expected number of 90 species based on jackknife1 estimator; dotted lines the SE of the jackknife1 estimation. The ant community was sampled sufficiently well, with 79% (71 species) of the expected total species number having been collected.

To account for trap-specific microhabitat conditions, we recorded litter depth, percent litter cover, percent vegetation cover of the herb layer (hereafter termed ‘vegetation cover’) and vegetation height of the herb layer (hereafter termed ‘vegetation height’) in a 1 m<sup>2</sup> quadrat centered on each trap during the 2009 sampling time.

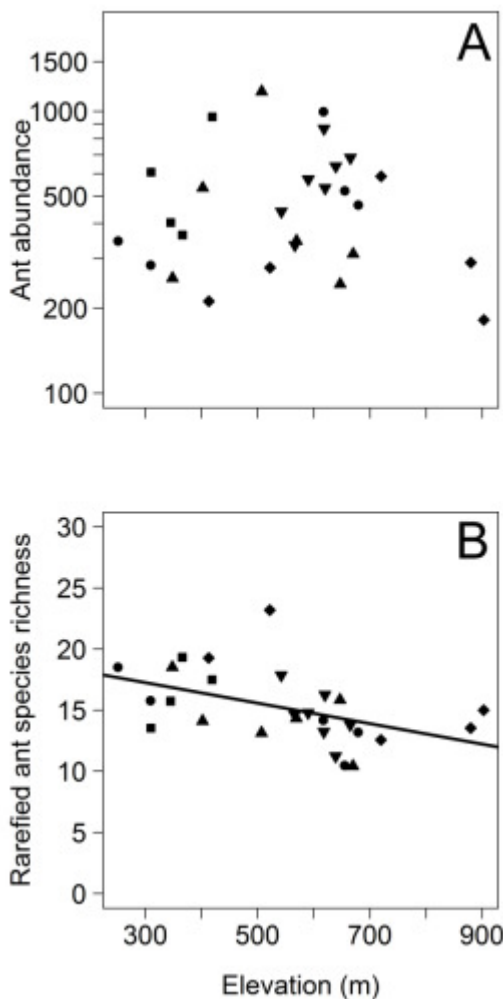
### Statistical analyses

All analyses were conducted with R 2.15.1 (<http://www.r-project.org>). Prior to analyses, the ten samples per trap and the four traps per plot were pooled, resulting in a single value per plot for ant abundance and species richness. Likewise, the four values of trap-specific microhabitat conditions were averaged per plot.

Sampling efficiencies for the total dataset and for subsets per successional stage were tested with plot-based species accumulation curves based on 999 permutations and the first-order jackknife (jackknife1) estimator in the R-package ‘vegan’ (<http://www.cran.r-project.org/package=vegan>). To account for

potential undersampling of species and for varying sampling efficiency between plots we only used rarefied and not observed species richness. Rarefied richness is calculated as the expected number of species in a standardized small sample of individuals drawn randomly from the pool of total samples (Gotelli and Colwell 2001). Calculations were based on the plot with the lowest number of individuals ( $N=182$ ). We also calculated the Shannon index to the power of  $e$  to obtain a measure of effective species diversity (Jost 2006). The relationships between the response variables ant abundance, ant species richness, Shannon index and the explanatory environmental variables were tested with linear models. Prior to analyses ant abundance was  $\log_e$ -transformed to meet assumptions of normality and variance homogeneity. Using only  $\log_e$ -transformed abundance data also accounts for possible biases in our data which may arise if e.g. a populous ant colony was located close to a pitfall trap.

We tested for collinearity between all environmental variables (see Table 10.1). When two variables were correlated with Spearman’s  $\rho > 0.7$  (Dormann et al. 2013), only one of the variables was retained. The use of Spearman’s  $\rho$  was appropriate as not all variables (e.g. canopy cover, tree abundance) were normally distributed. Plot elevation was strongly correlated with mean temperature ( $\rho=-0.85$ ,  $P<0.01$ ) and soil moisture ( $\rho=0.74$ ,  $P<0.01$ ). Thus only elevation was included in the analyses as it is a more comprehensive measure of the interacting environmental conditions. The successional age of the forest was strongly correlated with tree abundance ( $\rho=-0.74$ ,  $P<0.01$ ), basal area ( $\rho=0.91$ ,  $P<0.01$ ) and canopy cover ( $\rho=0.77$ ,  $P<0.01$ ), so the latter three variables describe patterns caused by successional age and were excluded from analyses. Successional age, however, was not correlated with tree species richness ( $\rho=0.25$ ,  $P=0.21$ ) and elevation ( $\rho=0.22$ ,  $P=0.28$ ). Vegetation cover surrounding a trap was strongly correlated with vegetation height ( $\rho=0.86$ ,  $P<0.01$ ), so vegetation height was omitted from the dataset. Hence, the initial full linear models contained tree species



**Figure 10.3.** Relationship between plot elevation and the abundance ( $\log_e$ -transformed; A) and rarefied species richness (B) of the ant community. The regression line shows a significant relationship at  $P < 0.05$  (see Table 10.2). Different symbols refer to different successional stages as explained in Fig. 10.1.

richness, successional age, elevation, soil pH, herb cover, herb species richness, vegetation cover, litter cover and litter depth as explanatory variables. The interaction term between tree species richness and successional age was also included to account for the possible interdependence of tree species richness and successional age. Because the environmental variables were recorded in different units, all environmental variables were standardized by z-transformation prior to modelling. Z-transformation sets the mean of a variable to 0 and the standard deviation

**Table 10.2.** Results of the linear models for ant species richness and Shannon index. Shown are standardized model estimate  $\pm$  SE, t-value, correlation coefficient  $R^2$  and probability P of the t-statistic

Variable <sup>a,b</sup>	Estimate $\pm$ SE	t	$R^2$	P
<i>Ant species richness</i>				
Elevation	$-1.4 \pm 0.5$	-2.7	0.23	0.01
AICc full <sup>c</sup> / minimal <sup>d</sup> :		169.2 / 133.8		
<i>Shannon index</i>				
Shrub cover	$-0.9 \pm 0.3$	-2.8	0.24	<0.01
AICc full <sup>c</sup> / minimal <sup>d</sup> :		139.1 / 107.3		

<sup>a</sup> herb cover, herb species richness, litter cover, litter depth, shrub cover, soil pH, successional age, tree species richness, vegetation cover and the interaction tree species richness:successional age were dropped during model simplification and are not shown.

<sup>b</sup> every variable accounted for one df of the numerator; full models always had 26 df in the denominator.

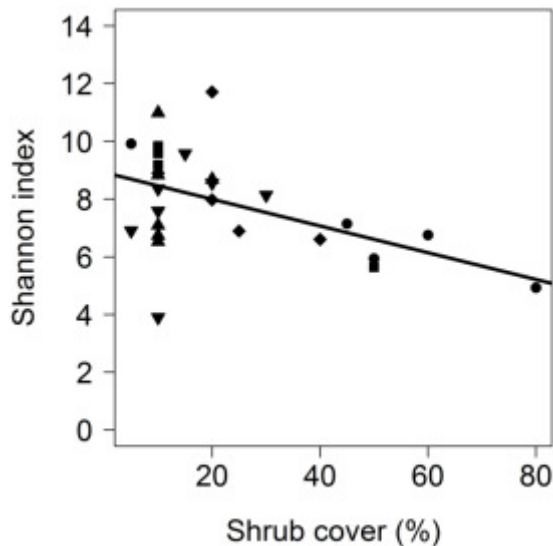
<sup>c</sup> initial linear model containing the entire set of variables.

<sup>d</sup> reduced minimal most parsimonious linear model.

to 1, and thus allows direct comparison of model parameters.

Based on the Akaike Information Criterion corrected for small sample sizes (AICc), full models were simplified in order to receive the most likely parsimonious models (Burnham et al. 2011). If two models were calculated to be equally likely ( $\Delta AICc \leq 2$ ) the model with the smaller number of variables was chosen. Model residuals were always checked for normality and homoscedasticity. To test for potential spatial autocorrelation we calculated Moran's I coefficients for the residuals of all minimal most parsimonious models with the R-package 'ape' (<http://www.cran.r-project.org/package=ape>). A permutation test ( $N=999$ ) was used to test for significant differences in expected and observed Moran's I coefficients. We used non-metric multidimensional scaling (NMDS) in 'vegan'





**Figure 10.4.** Relationship between the Shannon index of the ant community on a plot and shrub cover. The regression line shows a significant relationship at  $P < 0.05$  (see Table 10.2). Different symbols refer to different successional stages as explained in Fig. 10.1.

to analyze ant community composition per plot and species variation amongst plots. The NMDS was calculated on the Morisita-Horn index of square root transformed, Wisconsin double standardized abundance data. This standardization method first standardizes matrix columns (i.e. species) by their maxima and then matrix rows (i.e. sites) by their column sums. We selected the Morisita-Horn similarity index as it is robust against potentially undersampled communities (Wolda 1981). Stable ordination solutions were centered and NMDS axes were rotated until maximum variance in the ordination was explained on the first NMDS axis (Quinn and Keough 2002). To test which environmental variables are associated with species variation, we fitted the same set of non-collinear variables that were tested in the linear models post-hoc to the ordination plot. The environmental fit was based on a regression analysis of all variables with the NMDS axes scores (Quinn and Keough 2002). P-values of the regressions were obtained from 999 permutations.

We calculated group-equalized phi coefficients based on species occurrences in 'vegan' to test if a particular ant species was

associated with one or several successional stages (De Cáceres and Legendre 2009). A permutation test ( $N=999$ ) was used to test for the significance of the association between phi coefficients and the successional stages.

## Results

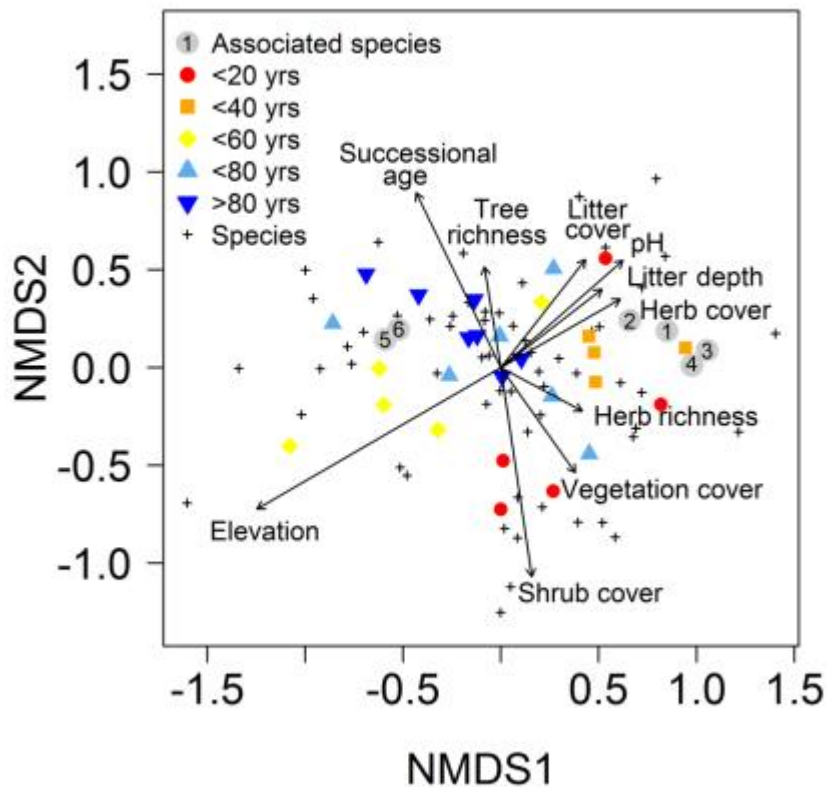
### Ant diversity and general community patterns

In total, we collected 13,441 ants belonging to nine subfamilies, 33 genera and 71 species (Appendix A), of which several species were found in Zhejiang province for the first time. The most species-rich subfamilies were Myrmicinae (24 species, 27% individuals; 13 genera), Formicinae (21 species, 28% individuals; 6 genera) and Ponerinae (12 species, 33% individuals; 6 genera). The three most species-rich genera were *Polyrhachis* (Formicinae, 7 species, 433 individuals), *Camponotus* (Formicinae, 6 species, 2979 individuals), and *Aenictus* (Aenictinae, 5 species, 1147 individuals).

The seven most common species accounted for 69% of total ant abundance: *Ectomomyrmex astutus* (12%), *Camponotus friedae* (11%), *Pheidole noda* (10%), *C. pseudoirritans* (10%), *Leptogenys kitteli* (9%), *Aphaenogaster* sp. CN01 (9%) and *Brachyponera luteipes* (9%). Twelve species (17%) were singletons, six species (8%) doubletons, and twenty species (28%) were only collected in one plot. No species was exotic to China.

The species accumulation curve and the jackknife1 species richness estimator of the total dataset revealed that sampling was not quite complete, with  $90 \pm 6$  (SE) ground-living ant species being expected to occur, of which the 71 observed species represent 79% (Fig. 10.2). The observed number of species did not differ between successional stages (range: 38-41). Sampling efficiency per successional stage was also similar and sufficient; 69-77% of the expected ant species (range:  $49 \pm 6$  -  $58 \pm 10$ ) were collected.

Ant abundance per plot ( $498 \pm 257$  SD, range: 182-1175) could not be explained by any of the environmental variables, including plot elevation (Fig. 10.3A). Rarefied ant species richness ( $15 \pm 3$  SD, range: 10-23) was explained best by a minimal linear model



**Figure 10.5.** NMDS ordination plot (stress=0.17) based on the Morisita-Horn index of square-root transformed, Wisconsin-double standardized abundance data of all ground-living ant species ( $N=71$ , crosses) collected in the 27 study plots. Successional stage of plots is indicated by colored symbols (see Fig. 10.1). Grey circles indicate location of species associated to specific stages (based on Phi coefficients, see Table 10.4 for species list). Arrows show the environmental variables fitted in a post-hoc procedure with the axes scores. Lengths of arrows indicate the strength of correlations (see Table 10.3).

only retaining a negative influence of elevation (estimate= $-1.4 \pm 0.5$ ,  $t=-2.7$ ,  $R^2=0.23$ ,  $P=0.01$ ; Table 10.2; Fig. 10.3B) after AICc based model selection. The Shannon index ( $7.9 \pm 1.8$  SD, range: 3.9-11.7) decreased with increasing shrub cover (estimate= $-0.9 \pm 0.3$ ,  $t=-2.8$ ,  $R^2=0.24$ ,  $P<0.01$ ; Table 10.2; Fig. 10.4) and was unrelated to all other environmental variables.

Tree species richness, successional age, soil pH, herb layer cover, herb layer species richness, litter cover, litter depth and vegetation cover did not influence ant abundance, ant species richness and Shannon index. Non-simplified full linear models for all response variables are shown in Appendix B. Residuals of all minimal models were normally

distributed. There was no significant spatial autocorrelation in the residuals of all minimal models. The differences between observed and expected Moran's I coefficients were small and the corresponding P-values larger 0.05 in all cases.

### Ant community composition and species variation

Multivariate analysis displayed a considerable spatial variation of ant species among the study plots, with clustering according to successional stage (Fig. 10.5). With the exception of two plots from the second-oldest successional stage (<80 yrs), ant communities

**Table 10.3.** Pearson correlation coefficients, explained variance ( $R^2$ ) and probabilities  $P$  (based on a permutation test with  $N=999$ ) for the relationship between the environmental variables (ordered by decreasing  $R^2$ ) and the axes scores of the first two NMDS axes (NMDS 1, NMDS 2). Significant  $P$ -values are indicated in bold

Variable	NMDS 1	NMDS 2	$R^2$	$P$
Elevation	-0.87	-0.50	0.84	<b>&lt;0.01</b>
Shrub cover	0.15	-0.99	0.47	<b>&lt;0.01</b>
Successional age	-0.44	0.90	0.40	<b>&lt;0.01</b>
Soil pH	0.75	0.66	0.28	<b>0.02</b>
Litter cover	0.62	0.79	0.20	0.07
Herb cover	0.87	0.50	0.20	0.07
Vegetation cover	0.58	-0.82	0.17	0.10
Litter depth	0.79	0.61	0.17	0.11
Tree species richness	-0.16	0.99	0.11	0.23
Herb species richness	0.88	-0.47	0.09	0.33

on younger plots were clearly separated from the communities on older plots. The post-hoc correlation of the environmental variables with the NMDS axes scores of plots was strongest for elevation ( $R^2=0.84$ ,  $P<0.01$ ; Table 10.3; Fig. 10.5). Successional age ( $R^2=0.40$ ,  $P<0.01$ ) and shrub cover ( $R^2=0.47$ ,  $P<0.01$ ) were also significantly correlated with the NMDS axes, but with opposing influences. Soil pH ( $R^2=0.28$ ,  $P=0.02$ ), was the only other variable with a significant correlation, being opposite to elevation. Tree species richness and the remaining environmental variables were not related to the spatial variation.

Only six species had phi values indicating significant association with one or more successional stages. The species *Prenolepis naoriji*, *Tetramorium aptum* and *Tetraoponera conexa* were associated with the two youngest stages, *Ectomomyrmex annamitus* with the second youngest stage, and *Camponotus compressus* as well as *C. friedae* were associated with the three oldest successional stages (Table 10.4; Fig. 10.5).

## Discussion

### Elevation as main driver of ant species richness

Elevation is known to have a direct influence on many abiotic variables, most prominently on mean annual temperature (Körner 2007) which across biomes decreases with about

0.5°C per 100 m increase in elevation. Being ectothermic organisms, ants are sensitive to elevation gradients (Hodkinson 2005) and mean annual temperature is globally the best predictor for ant species richness (Jenkins et al. 2011). Regionally, ant species richness generally declines with increasing elevation (e.g. Brühl et al. 1999; Sanders et al. 2007) and the decline is accompanied by a profound change in species composition as most ant species have narrow temperature niches (e.g. McGlynn et al. 2013; Mezger and Pfeiffer 2010).

In the GNNR, elevation provided the best explanation for ant species variation, even though the elevation gradient was relatively small (~650 m) and associated with a difference in mean temperature of only 2.9°C. At lower elevations, species of widespread ant genera such as *Camponotus* or tropical genera such as *Polyrhachis* were prevalent. The species richness of these genera was reduced at higher elevations, where species of typical temperate genera such as *Formica* and *Lasius* started to occur, as it is characteristic for the boundary between the Oriental and Palearctic zoogeographic regions in South-East China (Fellowes 2006).

However, mountain ranges in South-East China are not tall by global standards; the highest peak in the GNNR is just above 1250 m. High elevation areas act as islands of temperate climate in a subtropical matrix and have distinct species communities of ants and

**Table 10.4.** Ant species that were significantly associated with at least one of the five successional stages (1-5: < 20, < 40, < 60, < 80 and > 80 years old), based on the correlation  $r_{\Phi}^g$  of the group-equalized phi coefficient. Numbers in brackets after species names refer to Fig. 10.5. P-values are based on a permutation test (N=999)

Species	Subfamily	Successional stage	$r_{\Phi}^g$	P
<i>Prenolepis naoroji</i> [1]	Formicinae	1+2	0.57	0.02
<i>Tetramorium aptum</i> [2]	Myrmicinae	1+2	0.57	0.03
<i>Tetraoponera convexa</i> [3]	Pseudomyrmicinae	1+2	0.59	0.02
<i>Ectomomyrmex annamitus</i> [4]	Ponerinae	2	0.74	<0.01
<i>Camponotus compressus</i> [5]	Formicinae	3+4+5	0.63	<0.01
<i>Camponotus friedae</i> [6]	Formicinae	3+4+5	0.79	<0.01

other organisms (e.g. Bruelheide et al. 2011). Global warming will not only directly cause up-slope migration of animal species (e.g. Chen et al. 2009; Lenoir et al. 2008) but also change forest structure by increasing the mortality of trees adapted to high elevations and by facilitating the immigration of lowland tree species (Feeley et al. 2011; 2013). Unfortunately, land area strongly decreases at higher elevations, so that up-slope range movements will increase the extinction risk of a species (Körner 2007) and lead to local extinction of species adapted to cooler climates such as temperate ants in subtropical forests.

### Responses of ant communities to forest succession

By directly influencing various ecosystem properties including microclimate (Aussenac 2000), trees are ecosystem engineers in forests (Jones et al. 1994), and thus directly influencing ground-living arthropods. Ecological theory predicts an increase of arthropod species richness with increasing plant species richness and habitat complexity, i.e. in forests with increasing tree species richness (Root 1973) and increasing successional age (Guariguata and Ostertag 2001). A more complex or tree species-rich forest will provide more heterogeneous and temporarily more stable resources, and will maintain more species-rich and more diverse consumers across trophic levels.

In ecological studies, it is usually assumed that disturbed or younger secondary

forests have reduced tree species richness, which must not be the case (Hector et al. 2011). In our study area, young plots were already characterized by a species-rich tree community, so effects of successional age are not caused by differences in tree species richness. Several other studies on ants showed that primary forests contained a more species-rich and more distinct species community compared to secondary forests (e.g. Floren and Linsenmair 2005; Klimes et al. 2012; Vasconcelos 1999). However, a direct positive relationship between ant species richness and tree species richness has mostly been found for canopy ants (e.g. Floren and Linsenmair 2005; Klimes et al. 2012; Ribas et al. 2003), which are in terms of taxonomic composition and habitat requirements markedly different from ground-living ants (e.g. Floren et al. 2014).

Most ground-living ant species nest and forage in or on the leaf litter (Blüthgen and Feldhaar 2010; Wilson and Hölldobler 2005). It appears that, as long as a litter layer is present, a habitat can maintain diversity and abundance of ants and other organisms (Burghouts et al. 1992), independent of anthropogenic disturbance, successional age and tree species richness (Belshaw and Bolton 1993; Woodcock et al. 2011). Our results support the findings by Donoso et al. (2010) and Gunawardene et al. (2012) who concluded that variables other than tree species richness influence ground ant communities. A possible explanation could be that the large morphological heterogeneity of living leaves in the canopy might be less pronounced in the

matrix of decaying leaf litter on the forest floor. However, tree identity on a plot might be a proxy for the ant community. In the GNNR the NMDS ordination of the tree community (Bruelheide et al. 2011) was very similar to the NMDS ordination of the ant community (Procrustes rotation, 999 permutations, Procrustes sum of squares=0.42,  $R^2=0.58$ ,  $P<0.01$ ). This correlation probably reflects a structuring role of the identity of the vegetation in higher strata on the ground-living ant communities. While we found no influence of either tree species richness or successional age on ant abundance and measures of diversity, successional age had a profound influence on ant species variation.

During forest succession the vertical and horizontal structure of the forest changes (Guariguata and Ostertag 2001). With increasing succession, for example, tree abundance declines, while canopy cover increases, resulting in a larger light interception which has negative effects on lower vegetation strata through changed microhabitat conditions (Lebrija-Trejos et al. 2011). In the NMDS ordination, shrub cover and successional age had opposing effects on ant species composition. We conclude that environmental conditions such as light availability (McGlynn et al. 2013) or moisture (Kaspari and Weiser 2000) may be mediated by lower vegetation strata and can have strong influences on ant communities. This is probably stronger in younger plots that are more dominated by low vegetation.

### Implications for subtropical forest conservation in South-East China

Before anthropogenic disturbance, there was a forest continuum from the equatorial tropical rainforests of Sundaland to the boreal coniferous forests of the Russian Far East where subtropical forests connected tropical and temperate biomes (Corlett 2009). In order to conserve the remaining forest patches in subtropical South-East China it is important to understand how biodiversity dynamics follow disturbance. However, in China only a few studies have examined how forest succession influences forest species communities. Both et al. (2011) for

herbaceous plants, Bruelheide et al. (2011) for trees and Schuldt et al. (2012) for spiders found that species communities in older successional forests are different from younger forests. For all other taxa there is no information available from subtropical Chinese forests. Ecological studies on ants are rare in non-tropical Asia (Guénard et al. 2010). For most of the over 900 ant species known from China the ecological knowledge is sparse (Guénard and Dunn 2012) and our study adds several new distribution records of genera and species to the South-East Chinese ant fauna.

Ant species richness in younger secondary forests was not composed of disturbance-tolerant generalist species. None of the collected species is exotic to China (see Guénard and Dunn 2012) and the species richness of the two main trophic groups of ants, exclusive predators and dietary opportunists, in the GNNR is not influenced by successional age (Staab et al. 2014). As shown in our study, regenerating secondary forests can be effective to conserve ants (*sensu* Wright and Dent 2009), and this could also apply to other ground-living arthropods, as long as forest fragments are large enough (e.g. Bickel et al. 2006; Brühl et al. 2003). However, our study also shows that ant communities in young successional forests consist of a different species assemblage than older forests. Besides ant species that were found across successional stages, several species did only occur either in young or in old plots (Appendix A). Possibly, the species associated to old-growth forest might be in need of conservation, as old-growth forests are nowadays rare in China.

For our particular study area, we found several ant species to be strongly associated with either young or old successional stages. These species might be restricted in their habitat requirements to the specific conditions provided by young or old growth forests. All these ant species are widely distributed in the region (Guénard and Dunn 2012) and we suggest that species associated to old-growth forest might, together with other taxa (Both et al. 2011; Bruelheide et al. 2011; Schuldt et al. 2012), assist forest evaluation by supporting classical methods

such as tree inventories and dbh measurements.

### Conclusions

Our study showed that elevation explains overall ground-living ant species richness in a heterogeneous secondary subtropical forests, but that succession influences the ant community, possibly through changing microhabitat conditions. We demonstrated that secondary forests already 20-40 years after land abandonment or the last logging cycle attain the ant species richness and diversity of old-growth forests, and they likely support diverse communities of other organisms as well (see Dunn 2004; Edwards et al. 2011). Thus, secondary forests, particularly those of longer regeneration time harboring species communities that probably resemble more closely the original communities, can be valuable for conservation, especially when primary habitats are almost eradicated as in South-East China. However, at higher elevations even old-growth secondary forest may not be able to protect species from extinction due to up-slope movements.

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### References

- Alonso LE (2000) Ants as indicators of diversity. In: Agosti D, Majer JD, Alonso LE, Schultz TR (eds) *Ants: Standard methods for measuring and monitoring biodiversity*. Smithsonian Institution Press, Washington, pp 80-88
- Andersen AN, Majer JD (2004) Ants show the way Down Under: Invertebrates as bioindicators in land management. *Frontiers in Ecology and the Environment* 2:291-298
- Aussenac G (2000) Interactions between forest stands and microclimate: Ecophysiological aspects and consequences for silviculture. *Annals of Forest Science* 57:287-301
- Barlow J et al. (2007) Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. *Proceedings of the National Academy of Sciences USA* 104:18555-18560
- Basset Y et al. (2012) Arthropod diversity in a tropical forest. *Science* 338:1481-1484
- Belshaw R, Bolton B (1993) The effect of forest disturbance on the leaf-litter ant fauna in Ghana. *Biodiversity and Conservation* 2:656-666
- Bickel TO, Brühl CA, Gadau JR, Hölldobler B, Linsenmair K (2006) Influence of habitat fragmentation on the genetic variability in leaf litter ant populations in tropical rainforests of Sabah, Borneo. *Biodiversity and Conservation* 15:157-175
- Bihn JH, Verhaagh M, Brändle M, Brandl R (2008) Do secondary forests act as refuges for old growth forest animals? Recovery of ant diversity in the Atlantic forest of Brazil. *Biological Conservation* 141:733-743
- Blüthgen N, Feldhaar H (2010) Food and shelter: How resources influence ant ecology. In: Lach L, Parr CL, Abbott KL (eds) *Ant Ecology*. Oxford University Press, Oxford, pp 115-136
- Bolton B (1994) *Identification guide to the ant genera of the world*. Harvard University Press, Cambridge
- Both S, Fang T, Böhnke M, Bruelheide H, Geissler C, Kühn P, Scholten T, Trogisch S, Erfmeier A (2011) Lack of tree layer control on herb layer characteristics in a subtropical forest, China. *Journal of Vegetation Science* 22:1120-1131
- Bruelheide H et al. (2011) Community assembly during secondary forest succession in a Chinese subtropical forest. *Ecological Monographs* 81:25-41
- Bruelheide H et al. (2014) Designing forest biodiversity experiments: General considerations illustrated by a new large

- experiment in subtropical China. *Methods in Ecology and Evolution* 5:74-89
- Brühl CA, Mohamed V, Linsenmair KE (1999) Altitudinal distribution of leaf litter ants along a transect in primary forests on Mount Kinabalu, Sabah, Malaysia. *Journal of Tropical Ecology* 15:265-277
- Brühl CA, Eltz T, Linsenmair KE (2003) Size does matter - effects of tropical rainforest fragmentation on the leaf litter ant community in Sabah, Malaysia. *Biodiversity and Conservation* 12:1371-1389
- Burghouts T, Ernsting G, Korthals G, Devries T (1992) Litterfall, leaf litter decomposition and litter invertebrates in primary and selectively logged dipterocarp forest in Sabah, Malaysia. *Philosophical Transactions of the Royal Society B* 335:407-416
- Burnham KP, Anderson DR, Huyvaert KP (2011) AIC model selection and multimodel inference in behavioral ecology: Some background, observations, and comparisons. *Behavioral Ecology and Sociobiology* 65:23-35
- Chen IC, Shiu HJ, Benedick S, Holloway JD, Cheye VK, Barlow HS, Hill JK, Thomas CD (2009) Elevation increases in moth assemblages over 42 years on a tropical mountain. *Proceedings of the National Academy of Sciences USA* 106:1479-1483
- Corlett R (2009) *The ecology of tropical East Asia*. Oxford University Press, Oxford
- De Cáceres M, Legendre P (2009) Associations between species and groups of sites: Indices and statistical inference. *Ecology* 90:3566-3574
- Del Toro I, Ribbons RR, Pelini SL (2012) The little things that run the world revisited: A review of ant-mediated ecosystem services and disservices (Hymenoptera: Formicidae). *Myrmecological News* 17:133-146
- Donoso DA, Johnston MK, Kaspari M (2010) Trees as templates for tropical litter arthropod diversity. *Oecologia* 164:201-211
- Dormann CF et al. (2013) Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 36:27-46
- Du YJ, Mi XC, Liu XJ, Ma KP (2012) The effects of ice storm on seed rain and seed limitation in an evergreen broad-leaved forest in east China. *Acta Oecologica* 39:87-93
- Dunn RR (2004) Recovery of faunal communities during tropical forest regeneration. *Conservation Biology* 18:302-309
- Edwards DP, Larsen TH, Docherty TDS, Ansell FA, Hsu WW, Derhe MA, Hamer KC, Wilcove DS (2011) Degraded lands worth protecting: The biological importance of Southeast Asia's repeatedly logged forests. *Proceedings of the Royal Society B* 278:82-90
- Feeley KJ, Silman MR, Bush MB, Farfan W, Cabrera KG, Malhi Y, Meir P, Salinas Revilla N, Quisipupanqui MNR, Saatchi S (2011) Upslope migration of Andean trees. *Journal of Biogeography* 38:783-791
- Feeley KJ, Hurtado J, Saatchi S, Silman MR, Clark DB (2013) Compositional shifts in Costa Rican forests due to climate-driven species migrations. *Global Change Biology* 19:3472-3480
- Fellowes JR (2006) Ant (Hymenoptera: Formicidae) genera in southern China: Observations on the Oriental-Palaeartic boundary. *Myrmecological News* 8:239-249
- Floren A, Linsenmair KE (2005) The importance of primary tropical rain forest for species diversity: An investigation using arboreal ants as an example. *Ecosystems* 8:559-567
- Floren A, Wetzell W, Staab M (2014) The contribution of canopy species to overall ant diversity (Hymenoptera: Formicidae) in temperate and tropical ecosystems. *Myrmecological News* 19:65-74
- Folgarait PJ (1998) Ant biodiversity and its relationship to ecosystem functioning: A review. *Biodiversity and Conservation* 7:1221-1244
- Gaston KJ (2000) Global patterns in biodiversity. *Nature* 405:220-227
- Geissler C, Kühn P, Böhnke M, Bruehlheide H, Shi X, Scholten T (2012) Splash erosion potential under tree canopies in subtropical SE China. *Catena* 91:85-93
- Gerlach J, Samways M, Pryke J (2013) Terrestrial invertebrates as bioindicators: An overview of available taxonomic groups. *Journal of Insect Conservation* 17:831-850
- Gibbs HK, Ruesch AS, Achard F, Clayton MK, Holmgren P, Ramankutty N, Foley JA (2010) Tropical forests were the primary sources of new agricultural land in the 1980s and 1990s. *Proceedings of the National Academy of Sciences USA* 107:16732-16737
- Gibson L, Lee TM, Koh LP, Brook BW, Gardner TA, Barlow J, Peres CA, Bradshaw CJA, Laurance WF, Lovejoy TE, Sodhi NS (2011) Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature* 478:378-381
- Gotelli NJ, Colwell RK (2001) Quantifying biodiversity: Procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters* 4: 379-391
- Guariguata MR, Ostertag R (2001) Neotropical secondary forest succession: Changes in structural and functional characteristics. *Forest*

- Ecology and Management 148:185-206
- Guénard B, Dunn RR (2012) A checklist of the ants of China. *Zootaxa* 3558:1-77
- Guénard B, Weiser MD, Dunn RR (2010) Global generic richness and distribution: New maps of the world of ants with examples of their use in the context of Asia. *Asian Myrmecology* 3:21-28
- Gunawardene NR, Majer JD, Edirisinghe JP (2012) Correlates of ant (Hymenoptera: Formicidae) and tree species diversity in Sri Lanka. *Myrmecological News* 17:81-90
- Haddad NM, Crutsinger GM, Gross K, Haarstad J, Knops JMH, Tilman D (2009) Plant species loss decreases arthropod diversity and shifts trophic structure. *Ecology Letters* 12:1029-1039
- Hansen MC, et al. (2013) High-resolution global maps of 21st-century forest cover change. *Science* 342:850-853
- Hector A et al. (2011) The Sabah Biodiversity Experiment: A long-term test of the role of tree diversity in restoring tropical forest structure and functioning. *Philosophical Transactions of the Royal Society B* 366:3303-3315
- Hodkinson ID (2005) Terrestrial insects along elevation gradients: Species and community responses to altitude. *Biological Reviews* 80:489-513
- Hoffmann BD, Andersen AN (2003) Responses of ants to disturbance in Australia, with particular reference to functional groups. *Austral Ecology* 28:444-464
- Jenkins CN et al. (2011) Global diversity in light of climate change: The case of ants. *Diversity and Distributions* 17:652-662
- Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. *Oikos* 69:373-386
- Jost L (2006) Entropy and diversity. *Oikos* 113:363-375
- Kaspari M, Weiser MD (2000) Ant activity along moisture gradients in a neotropical forest. *Biotropica* 32:703-711
- Klimes P, Idigel C, Rimandai M, Fayle TM, Janda M, Weiblen GD, Novotny V (2012) Why are there more arboreal ant species in primary than in secondary tropical forests? *Journal of Animal Ecology* 81:1103-1112
- Körner C (2007) The use of 'altitude' in ecological research. *Trends in Ecology and Evolution* 22:569-574
- Lebrija-Trejos E, Perez-Garcia EA, Meave JA, Poorter L, Bongers F (2011) Environmental changes during secondary succession in a tropical dry forest in Mexico. *Journal of Tropical Ecology* 27:477-489
- Legendre P, Mi XC, Ren HB, Ma KP, Yu MJ, Sun IF, He FL (2009) Partitioning beta diversity in a subtropical broad-leaved forest of China. *Ecology* 90:663-674
- Lenoir J, Gegout JC, Marquet PA, de Ruffray P, Brisse H (2008) A significant upward shift in plant species optimum elevation during the 20th century. *Science* 320:1768-1771
- López-Pujol J, Zhang FM, Ge S (2006) Plant biodiversity in China: Richly varied, endangered, and in need of conservation. *Biodiversity and Conservation* 15:3983-4026
- McGlynn TP, Fawcett RM, Clark DA (2009) Litter biomass and nutrient determinants of ant density, nest size, and growth in a Costa Rican tropical wet forest. *Biotropica* 41:234-240
- McGlynn TP, Alonso-Rodriguez AM, Weaver M (2013) A test of species-energy theory: Patch occupancy and colony size in tropical rainforest litter-nesting ants. *Oikos* 122:1357-1361
- Mezger D, Pfeiffer M (2010) Is nest temperature an important factor for niche partitioning by leaf-litter ants (Hymenoptera: Formicidae) in Bornean rain forests? *Journal of Tropical Ecology* 26:445-455
- Miettinen J, Shi C, Liew SC (2011) Deforestation rates in insular Southeast Asia between 2000 and 2010. *Global Change Biology* 17:2261-2270
- Primack RB, Corlett R (2005) *Tropical Rain Forests: An ecological and biogeographical comparison*. Blackwell Publishing, Oxford
- Quinn GP, Keough MJ (2002) *Experimental design and data analysis for biologists*. Cambridge University Press, Cambridge
- Ribas CR, Schoereder JH, Pic M, Soares SM (2003) Tree heterogeneity, resource availability, and larger scale processes regulating arboreal ant species richness. *Austral Ecology* 28:305-314
- Root RB (1973) Organization of a plant-arthropod association in simple and diverse habitats: The fauna of collards (*Brassica oleracea*). *Ecological Monographs* 43:95-120
- Sanders NJ, Lessard JP, Fitzpatrick MC, Dunn RR (2007) Temperature, but not productivity or geometry, predicts elevational diversity gradients in ants across spatial grains. *Global Ecology and Biogeography* 16:640-649
- Scherber C et al. (2010) Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. *Nature* 468:553-556
- Schuldt A, Both S, Bruelheide H, Härdtle W, Schmid B, Zhou H, Assmann T (2011) Predator diversity and abundance provide little



- support for the enemies hypothesis in forests of high tree diversity. *PLoS ONE* 6:e22905
- Schuldt A, Bruelheide H, Härdtle W, Assmann T (2012) Predator assemblage structure and temporal variability of species richness and abundance in forests of high tree diversity. *Biotropica* 44:793-800
- Staab M, Schuldt A, Assmann T, Klein AM (2014) Tree diversity promotes predator but not omnivore ants in a subtropical Chinese forest. *Ecological Entomology*, DOI:10.1111/een.12143.
- Vasconcelos HL (1999) Effects of forest disturbance on the structure of ground-foraging ant communities in central Amazonia. *Biodiversity and Conservation* 8:409-420
- Wilson EO, Hölldobler B (2005) The rise of the ants: A phylogenetic and ecological explanation. *Proceedings of the National Academy of Sciences USA* 102:7411-7414
- Wolda H (1981) Similarity indices, sample size and diversity. *Oecologia* 50:296-302
- Woodcock P, Edwards DP, Fayle TM, Newton RJ, Khen CV, Bottrell SH, Hamer KC (2011) The conservation value of South East Asia's highly degraded forests: Evidence from leaf-litter ants. *Philosophical Transactions of the Royal Society B* 366:3256-326.
- Wright JS, Dent DH (2009) The future of tropical species in secondary forests: A quantitative review. *Biological Conservation* 142:2833-2843

## Supplementary Material

**Appendix A.** Ant species collected by pitfall traps in the 27 study plots in the GNNR. Shown is the number of individuals per species, the number of plots on which a species was collected, the abundance rank of the species in the ant community, and the successional stages a species occurred in. The genus level taxonomy of Ponerinae follows (Schmidt & Shattuck 2014). High resolution photographs of most species can be found on [www.antweb.org](http://www.antweb.org) and [www.antbase.net](http://www.antbase.net).

Species	Individuals	Plots	Rank	Stages	Identification source
<b>Aenictinae</b>					
<i>Aenictus bobaiensis</i> Zhou & Chen, 1999	514	4	9	1-4	Jaitrong & Wiwatwitaya 2013
<i>Aenictus fuchuanensis</i> Zhou, 2001	132	6	17	2-5	Jaitrong & Yamane 2013
<i>Aenictus gutianshanensis</i> Staab, 2014	6	1	47	1	Staab 2014
<i>Aenictus benanensis</i> Li & Wang, 2005	4	1	52	3	Li & Wang 2005
<i>Aenictus hodgsoni</i> Forel, 1901	518	12	8	1-5	Jaitrong & Yamane 2011
<b>Cerapachyinae</b>					
<i>Cerapachys sulcinodis</i> Emery, 1898	1	1	71	3	Brown 1975
<b>Dolichoderinae</b>					
<i>Dolichoderus incisus</i> Xu, 1995	2	2	59	4,5	Xu 2001
<i>Liometopum sinense</i> Wheeler, 1921	5	2	50	5	Del Toro et al. 2009
<i>Technomyrmex antennus</i> Zhou, 2001	11	6	37	2-5	Bolton 2007
<i>Technomyrmex obscurior</i> Wheeler, 1928	311	23	12	1-5	Bolton 2007
<b>Ectatomminae</b>					
<i>Gnamptogenys panda</i> (Brown, 1948)	42	12	27	1-5	Lattke 2004
<b>Formicinae</b>					
<i>Camponotus compressus</i> (Fabricius, 1787)	31	12	30	3-5	antweb.org
<i>Camponotus friedae</i> Forel, 1912	1540	15	2	3-5	Wang & Wu 1994
<i>Camponotus itoi</i> Forel, 1912	1	1	71	4	Wang & Wu 1994
<i>Camponotus pseudoirritans</i> Wu & Wang, 1989	1277	27	4	1-5	Wang & Wu 1994
<i>Camponotus rubidus</i> Xiao & Wang, 1989	129	5	18	1,3,5	Wang & Wu 1994
<i>Camponotus</i> sp. CN08	1	1	71	3	
<i>Formica japonica</i> Motschoulsky, 1866	167	5	15	1,3,4	antweb.org
<i>Lasius alienus</i> (Foerster, 1850)	18	1	34	3	Seifert 1992
<i>Nylanderia</i> sp. CN02	5	4	50	2,5	
<i>Nylanderia</i> sp. CN03	7	4	43	1,3	
<i>Nylanderia</i> sp. CN05	11	4	37	3-5	
<i>Nylanderia</i> sp. CN06	18	10	34	1,2,5	
<i>Polyrhachis cyphonota</i> Xu, 1998	7	2	43	1,4	Xu 2002

<i>Polyrhachis dives</i> Smith, 1857	14	2	35	1	W. Dorow pers. comm.
<i>Polyrhachis illaudata</i> Walker, 1859	335	26	11	1-5	W. Dorow pers. comm.
<i>Polyrhachis lamellidens</i> Smith, 1874	44	1	25	1	Kohout 2014
<i>Polyrhachis shixingensis</i> Wu & Wang, 1995	31	1	30	1	Kohout 2013
<i>Polyrhachis striata</i> Mayr, 1862	1	1	71	1	antweb.org
<i>Polyrhachis (Myrmobopla) sp.</i> CN04	1	1	71	1	
<i>Prenolepis naoroji</i> Forel, 1902	23	8	32	1-4	Wang & Wu 2007
<i>Prenolepis umbra</i> Zhou & Zheng, 1998	72	10	23	1-5	Wang & Wu 2007
Myrmicinae					
<i>Aphaenogaster sp.</i> CN01	1176	23	6	1-5	
<i>Aphaenogaster sp.</i> CN02	114	14	19	1-5	
<i>Aphaenogaster sp.</i> CN03	77	10	21	1-5	
<i>Carebara jiangxiensis</i> (Wu & Wang, 1995)	2	2	59	3,5	Xu 2003
<i>Carebara sp.</i> CN01	1	1	71	3	
<i>Crematogaster cf. biroi</i> Mayr, 1897	1	1	71	2	antweb.org
<i>Crematogaster cf. rogenhoferi</i> Mayr, 1879	73	11	22	1-5	antweb.org
<i>Crematogaster cf. subnuda</i> Mayr, 1879	6	5	47	3,5	antweb.org
<i>Crematogaster sp.</i> CN05	6	3	47	1-3	
<i>Dilobocondyla fouqueti</i> Santschi, 1910	2	2	59	2,4	Bharti & Kumar 2013
<i>Kartidris galos</i> Bolton, 1991	113	2	20	2,5	Xu 1999
<i>Myrmecina sauteri</i> Forel, 1912	3	3	53	3-5	Zhou et al. 2008
<i>Myrmecina taiwana</i> Terayama, 1985	1	1	71	5	Zhou et al. 2008
<i>Pheidole noda</i> Smith, 1874	1308	16	3	1-5	Zhou & Zheng, 1999
<i>Pheidole sp.</i> CN04	55	2	24	1,4	
<i>Pheidologeton melasolenus</i> Zhou & Zheng, 1997	39	14	28	1-5	Zhou et al. 2006
<i>Pristomyrmex punctatus</i> Smith, 1860	6	1	47	4	Wang 2003
<i>Rhoptromyrmex wrightonii</i> Forel, 1902	151	1	16	2	Bolton 1986
<i>Rotastruma stenoceps</i> Bolton, 1991	2	2	59	2,4	Bolton 1991
<i>Temnothorax sp.</i> CN01	2	1	59	5	
<i>Tetramorium aptum</i> Bolton, 1977	30	8	31	1,2,4,5	Bolton 1977
<i>Tetramorium bicarinatum</i> (Nylander, 1846)	1	1	71	2	Bolton 1977
<i>Tetramorium shensiense</i> Bolton, 1977	505	17	10	1-5	Bolton 1977
<i>Tetramorium sp.</i> CN08	7	2	43	4,5	
Ponerinae					
<i>Anochetus risii</i> Forel, 1900	9	5	39	1-4	Brown 1978
<i>Brachyponera chinensis</i> (Emery, 1895)	222	23	13	1-5	Xu 1998
<i>Brachyponera luteipes</i> (Mayr, 1862)	1151	25	7	1-5	Xu 1998
<i>Brachyponera sp.</i> CN01	1	1	71	3	
<i>Cryptopone sauteri</i> (Wheeler, 1906)	1	1	71	5	Zhou 2001

<i>Ectomomyrmex annamitus</i> (Andre, 1892)	8	5	40	1,2	Xu 1998
<i>Ectomomyrmex astutus</i> (Smith, 1858)	1579	27	1	1-5	Xu 1998
<i>Ectomomyrmex javanus</i> Mayr, 1867	5	4	50	1-4	Xu 1998
<i>Leptogenys kitteli</i> (Mayr, 1870)	1240	23	5	1-5	Zhou et al. 2012
<i>Leptogenys laozi</i> Xu, 2000	42	9	27	3-5	Zhou et al. 2012
<i>Odontomachus monticola</i> Emery, 1892	207	25	14	1-5	Brown 1976
<i>Odontomachus</i> sp. CN02	2	2	59	4,5	
Proceratiinae					
<i>Discothyrea sauteri</i> Forel, 1912	4	3	52	1,2,5	Xu et al 2014
Pseudomyrmecinae					
<i>Tetraponera allaborans</i> (Walker, 1859)	1	1	71	2	Xu & Chai 2004
<i>Tetraponera convexa</i> Xu & Chai, 2004	9	4	39	1,2	Xu & Chai 2004

## References

- Antbase (2014) Mongolian National University, Ulan Bator, Available at [www.antbase.net](http://www.antbase.net). Accessed 24. July 2014
- Antweb (2014) California Academy of Science, San Francisco, Available at [www.antweb.org](http://www.antweb.org). Accessed 24. July 2014
- Bharti H, Kumar R (2013) Five new species of *Dilobocondyla* (Hymenoptera: Formicidae) with a revised key to the known species. *Asian Myrmecology* 5:29-44
- Bolton B (1977) The ant tribe Tetramoriini (Hymenoptera: Formicidae). The genus *Tetramorium* Mayr in the Oriental and Indo-Australian regions, and in Australia. *Bulletin of the British Museum (Natural History) Entomology* 36:67-151
- Bolton B (1986) A taxonomic and biological review of the tetramoriine ant genus *Rhoptromyrmex* (Hymenoptera: Formicidae). *Syst. Entomol.* 11:1-17
- Bolton B (1991) New myrmecine ant genera from the Oriental region (Hymenoptera, Formicidae). *Syst. Entomol.* 16:1-13
- Bolton B (2007) Taxonomy of the dolichoderine ant genus *Technomyrmex* Mayr (Hymenoptera: Formicidae) based on the worker caste. *Contributions of the American Entomological Institute* 35:1-150
- Brown WL (1975) Contributions toward a reclassification of the Formicidae. V. Ponerinae, tribes Platythyreini, Cerapachyini, Cylindromyrmecini, Acanthostichini, and Aenictogitini. *Search. Agri.* 5:1-115
- Brown WL (1976) Contributions toward a reclassification of the Formicidae. Part VI. Ponerinae, tribe Ponerini, subtribe Odontomachiti. Section A. Introduction, subtribal characters. Genus *Odontomachus*. *Studia. Ent.* 19:67-171
- Brown WL (1978) Contributions toward a reclassification of the Formicidae. Part VI. Ponerinae, tribe Ponerini, subtribe Odontomachiti. Section B. Genus *Anocheetus* and bibliography. *Studia. Ent.* 20:549-638
- Del Toro I, Pacheco JA, Mackay WP (2009) Revision of the ant genus *Liometopum* (Hymenoptera: Formicidae). *Sociobiology* 53:299-369
- Jaitrong W, Wiwatwitaya D (2013) Two new species fo the *Aenictus pachyverus* species group (Hymenoptera: Formicidae: Aenictinae) from Southeast Asia. *Raff. Bull. Zool.* 61:97-102
- Jaitrong W, Yamane S (2011) Synopsis of *Aenictus* species groups and revision of the *A. currax* and *A. laeviceps* groups in the eastern Oriental, Indo-Australian, and Australasian regions (Hymenoptera: Formicidae: Aenictinae). *Zootaxa* 3128:1-46
- Jaitrong W, Yamane S (2013) The *Aenictus ceylonicus* species group (Hymenoptera, Formicidae, Aenictinae) from Southeast Asia. *J. Hymenopt. Res.* 31:165-233
- Kohout RJ (2013) A review of the *Polyrbachis xiphias* species-group of the subgenus *Campomyrma* Wheeler (Hymenoptera: Formicidae: Formicinae). *Asian Myrmecology* 5:21-27
- Kohout RJ (2014) A review of the subgenus *Polyrbachis* (*Polyrbachis*) Fr. Smith (Hymenoptera:

- Formicidae: Formicinae) with keys and description of a new species. *Asian Myrmecology* 6:1-31
- Lattke JE (2004) A taxonomic revision and phylogenetic analysis of the ant genus *Gnamptogenys* Roger in Southeast Asia and Australasia (Hymenoptera: Formicidae: Ponerinae). University of California Publications in Entomology 122:1-266
- Li SP, Wang YL (2005) A new species of the ant genus *Aenictus* Shuckard (Hymenoptera: Formicidae) from Henan, China. *Entomotaxonomia* 27:157-160
- Schmidt CA, Shattuck SO (2014) The higher classification of the ant subfamily Ponerinae (Hymenoptera: Formicidae), with a review of ponerine ecology and behavior. *Zootaxa* 3817:1-242
- Seifert B (1992) A taxonomic revision of the Palaearctic members of the ant subgenus *Lasius* s.str. (Hymenoptera: Formicidae). *Abh. Ber. Naturkundemus. Görlitz* 66:1-67
- Staab M (2014) A new species of the *Aenictus wroughtonii* group (Hymenoptera, Formicidae) from South-East China. *ZooKeys* 391:65-73
- Wang CL, Wu J (1994) Second revisionary studies on genus *Camponotus* Mayr of China (Hymenoptera: Formicidae). *Journal of Beijing Forestry University (English Edition)* 3:23-34
- Wang MS (2003) A monographic revision of the ant genus *Pristomyrmex* (Hymenoptera: Formicidae). *Bulletin of the Museum of Comparative Zoology* 157:383-542
- Wang W, Wu WL (2007) Two new species of Formicidae (Hymenoptera) from Hubei province, China. *Acta Zootaxonomica Sinica* 22:721-723. (in Chinese)
- Xu ZH (1998) The Chinese species of the ant genus *Pachycondyla* Smith (Hymenoptera: Formicidae: Ponerinae). *Journal of Southwest Forestry College* 18:209-220. (in Chinese)
- Xu ZH (1999) Systematic studies on the ant genera of *Carebara*, *Rhopalomastix* and *Kartidris* in China (Hymenoptera: Formicidae: Myrmicinae). *Acta Biologica Plateau Sinica* 14:129-136
- Xu ZH (2001) Two new species of the ant genus *Dolichoderus* Lund from Yunnan, China. *Acta Zootaxonomica Sinica* 26:355-360
- Xu ZH (2002) A systematic study of the ant subgenus *Cyrtomyrma* Forel of the genus *Polyrhachis* Smith of China (Hymenoptera: Formicidae). *Acta Entomologica Sinica* 45:522-530
- Xu ZH (2003) A systematic study on Chinese species of the ant genus *Oligomyrmex* Mayr (Hymenoptera, Formicidae). *Acta Zootaxonomica Sinica* 28:310-322
- Xu ZH, Chai ZQ (2004) Systematic study on the ant genus *Tetraponera* F. Smith (Hymenoptera: Formicidae) of China. *Acta Zootaxonomica Sinica* 29:63-76
- Xu ZH, Burwell CJ, Nakamura A (2014) Two new species of the proceratiine ant genus *Discothyrea* Roger from Yunnan, China, with a key to the known Oriental species. *Asian Myrmecology* 6:33-41
- Zhou SY (2001) *Ants of Guangxi*. Guangxi Normal University Press, Guilin. (in Chinese)
- Zhou SY, Huang JJ, Ma LB (2008) Two new species of the ant genus *Myrmecina* (Hymenoptera : Formicidae), with a key to Chinese species. *Sociobiology* 52:283-291
- Zhou SY, Zhao S, Jia FL (2006) A taxonomic study on the ant genus *Pheidologeton* Mayr (Hymenoptera, Formicidae, Myrmicinae) from China. *Acta Zootaxonomica Sinica* 31:870-873
- Zhou SY, Zheng ZM (1999) Taxonomic study of the ant genus *Pheidole* Westwood from Guangxi, with descriptions of three new species. *Acta Zootaxonomica Sinica* 24:83-88
- Zhou SY, Chen Y, Chen ZL, Zhou P, Ban DX, Huang MY (2012) Two new species of the genus *Leptogenys* from Guangxi, China (Hymenoptera: Formicidae). *Sociobiology* 59:885-892.

**Appendix B.** Results of the full initial linear models for log-transformed ant abundance, rarefied ant species richness and Shannon index. Shown are standardized model estimate  $\pm$  SE, t-value, correlation coefficient  $R^2$  and probability P of the t-statistic. The results are only shown to provide general trends of correlations. As environmental variables in a heterogeneous landscape might be non-independent, parameters and P-values of non-reduced full models should be interpreted with great caution. Significant P-values are indicated in bold.

Variable <sup>a</sup>	Estimate $\pm$ SE	t	R <sup>2</sup>	P
<b>Ant abundance<sup>b</sup></b>				
Elevation	-0.2 $\pm$ 0.2	-0.9	<0.01	0.37
Herb cover	-0.3 $\pm$ 0.2	-1.8	0.11	0.09
Herb species richness	-0.3 $\pm$ 0.2	-1.4	0.08	0.18
Litter cover	0.05 $\pm$ 0.1	0.4	<0.01	0.69
Litter depth	-0.07 $\pm$ 0.1	-0.5	0.01	0.62
Shrub cover	0.1 $\pm$ 0.2	0.7	<0.01	0.51
Soil pH	0.09 $\pm$ 0.2	0.6	0.02	0.58
Successional age	-0.03 $\pm$ 0.1	-0.2	0.01	0.82
Tree species richness	-0.09 $\pm$ 0.1	-0.3	0.05	0.75
Vegetation cover	0.08 $\pm$ 0.1	0.6	0.02	0.58
Successional age: tree species richness	0.05 $\pm$ 0.2	0.2	<0.01	0.84
AICc	80.7			
<b>Rarefied ant species richness</b>				
Elevation	-1.3 $\pm$ 0.9	-1.3	0.23	0.2
Herb cover	0.3 $\pm$ 0.9	0.3	<0.01	0.79
Herb species richness	0.08 $\pm$ 0.9	<0.1	<0.01	0.93
Litter cover	-0.9 $\pm$ 0.6	-1.6	0.08	0.14
Litter depth	-0.2 $\pm$ 0.7	-0.3	<0.01	0.8
Shrub cover	-1.3 $\pm$ 0.9	-1.4	0.1	0.17
Soil pH	0.04 $\pm$ 0.8	<0.1	<0.01	0.96
Successional age	-1.0 $\pm$ 0.7	-1.3	<0.01	0.21
Tree species richness	0.9 $\pm$ 0.6	1.4	0.06	0.19
Vegetation cover trap	-0.6 $\pm$ 0.7	-0.8	0.02	0.44
Successional age: tree species richness	0.06 $\pm$ 1.2	<0.1	<0.01	0.96
AICc	169.2			
<b>Shannon index</b>				
Elevation	-0.3 $\pm$ 0.6	-0.6	0.15	0.57
Herb cover	0.2 $\pm$ 0.5	0.3	<0.01	0.78
Herb species richness	0.3 $\pm$ 0.5	-0.2	0.03	0.87
Litter cover	-0.4 $\pm$ 0.3	-1.2	0.04	0.23
Litter depth	0.04 $\pm$ 0.4	0.1	<0.01	0.92
Shrub cover	-1.4 $\pm$ 0.5	-2.8	0.21	<b>0.02</b>
Soil pH	0.02 $\pm$ 0.5	<0.1	<0.01	0.97
Successional age	-0.7 $\pm$ 0.4	-0.7	0.01	0.48
Tree species richness	0.6 $\pm$ 0.4	-0.2	0.11	0.87
Vegetation cover	-0.2 $\pm$ 0.4	0.4	<0.01	0.7
Successional age: tree species richness	0.3 $\pm$ 0.7	0.5	<0.01	0.62
AICc	139.1			

<sup>a</sup> every variable accounted for one df of the numerator; full models always had 26 df in the denominator.

<sup>b</sup> log-transformed.

# CHAPTER 11

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# Effects of ants on the functional composition of spider assemblages increase with tree species richness in a highly diverse forest

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## Abstract

In species-rich ecosystems such as (sub)tropical forests, higher trophic level interactions often play key functional roles. Plant species loss may alter these interactions, but particularly among predators intraguild interactions might modify effects in the interplay with plant diversity. Empirical evidence is scarce, however, and we lack knowledge of these relationships in species-rich systems. Here, we analyze the relationship between spiders and ants—two of the dominant predatory arthropod taxa—on tree saplings across a gradient from medium to high woody plant species richness in a subtropical forest in South-East China. Neither ant nor spider total biomass were significantly related to woody plant species richness. In contrast, the biomass distribution of spider functional groups shifted and spider family richness increased in the presence of ants to more web builder-dominated assemblages. However, ant effects depended on the species richness of the plant communities, becoming more pronounced in plots with higher plant species richness. Our results suggest that besides direct effects of ants particularly on hunting spiders, ants might also indirectly influence intraguild interactions within spider assemblages. The observed shifts in the spider assemblages with increasing ant presence and plant species richness may affect their functional impact by changing the prey spectrum being particularly impacted. Altogether, the relationships among ants, spiders and plant species richness might contribute to explaining the non-significant relationship between the overall effects of predators and plant diversity previously observed in these forests. Our findings can thus help to better understand the complexity of biotic interactions in such species-rich ecosystems.

**Key words:** arthropods; BEF-China; biodiversity; ecosystem function; intraguild interactions; predators; trophic interactions

## Introduction

Biotic interactions, such as top-down effects of predators, can have a substantial impact on community dynamics and ecosystem functioning (Terborgh et al. 2001; Symondson et al. 2002; Duffy 2003), mediating nutrient fluxes, biomass production, and the structure and diversity of primary producer communities (e.g. Lawrence and Wise 2004; Schmitz 2009). Theory predicts, and some studies have provided empirical evidence (e.g. Haddad et al. 2009), that predator effects increase with plant diversity, as more diverse plant communities are expected to provide a higher diversity and stability of resources (e.g.

prey, shelter, habitats) that promote predator abundance and diversity (Root 1973; Haddad et al. 2009; Dinnage et al. 2012). Considering that global change increasingly alters ecosystems and threatens biodiversity (Sala et al. 2000; Barnosky et al. 2012), such relationships could have important ecological consequences for the long-term functioning of many ecosystems. However, knowledge on the relationship between predator impact and plant diversity is scarce for those ecosystems that are particularly threatened by biodiversity loss and where biotic interactions probably play an essential role, such as species-rich (sub)tropical forests (Schemske et al. 2009;

Zhang and Adams 2011).

Results from a comparatively well-studied subtropical forest ecosystem in South-East China indicate that plant diversity does not necessarily promote predator top-down control in such highly diverse forests (Schuldt et al. 2010), and that diversity-dependent differences in biotic interactions are largely bottom-up controlled (Schuldt et al. 2014b). The overall biomass of predators, and particularly the abundance, biomass and species richness of spiders as one of the dominant taxa of generalist predators in these forests were not related to, or even decreased with, increasing woody plant diversity (Schuldt et al. 2011; Schuldt et al. 2014b). However, individual taxa such as predatory ants in part exhibited a positive relationship with plant diversity (Schuldt et al. 2014c; Staab et al. 2014), emphasizing the complexity of diversity effects across trophic levels in such forests. One reason for the lack of an overall effect of predators in relation to changing woody plant diversity could thus be that interactions among predators, such as intraguild predation and interference competition (Sih et al. 1998), weakened the overall predator effect. Ants and spiders are two of the dominant predatory taxa in many ecosystems and strong interactions between these taxa have repeatedly been documented, in most cases indicating antagonistic relationships and negative effects on top-down control (e.g. Halaj et al. 1997; Del-Claro and Oliveira 2000; Mooney 2007; Sanders et al. 2011; Nahas et al. 2012; Mestre et al. 2013). Often, particular functional groups of spiders, such as active hunters, have been found to be more strongly affected by ants than other groups of spiders (Halaj et al. 1997; Mooney 2007; Mestre et al. 2013), suggesting that ants can cause shifts in the structure and functional impact of spider assemblages. However, relationships between ants and spiders at the level of whole plant communities are poorly studied, and thus knowledge of their ecosystem-level consequences is largely lacking. Moreover, to our knowledge, no study has yet directly addressed the role that changes in plant diversity play in affecting the interactions between these major predator taxa—particularly not for species-rich

(sub)tropical forests.

Here, we address these shortcomings by analyzing the relationship between spiders and ants across a gradient from medium to high woody plant species richness in the above-mentioned species-rich forests in South-East China. Specifically, we test for the interactive effects of ant presence and tree species richness on the biomass and functional composition of spider assemblages, aiming to provide insight into the potential mechanisms underlying the previously observed lack of an overall effect of predator top-down control in relation to changing woody plant species richness in this system (Schuldt et al. 2014b). While observational in character, our study is based on direct and simultaneous assessments of spiders and ants on a large number of tree and shrub individuals across 27 forest stands, allowing for a direct comparison under natural conditions. We hypothesize that (i) ant presence and biomass decrease the biomass and shift the functional composition of spider assemblages at the plant community level. Ants may directly predate on spiders, ant-controlled trees might be avoided by spiders (interference competition), and/or ants might reduce prey-availability (exploitative competition) (Halaj et al. 1997; Sanders et al. 2011; Mestre et al. 2013). Freely hunting spiders are more likely to encounter and be negatively affected by ants than web-building spiders (Halaj et al. 1997; Mooney 2007), which suggests that the composition and thus the functional structure of spider assemblages could shift under an increasing impact of ants. Moreover, we expect that (ii) the effects of ants on spiders will be mediated by woody plant species richness. Higher resource availability and diversity in more plant species-rich forest stands might reduce direct interactions between ants and spiders. However, the response to changes in tree species richness might differ in strength between spiders and ants (see e.g. Schuldt et al. 2011; Staab et al. 2014). A stronger impact of ants on spiders in more species-rich stands could strengthen the negative impact on spiders, potentially weakening overall predator top-down effects (Schuldt et al. 2014b).

## Methods

### Study site and plot selection

The study was conducted in the Gutianshan National Nature Reserve (29°14' N; 118°07' E) in Zhejiang province, South-East China. The reserve covers about 80 km<sup>2</sup> of evergreen mixed broadleaved forest in a mountainous area at 250–1260 m a.s.l. The subtropical monsoon climate is characterized by a mean annual temperature of 15.3°C and a mean annual precipitation of about 2000 mm (Hu and Yu 2008), with most of the rainfall occurring in May and June (Geißler et al. 2012).

In 2008, 27 study plots of 30 m x 30 m were established following a stratified sampling design based on stand age (> 20 – < 80 yr) and woody plant species richness (between 25–69 species per plot). The 27 study plots were randomly spread across the accessible parts of the reserve. Details on plot selection and plot characteristics are provided by Bruelheide et al. (2011).

### Sampling of spiders and ants

Spiders and ants were collected on a plant-individual basis with beating sheets during the main vegetation periods in 2011 and 2012. Samples were taken directly from individual trees and shrubs by hand-holding a funnel-shaped cloth sheet (70 cm diameter) beneath the plant and hitting the stem quickly with a beating stick seven times in a row. This beating procedure knocks down arthropods from the plant and causes them to fall down onto the cloth sheet, from which they are collected with forceps or aspirators (Ødegaard et al. 2005; Wardhaugh et al. 2012). In each plot, 25 tree and shrub saplings (average height 1.7 m ± 0.48 SD) were sampled along transects running diagonally through the plots. Every two meters, the woody plant sapling growing closest to the transect line was selected, resulting in a random selection of tree and shrub species in each plot (with the composition of these saplings mirroring the differences in the community composition among plots of the overall woody plant communities; see Schuldt et al. 2014b). Sapling species identity was determined with the help of local experts. The height of each

sapling was recorded in the field. Samples were taken at three time points to obtain a representative sample of arthropod abundance and diversity across important parts of the growing season (toward the end of the main growing season in September/October 2011, at the beginning of the growing season in April 2012, and at the peak of the growing season in June 2012). Transect lines varied between the fall and spring surveys, thus sampling a different set of tree and shrub individuals, but were identical between the spring and summer surveys for logistical reasons.

Ants and adult spiders were identified to the level of (morpho-)species within families (spiders)/subfamilies (ants) or genera based on morphological characters—in the case of adult spiders based on their genitalia. Juvenile spiders (which accounted for 88% of all spiders caught) were identified to family level. The body length of each ant and spider individual (excluding body appendages such as antennae or spinnerets) was measured to the closest 0.1 mm under a stereo-microscope. The biomass of each sampled individual was estimated on the basis of taxon-specific body length-biomass equations of Hódar (1996). Spiders were classified into web-builders and active hunters based on their family affiliation (Jocqué and Dippenaar-Schoeman 2007). For ants, the degree to which species exhibited a predatory lifestyle was estimated from a cafeteria experiment conducted on tree saplings in the same study plots, where ants were offered honey baits as a carbohydrate source and fish baits as a protein source. Cafeteria experiments are commonly used for investigating feeding preferences and trophic positions of ant communities (e.g. Dejean et al. 2014). The relative number of feeding occurrences of each ant species (where all individuals of a given species on a given tree were counted as one occurrence) on each bait type were recorded and used as an indicator of feeding preferences, expressed as the degree of predatory feeding behavior (see Supplementary Material for details).

### Environmental predictors

The species richness of woody plants in each plot was assessed at the time of plot

establishment in 2008 for all tree and shrub individuals > 1 m height. Plot age was based on stem core and diameter at breast height (dbh) measurements (Bruehlheide et al. 2011). Plot age was strongly correlated with plot characteristics that change with succession (e.g. canopy cover, tree density) and used as a comprehensive measure of successional changes in (a)biotic plot conditions (see Schuldt et al. 2010). We also included the elevation (m a.s.l.) of the plots in our analyses, as the topographic variability of the study site may further affect environmental plot conditions.

### Statistical analysis

Spider and ant data were averaged across the three sampling times and the 25 saplings sampled per plot to obtain mean values that reflect the average load of spiders and ants per tree and plot across the growing season. The effects of woody plant species richness and ants on spiders were tested with linear regression models.

As response variables, we used spider biomass (which was strongly correlated with the number of spider individuals: Pearson's  $r = 0.78$ ,  $P < 0.001$ ), spider family richness (as most spiders were juveniles and only identified to family level), and the biomass ratio of web-building to actively hunting spiders (reflecting the functional composition of spider assemblages based on their main hunting type, which might be particularly affected by the presence of ants). We initially also calculated biomass and family richness separately for web-builders and hunting spiders, but as these values were strongly correlated with overall spider biomass ( $r = 0.83$  and  $0.86$  for web-builder and hunter biomass, respectively;  $P < 0.001$ ) and family richness ( $r = 0.73$  and  $0.62$  for web-builder and hunter family richness, respectively,  $P < 0.001$ ), we only used spider guild-specific data for the biomass ratio analysis.

As predictors (all standardized to mean = 0 and  $SD = 1$ ), we included in the regression models the mean sapling height, elevation, woody plant species richness, plot age, the probability of ant presence, total ant biomass, as well as the two- and three-way interactions among plant species richness, plot

age and each of the two ant metrics. The probability of ant presence was expressed as the proportion of sampled trees on which ants had been recorded at the three sampling times. We used this variable as a conservative measure of ant effects, as it is based on presence-absence data and thus less affected by potential sampling effects that may occur when abundance data are used for a social taxon such as ants. Nevertheless, ant presence was highly correlated with, and thus well represents, the number of ant individuals ( $r = 0.92$ ,  $P < 0.001$ ) as well as ant species richness ( $r = 0.98$ ,  $P < 0.001$ ). Total ant biomass was only moderately correlated with the probability of ant presence ( $r = 0.48$ ,  $P = 0.011$ ), and we thus included ant biomass as an additional predictor. Both ant presence and biomass were strongly positively correlated with the degree of predatory feeding behavior exhibited by the ant communities across the 27 study plots ( $r = 0.60$  and  $r = 0.85$ , respectively;  $P \leq 0.001$ ), meaning that plots with a higher presence and biomass of ants were dominated by species that are more likely to act as predators. Due to the strong correlations with ant presence and biomass, we did not include the degree of predatory feeding behavior into the analyses. The biomass ratio of web-building to hunting spiders, the probability of ant presence and ant biomass were log-transformed to improve modeling assumptions.

We used an automated variable selection procedure to simplify the full models based on the reduction in AICc with the stepwise exclusion of uninformative predictor variables (Burnham and Anderson 2004). The models with the smallest number of predictors and the lowest global AICc were chosen as the most parsimonious, best-fit models for each response variable. Model residuals were checked for normality and homogeneity of variances.

To evaluate the extent to which changes in spider family richness were driven by changes in spider family composition across the study plots, we used non-metric multi-dimensional scaling (NMDS) analysis, based on a Morisita-Horn dissimilarity matrix of square-root transformed abundance data. A stable solution for a two-dimensional

**Table 11.1.** Results (standardized estimates, standard errors, t- and P-values of the predictors and overall model fit) of the minimal regression models for spider biomass, spider family richness, and the ratio of web-building to freely hunting spiders across 27 forest plots in subtropical China

Predictor	Spider biomass			Spider family richness			Biomass ratio web/hunting spiders		
	Stand. est. (± SE)	t	P	Stand. est. (± SE)	t	P	Stand. est. (± SE)	t	P
Plot age	0.69 (±0.18)	3.8	<0.001	0.15 (±0.05)	2.8	0.010	-	-	-
Woody plant species richness	-	-	-	-0.003 (±0.05)	-0.1	0.951	0.08 (±0.10)	0.8	0.416
Probability of ant presence	-	-	-	0.09 (±0.05)	1.7	0.108	0.16 (±0.10)	1.6	0.116
Plant species richness x ant presence	-	-	-	0.10 (±0.04)	2.3	0.034	0.19 (±0.08)	2.3	0.032
R <sup>2</sup> adj.	0.34			0.33			0.17		
F	14.3			4.2			2.7		
Deg. of Freedom	1, 25			4, 22			3, 23		
P	<0.001			0.011			0.066		

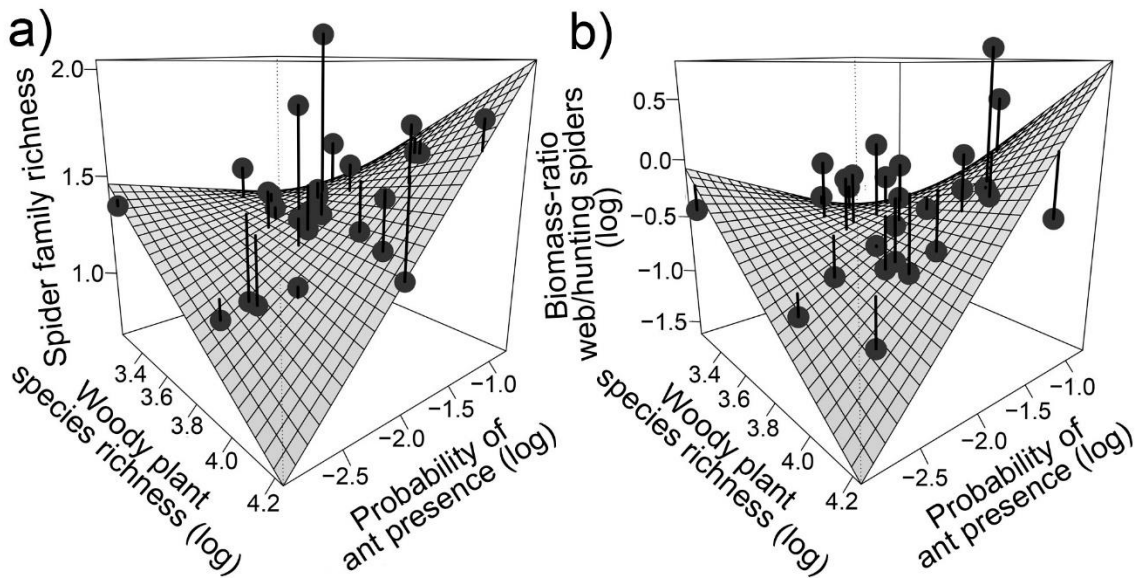
ordination was computed from multiple random starting configurations. Results were centered, and principal components rotation was used to obtain maximum variance of points on the first dimension. Predictors retained in the minimal model for spider family richness were standardized and fitted to the ordination plot on the basis of a regression analysis with the NMDS axes scores. Significance of the correlations was assessed with permutation tests (N = 1000).

All analyses were conducted in R 3.0.0 (<http://www.R-project.org>).

**Results**

In total, we recorded 3732 spiders (with a total biomass of 6191 mg) and 674 ants (total biomass 398 mg). The spiders belonged to 22 families, of which Theridiidae, Salticidae, Araneidae, and Thomisidae were the most abundant and contributed most to total biomass (accounting for 23, 19, 18, and 13%, respectively, of all individuals, and 10, 35, 15, and 9% of the total spider biomass). Of the 3732 spiders, 434 were adults (belonging to 131 morphospecies, with Theridiidae (46 species) and Salticidae (19) as the most

species-rich families) and 3298 (88%) juveniles (Table S11.1 in Supplementary Material). The ants belonged to 40 (morpho)species. Four species accounted for 65% of all ant individuals (*Paraparatrechina sauteri* (Forel, 1913) (Formicinae; 180 individuals), *Crematogaster rogenhoferi* Mayr, 1879 (subfamily Myrmicinae; 158), *Camponotus humerus* Wang & Wu, 1994 (Formicinae; 56), and *Polyrbachis illaudata* Walker, 1859 (Formicinae; 45). Three of the four most common species (excluding *P. sauteri*, which contributed little to overall biomass due to its small body size of around 1.5 mm) also belonged to the four species contributing most (63% in total) to overall ant biomass: *P. illaudata* (168 mg), *C. rogenhoferi* (37 mg), *Camponotus friedae* Forel, 1912 (28 mg), and *C. humerus* (18 mg). Only one species (*Pachycondyla luteipes* (Mayr, 1862), a singleton of the subfamily Ponerinae) was classified as a strict predator. However, of the remaining omnivore species, 24 out of 26 species tested in the cafeteria experiment (94% of all ant individuals, 88% of total ant biomass) showed evidence for at least a partially predatory lifestyle by foraging on fish baits. The degree of predatory feeding behavior in these species ranged from 7% to 80%, with a mean of 45 ±



**Figure 11.1.** Relationships between woody plant species richness, ant presence and a) spider family richness and b) the biomass ratio of web-building to freely hunting spiders. All relationships significant at  $P < 0.005$  (see Table 11.1).

19% *SD* (Table S11.2).

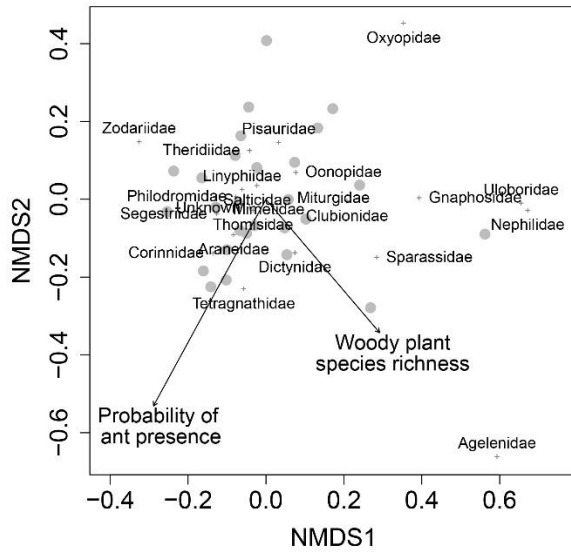
Mean spider biomass and spider family richness were positively related to plot age, but spider biomass showed no significant relationship with the probability of ant presence (Table 11.1). In contrast, spider family richness and also the biomass ratio of web-building to hunting spiders showed an effect of ant presence that was mediated by woody plant species richness (Table 11.1). Ant presence was strongly positively related to spider family richness and the biomass ratio of web-building to hunting spiders at high levels of woody plant species richness, leading to an increase in family richness and a shift in the dominance from hunting to web-building spiders with increasing ant presence (Fig. 11.1). In contrast, ant presence was only weakly related to spider family richness and the biomass ratio at low levels of woody plant species richness. Separately testing for effects on hunting and web-building family richness showed no effect on hunting spider richness ( $F_{2, 23} = 0.85$ ,  $P = 0.482$  for the ant–woody plant species richness interaction) and a slight positive (but non-significant) tendency for an effect on web-building spider family richness ( $F_{2, 23} = 1.73$ ,  $P = 0.190$ ). Total ant biomass did not contribute to explaining additional variance beyond that accounted for by ant presence in any of the models.

The NMDS analysis indicated that the probability of ant presence particularly promoted the relative abundance of the web-building Araneidae and Tetragnathidae as well as that of freely hunting Corinnidae (all of which also tended to be positively related to woody plant species richness), whereas several hunting families, such as Oxyopidae and Pisauridae, appeared to be negatively related to ant presence (Fig. 11.2). Families such as Zodariidae and Theridiidae appeared to be negatively related to woody plant species richness. However, the overall effect of woody plant species richness was not significant (Fig. 11.2).

Ants, in turn, appeared to be not directly affected by woody plant species richness. Neither the probability of ant presence ( $F_{1,25} = 0.23$ ,  $P = 0.638$ ) nor mean ant biomass ( $F_{1,25} = 0.03$ ,  $P = 0.857$ ) or the degree of predatory feeding behavior ( $F_{1,25} = 0.47$ ,  $P = 0.501$ ) were significantly related to the species richness of woody plants.

## Discussion

Our study shows that the presence of ants, while not directly influencing overall spider biomass, caused shifts in the richness and composition of spider assemblages that might affect their functional impact in the studied



**Figure 11.2.** NMDS ordination plot (based on Morisita-Horn index of square root-transformed relative abundance data) of the assemblages of spider families (crosses) on tree and shrub saplings across 27 forest plots (filled circles). Stress = 0.199. Ant presence ( $R^2 = 0.23$ ;  $P = 0.050$ ) and woody plant species richness ( $R^2 = 0.13$ ;  $P = 0.190$ ) were standardized and fitted in a post-hoc correlation procedure with the axes scores.

forest stands. Interestingly, the effect of ants depended on the woody plant species richness of the forest stands, becoming more pronounced with increasing plant species richness. This underlines the importance of plant species richness for higher trophic level interactions. At the same time, however, the dependence of the interactions between ants and spiders on woody plant species richness might result in an overall non-significant net relationship between total predator effects and plant species richness. Neither ant nor spider biomass were significantly related to woody plant species richness, and previous studies in these forests found no indications of the often hypothesized positive effect of plant species richness on predator top-down control (Schuldt et al. 2014a; Schuldt et al. 2014b). Our results can thus help to better understand the complexity of biotic interactions in species-rich ecosystems that might not be apparent at first sight.

Ants and spiders play a dominant role in the arthropod assemblages of many ecosystems, with a significant impact on other trophic groups and on each other (e.g.

Symondson et al. 2002; Rosumek et al. 2009; Sanders et al. 2011). A range of studies in tree-dominated systems have documented primarily negative effects of ants on spiders (Halaj et al. 1997; Del-Claro and Oliveira 2000; Philpott et al. 2004; Mooney 2007; Nahas et al. 2012; Mestre et al. 2013). However, closer inspection often revealed particularly strong effects of ants on freely hunting spiders, whereas web builders were found to be less affected in several cases (e.g. Halaj et al. 1997; Mooney 2007; but see Nahas et al. 2012; Mestre et al. 2013). Freely hunting spiders are more likely to be encountered by ants than many web builders (which are often out of the direct reach of ants when sitting in their webs), making hunting spiders more prone to experience predation or competitive pressure exerted by ants. This is in line with our findings that an increasing probability of ant presence shifted the biomass distribution of spiders to more web builder dominated assemblages and that the increase in spider family richness with increasing ant presence tended to be driven to a larger extent by web-building families. Moreover, the NMDS analysis indicated that the biomass of several web-building spider families increased in the presence of ants, whereas that of several hunting spider families decreased. However, our study also shows that total spider biomass is not necessarily affected by these shifts in the structure of the spider assemblages. This contrasts with findings from other studies in forest ecosystems (Halaj et al. 1997; Del-Claro and Oliveira 2000; Mooney 2007; Nahas et al. 2012) and might be due to the fact that the effects of ants were mediated by woody plant species richness—a component of plant communities not considered in previous studies.

Plant species richness can strongly affect assemblages and biotic interactions at higher trophic levels (Cardinale et al. 2012). To our knowledge, our study is the first to document that plant species richness determined the extent to which ants affected spiders. This finding can have important implications for our understanding of how plant species richness and its loss might affect interaction networks among different trophic groups and their impact on important

ecosystem functions (such as pest control). Only at high levels of woody plant species richness did a higher probability of ant presence increase the spider family richness and the web builder to hunting spider biomass ratio. This pattern was not evident in plots with comparatively low woody plant species richness. Interestingly, however, a low probability of ant presence at high levels of plant species richness in turn decreased the spider family richness and the biomass ratio below the values observed in less plant species-rich plots. These patterns underline the complexity of the interactions between ants and spiders. The degree to which the ant species observed in our study showed an indication of a predatory lifestyle (< 50% on average) suggests that other factors besides direct predation play a role in driving these patterns (see e.g. also Halaj et al. 1997). The majority of vegetation-foraging ant species are involved in trophobiotic interactions with sap-sucking Hemiptera and show aggressive behavior toward potential enemies of their trophobiotic partners (Del-Claro and Oliveira 2000; Philpott and Armbrrecht 2006; Rosumek et al. 2009). Asymmetric interference competition of ants with particular groups of hunting spiders could benefit web builders and less dominant hunting spiders, which otherwise might be more strongly affected by intraguild interactions with those particular groups of hunting spiders (e.g. Nyffeler 1999). Schuldt et al. (2014c) showed that highly competitive hunting spiders might have severe effects on the structure of the overall spider assemblages in such species-rich forests, and, as was also the case in our study, that such effects can indirectly depend on plant species richness. Note that ant presence and biomass were not affected by woody plant species richness, such that the effects of woody plant species richness are not due to changes in the direct impact of ants. Moreover, they were also not due to potential changes in the availability or presence of 'ant-plants' that attract ants with the help of extrafloral nectaries in many tropical forest systems (Rosumek et al. 2009), as extrafloral nectaries are uncommon and only found on very few of the woody plant species at our study site. In general, an increase in the species richness of

plants can be assumed to provide an increase in the resources available to predators such as spiders (Root 1973; Haddad et al. 2009). Under negative impacts of ants on hunting spiders such resources would benefit primarily other spiders, particularly web builders that are not strongly affected by ants. In the absence or at a low probability of ant presence, however, those active hunting spiders would benefit from more available resources as well. In this case, family richness and the biomass ratio of web-building to hunting spiders could decrease if a better performance of particular active hunters would result in stronger intraguild competitive or predation effects within the spider assemblages. While difficult to verify with our observational data, changes in the spider assemblages might thus in part be related to ant-mediated intraguild interactions between spider families (see also Moya-Laraño and Wise 2007).

The patterns we observed may have strong effects on the functional impact of important generalist predators in these forests. The shift toward more web builder dominated and more family-rich spider assemblages with increasing ant presence and woody plant species richness can lead to changes in the prey spectrum being particularly affected by the spider assemblages. For instance, many lepidopteran larvae and other herbivores with limited mobility are more likely to be encountered, and thus experience higher predation pressure, by hunting spiders (Nyffeler 1999). Many herbivores may thus benefit from a higher dominance of web-building spiders, which also capture a high proportion of flying insects and can thus negatively affect the densities of hymenopteran and dipteran parasitoids attacking herbivores (Nentwig 1987; Brodeur and Rosenheim 2000). In contrast, ants are known to cause reductions in the densities of many herbivores (Floren et al. 2002; Mooney 2007; Rosumek et al. 2009). However, direct negative effects on herbivores are unlikely to be driven by plant species richness in the studied forests, as ant presence and biomass were not affected by woody plant species richness. This lack of a tree species richness effect on ants differs from the findings of



Ribas et al. (2003) and Klimes et al. (2012) and could be due to a focus on different vegetation strata (our study: understory, above studies: canopy). Altogether, our findings may thus contribute to explaining the fact that previous studies in the same forest stands did not detect a general plant diversity dependent top-down effect of predators on herbivores (Schuldt et al. 2014a; Schuldt et al. 2014b). However, the explained variation of the regression models (17-34%) shows that ant presence, woody plant species richness and plot age alone cannot fully explain the patterns observed for spiders. While observational studies have the advantage of investigating established and natural assemblages of species under real-world conditions, they often face a variety of confounding factors that are difficult to control. The actual strength of these effects thus needs to be verified with controlled experiments that not only manipulate ant presence or biomass, but also tree species richness. In several regions across the globe, and also in our study region, larger-scale tree diversity experiments have recently been established (Bruehlheide et al. 2014; www.treedivnet.ugent.be). These might further our mechanistic understanding of the role of plant species richness in influencing biotic interactions at higher trophic levels and their overall functional impact on ecosystem processes in species-rich forests.

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### References

Barnosky AD, Hadly EA, Bascompte J, Berlow EL, Brown JH (2012) Approaching a state shift in Earth's biosphere. *Nature* 486:52-58  
 Brodeur J, Rosenheim JA (2000) Intraguild

interactions in aphid parasitoids. *Entomologia Experimentalis et Applicata* 97:93-108  
 Bruehlheide H et al. (2011) Community assembly during secondary forest succession in a Chinese subtropical forest. *Ecological Monographs* 81:25-41  
 Bruehlheide H et al. (2014) Designing forest biodiversity experiments: general considerations illustrated by a new large experiment in subtropical China. *Methods in Ecology and Evolution* 5:74-89  
 Burnham KP, Anderson DR (2004) Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York  
 Cardinale BJ et al. (2012) Biodiversity loss and its impact on humanity. *Nature* 486:59-67  
 Dejean A, Labrière N, Touchard A, Petitclerc F, Roux O (2014) Nesting habits shape feeding preferences and predatory behavior in an ant genus. *Naturwissenschaften* 101:323-330  
 Del-Claro K, Oliveira PS (2000) Conditional outcomes in a neotropical treehopper-ant association: temporal and species-specific variation in ant protection and homopteran fecundity. *Oecologia* 124:156-165  
 Dinnage R, Cadotte MW, Haddad NM, Crutsinger GM, Tilman D (2012) Diversity of plant evolutionary lineages promotes arthropod diversity. *Ecology Letters* 15:1308-1317  
 Duffy JE (2003) Biodiversity loss, trophic skew and ecosystem functioning. *Ecology Letters* 6:680-687  
 Floren A, Biun A, Linsenmair KE (2002) Arboreal ants as key predators in tropical lowland rainforest trees. *Oecologia* 131:137-144  
 Geißler C, Kühn P, Böhnke M, Bruehlheide H, Shi X, Scholten T (2012) Splash erosion potential under tree canopies in subtropical SE China. *CATENA* 91:85-93  
 Haddad NM, Crutsinger GM, Gross K, Haarstad J, Knops JMH, Tilman D (2009) Plant species loss decreases arthropod diversity and shifts trophic structure. *Ecology Letters* 12:1029-1039  
 Halaj J, Ross DW, Moldenke AR (1997) Negative effects of ant foraging on spiders in Douglas-fir canopies. *Oecologia* 109:313-322  
 Hódar JA (1996) The use of regression equations for estimation of arthropod biomass in ecological studies. *Acta Oecologica* 17:421-433  
 Hu Z, Yu M (2008) Study on successions sequence of evergreen broad-leaved forest in Gutian Mountain of Zhejiang, Eastern China: species diversity. *Frontiers of Biology in China* 3:45-49  
 Jocqué R, Dippenaar-Schoeman AS (2007) Spider

- families of the world. Royal Museum for Central Africa, Tervuren
- Klimes P et al. (2012) Why are there more arboreal ant species in primary than secondary tropical forests? *Journal of Animal Ecology* 81:1103-1112
- Lawrence KL, Wise DH (2004) Unexpected indirect effect of spiders on the rate of litter disappearance in a deciduous forest. *Pedobiologia* 48:149-157
- Mestre L, Pinol J, Barrientos JA, Espadaler X (2013) Ant exclusion in citrus over an 8-year period reveals a pervasive yet changing effect of ants on a Mediterranean spider assemblage. *Oecologia* 173:239-248
- Mooney KA (2007) Tritrophic effects of birds and ants on a canopy food web, tree growth, and phytochemistry. *Ecology* 88:2005-2014
- Moya-Laraño J, Wise DH (2007) Direct and indirect effects of ants on a forest-floor food web. *Ecology* 88:1454-1465
- Nahas L, Gonzaga MO, Del-Claro K (2012) Emergent impacts of ant and spider interactions: herbivory reduction in a tropical savanna tree. *Biotropica* 44:498-505
- Nentwig W (1987) The prey of spiders. In: Nentwig W (ed) *Ecophysiology of spiders*. Springer Berlin Heidelberg, pp 249-263
- Nyffeler M (1999) Prey selection of spiders in the field. *Journal of Arachnology* 27:317-324
- Ødegaard F, Diserud OH, Østbye K (2005) The importance of plant relatedness for host utilization among phytophagous insects. *Ecology Letters* 8:612-617
- Philpott SM, Armbrecht I (2006) Biodiversity in tropical agroforests and the ecological role of ants and ant diversity in predatory function. *Ecological Entomology* 31:369-377
- Philpott SM, Greenberg R, Bichier P, Perfecto I (2004) Impacts of major predators on tropical agroforest arthropods: comparisons within and across taxa. *Oecologia* 140:140-149
- Ribas CR, Schoereder JH, Pic M, Soares SM (2003) Tree heterogeneity, resource availability, and larger scale processes regulating arboreal ant species richness. *Austral Ecology* 28:305-314
- Root RB (1973) Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). *Ecological Monographs* 43:95-124
- Rosumek FB et al. (2009) Ants on plants: a meta-analysis of the role of ants as plant biotic defenses. *Oecologia* 160:537-549
- Sala OE et al. (2000) Global biodiversity scenarios for the year 2100. *Science* 287:1770-1774
- Sanders D, Schaefer M, Platner C, Griffi GJK (2011) Intraguild interactions among generalist predator functional groups drive impact on herbivore and decomposer prey. *Oikos* 120:418-426
- Schemske DW, Mittelbach GG, Cornell HV, Sobel JM, Roy K (2009) Is there a latitudinal gradient in the importance of biotic interactions? *Annual Review of Ecology Evolution and Systematics* 40:245-269
- Schmitz OJ (2009) Effects of predator functional diversity on grassland ecosystem function. *Ecology* 90:2339-2345
- Schuldt A et al. (2014a) Functional and phylogenetic diversity of woody plants drive herbivory in a highly diverse forest. *New Phytologist* 202:864-873
- Schuldt A et al. (2010) Tree diversity promotes insect herbivory in subtropical forests of south-east China. *Journal of Ecology* 98:917-926
- Schuldt A et al. (2014b) Woody plant phylogenetic diversity mediates bottom-up control of arthropod biomass in species-rich forests. *Oecologia*: DOI: 10.1007/s00442-014-3006-7
- Schuldt A et al. (2011) Predator diversity and abundance provide little support for the enemies hypothesis in forests of high tree diversity. *PLoS ONE* 6:e22905
- Schuldt A, Bruelheide H, Durka W, Michalski SG, Purschke O, Assmann T (2014c) Tree diversity promotes functional dissimilarity and maintains functional richness despite species loss in predator assemblages. *Oecologia* 174:533-543
- Sih A, Englund G, Wooster D (1998) Emergent impacts of multiple predators on prey. *Trends in Ecology & Evolution* 13:350-355
- Staab M, Schuldt A, Assmann T, Klein AM (2014) Tree diversity promotes predator but not omnivore ants in a subtropical Chinese forest. *Ecological Entomology*: in press
- Symondson WOC, Sunderland KD, Greenstone MH (2002) Can generalist predators be effective biocontrol agents? *Annual Review of Entomology* 47:561-594
- Terborgh J et al. (2001) Ecological meltdown in predator-free forest fragments. *Science* 294:1923-1926
- Wardhaugh CW, Stork NE, Edwards W (2012) Feeding guild structure of beetles on Australian tropical rainforest trees reflects microhabitat resource availability. *Journal of Animal Ecology* 81:1086-1094
- Zhang Y, Adams J (2011) Top-down control of herbivores varies with ecosystem types. *Journal of Ecology* 99:370-372

## Supplementary material

### Methods: cafeteria experiment

The feeding preferences of vegetation-foraging ants in the Gutianshan National Nature Reserve were assessed with standardized cafeteria experiments. On each of the 27 study plots, nine pairwise feeding platforms were installed. Each feeding platform consisted of two flat plastic dishes (diameter: 5 cm, height: 1 cm) that were fixed next to each other with standard electricity insulation tape on a small tree at breast height (Figure S1). In each of the nine 10 m x 10 m subplots of the entire 30 m x 30 m plot one such feeding platform was set up. One of the two platforms was always baited with a cotton ball soaked in around 3 ml honey water (1 part honey, 2 parts water)

as a surrogate for plant-based carbohydrate-rich food, while the other platform was baited with around 3 g of canned fish as a surrogate for animal-based protein-rich food.

After baiting, feeding platforms were checked after 180 minutes and all ants feeding on the baits were collected (Figure S2). Ants were stored in 95 % ethanol until point mounting and identification. For every ant species, the relative number of feeding occurrences on each bait type was recorded and the relative proportion of feeding occurrences on fish baits was taken as a measure for the degree of predatory feeding behavior of a species.



**Figure S11.1.** Photograph illustrating the cafeteria experiments performed to assess the feeding behavior of vegetation-foraging ants in the Gutianshan National Nature Reserve. A cotton ball soaked with honey water (as carbohydrate source; left side) and a piece of canned fish (as protein source; right side) were offered next to each other.

**Table S11.1.** Spider morphospecies and the number of individuals per morphospecies collected in the beating samples of the 27 forest plots in South-East China. Juvenile spiders were only identified to family level

Morphospecies	Family	Individuals
Agelenidae juvenile	Agelenidae	4
Agelenidae sp.1	Agelenidae	1
Araneidae juvenile	Araneidae	654
Araneidae sp.1	Araneidae	1
Araneidae sp.10	Araneidae	1
Araneidae sp.2	Araneidae	1
Araneidae sp.3	Araneidae	1
Araneidae sp.4	Araneidae	2
Araneidae sp.5	Araneidae	1
Araneidae sp.6	Araneidae	1
Araneidae sp.7	Araneidae	1
Araneidae sp.8	Araneidae	1
Araneidae sp.9	Araneidae	1
Clubionidae juvenile	Clubionidae	63
Clubionidae sp.1	Clubionidae	5
Clubionidae sp.2	Clubionidae	3
Clubionidae sp.3	Clubionidae	2
Clubionidae sp.4	Clubionidae	1
Clubionidae sp.5	Clubionidae	2
Corinnidae juvenile	Corinnidae	32
Corinnidae sp.1	Corinnidae	2
Dictynidae juvenile	Dictynidae	32
Dictynidae sp.1	Dictynidae	30
Dictynidae sp.2	Dictynidae	1
Dictynidae sp.3	Dictynidae	1
Erigoninae juvenile	Linyphiidae	1
Erigoninae sp.1	Linyphiidae	1
Erigoninae sp.2	Linyphiidae	2
Erigoninae sp.3	Linyphiidae	1
Gnaphosidae juvenile	Gnaphosidae	9
Gnaphosidae sp.1	Gnaphosidae	1
Gnaphosidae sp.2	Gnaphosidae	1
Linyphiinae juvenile	Linyphiidae	323
Linyphiinae sp.1	Linyphiidae	26
Linyphiinae sp.2	Linyphiidae	1
Linyphiinae sp.3	Linyphiidae	1
Linyphiinae sp.4	Linyphiidae	2
Linyphiinae sp.5	Linyphiidae	1
Linyphiinae sp.6	Linyphiidae	5
Linyphiinae sp.7	Linyphiidae	1
Lycosidae juvenile	Lycosidae	1
Mimetidae juvenile	Mimetidae	10
Mimetidae sp.1	Mimetidae	4

Mimetidae sp.2	Mimetidae	3
Miturgidae juvenile	Miturgidae	28
Nephilidae sp.1	Nephilidae	2
Nephilidae sp.2	Nephilidae	4
Oonopidae juvenile	Oonopidae	5
Oonopidae sp.1	Oonopidae	1
Oonopidae sp.2	Oonopidae	4
Oonopidae sp.3	Oonopidae	7
Oxyopidae juvenile	Oxyopidae	112
Oxyopidae sp.1	Oxyopidae	3
Philodromidae juvenile	Philodromidae	116
Philodromidae sp.1	Philodromidae	1
Philodromidae sp.2	Philodromidae	5
Pisauridae juvenile	Pisauridae	23
Pisauridae sp.1	Pisauridae	1
Pisauridae sp.2	Pisauridae	2
Salticidae juvenile	Salticidae	612
Salticidae sp.1	Salticidae	6
Salticidae sp.10	Salticidae	2
Salticidae sp.11	Salticidae	1
Salticidae sp.12	Salticidae	1
Salticidae sp.13	Salticidae	1
Salticidae sp.14	Salticidae	1
Salticidae sp.15	Salticidae	1
Salticidae sp.16	Salticidae	1
Salticidae sp.17	Salticidae	1
Salticidae sp.18	Salticidae	2
Salticidae sp.2	Salticidae	30
Salticidae sp.29	Salticidae	1
Salticidae sp.3	Salticidae	37
Salticidae sp.4	Salticidae	8
Salticidae sp.5	Salticidae	6
Salticidae sp.6	Salticidae	1
Salticidae sp.7	Salticidae	3
Salticidae sp.8	Salticidae	3
Salticidae sp.9	Salticidae	3
Segestriidae juvenile	Segestriidae	2
Sparassidae juvenile	Sparassidae	11
Sparassidae sp.1	Sparassidae	1
Sparassidae sp.2	Sparassidae	1
Tetragnathidae juvenile	Tetragnathidae	28
Tetragnathidae sp.1	Tetragnathidae	5
Tetragnathidae sp.2	Tetragnathidae	5
Tetragnathidae sp.3	Tetragnathidae	1
Tetragnathidae sp.4	Tetragnathidae	7
Tetragnathidae sp.5	Tetragnathidae	1
Tetragnathidae sp.6	Tetragnathidae	5

Tetragnathidae sp.7	Tetragnathidae	1
Theridiidae juvenile	Theridiidae	742
Theridiidae sp.1	Theridiidae	6
Theridiidae sp.10	Theridiidae	1
Theridiidae sp.11	Theridiidae	1
Theridiidae sp.12	Theridiidae	2
Theridiidae sp.13	Theridiidae	6
Theridiidae sp.14	Theridiidae	2
Theridiidae sp.15	Theridiidae	2
Theridiidae sp.16	Theridiidae	2
Theridiidae sp.17	Theridiidae	1
Theridiidae sp.18	Theridiidae	1
Theridiidae sp.19	Theridiidae	1
Theridiidae sp.2	Theridiidae	24
Theridiidae sp.20	Theridiidae	8
Theridiidae sp.21	Theridiidae	1
Theridiidae sp.22	Theridiidae	1
Theridiidae sp.23	Theridiidae	2
Theridiidae sp.24	Theridiidae	1
Theridiidae sp.25	Theridiidae	3
Theridiidae sp.26	Theridiidae	5
Theridiidae sp.27	Theridiidae	2
Theridiidae sp.28	Theridiidae	2
Theridiidae sp.29	Theridiidae	1
Theridiidae sp.3	Theridiidae	4
Theridiidae sp.30	Theridiidae	1
Theridiidae sp.31	Theridiidae	1
Theridiidae sp.32	Theridiidae	2
Theridiidae sp.33	Theridiidae	6
Theridiidae sp.34	Theridiidae	1
Theridiidae sp.35	Theridiidae	1
Theridiidae sp.36	Theridiidae	1
Theridiidae sp.37	Theridiidae	4
Theridiidae sp.38	Theridiidae	3
Theridiidae sp.39	Theridiidae	1
Theridiidae sp.4	Theridiidae	2
Theridiidae sp.40	Theridiidae	1
Theridiidae sp.41	Theridiidae	2
Theridiidae sp.42	Theridiidae	2
Theridiidae sp.43	Theridiidae	7
Theridiidae sp.44	Theridiidae	1
Theridiidae sp.45	Theridiidae	1
Theridiidae sp.46	Theridiidae	1
Theridiidae sp.5	Theridiidae	1
Theridiidae sp.6	Theridiidae	4
Theridiidae sp.7	Theridiidae	3
Theridiidae sp.8	Theridiidae	1

Theridiidae sp.9	Theridiidae	1
Thomisidae juvenile	Thomisidae	462
Thomisidae sp.1	Thomisidae	7
Thomisidae sp.2	Thomisidae	5
Thomisidae sp.3	Thomisidae	4
Thomisidae sp.4	Thomisidae	3
Thomisidae sp.5	Thomisidae	2
Thomisidae sp.6	Thomisidae	1
Uloboridae juvenile	Uloboridae	4
Uloboridae sp.1	Uloboridae	1
Uloboridae sp.2	Uloboridae	2
Uloboridae sp.3	Uloboridae	1
Uloboridae sp.4	Uloboridae	1
Unidentified juvenile	Unidentified	11
Zodariidae juvenile	Zodariidae	13
Zodariidae sp.1	Zodariidae	2
Zodariidae sp.2	Zodariidae	1
Zodariidae sp.3	Zodariidae	2

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**Table S11.2.** Ant species collected in the beating samples of the 27 forest plots in South-East China. Shown are the number of individuals and the occurrence (i.e. the number of samples in which the species was collected) per species, as well as the percentage of occurrences per species on fish baits (based on the cafeteria experiment described above)

Species	Subfamily	Occurrence	Individ.	% occurrence on fish baits
<i>Aphaenogaster</i> sp.2	Myrmicinae	1	1	0.57
<i>Camponotus compressus</i> (Fabricius, 1787)	Formicinae	3	2	0.25
<i>Camponotus friedae</i> Forel, 1912	Formicinae	9	10	0.39
<i>Camponotus humerus</i> Wang & Wu, 1994	Formicinae	44	56	0.40
<i>Camponotus pseudoirritans</i> Wu & Wang, 1989	Formicinae	4	4	0.33
<i>Camponotus rubidus</i> Xiao & Wang, 1989	Formicinae	2	2	0.56
<i>Camponotus</i> sp.10	Formicinae	2	2	0.00
<i>Camponotus</i> sp.11	Formicinae	1	1	0.50
<i>Camponotus</i> sp.8	Formicinae	2	2	NA
<i>Crematogaster rogenhoferi</i> Mayr, 1879	Myrmicinae	84	158	0.56
<i>Crematogaster</i> sp.5	Myrmicinae	6	11	0.75
<i>Dolichoderus incisus</i> Xu, 1995	Dolichoderinae	2	2	NA
<i>Dolichoderus</i> sp.2	Dolichoderinae	1	1	NA
<i>Formica japonica</i> Motschoulsky, 1866	Formicinae	1	1	0.33
<i>Gauromyrmex acanthinus</i> (Karavaiev, 1935)	Myrmicinae	2	2	NA
<i>Liometopum sinense</i> Wheeler, 1921	Dolichoderinae	1	1	NA
<i>Nylanderia</i> sp.3	Formicinae	1	26	0.80
<i>Nylanderia</i> sp.6	Formicinae	22	1	0.27
<i>Pachycondyla luteipes</i> (Mayr, 1862)	Ponerinae	1	1	1.00
<i>Paraparatrechina santeri</i> (Forel, 1913)	Formicinae	110	180	0.07
<i>Pheidole noda</i> Smith, 1874	Myrmicinae	18	40	0.46
<i>Plagiolepis</i> sp.1	Formicinae	2	3	0.25
<i>Plagiolepis</i> sp.2	Formicinae	4	5	NA
<i>Polyrbachis dives</i> Smith, 1857	Formicinae	2	2	NA
<i>Polyrbachis illaudata</i> Walker, 1859	Formicinae	41	45	0.26
<i>Polyrbachis lamellidens</i> Smith, 1874	Formicinae	3	3	0.56
<i>Polyrbachis</i> sp.4	Formicinae	1	1	NA
<i>Polyrbachis striata</i> Mayr, 1862	Formicinae	2	2	0.00
<i>Prenolepis</i> sp.5	Formicinae	1	2	NA
<i>Prenolepis</i> sp.6	Formicinae	1	1	NA
<i>Recurvidris glabriceps</i> Zhou, 2000	Myrmicinae	2	5	0.40
<i>Rhoptromyrmex wrightonii</i> Forel, 1902	Myrmicinae	3	4	NA
<i>Rotastruma stenoceps</i> Bolton, 1991	Myrmicinae	10	11	0.71
<i>Tapinoma indicum</i> Forel, 1895	Dolichoderinae	2	2	0.33
<i>Technomyrmex brunneus</i> Forel, 1895	Dolichoderinae	1	1	NA
<i>Technomyrmex obscurior</i> Wheeler, 1928	Dolichoderinae	16	36	0.37
<i>Tetramorium shensiense</i> Bolton, 1977	Myrmicinae	19	25	0.80
<i>Tetraoponera allaborans</i> (Walker, 1859)	Pseudomyrmicinae	9	9	0.50
<i>Tetraoponera amargina</i> Xu & Chai, 2004	Pseudomyrmicinae	8	8	NA
<i>Tetraoponera convexa</i> Xu & Chai, 2004	Pseudomyrmicinae	5	5	NA



# CHAPTER 12

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# Scale-dependent diversity patterns affect spider assemblages of two contrasting forest ecosystems

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## Abstract

Spiders are important generalist predators in forests. However, differences in assemblage structure and diversity can have consequences for their functional impact. Such differences are particularly evident across latitudes, and their analysis can help to generate a better understanding of region-specific characteristics of predator assemblages. Here, we analyze the relationships between species richness, family richness and functional diversity (FD) as well as  $\alpha$ - and  $\beta$ -components of epigeic spider diversity in semi-natural temperate and subtropical forest sites. As expected, within-plot and overall spider species and family richness were higher in the subtropical plots. In contrast, local FD within plots was similar between sites, and differences in FD only became evident at larger spatial scales due to higher species turnover in the subtropical forests. Our study indicates that the functional effects of predator assemblages can change across spatial scales. We discuss how differences in richness and functional diversity between contrasting forest ecosystems can depend on environmental heterogeneity and the effects of species filters acting at local scales. The high turnover observed in the species-rich subtropical forests also requires a more regional perspective for the conservation of the overall diversity and the ecological functions of predators than in less diverse forests, as strategies need to account for the large spatial heterogeneity among plots.

**Key words:** BEF China; beta-diversity; ecosystem function; latitude; plant diversity; predators; spatial scale; turnover

## Introduction

It is well established that the species richness of many taxa generally increases from the poles toward the tropics (but exceptions are also known; Hillebrand 2004). Concomitantly, the strength of biotic interactions and their impact on ecosystem functions are expected to increase from higher toward lower latitudes (Schemske et al. 2009). Predation and predator effects on herbivores are an often-cited example of biotic interactions that show a correlation with latitude (e.g. Schemske et al. 2009; Rodriguez-Castaneda 2013) but the generality of these patterns is not well established (Zhang and Adams 2011). In particular, it has become clear that the functional impact of organism groups such as predators is determined much less by their species richness *per se*, but rather by the species' functional differentiation and

potential niche complementarity (Finke and Snyder 2008; Woodcock and Heard 2011). Interestingly, a recent study on spider diversity indicated that functional guild richness and diversity do not differ consistently between temperate and tropical regions, possibly due to higher functional redundancy among species in the much more species-rich tropical sites (Cardoso et al. 2011). This, in turn, might suggest that the strength of biotic interactions such as predation, while confirmed in some cases and for some taxa (particularly for ants: Jeanne 1979; Rosumek et al. 2009), does not necessarily have to differ between latitudes in all cases and for all taxa (Cornell et al. 1998; Andrew and Hughes 2005; Cardoso et al. 2011).

For a better understanding, more studies are needed that address patterns in the functional diversity of predators and that take into account the potential scale-dependence of

these patterns. Latitudinal diversity patterns are particularly pronounced at larger spatial scales (Hillebrand 2004). At a local scale, relevant for direct interactions between predator species and their prey, the spatial heterogeneity in local environmental conditions and the factors determining local community assembly and species turnover can lead to patterns that deviate from those observed at larger scales (Hortal et al. 2012). As the mechanisms underlying these patterns can differ between regions (Algar et al. 2011), this might influence the degree to which species richness affects functional diversity and thus ultimately biotic interactions such as predation (Hooper et al. 2005).

Here, we analyze to what extent species richness, family richness and the functional diversity of epigeic spiders differ between temperate and subtropical forest sites, and assess the contribution of  $\alpha$ - and  $\beta$ -richness components to overall species richness in these forests. Forests harbor a large diversity of biota, and spiders play an important role as a dominant group of generalist predators in these ecosystems (Wise 2004; Schuldt et al. 2011). While our study is limited to two large forest expanses, it considers a total of 18 forest stands representative of the range of tree richness variation found in the study regions; i.e. Central Europe and southeast China. Despite restrictions regarding the general transferability to other forest ecosystems, our study thus provides an important baseline and insights into scale-dependent patterns of species richness and functional diversity for more detailed studies in species-rich forests. We hypothesize that while (i) the subtropical forest plots feature both a higher overall richness and a higher small-scale  $\alpha$ -richness than temperate plots, as might generally be expected with decreasing latitude (Hillebrand 2004), (ii) overall richness in the subtropical forests will be shaped more strongly by species turnover ( $\beta$ -richness) than in the temperate forest plots. With higher species richness in the subtropical forests, we also expect (iii) to find an overall higher functional diversity of epigeic spiders (but see Cardoso et al. 2011), which can be indicative of higher predator pressure (e.g. Finke and Snyder 2008).

## Methods

### Study sites

Two sites were selected for this study. Both sites are characterized by semi-natural, broad-leaved forests which comprise stands of high tree diversity within the respective regions. The temperate study site was located in the Hainich National Park, Thuringia, Germany (51°01'N, 10°05'E). The national park covers 76 km<sup>2</sup> of deciduous forest, with *Fagus sylvatica* L., *Tilia platyphyllos* Scop., *Tilia cordata* L. and *Fraxinus excelsior* L. as dominant tree species. In 2005, nine study plots of 50 x 50 m, with a stand age of 80–120 yr, were established along a tree diversity gradient ranging from 1 to 10 tree species. The subtropical study site was located in the Gutianshan National Nature Reserve, Zhejiang Province, south-east China (29°14'N, 118°07'E). The reserve is characterized by 81 km<sup>2</sup> of broad-leaved, semi-evergreen forest, with dominant tree species being *Castanopsis eyrei* (Champ. ex Benth.) and *Schima superba* Gardn. et Champ. For the present study, we selected nine plots of 30 x 30 m that were comparable in age to the Hainich study plots (Table 12.1). Plots were established in 2008 and differed in age (60–115 yr) and the diversity of woody plants (29–69 species). The average distance among the temperate plots was 1.8 ( $\pm 0.23$  SE) km. The average distance among the subtropical plots was 2.6 ( $\pm 0.37$  SE) km. However, this was due to one plot with a particularly large distance to all other plots. Removing this plot resulted in an average distance of 1.8 ( $\pm 0.25$  SE) km, very similar to the temperate plots, and did not change the outcome of our statistical analyses (most importantly, this had no effect on the potential site effects we found; data not shown). For details on plot establishment and plot characteristics at the two sites, see Leuschner et al. (2009) and Bruelheide et al. (2011).

### Sampling design and spider identification

At both sites, spiders were sampled by pitfall traps over the course of one growing season. At the temperate site Hainich, sampling was conducted from 27 April to 26 October 2005 (see Schuldt et al. 2008). We used four randomly selected traps (0.4 L cups, upper diameter 5.5 cm)—of the originally six pitfall

traps that were installed along three transects in each of the nine plots—for our comparison with the subtropical site. Mean distance between these traps was 25 m. Sampling at the subtropical site was from 30 March–2 September 2009. In the center of each plot (note: out of logistical reasons the sampling area layout within the plots slightly differed from that at the temperate site), four traps (0.5 L cups, upper diameter 8.5 cm) were set up in the corners of a 10 x 10 m square (see Schuldt et al. 2011). Traps at both sites were emptied at fortnightly intervals. Potential differences in trap catches due to slightly deviating trap dimensions between regions were accounted for by using rarefied spider data (see below). While the larger distance between traps at the temperate site might potentially increase beta diversity within plots, the temperate study plots were much more homogeneous than the subtropical plots, and our results show that interpretation of our data is not affected by these differences in trapping design.

Adult spiders were identified to species or morphospecies (within families or genera; most of the subtropical spiders) based on their genitalia.

### Habitat characteristics

Aiming at reducing differences among study sites to a minimum (i.e. by using the same number of traps, similar trapping periods, and having the possibility to analyze the same number of plots of similar age at each site), we were not able to replicate sites within regions (datasets with similar sampling characteristics were not available). This limits our ability to generalize results beyond our study sites (the plots of which, however, represent the typical range of tree diversity found in both regions). However, we included habitat characteristics in our models that represent the range of factors known to affect spiders at a local scale and act independent of the specific study region. These characteristics included soil pH, litter depth, and percentage herb cover, which were assessed at the time of spider trapping (for details on measurements, see Schuldt et al. 2008 2011). We also included the stand age of the study plots as a predictor in our models. Observed differences among sites despite inclusion of these local-scale habitat

characteristics might thus indicate region effects, as these differences represent those effects that are not explained by local-scale variation (i.e. effects that point to larger-scale impacts).

Spider diversity might also be affected by tree diversity, which strongly differed between the subtropical and temperate sites ( $t = -18.8$ ,  $df = 38.7$ ;  $P < 0.001$ ). Yet, with our data it is difficult to differentiate actual effects of tree diversity and simple covariation due to similar mechanisms underlying large-scale diversity patterns of different organism groups. However, using tree diversity instead of site (as a potential region effect) in our statistical analyses always resulted in models with a slightly lower fit (data not shown), which indicates that site differences include additional information beyond pure tree diversity data. We thus used the potential region effect of site differences rather than tree diversity in our analyses and address the interrelation between the two variables in the Discussion.

### Data analysis

We used rarefaction (for between-site comparisons we used sample-based rarefaction with values rescaled to  $n=1000$  individuals; plot-level comparisons were based on  $n=24$  individuals) to compare species and family richness between the subtropical and temperate sites. Likewise, we used rarefied spider assemblage data ( $n=24$  individuals per trap, using the function *rarefy* in the *vegan* package in R; Oksanen et al. 2010) to calculate the functional diversity (FD) of spider guild composition at both sites. Guild data was based on the UPGMA cluster analysis of ecological characteristics (in particular foraging strategy) by Cardoso et al. (2011). We calculated FD as the sum of branch lengths connecting all terminal guild clusters in the dendrogram of Cardoso et al. (2011) that contained spider families observed at our study sites (Petchey and Gaston 2006). Rarefied assemblage data were used to ensure that results were independent of the number of individuals (and the resulting number of species) sampled at each site.

**Table 12.1.** Summary statistics of overall richness measures and sampling design

Variable	Temperate site (Hainich)	Subtropical site (Gutianshan)
Adult spiders	2979	1823
Species richness	62	108
Rarefied richness	45.3 (CI: 38.9-51.8) <sup>a</sup>	83.9 (CI: 73.0-94.7) <sup>a</sup>
Families	17	23
Families rarefied	13.6 (CI: 10.6-16.6) <sup>a</sup>	21.6 (CI: 19.5-23.8) <sup>a</sup>
Functional diversity FD	3.53	3.88
FD rarefied communities	3.01	3.88
Total # of plots	9	9
Total # of traps (4 per plot)	36	36
# of trap days	182	157
Stand age	80-120	60-115

<sup>a</sup>CI=Lower and upper 95% confidence intervals

Richness variables and functional diversity were log-transformed to increase normality and homoscedasticity of the data (Figures show untransformed data for clarity). The between-site ('region', see above) effect on these richness measures was tested with linear mixed-effects models, with soil pH, litter depth, percentage herb cover, and stand age included as covariables. Plot identity was included as a random effect to account for the hierarchical data structure (traps nested within plots). We used a stepwise selection procedure of explanatory variables based on the AICc to fit the most parsimonious, minimal adequate model with the lowest global AICc for each of the response variables.

To assess the relative importance of  $\alpha$ - and  $\beta$ -richness components on overall  $\gamma$ -richness of spiders at both sites, we used additive partitioning of species richness (Lande 1996). Overall richness at the subtropical and temperate sites was partitioned into mean species richness per trap within plots ( $\alpha_{\text{within}}$ ) and the spatial turnover within plots (between traps:  $\beta_{\text{within}}$ ) and between plots ( $\beta_{\text{between}}$ ). Due to the additive nature of the components,  $\alpha_{\text{within}} + \beta_{\text{within}} + \beta_{\text{between}} = \gamma$ , and  $\alpha_{\text{within}} + \beta_{\text{within}} = \alpha_{\text{between}}$  (mean richness per plot). Again, analyses were based on rarefied assemblage data (Crist and Veech 2006). Richness components were expressed

as percentages of total rarefied richness and tested against study site and the covariables pH, litter depth, herb cover, and stand age in linear models. Minimal adequate models were fit by stepwise variable selection based on the reduction in AICc compared to the full model.

All analyses were performed in R 2.12.0 (<http://www.R-project.org>) and EstimateS 8.0.0 (R. K. Colwell, <http://purl.oclc.org/estimates>).

## Results

The overall richness of species and families was higher at the subtropical site, even though the total number of adult spiders was higher at the temperate site (Table 12.1). These richness patterns became even more pronounced after accounting for differences in spider abundance by rarefaction. Similarly, overall functional diversity was higher at the subtropical site, in particular when rarefied assemblage data was used (Table 12.1).

Mean rarefied species richness of spiders per trap differed between sites (Table 12.2, Fig. 12.1a), with higher richness in the subtropical compared to the temperate plots ( $0.24 \pm 0.06$  SE species for log-transformed trap data). Along with pH, which, however, had no significant overall effect, site differences were retained in the minimal model for species richness (Fig. 12.2). They

**Table 12.2.** Results (degrees of freedom;  $F$ -value and probabilities  $P$ ) for the fixed effects of (a) the minimal mixed-effects models for rarefied species, family and foraging guild richness, and (b) the linear models for the proportions of  $\alpha$ - and  $\beta$ -components of partitioned overall species richness (see Fig. 12.2 for details)

Model	Fixed effects	df	$F$	$P$
<i>(a) Rarefied richness measures</i>				
Species richness	pH	1, 15	0.65	0.432
	Region	1, 15	18.18	<0.001
Family richness	Region	1, 16	89.82	<0.001
Functional diversity	-	-	-	<i>n.s.</i>
<i>(b) Partitioning of overall richness</i>				
Richness $\alpha_{\text{within}}$	pH	1, 15	53.88	<0.001
	Region	1, 15	22.11	<0.001
Richness $\beta_{\text{within}}$	Stand age	1, 13	0.35	0.56
	Litter depth	1, 13	1.99	0.181
	pH	1, 13	2.21	0.16
	Region	1, 13	18.95	<0.001
Richness $\beta_{\text{between}}$	Region	1, 16	27.06	<0.001

were also retained, as the only variable, in the minimal model for family richness. Rarefied family richness per trap was higher in the subtropical plots ( $0.49 \pm 0.05$   $SE$  for log-transformed data) (Fig. 12.1b). Interestingly, functional diversity at the plot level was also higher at the subtropical site ( $F_{1,15} = 11.99$ ;  $P = 0.004$  in a minimal model with herb cover as a second predictor), whereas there was no significant difference in functional diversity between the subtropical and temperate sites at the smaller scale of the individual traps (Fig. 12.1c).

Additive partitioning revealed a prominent role of spatial turnover between plots for overall species richness (using rarefied assemblage data), in particular for the subtropical plots (Fig. 12.2). Site was retained as a significant explanatory variable in the minimal models for all richness proportions (Table 12.2). The subtropical site had a proportionally higher species turnover between plots ( $10.28\% \pm 3.16$   $SE$  for  $\beta_{\text{between}}$ ), and a lower  $\alpha$ -richness and turnover within plots at the level of the individual traps ( $-6.92\% \pm 1.47$   $SE$  for  $\alpha_{\text{within}}$ , and  $-4.54\% \pm 1.71$   $SE$  for  $\beta_{\text{within}}$ , respectively) (Fig. 12.2). The mean proportion of total species richness represented by the individual plots ( $\alpha_{\text{between}}$ )

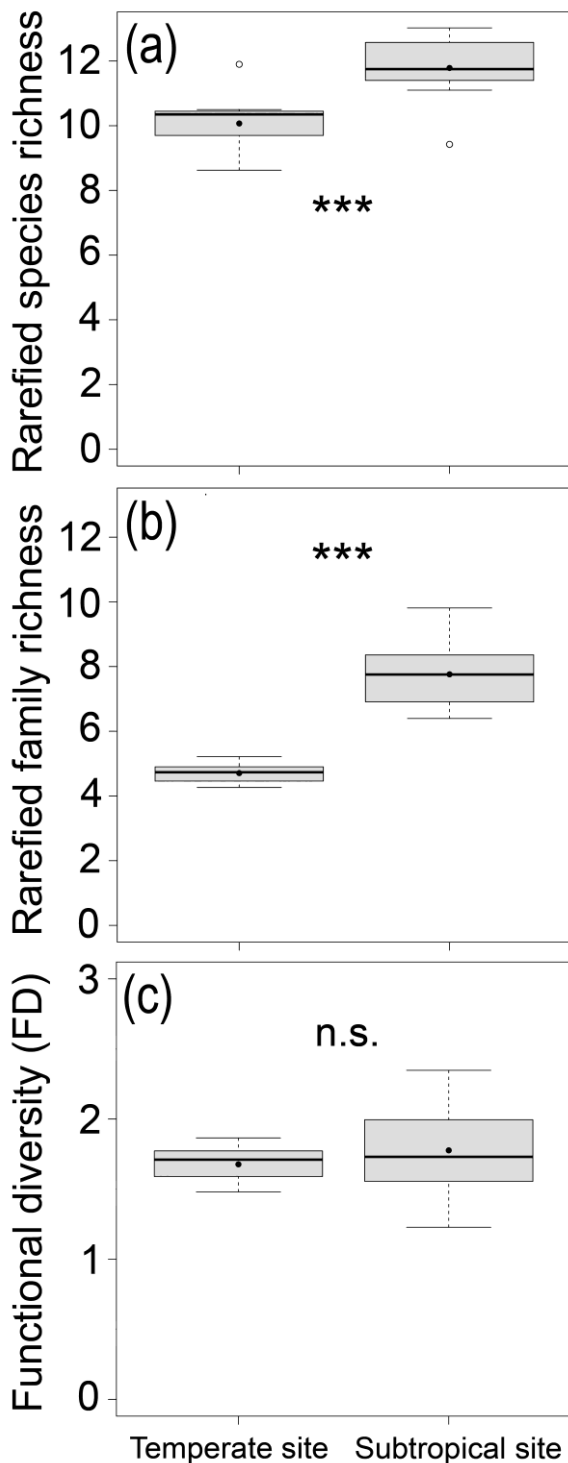
was higher at the temperate (43.7% of total species richness) compared to the subtropical site (29.1%) (Fig. 12.2). Stand age of the plots was only retained, but as a non-significant predictor, in the minimal model for  $\beta_{\text{within}}$ .

## Discussion

Our analysis provides insight into scale-dependent patterns of predator assemblages in species-rich forests that should motivate further analysis in future studies. The lack of replication within regions (as comparable datasets were not available) limits our ability to generalize results. However, significant differences between sites despite consideration of potential local-scale effects of plot-specific habitat characteristics point to effects that might be attributed to larger-scale, more regional impacts.

### Species richness and functional diversity

Our results of higher species and family richness of epigeic spiders in the subtropical plots are in line with the general observation of increasing diversity toward lower latitudes (e.g. Hillebrand 2004). The overall functional diversity was also higher at the subtropical than at the temperate site. However, while this was true of differences at the site and plot levels, functional diversity at the finest spatial scale, i.e. at the level of the individual traps, did not differ significantly between the two sites. This indicates that on a very local scale, spider assemblages in the temperate plots seem to be able to take on similar functional roles as in the subtropical plots, despite higher species and family richness in the latter at this local scale (see also Lange et al. 2011). In contrast to our study, Cardoso et al. (2011) found for larger-scale data that functional diversity did not necessarily differ between high and low latitudes. In their study, functional diversity of plots at higher latitudes was similar to that of tropical plots located at higher elevations, whereas tropical plots at lower elevations showed a significantly higher functional diversity (Cardoso et al. 2011). Our study indicates that such patterns can be in part due to differences in the spatial heterogeneity within plots and the resulting species turnover. For heterogeneous forests characterized by high plant diversity, such as

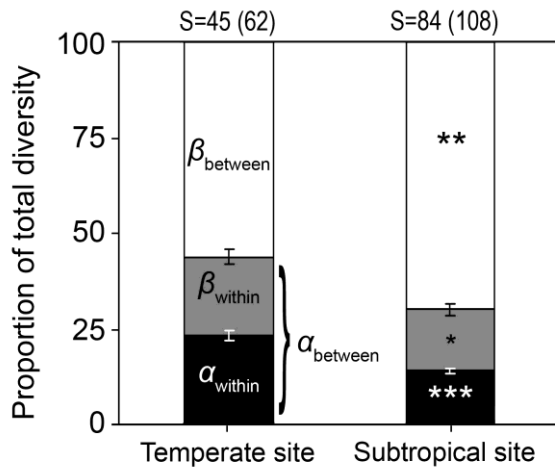


**Figure 12.1.** Rarefied (a) species richness, (b) family richness, and (c) functional diversity of epigeic spiders per trap in 9 temperate and 9 subtropical broad-leaved forest stands. Filled circles indicate mean values, black lines show medians. \*\*\* indicates significant differences between regions with  $P < 0.001$ ; n.s. = not significant.

our subtropical plots, species turnover at larger scales can override similarities in the functional diversity with forests at higher latitudes.

Similar functional diversity at the temperate and the subtropical sites at the smallest scale of our analysis, despite higher overall species richness at the subtropical plots, can be explained by the fact that the proportional  $a_{\text{within}}$  richness of the plots was lower at the subtropical site. Likewise, the observed differences in species richness between traps at both sites, even though statistically significant, were apparently not large enough to cause significant differences in functional diversity at the level of individual traps. However, functional diversity (FD) increased much stronger from the trap to the site level at the subtropical site, due to higher species turnover than at the temperate site. In a comparison of nesting ant diversity in natural and structurally less diverse secondary forest sites, Klimes et al. (2012) found that despite higher overall diversity in the structurally more complex natural forests, ant diversity did not differ between sites at the level of individual trees. Thus, while simpler environments might show similar local variability and a resulting similar local-scale diversity than more complex environments, larger microhabitat turnover in structurally more complex environments increases overall diversity in these environments at larger scales (Klimes et al. 2012). Small-scale vegetational heterogeneity was much higher within the subtropical plots of our study (mean tree richness of 43.8 compared to the temperate plots with 5.8 species) and can have provided more niches for additional spider functional groups at both the plot and the site levels (note that despite higher contribution of the  $\beta_{\text{within}}$ -component to overall richness at the temperate site, this component comprised many more species at the subtropical site). The observed high proportions of  $\beta$ -richness at the subtropical site were not affected by a potential undersampling of rare species. Proportions of  $\alpha$ - and  $\beta$ -components did not change when only common species were considered for the partitioning of overall species richness (Schuldt et al. 2012).





**Figure 12.2.** Partitioning of overall ( $\gamma$ ) rarefied species richness into proportional components (mean  $\pm$  SE) of richness per trap within plots ( $\alpha_{within}$ ), species turnover between traps within plots ( $\beta_{within}$ ), and turnover between plots ( $\beta_{between}$ ). \*\*\*, \*\*, and \* indicate significant differences in the individual components between regions with  $P < 0.001$ ,  $P < 0.01$ , and  $P < 0.05$ , respectively.  $\alpha_{between}$  = mean proportion of overall species richness per plot. S = rarefied (total observed) species richness per study site.

Yet, differences in tree diversity *per se* and their influence on habitat characteristics probably do not completely explain the observed patterns at the two sites. Although tree diversity can affect abiotic and biotic characteristics important to spiders (e.g. litter and vegetation structure, microclimate, prey availability; Scheu 2005), we found significant differences between sites despite inclusion of such potentially important plot characteristics as covariables (see also Klimes et al. 2012). Strong site effects despite inclusion of these local-scale characteristics point to larger-scale impacts on these patterns. One factor that is well known to cause such larger-scale impacts are differences in regional climate characteristics (Field et al. 2009), which can influence the way regional and local species filters affect diversification and species turnover (Bond and Chase 2002; Algar et al. 2011). We might thus hypothesize that environmental stability at lower latitudes has promoted local-scale competition and niche-partitioning among a large number of species (Mittelbach et al. 2007), whereas less stable conditions at higher latitudes have limited regional diversification and the number of

potentially available species (Wiens et al. 2010). Our dataset, however, does not allow for a direct analysis of the underlying mechanisms, and further studies are needed to develop a better mechanistic understanding.

### Functional redundancy and biodiversity conservation

Spider assemblages in species-rich forests at lower latitudes have previously been proposed to be more resistant to disturbances or invasions (Cardoso et al. 2011). In our study, functional diversity increased less than species richness from the trap to the site level, and differences in functional diversity between sites were less pronounced than differences in species richness. This indicates that redundancy among species increased with scale particularly at the subtropical site. Such redundant species can act as insurance and promote functional stability (Fonseca and Ganade 2001; Hooper et al. 2005). Together with the fact that the main cause of higher species richness in the subtropical forest stands of our study was the strong spatial turnover in species among plots, these findings can have important implications for the conservation of biodiversity and the associated functions in the studied forests. While conservation efforts can already be effective by focusing on a few, particularly species-rich forest plots at the temperate site, preserving regional diversity (and potentially functional stability) at the subtropical site requires a larger-scale perspective. Conservation strategies will need to account for the large spatial heterogeneity in species composition of such species-rich forests by devoting efforts to a larger area, and not only to the most species-rich plots (see also Baselga 2010). This is of particular relevance in light of increasing fragmentation and loss of natural and semi-natural forests in many species-rich regions due to increasing socioeconomic pressure (e.g. Lopez-Pujol et al. 2006).

### Conclusions

Further studies are needed to test the generality of the observed patterns, as we were not able to replicate study sites within regions. Nevertheless, our study underscores the importance of considering multiple study

plots and scale-dependent patterns when analyzing the structure of predator assemblages in contrasting forest ecosystems. As functional diversity patterns of predator assemblages can be scale-dependent, differences in the effects of predator pressure reported from comparisons of different forests ecosystems or regions might also depend on the spatial scale considered. More high-quality data based on replicated and methodologically comparable assessments are needed for further studies. In many cases, methodological data constraints hinder consistent comparisons of diversity patterns and trophic interaction strength between regions (Andrew and Hughes 2005; Beck et al. 2012). In this regard, our study, being based on comparable sampling effort and sampling design between study sites, provides insight into the spatial dynamics of predator diversity of semi-natural forests and calls attention to research needs that should be addressed in future studies.

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### References

- Algar AC, Kerr JT, Currie DJ (2011) Quantifying the importance of regional and local filters for community trait structure in tropical and temperate zones. *Ecology* 92:903-914
- Andrew NR, Hughes L (2005) Arthropod community structure along a latitudinal gradient: Implications for future impacts of climate change. *Austral Ecology* 30:281-297
- Baselga A (2010) Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography* 19:134-143
- Beck J, Holloway JD, Khen CV, Kitching IJ (2012) Diversity partitioning confirms the importance of beta diversity components in tropical rainforest lepidoptera. *American Naturalist* 180:E64-E74
- Bond EM, Chase JM (2002) Biodiversity and ecosystem functioning at local and regional spatial scales. *Ecology Letters* 5:467-470
- Bruehlheide H et al. (2011) Community assembly during secondary forest succession in a Chinese subtropical forest. *Ecological Monographs* 81:25-41
- Cardoso P, Pekar S, Jocque R, Coddington JA (2011) Global patterns of guild composition and functional diversity of spiders. *Plos One* 6:e21710
- Cornell HV, Hawkins BA, Hochberg ME (1998) Towards an empirically-based theory of herbivore demography. *Ecological Entomology* 23:340-349
- Crist TO, Veech JA (2006) Additive partitioning of rarefaction curves and species-area relationships: unifying  $\alpha$ -,  $\beta$ - and  $\gamma$ -diversity with sample size and habitat area. *Ecology Letters* 9:923-932
- Field R et al. (2009) Spatial species-richness gradients across scales: a meta-analysis. *Journal of Biogeography* 36:132-147
- Finke DL, Snyder WE (2008) Niche partitioning increases resource exploitation by diverse communities. *Science* 321:1488-1490
- Fonseca CR, Ganade G (2001) Species functional redundancy, random extinctions and the stability of ecosystems. *Journal of Ecology* 89:118-125
- Hillebrand H (2004) On the generality of the latitudinal diversity gradient. *American Naturalist* 163:192-211
- Hooper DU et al. (2005) Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecological Monographs* 75:3-35
- Hortal J, De Marco P, Santos AMC, Diniz-Filho JAF (2012) Integrating biogeographical processes and local community assembly. *Journal of Biogeography* 39:627-628
- Jeanne RL (1979) A latitudinal gradient in rates of ant predation. *Ecology* 60:1211-1224
- Klimes P et al. (2012) Why are there more arboreal ant species in primary than secondary tropical forests? *Journal of Animal Ecology* 81:1103-1112
- Lande R (1996) Statistics and partitioning of species diversity, and similarity among multiple communities. *Oikos* 76:5-13
- Lange M et al. (2011) The impact of forest management on litter-dwelling invertebrates: a

- subtropical-temperate contrast. *Biodiversity and Conservation* 20:2133-2147
- Leuschner C, Jungkunst HF, Fleck S (2009) Functional role of forest diversity: Pros and cons of synthetic stands and across-site comparisons in established forests. *Basic and Applied Ecology* 10:1-9
- Lopez-Pujol J, Zhang FM, Ge S (2006) Plant biodiversity in China: richly varied, endangered, and in need of conservation. *Biodiversity and Conservation* 15:3983-4026
- Mittelbach GG et al. (2007) Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecology Letters* 10:315-331
- Oksanen E et al. (2010) vegan: Community Ecology Package. R package version 1.17-4. Available from <http://cran.r-project.org>.
- Petchey OL, Gaston KJ (2006) Functional diversity: back to basics and looking forward. *Ecology Letters* 9:741-758
- Rodriguez-Castaneda G (2013) The world and its shades of green: a meta-analysis on trophic cascades across temperature and precipitation gradients. *Global Ecology and Biogeography* 22:118-130
- Rosumek FB et al. (2009) Ants on plants: a meta-analysis of the role of ants as plant biotic defenses. *Oecologia* 160:537-549
- Schemske DW, Mittelbach GG, Cornell HV, Sobel JM, Roy K (2009) Is there a latitudinal gradient in the importance of biotic interactions? *Annual Review of Ecology Evolution and Systematics* 40:245-269
- Scheu S (2005) Linkages between tree diversity, soil fauna and ecosystem processes. In: Scherer-Lorenzen M, Körner C, Schulze ED (eds) *Forest diversity and function: Temperate and boreal systems*. Springer, Berlin, Heidelberg, pp 211-233
- Schuldt A et al. (2011) Predator diversity and abundance provide little support for the enemies hypothesis in forests of high tree diversity. *PLoS ONE* 6:e22905
- Schuldt A, Bruelheide H, Härdtle W, Assmann T (2012) Predator assemblage structure and temporal variability of species richness and abundance in forests of high tree diversity. *Biotropica* 44:793-800
- Schuldt A, Fahrenholz N, Brauns M, Migge-Kleian S, Platner C, Schaefer M (2008) Communities of ground-living spiders in deciduous forests: Does tree species diversity matter? *Biodiversity and Conservation* 17:1267-1284
- Wiens JJ et al. (2010) Niche conservatism as an emerging principle in ecology and conservation biology. *Ecology Letters* 13:1310-1324
- Wise DH (2004) Wandering spiders limit densities of a major microbi-detritivore in the forest-floor food web. *Pedobiologia* 48:181-188
- Woodcock BA, Heard MS (2011) Disentangling the effects of predator hunting mode and habitat domain on the top-down control of insect herbivores. *Journal of Animal Ecology* 80:495-503
- Zhang YA, Adams J (2011) Top-down control of herbivores varies with ecosystem types. *Journal of Ecology* 99:370-372



# CHAPTER 13

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# Non-native tree species (*Pseudotsuga menziesii*) strongly decreases predator biomass and abundance in mixed-species plantations of a tree diversity experiment

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## Abstract

Stand diversification increasingly emerges as a promising means for improving the multi-functionality and sustainability of management in plantation forests. Increasing tree species richness might potentially also benefit natural enemies, which can substantially contribute to sustainable forest management via top-down control of forest pests. However, there is little empirical evidence on how tree species richness affects the diversity and abundance of predators, as the majority of analyses to date have rarely gone beyond comparisons of monocultures and two species mixtures. Here, we analyzed the performance of spiders as important generalist predators in a tree diversity experiment that uses four of the economically most important broadleaved and coniferous tree species in Europe. We tested the extent to which tree species richness and the identity of the planted tree species affect the abundance, biomass, species richness and functional diversity of spiders. Whereas tree species richness in general had no significant effect, tree species identity strongly affected spider biomass and abundance—with a particularly strong negative effect of the non-native Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco). Our results indicate that increasing tree species richness does not necessarily promote characteristics of natural enemy assemblages relevant for pest control in forests and thus not all functions that may be important in a multi-functional management context. Rather, tree species composition and identity will often be of crucial importance in determining forest ecosystem functions and services. The fact that the severe impact of Douglas fir persisted even in diversified tree species mixtures suggests that stand-level predator efficiency can be reduced for tree species growing adjacent to or in mixture with this species. This calls for a more thorough examination of the ecological consequences of the increasing use of this species in forestry across Europe, in particular considering that climate change may increase the potential of pest outbreaks and thus the need for adequate control in the next decades.

**Keywords:** Arthropods; biodiversity; ecosystem function; herbivore control; identity effects; spiders

## Introduction

The relationship between biodiversity and the provisioning of ecosystem functions and services has become a major focus of ecological research and is increasingly being integrated into economic decision making and environmental management schemes (Gómez-Baggethun et al. 2010; Cardinale et al. 2012; Ruckelshaus et al. 2014). Forest ecosystems, which provide key services essential to human well-being (Kremen et al. 2000; Bonan 2008), have only relatively recently been incorporated

more thoroughly into the biodiversity-ecosystem function and service framework (Scherer-Lorenzen et al. 2007). Several studies have shown not only increased biomass production, but also higher stability and insurance against biotic and abiotic disturbances, even with only moderate increases in tree species richness (e.g. Jactel and Brockerhoff 2007; Morin et al. 2011; Gamfeldt et al. 2013; for a review see Scherer-Lorenzen 2014). All of this may enhance the long-term economic value of forests (Knoke et al. 2008) and, moreover, promote the

overall biodiversity of plants and animals associated with these forest ecosystems. This corresponds well with the goals of sustainable forest management approaches that are being pursued in many regions with a long history of intensive forest management, such as in Europe (Rametsteiner and Mayer 2004; Wolfslehner et al. 2005). However, despite efforts of promoting the establishment of mixtures (usually two species mixtures) over the last decades, to date the largest proportion of forests even in Europe is still made up of monoculture plantations (Knoke et al. 2008). To create stronger incentives to re-evaluate traditional forest management practices, particularly regarding sustainable forest management, a better understanding may be required of how tree species diversity actually affects many of the vital functions and services provided by forests that have received little attention in this respect so far (Nadrowski et al. 2010).

A key function that is often considered to be positively associated with more diverse plant communities (Root 1973; Haddad et al. 2009) and of high economic importance is pest control (Losey and Vaughan 2006). Predators may benefit from increased resource and prey diversity in more diverse plant communities (Root 1973; Haddad et al. 2009) and thus contribute to the reduction of herbivore damage and pest outbreaks often observed with an increase in the tree diversity of forest stands (Jactel and Brockerhoff 2007; Castagnyrol et al. 2014). The role of predators in stabilizing forest ecosystem functioning by controlling herbivores is particularly relevant considering that climate change will increase the risk of pest outbreaks and facilitate the immigration and establishment of exotic pest species in the next decades (Dale et al. 2001; Lindner et al. 2010; Netherer and Schopf 2010). However, whether tree diversity actually promotes predator effects under real-world conditions is far from clear (Zhang and Adams 2011). There are comparatively few studies on the relationship between tree diversity and the abundance and diversity of predators that went beyond comparisons of monocultures and two species mixtures. Those that did found either positive (e.g. Sobek et al. 2009),

negative (Schuldt et al. 2011; Zou et al. 2013), or no clear effects on predators (Schuldt et al. 2008; Vehviläinen et al. 2008). In the latter case, tree species composition and species identity were often found to have stronger effects than tree species richness *per se* (Zhang and Adams 2011). The observational character of most of these studies, with varying degrees of environmental variation among study locations, could be one of the reasons for the heterogeneous results.

Here, we make use of a controlled tree diversity experiment with early successional forest that is based on tree species of high economic importance to forestry in Central Europe. We test for the effects of tree species richness and species identity on the abundance, biomass and diversity of a functionally important group of generalist predators, epigeic spiders (Symondson et al. 2002). Epigeic predators have been shown to be able to strongly affect the densities of forest pests, many of which spend part of their life cycle in the forest floor stratum (e.g. Tanhuanpää et al. 1999). Most previous studies analyzing plant diversity effects on predators have focused on predator abundance and species richness. However, the functional impact and thus the pest-control potential of predators may be more strongly determined by their biomass and functional diversity (Saint-Germain et al. 2007; Schmitz 2009; Reiss et al. 2011), and we thus include these two assemblage characteristics for a more comprehensive analysis. The experimental design with up to four tree species planted in mixture well represents large-scale forest diversity in the temperate and boreal parts of Europe (see e.g. Gamfeldt et al. 2013). A mix of broadleaved and coniferous species as well as the inclusion of a non-native tree species that has become the economically most important exotic tree species in Europe (Douglas fir; Schmid et al. 2014) reflects two important trends in forest management practices that are in need of further exploration in the framework of biodiversity and ecosystem function research. Considering that plant species richness may increase the diversity of resources and prey (Root 1973; Haddad et al. 2009) and that non-native tree species might provide generalist



predators with less diverse prey (Goßner and Ammer 2006), we hypothesize that (i) tree species richness promotes the abundance, biomass, species richness and functional diversity of spiders, and thus the pest-control potential of forest stands, and that (ii) tree species identity plays an important additional role in structuring spider assemblages in that (locally) non-native conifers may decrease spider diversity and abundance (in particular of typical forest species).

## Methods

### Study site and experimental design

The study was conducted on the 'Kaltenborn' site of the BIOTREE tree diversity experiment (Scherer-Lorenzen et al. 2007) in southwest Thuringia, Germany (50°47' N, 10°13' E). The study site is located on acidic bedrock at a height of 320-350 m a.s.l. It is characterized by a subatlantic climate, with a mean annual temperature of 7.8°C and a mean annual precipitation of 650 mm (Scherer-Lorenzen et al. 2007).

Details on the experiment, designed to study the relationships between tree species richness and ecosystem functions, are provided by Scherer-Lorenzen et al. (2007). In short, the experimental setup at the 'Kaltenborn' site consists of 16 study plots of 0.58 ha (120 m x 48 m), established in 2003/2004 and thus representing early successional forest, which cover a total area of 20 ha under homogeneous site conditions directly adjacent to a pine-beech forest. The 16 study plots comprised of the monocultures (4 plots), all possible two (six plots) and three species mixtures (four plots), and the four species mixture (2 plots) of four tree species: the broadleaved, deciduous European beech (*Fagus sylvatica* L.) and sessile oak (*Quercus petraea* Liebl.), and the coniferous Norway spruce (*Picea abies* (L.) H. Karst.) and Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco). While the latter is an exotic species, all four tree species are commonly found in the surrounding forests and economically highly important for local forestry. Diversity treatments were randomly allocated across the 16 plots of the study site. Within each plot, tree species were planted in monospecific

patches of 8 m x 8 m (the size of these patches being based on the canopy properties of full-grown tree individuals), with the aim of retaining one tree individual per species-specific patch in the long term while avoiding outcompetition of slow-growing species at the early stage of the experiment. Tree individuals were planted in rows of 2 m distance, with the distance within rows following common planting practice (2 m for the two conifers, 1 m for the two deciduous species). Each plot was divided into three subplots that will receive different treatments in the future (unmanaged, managed, managed with addition of further tree species; see Scherer-Lorenzen et al. 2007). For details on plot conditions, see Table S13.1 (Appendix A in Supplementary Material).

### Spider data and plot characteristics

Spiders were captured with pitfall traps, which were exposed over the main growing season in 2012 (17 April – 02 October) and emptied every three weeks. Five traps (0.5 L plastic cups with an upper diameter of 9.5 cm) were installed in each of the 16 study plots and filled with 0.15 L of a preserving solution (40% ethanol, 30% water, 20% glycerol, 10% acetic acid, and a few drops of detergent to reduce surface tension). The traps were arranged in a 16 m x 16 m square in the center of the unmanaged subplots, with one trap in each of the four corners and the fifth trap in the center of the square. The square's corners were arranged such that each trap was located at the intersection of four neighboring monospecific planting patches (with all four patches of the same species in monocultures and up to four different species in the most diverse mixtures). This ensured that each trap was positioned at a location that represented a mix of the environmental conditions associated with each of the tree species planted in a given plot.

Spiders were sorted and adults were determined to species. Data for each of the 80 traps were pooled over the whole sampling period. For the analysis of biomass data and the functional diversity of the spider assemblages, we retrieved data on traits related to the resource use of the spider species from the literature (Platen and von Broen 2005;

Nentwig et al. 2014). Specifically, these were mean body length (average of male and female lengths), from which we estimated biomass using the taxon-specific body length-biomass equations of Hódar (1996), hunting type (web-building or cursorial; based on family level data), vegetation stratum used (mean of 1 = ground level, 2 = herb layer, 3 = shrub and tree layer), and two phenological variables (the length in months of the activity period of adults, and the month (coded as, e.g., 3 for March, 6 for June) marking the middle of the activity period to distinguish among early, mid or late season activity peaks). These traits are considered to have a major effect on the foraging characteristics of spiders and may thus be particularly important to determining their functional effect (Cardoso et al. 2011; Schuldt et al. 2014). Furthermore, we distinguished between spider species particularly associated and those not associated with forest habitats (based on Platen and von Broen 2005; Nentwig et al. 2014).

For additional information on the plots we recorded a number of plot characteristics that may help to interpret treatment effects on spiders. These characteristics included mean tree height (m) in each plot, herb layer height (cm), total herb layer cover (%), grass cover (%), moss cover (%), litter cover (%) and litter depth (cm). Mean tree height per plot was calculated from the average height of individuals of each tree species growing in a given plot (four randomly selected individuals of each species were measured per plot). Herb layer and litter layer characteristics were assessed in a 1 m<sup>2</sup> quadrat around each pitfall trap. Herb layer height and litter depth were measured with a yardstick, vegetation and litter cover were visually estimated to the closest 5%. Measurements were conducted in July 2012 at the peak of the main growing season. We did not account for herb layer plant diversity, as it was shown in previous studies that epigeic spiders in forests are often most strongly affected by tree layer-mediated characteristics of the forest stands, which strongly determine overall plant biomass, litter structure, microclimate and prey availability (e.g. Scheu 2005; Schuldt et al. 2011).

### Statistical analysis

Spider species richness in the pitfall traps was strongly correlated with spider abundance (Pearson's  $r = 0.77$ ;  $P < 0.001$ ), and we used rarefaction to calculate the abundance-independent, rarefied species richness of spiders (based on the trap with the smallest number ( $N = 28$ ) of adult individuals; using the *vegan* package in R; Oksanen et al. 2013). The functional diversity of the spider assemblages was calculated as the abundance-weighted Rao's  $Q$ , based on spider biomass, hunting type, mean vegetation stratum, and the two phenology variables (length and mean month of the activity period). Rao's  $Q$  is calculated as the variance in pairwise dissimilarities among all individuals in an assemblage, and it is one of the most widely used indices quantifying functional diversity (Schleuter et al. 2010). Calculation of Rao's  $Q$  was conducted with the R-package *FD* (Laliberté and Legendre 2010). Since in many cases spiders recorded with very few individuals might represent accidental occurrences of vagrant species that are not biologically associated to the plots they were captured in, we focused our analysis of functional diversity patterns on species that were recorded with more than three individuals in the total catch (see also Bihn et al. 2010; Schuldt et al. 2014). On average, the species excluded made up 0.9% ( $\pm 0.4$  SD) of the total number of adult spiders per plot. Moreover, additional analyses with the full spider dataset showed that our results are robust and not influenced by the exclusion of potential vagrants (Table S13.5 in Appendix A).

For the analyses, pitfall trap data were averaged as trap means per plot. We used spider abundance, biomass, rarefied richness and Rao's  $Q$  as response variables, with the first three variables log-transformed to improve modeling assumptions. Patterns of forest species were highly correlated with those of the overall spider catch, and we thus only tested for patterns in the overall spider catch (see Results). The species richness of experimental communities is not independent of the communities' species composition: if the presence or absence of all species is known, species richness will automatically

**Table 13.1.** Linear model results for the relationships between tree species richness and spider abundance, biomass and diversity across the 16 experimental study plots of the BIOTREE tree diversity experiment

	Abundance			Biomass			Rarefied richness			Rao's Q		
	Std. Est. ( $\pm$ SE)	<i>t</i>	<i>P</i>	Std. Est. ( $\pm$ SE)	<i>t</i>	<i>P</i>	Std. Est. ( $\pm$ SE)	<i>t</i>	<i>P</i>	Std. Est. ( $\pm$ SE)	<i>t</i>	<i>P</i>
Richness effect												
Tree species richness	0.05 ( $\pm$ 0.12)	0.3	0.706	-0.07 ( $\pm$ 0.13)	-0.6	0.584	-0.01 ( $\pm$ 0.02)	-0.6	0.576	-0.24 ( $\pm$ 0.15)	-1.6	0.133
<i>F</i> -value	0.15			0.31			0.33			2.54		
DF (n,d)	1,14			1,14			1,14			1,14		
<i>P</i>	0.706			0.584			0.576			0.133		
R <sup>2</sup>	0.01			0.02			0.02			0.15		

<sup>a</sup>DF (n,d): nominator and denominator degrees of freedom

been known (Schmid et al. 2002; Bell et al. 2009). Statistical approaches need to account for this inevitable interdependence, as simultaneous inclusion of linear species richness and species identity predictors would lead to overdetermination of statistical models (Bell et al. 2009). We thus used a sequential linear regression modeling approach after Bell et al. (2009; see also Hantsch et al. 2013), where we first tested for the effects of tree species richness as the main predictor and then used the residuals of this regression to test whether the effects of tree species identity (coded as binary variables for the presence and absence of each species) explained any of the remaining variation in the spider data. This approach enables a straightforward separation of species diversity and identity effects (Bell et al. 2009). The additional plot characteristics that we had assessed can be expected to largely reflect tree species identity effects that are already accounted for by the inclusion of the identity terms in the models. However, to test whether additional effects of these plot characteristics that were not due to tree species composition might affect spiders, we analyzed in a third step the effects of these plot characteristics on the residuals of the regression on tree species identity. As these plot characteristics were in part correlated and we were primarily interested in the main effects of a combined set of variables, we subjected the standardized plot characteristics to a principal components analysis (PCA) for dimension reduction. The first three principal

components (PC1-3) explained 88% of the variability in the plot characteristics data (Table S13.2 in Appendix A) and were subsequently used in the regression analyses. We also directly tested for correlations between plot characteristics and the presence or absence of the four individual tree species to assess the extent to which identity effects might be due to any of these characteristics.

Moreover, in an alternative approach we assessed the effects of tree species richness, the proportion of each tree species in each of the plots (instead of species identity, which, as detailed above, would have hindered such an analysis), the interactions between species richness and the proportion of each tree species per plot, and the three PCs representing the general plot characteristics, as predictors of the spider data with mixed-effects models (i.e. trap-level spider data with plot included as a random effect). Starting from full models with all predictors, we used a stepwise selection procedure based on the AICc (Burnham and Anderson 2004) to obtain the most parsimonious models with the fewest number of predictors and the lowest global AICc. Finally, as our main analytical approach using sequential regression models does not allow for direct inclusion of interactions between tree species richness and tree species identity, we analyzed additional regression models containing only the interaction term between species richness and species identity for each tree species. Modeling assumptions of

**Table 13.2.** Linear model results for the relationships between tree species identity and spider abundance, biomass and diversity across the 16 experimental study plots of the BIOTREE tree diversity experiment. Significant relationships are indicated in bold font

Identity effect	Abundance			Biomass			Rarefied richness			Rao's Q		
	Std. Est. (± SE)	<i>t</i>	<i>P</i>	Std. Est. (± SE)	<i>t</i>	<i>P</i>	Std. Est. (± SE)	<i>t</i>	<i>P</i>	Std. Est. (± SE)	<i>t</i>	<i>P</i>
Beech	0.13 (± 0.09)	1.4	0.186	0.12 (± 0.08)	1.4	0.177	-0.03 (± 0.02)	-1.5	0.170	-0.27 (± 0.14)	-1.9	0.083
Oak	0.14 (± 0.09)	1.5	0.159	0.22 (± 0.08)	2.7	<b>0.019</b>	-0.01 (± 0.02)	-0.4	0.729	0.05 (± 0.14)	0.4	0.714
Fir	-0.28 (± 0.09)	-3.0	<b>0.011</b>	-0.30 (± 0.08)	-3.7	<b>0.003</b>	0.02 (± 0.02)	1.1	0.277	0.17 (± 0.14)	1.3	0.229
Spruce	0.01 (± 0.09)	0.1	0.915	-0.03 (± 0.08)	-0.4	0.670	0.01 (± 0.02)	0.7	0.511	0.04 (± 0.14)	0.3	0.799
<i>F</i> -value	3.43			6.07			1.03			1.39		
DF (n,d)	4,11			4,11			4,11			4,11		
<i>P</i>	0.047			0.008			0.434			0.299		
R <sup>2</sup> adj.	0.39			0.57			0.01			0.09		

<sup>a</sup>DF (n,d): nominator and denominator degrees of freedom

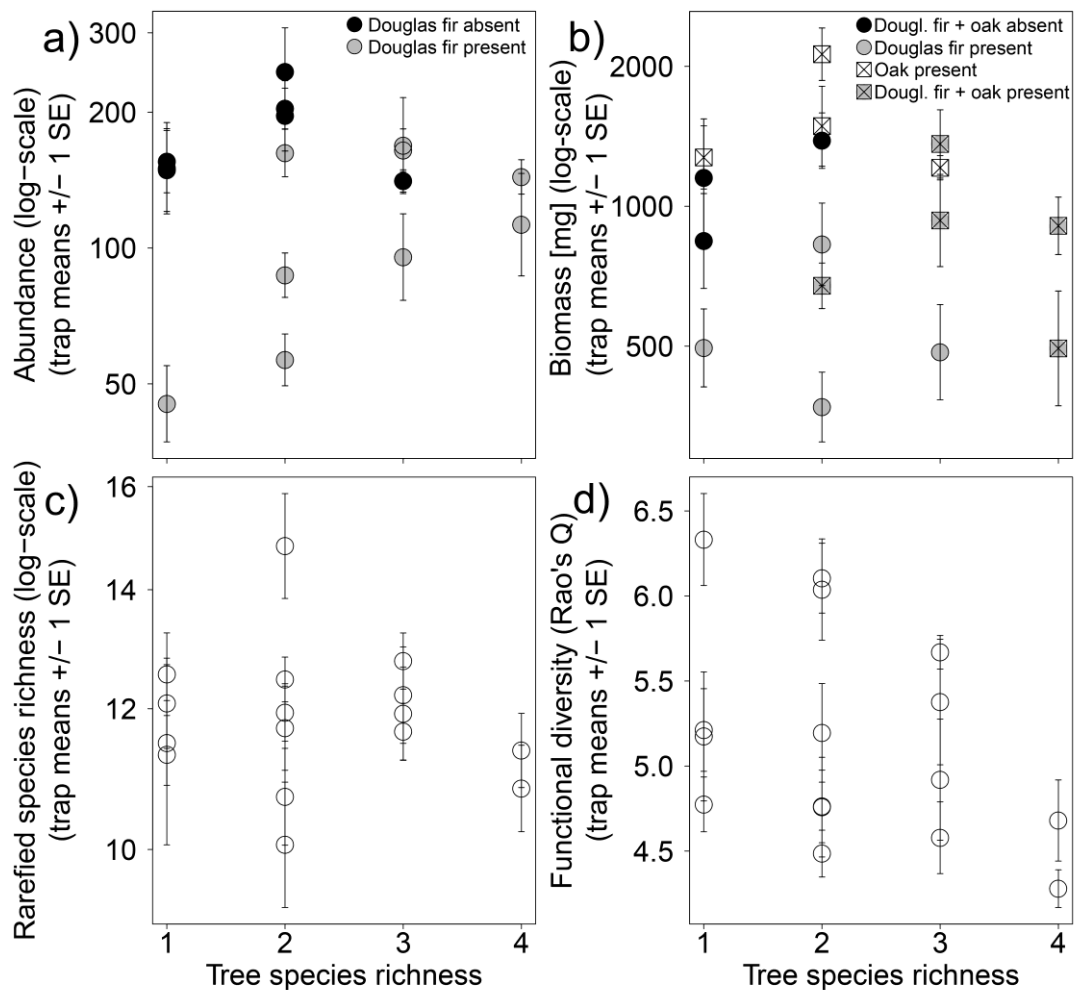
normality and homoscedasticity were checked for all models.

The similarity in spider assemblages between the 16 study plots was analyzed with non-metric multidimensional scaling (NMDS; package *vegan* in R; Oksanen et al. 2013) based on the Morisita-Horn index of square root-transformed abundance data (Jost et al. 2011). The minimal number of required dimensions was determined based on the reduction in stress for solutions with one to six dimensions, with two dimensions being indicated as the most suitable solution in our case. A stable solution was computed from multiple random starting configurations. To evaluate the potential impact of the treatment factors on spider assemblage structure, tree species richness and tree species identity were fitted to the ordination plot on the basis of a regression analysis with the NMDS axes scores (Quinn and Keough 2002). Significance of the correlations was assessed with permutation tests ( $N = 1000$ ). As in the calculation of Rao's Q, the NMDS analysis was based on all spider species with > 3 individuals in the total catch (see Table S13.5 in Appendix A for an analysis of the full dataset including all spider species, which shows that results are robust to the exclusion

of potentially vagrant species). To verify the significance of the effects indicated by the correlative NMDS approach, we used permutational multivariate analysis of variance (as a method that is less sensitive to dispersion effects than alternative methods such as ANOSIM; Oksanen et al. 2013), based on the Morisita-Horn index of square root-transformed spider abundances (function *adonis* in the R-package *vegan*). In this analysis, we included all predictors that were found to be significantly associated with the NMDS axes scores. All analyses were conducted in R 3.0.2 (<http://www.R-project.org>).

## Results

In total, we captured 12,116 spiders, 10,097 of which were adults. The adult spiders belonged to 122 species, with most species belonging to the families Linyphiidae (55 species) and Theridiidae (17 species). Lycosidae (6180 individuals) and Linyphiidae (2929 individuals) accounted for the bulk of individuals, with the three lycosids *Pardosa pullata* (Clerck) (2206 individuals), *Trochosa terricola* Thorell (1843), *Piratula latitans* (Blackwall) (788), and the linyphiid *Cnephalocotes obscurus* (Blackwall) (737) being the most abundant species. Sixty-eight



**Figure 13.1.** Relationships between tree species richness and the abundance (a), biomass (b), rarefied species richness (c) and functional diversity (d) of spiders across the 16 experimental study plots.

species with 5013 individuals were typical forest species, whereas the remaining taxa exhibited more ubiquitous habitat associations. The biomass (Pearson's  $r = 0.99$ ;  $P < 0.001$ ), abundance ( $r = 0.82$ ;  $P < 0.001$ ), and rarefied species richness ( $r = 0.99$ ;  $P < 0.001$ ) distributions across the study plots were highly correlated between the overall catch and forest spiders, and we only report results for overall spider patterns in the following.

Tree species richness had no significant effect on spider abundance, biomass, or rarefied species richness (Table 13.1). There was a non-significant ( $P = 0.133$ ) tendency of decreasing functional diversity of spiders with increasing tree species richness (Table 13.1; Fig. 13.1d). At the same time, the presence of beech in the study plots likewise

tended to decrease spider functional diversity (Table 13.2). Tree species composition also strongly determined spider abundance and biomass patterns. The presence of Douglas fir in the study plots significantly decreased both spider abundance and biomass (Table 13.2; Fig. 13.1a-b). For biomass patterns, this effect was counteracted to some extent by a positive impact of the presence of oak in the plots (Table 13.2, Fig. 13.1b), but standardized effects of Douglas fir on spider abundance and biomass were always stronger than those of any of the other tree species (Table 13.2). The presence of Douglas fir, and for biomass patterns also of oak, explained 39% and 57%, respectively, of the variation among plots in spider abundance and biomass. Separate regression analyses testing for interaction

**Table 13.3.** Results of permutational multivariate analysis of variance (based on Morisita-Horn distances of square root-transformed abundance data) testing the effects of predictors that were significantly associated with the NMDS axes scores (see Fig. 13.2). P-values based on 999 permutations

	DF	SS	MS	F	R <sup>2</sup>	P
Tree species richness	1	0.09	0.09	1.9	0.09	0.051
Beech	1	0.11	0.11	2.2	0.11	0.033
Douglas fir	1	0.15	0.15	3.2	0.15	0.008
PC1	1	0.13	0.13	2.6	0.13	0.008
Residuals	11	0.54	0.05	0.5		

<sup>a</sup>DF = degrees of freedom; SS = sums of squares; MS = mean squares

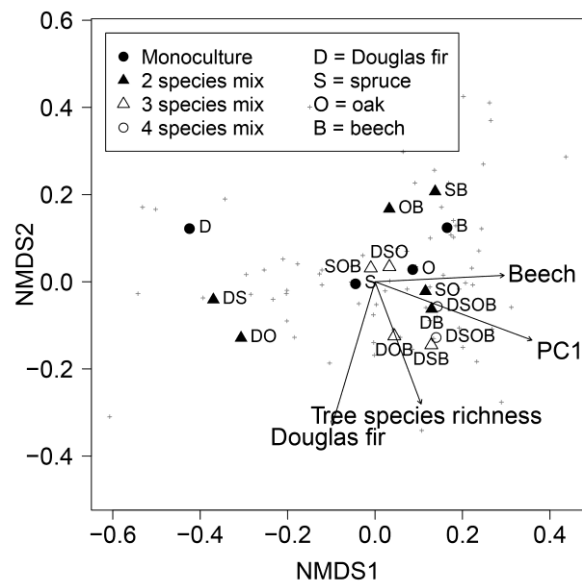
<sup>b</sup>PC1 = Principal component 1 of a PCA on environmental plot characteristics (see Methods)

effects of tree species richness and species identity for each tree species indicated that the significant effects of Douglas fir and oak on spider abundance and diversity were not dependent on tree species richness ( $P > 0.2$  for all interaction effects). Only the rarefied species richness of spiders showed very weak relationships with tree species composition (Table 13.2). After the effects of tree species richness and tree species identity were accounted for, the general plot characteristics (tree height, herb layer and litter characteristics) did not have any significant additional effects on spiders (Table S13.3 in Appendix A). The alternative mixed model approach confirmed the general lack of effect of tree species richness and richness-species identity interactions, and supported the strong effects of Douglas fir on spider abundance and biomass (Table S13.4 in Appendix A). At the same time, it indicated an effect of plot characteristics related to tree height and moss and grass cover (PC1; Table S13.2) on spider abundance and biomass that was independent of, but much weaker (based on the standardized effects), than the effects of Douglas fir (Table S13.3).

In contrast to the univariate measures of abundance, biomass, species richness and functional diversity, the multivariate analyses of spider assemblage patterns indicated an effect of tree species richness on spider assemblage composition (Tables 3 and S5, Fig. 13.2). Tree species identity likewise affected

spider assemblage structure (Tables 3 and S5). Particularly, the presence of Douglas fir and beech strongly determined differences in spider assemblage composition among the study plots (Table 13.3, Fig. 13.2). Plot characteristics represented by PC1 had additional effects on spider assemblage composition.

Regarding the effects of tree species identity on general environmental plot characteristics, plots containing Douglas fir had a larger mean height of tree individuals (Table 13.4). In contrast, the presence of beech was significantly negatively related to mean tree height of the plots, and plots containing beech had a higher grass cover than those without beech. The presence of oak and spruce was negatively related to moss and the overall herb layer cover, respectively (Table 13.4). Litter cover and litter depth showed no significant relationship with the presence of any of the four tree species.



**Figure 13.2.** NMDS ordination plot (based on Morisita-Horn index of square root-transformed relative abundance data) of the assemblages of epigeic spider species in the 16 experimental study plots. Stress = 0.082. Environmental variables were standardized and fitted in a post-hoc correlation procedure with the axes scores. PC1 = Principal component 1 of a PCA on environmental plot characteristics (see Methods). See Table S13.5 for significance of correlations. Crosses represent spider species.

## Discussion

For a set of economically important tree species, our study shows that increasing tree species richness does not necessarily promote characteristics of natural enemy assemblages relevant for pest control in forests. Rather, the abundance and biomass of our focal generalist predator taxon, spiders, were strongly affected by tree species identity. Particularly the non-native Douglas fir had a strong negative effect on spiders. The fact that this severe impact persisted even in diversified tree species mixtures calls for a more thorough examination of the ecological consequences of the increasing use of this species in forestry across Europe.

### Tree species richness and predator assemblages

The lack of an effect of tree species richness on the abundance, biomass and diversity of spiders contrasts with ecological theory and findings from grassland ecosystems that predict an impact of plant species richness also on higher trophic levels (e.g. Haddad et al. 2009; Scherber et al. 2010). Although this impact might be lower for secondary than for primary consumers (Scherber et al. 2010), predators may benefit from a higher structural and resource diversity (particularly prey diversity) brought about by plant species richness. And while our experimental design only considers a moderate increase in tree species richness, effects may be expected to be particularly pronounced across such gradients from monospecific to moderately diverse plant communities (Schmid et al. 2009). For the provisioning of several ecosystem services, this has previously been shown for forests of similar tree species richness as our study plots (Morin et al. 2011; Gamfeldt et al. 2013). That we did not find a similar pattern for predators may have several, mutually non-exclusive reasons.

For one, our study system represents an early stage of the forest cycle. While enhancing top-down control by predators may be particularly beneficial for young trees that are often highly vulnerable to herbivore damage, recent studies have shown that diversity effects can become much stronger

over time (discussed in Cardinale et al. 2012). Since crown closure in the study plots is not yet complete, differences in prey assemblages and structural aspects among plots that are important for spiders may not be as pronounced as in older forest stands that are characterized by more distinct stand characteristics. However, even for older forests several studies have similarly reported a lack of a consistent effect of tree species richness on the abundance and diversity of predatory arthropods (e.g. Schuldt et al. 2008; Vehviläinen et al. 2008). Moreover, our results were not affected by a potential impact of non-forest spider species, as the overall patterns of spider diversity, abundance and biomass were highly correlated with the patterns of typical forest species.

Another possibility is that interaction effects across trophic levels could be less pronounced in our moderately diverse temperate study system, as biotic interactions are often assumed to be stronger at the highly diverse lower latitudes (Schemske et al. 2009). Yet, such latitudinal differences can be scale-dependent (Schuldt et al. 2013) and even in highly diverse forests predator abundance and diversity are not necessarily promoted by plant diversity (Schuldt et al. 2011; Zou et al. 2013; but see Basset et al. 2012). Of course, like most of the previous studies that investigated tree diversity effects on predators, our study can only provide insights into patterns of a rather generalistic predator taxon.

**Table 13.4.** Correlations (Pearson's  $r$ ) between tree species richness, tree species identity and environmental characteristics of the 16 experimental study plots. Significant relationships are indicated in bold font

Plot characteristics	Tree species				
	richness	Beech	Oak	Spruce	Fir
Mean tree height	-0.03	<b>-0.56*</b>	-0.28	0.25	<b>0.54*</b>
Herb layer height	0.36	0.25	0.36	-0.30	0.39
% herb layer cover	-0.34	-0.33	0.11	<b>-0.67**</b>	0.23
% moss cover	-0.30	-0.46	<b>-0.52*</b>	0.37	0.03
% grass cover	0.45	<b>0.61*</b>	0.43	-0.01	-0.16
Litter depth	0.16	0.24	-0.25	0.26	0.06
% litter cover	-0.14	-0.19	-0.45	0.18	0.18

\* $P < 0.05$ ; \*\* $P < 0.01$

However, these generalist predators have been shown to often play a crucial role in pest control (Symondson et al. 2002). Spider assemblage structure was the only aspect that showed a strong relationship with tree species richness in our study, but this effect did not translate into a significant impact on spider functional diversity. Changes in the species composition of the spider assemblages with increasing tree species richness across our study plots thus obviously did not result in a substantial change of the functional impact of these assemblages. Moreover, the effects of tree species richness and the presence of Douglas fir acted in a similar way on spider assemblage structure (see Fig. 13.2). This indicates that a sampling effect of increasing the probability of including a tree species with a particularly strong effect on spiders may to some extent underlie the relationship between spider assemblage structure and tree species richness.

#### Tree species identity effects on predators

In general, tree species identity has been found in the majority of studies in forest ecosystems to more strongly affect predator assemblages than tree species richness (Zhang and Adams 2011), and our study makes no exception to this trend. Zhang and Adams (2011) estimate that many predator species may numerically respond to the presence of a particular tree species and its associated herbivores. In addition, epigeic taxa might be strongly influenced by the effects of individual tree species on litter structure and microclimatic conditions (e.g. Schuldt et al. 2008; Vehviläinen et al. 2008).

In our case, the coniferous and non-native Douglas fir had strong negative effects on spider abundance and biomass—two characteristics that strongly determine predator functional impact (Saint-Germain et al. 2007)—irrespective of tree species richness. In contrast, oak positively affected spider biomass and beech to some extent counteracted the effects of Douglas fir on spider assemblage structure, but neither of the two broadleaved species was able to completely make up for the negative effects of the presence of Douglas fir on spiders (standardized effects were much weaker for

the two broadleaved species than for Douglas fir). This may be critical, as the use of Douglas fir in forestry is strongly increasing across large parts of Europe and the species is expected to become the economically third most important conifer species in many regions (Schmid et al. 2014).

The effects of Douglas fir on the associated arthropod diversity have often been found to be potentially less severe or even comparable to other conifers when the species is planted in low densities and interspersed into mixtures with other tree species (reviewed in Schmid et al. 2014). However, comparisons of Douglas fir stands with stands of other tree species are often difficult due to confounding site characteristics (Schmid et al. 2014). Experimental approaches such as in our study may provide deeper insight into the effects of individual tree species under environmentally homogeneous site conditions. And yet, dense stands of Douglas fir have been shown in previous studies to affect litter characteristics, microclimate and the associated arthropod assemblages (Finch and Szumelda 2007; Schmid et al. 2014). For instance, Goßner and Ammer (2006) found temporally reduced abundances of arthropods in forest stands dominated by Douglas fir, which might negatively affect prey availability for predators. This particularly applies when compared to native broadleaved tree species such as beech and oak (Schmid et al. 2014). In our study, the presence of Douglas fir was strongly correlated with the mean tree height of the study plots, which may have strong effects on environmental conditions important to spiders (Oxbrough et al. 2010). Further studies, however, are needed to identify the ultimate drivers underlying the effects of Douglas fir, and the above cited studies indicate that various factors might interact to cause the observed effects (see also Schmid et al. 2014). Nevertheless, the experimental tree planting design and homogeneous site conditions of our study make a strong case for demonstrating the causality of Douglas fir effects—a scenario that is not necessarily met with observational studies where many factors may potentially confound the results. Moreover, our findings not only apply to overall spider biomass and abundance, but



also to that of more specialized forest species, which were highly correlated with overall spider patterns.

The strong negative effect of Douglas fir on spider biomass and abundance even in diverse mixtures with broadleaved tree species may to some extent be due to the monospecific patch planting design in our study plots, which could promote identity effects by creating locally dense planting conditions of individual species. However, similar planting approaches are increasingly being explored in forest management and recommended for enhancing biodiversity (e.g. Oxbrough et al. 2012; Saha et al. 2012). The fact that the negative effects persisted even in plots where Douglas fir patches made up a low proportion of the overall tree cover underscores the strength of this effect (see also Oxbrough et al. 2012). Considering the increasing use of Douglas fir in forestry, this may have far-reaching consequences, also in terms of biodiversity conservation, for plantation forests.

For forest management and pest regulation, the results of our study indicate (and, of course, call for additional studies on herbivore performance) that although Douglas fir so far has not been subject to severe pest outbreaks in its non-native European range (Schmid et al. 2014), stand-level predator efficiency can be reduced for tree species growing adjacent to or in mixture with this species. Moreover, climate change might increase the risk of more severe herbivore damage due to host switches or the establishment of previously absent herbivores also for Douglas fir (Schmid et al. 2014). A low pest control potential would then be directly detrimental also to this species and the forest areas where it is present.

### Conclusions

Enhancing the multi-functionality of plantation forests is a goal of modern and sustainable forest management that tries to balance a multitude of economic, ecological and societal demands (Rametsteiner and Mayer 2004; Cabbage et al. 2007). Increasing the tree species richness of forests has been shown to be particularly promising in this respect (Morin et al. 2011; Gamfeldt et al.

2013). However, the lack of a tree species richness effect on predator diversity and abundance in our study indicates that tree species richness does not necessarily promote all functions and services that may be crucial in a multi-functional context. The diversity and abundance of natural enemies can contribute significantly to a sustainable forest management, in particular if climate change increases the probability of pest outbreaks (Lindner et al. 2010; Netherer and Schopf 2010) and at the same time decreases the habitat quality for economically important tree species (Hanewinkel et al. 2013). While tree species richness may act as a general insurance against many species-specific environmental risks, our study supports the view that tree species composition and identity will often be of crucial importance in determining forest ecosystem functions and services. In our case, the severe impact of the non-native but economically important Douglas fir, with negative effects on spider biomass and abundance irrespective of the planted tree species richness, calls for a more detailed investigation into the role of this species in impacting important ecosystem functions and the overall multi-functionality of forest ecosystems. Based on our results, a management recommendation that agrees with the precautionary measures recommended in previous studies (e.g. Goßner and Ammer 2006; Finch and Szumelda 2007) is to reduce monocultures and high-density planting of Douglas fir in mixtures in order to avoid detrimental effects on predator top-down control and possibly also on the future biodiversity conservation potential of plantation forests.

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## References

- Basset Y et al. (2012) Arthropod diversity in a tropical forest. *Science* 338:1481-1484
- Bell T, Lilley AK, Hector A, Schmid B, King L, Newman JA (2009) A linear model method for biodiversity-ecosystem functioning experiments. *American Naturalist* 174:836-849
- Bihn JH, Gebauer G, Brandl R (2010) Loss of functional diversity of ant assemblages in secondary tropical forests. *Ecology* 91:782-792
- Bonan GB (2008) Forests and climate change: forcings, feedbacks, and the climate benefits of forests. *Science* 320:1444-1449
- Burnham KP, Anderson DR (2004) Model selection and multimodel inference : a practical information-theoretic approach. Springer, New York
- Cardinale BJ et al. (2012) Biodiversity loss and its impact on humanity. *Nature* 486:59-67
- Cardoso P, Pekar S, Jocque R, Coddington JA (2011) Global patterns of guild composition and functional diversity of spiders. *Plos ONE* 6:e21710
- Castagneyrol B, Jactel H, Vacher C, Brockerhoff EG (2014) Effects of plant phylogenetic diversity on herbivory depend on herbivore specialization. *Journal of Applied Ecology* 51:134-141
- Cubbage F, Harou P, Sills E (2007) Policy instruments to enhance multi-functional forest management. *Forest Policy and Economics* 9:833-851
- Dale VH et al. (2001) Climate change and forest disturbances. *Bioscience* 51:723-734
- Finch OD, Szumelda A (2007) Introduction of Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) into Western Europe: Epigaic arthropods in intermediate-aged pure stands in northwestern Germany. *Forest Ecology and Management* 242:260-272
- Gamfeldt L et al. (2013) Higher levels of multiple ecosystem services are found in forests with more tree species. *Nature Communications* 4:1340
- Gómez-Baggethun E, de Groot R, Lomas PL, 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
- Goßner M, Ammer U (2006) The effects of Douglas-fir on tree-specific arthropod communities in mixed species stands with European beech and Norway spruce. *European Journal of Forest Research* 125:221-235
- Haddad NM, Crutsinger GM, Gross K, Haarstad J, Knops JMH, Tilman D (2009) Plant species loss decreases arthropod diversity and shifts trophic structure. *Ecology Letters* 12:1029-1039
- Hanewinkel M, Cullmann DA, Schelhaas M-J, Nabuurs G-J, Zimmermann NE (2013) Climate change may cause severe loss in the economic value of European forest land. *Nature Climate Change* 3:203-207
- Hantsch L, Braun U, Scherer-Lorenzen M, Bruehlheide H (2013) Species richness and species identity effects on occurrence of foliar fungal pathogens in a tree diversity experiment. *Ecosphere* 4:art81
- Hódar JA (1996) The use of regression equations for estimation of arthropod biomass in ecological studies. *Acta Oecologica* 17:421-433
- Jactel H, Brockerhoff EG (2007) Tree diversity reduces herbivory by forest insects. *Ecology Letters* 10:835-848
- Jost L, Chao A, Chazdon RL (2011) Compositional similarity and  $\beta$  (beta) diversity. In: Magurran AE, McGill BJ (eds) *Biological diversity: frontiers in measurement and assessment*. Oxford Univ. Press, New York, pp 66-84
- Knoke T, Ammer C, Stimm B, Mosandl R (2008) Admixing broadleaved to coniferous tree species: a review on yield, ecological stability and economics. *European Journal of Forest Research* 127:89-101
- Kremen C et al. (2000) Economic incentives for rain forest conservation across scales. *Science* 288:1828-1832
- Laliberté E, Legendre P (2010) A distance-based framework for measuring functional diversity from multiple traits. *Ecology* 91:299-305
- Lindner M et al. (2010) Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. *Forest Ecology and Management* 259:698-709
- Losey JE, Vaughan M (2006) The economic value of ecological services provided by insects. *Bioscience* 56:311-323
- Morin X, Fahse L, Scherer-Lorenzen M, Bugmann H (2011) Tree species richness promotes productivity in temperate forests through strong complementarity between species. *Ecology Letters* 14:1211-1219
- Nadrowski K, Wirth C, Scherer-Lorenzen M (2010) Is forest diversity driving ecosystem functioning and service? *Current Opinion in Environmental Sustainability* 2:75-79

- Nentwig W, Blick T, Gloor D, Hänggi A, Kropf C (2014) Spiders of Europe. Version 02.2014. Available at [www.araneae.unibe.ch](http://www.araneae.unibe.ch). Accessed 10 February 2014.
- Netherer S, Schopf A (2010) Potential effects of climate change on insect herbivores in European forests—General aspects and the pine processionary moth as specific example. *Forest Ecology and Management* 259:831-838
- Oksanen E et al. (2013) vegan: Community Ecology Package. R package version 2.0-9. Available from <http://cran.r-project.org>.
- Oxbrough A, French V, Irwin S, Kelly TC, Smiddy P, O'Halloran J (2012) Can mixed species stands enhance arthropod diversity in plantation forests? *Forest Ecology and Management* 270:11-18
- Oxbrough A, Irwin S, Kelly TC, O'Halloran J (2010) Ground-dwelling invertebrates in reforested conifer plantations. *Forest Ecology and Management* 259:2111-2121
- Platen R, von Broen B (2005) Gesamtartenliste und Rote Liste der Webspinnen und Weberknechte (Arachnida: Araneae, Opiliones) des Landes Berlin. In: Der Landesbeauftragte für Naturschutz und Landschaftspflege (ed) Rote Listen der gefährdeten Pflanzen und Tiere von Berlin. Available at [http://www.stadtentwicklung.berlin.de/natur\\_gruen/naturschutz/downloads/artenschutz/ro\\_telisten/28\\_spinnen\\_print.pdf](http://www.stadtentwicklung.berlin.de/natur_gruen/naturschutz/downloads/artenschutz/ro_telisten/28_spinnen_print.pdf). Accessed 10 February 2014
- Quinn GP, Keough MJ (2002) Experimental design and data analysis for biologists. University Press, Cambridge
- Rametsteiner E, Mayer P (2004) Sustainable forest management and Pan-European forest policy. *Ecological Bulletins* 51:51-57
- Reiss J, Bailey RA, Perkins DM, Pluchinotta A, Woodward G (2011) Testing effects of consumer richness, evenness and body size on ecosystem functioning. *Journal of Animal Ecology* 80:1145-1154
- Root RB (1973) Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). *Ecological Monographs* 43:95-124
- Ruckelshaus M et al. (2014) Notes from the field: Lessons learned from using ecosystem service approaches to inform real-world decisions. *Ecological Economics* doi: 10.1016/j.ecolecon.2013.07.009
- Saha S et al. (2012) Growth and quality of young oaks (*Quercus robur* and *Quercus petraea*) grown in cluster plantings in central Europe: A weighted meta-analysis. *Forest Ecology and Management* 283:106-118
- Saint-Germain M et al. (2007) Should biomass be considered more frequently as a currency in terrestrial arthropod community analyses? *Journal of Applied Ecology* 44:330-339
- Schemske DW, Mittelbach GG, Cornell HV, Sobel JM, Roy K (2009) Is there a latitudinal gradient in the importance of biotic interactions? *Annual Review of Ecology Evolution and Systematics* 40:245-269
- Scherber C et al. (2010) Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. *Nature* 468:553-556
- Scherer-Lorenzen M (2014) The functional role of biodiversity in the context of global change. In: Burslem D, Coomes D, Simonson W (eds) *Forests and global change*. Cambridge University Press, Cambridge, pp 195-238
- Scherer-Lorenzen M, Schulze ED, Don A, Schumacher J, Weller E (2007) Exploring the functional significance of forest diversity: A new long-term experiment with temperate tree species (BIOTREE). *Perspectives in Plant Ecology Evolution and Systematics* 9:53-70
- Scheu S (2005) Linkages between tree diversity, soil fauna and ecosystem processes. In: Scherer-Lorenzen M, Körner C, Schulze ED (eds) *Forest diversity and function: Temperate and boreal systems*. Springer, Berlin, Heidelberg, pp 211-233
- Schleuter D, Daufresne M, Massol F, Argillier C (2010) A user's guide to functional diversity indices. *Ecological Monographs* 80:469-484
- Schmid B et al. (2009) Consequences of species loss for ecosystem functioning: meta-analyses of data from biodiversity experiments. In: Naeem S, Bunker DE, Hector A, Loreau M, Perrings C (eds) *Biodiversity, ecosystem functioning, and human wellbeing. An ecological and economic perspective*. Oxford Univ. Press, Oxford, pp 14-29
- Schmid B et al. (2002) The design and analysis of biodiversity experiments. In: Loreau M, Naeem S, Inchausti P (eds) *Biodiversity and ecosystem functioning. Synthesis and perspectives*. Oxford University Press, Oxford, pp 61-75
- Schmid M, Pautasso M, Holdenrieder O (2014) Ecological consequences of Douglas fir (*Pseudotsuga menziesii*) cultivation in Europe. *European Journal of Forest Research* 133:13-29
- Schmitz OJ (2009) Effects of predator functional diversity on grassland ecosystem function. *Ecology* 90:2339-2345
- Schuldt A, Assmann T, Schaefer M (2013) Scale-dependent diversity patterns affect spider assemblages of two contrasting forest ecosystems. *Acta Oecologica* 49:17-22

- Schuldt A et al. (2011) Predator diversity and abundance provide little support for the enemies hypothesis in forests of high tree diversity. *PLoS ONE* 6:e22905
- Schuldt A, Bruelheide H, Durka W, Michalski SG, Purschke O, Assmann T (2014) Tree diversity promotes functional dissimilarity and maintains functional richness despite species loss in predator assemblages. *Oecologia* 174:533-543
- Schuldt A, Fahrenholz N, Brauns M, Migge-Kleian S, Platner C, Schaefer M (2008) Communities of ground-living spiders in deciduous forests: Does tree species diversity matter? *Biodiversity and Conservation* 17:1267-1284
- Sobek S, Scherber C, Steffan-Dewenter I, Tscharntke T (2009) Sapling herbivory, invertebrate herbivores and predators across a natural tree diversity gradient in Germany's largest connected deciduous forest. *Oecologia* 160:279-288
- Symondson WOC, Sunderland KD, Greenstone MH (2002) Can generalist predators be effective biocontrol agents? *Annual Review of Entomology* 47:561-594
- Tanhuanpää M, Ruohomäki K, Kaitaniemi P, Klemola T (1999) Different impact of pupal predation on populations of *Epirrita autumnata* (Lepidoptera; Geometridae) within and outside the outbreak range. *Journal of Animal Ecology* 68:562-570
- Vehviläinen H, Koricheva J, Ruohomäki K (2008) Effects of stand tree species composition and diversity on abundance of predatory arthropods. *Oikos* 117:935-943
- Wolfslehner B, Vacik H, Lexer MJ (2005) Application of the analytic network process in multi-criteria analysis of sustainable forest management. *Forest Ecology and Management* 207:157-170
- Zhang Y, Adams J (2011) Top-down control of herbivores varies with ecosystem types. *Journal of Ecology* 99:370-372
- Zou Y, Sang W, Bai F, Axmacher JC (2013) Relationships between plant diversity and the abundance and  $\alpha$ -diversity of predatory ground beetles (Coleoptera: Carabidae) in a mature Asian temperate forest ecosystem. *PLoS ONE* 8:e82792

## Supplementary Material

## Appendix A

**Table S13.1.** Tree species composition, species richness and mean values ( $\pm$  SD) of important plot characteristics (see Methods for measurement details) of the 16 experimental study plots of the BIOTREE tree diversity experiment

Plot	Tree species	Tree							
		species richness	Tree height [m]	Herb layer height [m]	Herb layer cover [%]	Moss cover [%]	Grass cover [%]	Litter depth [cm]	Litter cover [%]
1	B	2.1 ( $\pm$ 0.3)	16.0 ( $\pm$ 18.2)	8.0 ( $\pm$ 8.4)	76.0 ( $\pm$ 23)	0.46 ( $\pm$ 0.1)	0.0 ( $\pm$ 0.0)	0.0 ( $\pm$ 0.0)	
2	O	2.3 ( $\pm$ 0.6)	32.0 ( $\pm$ 11)	2.0 ( $\pm$ 4.5)	66.0 ( $\pm$ 13.4)	0.62 ( $\pm$ 0.1)	0.1 ( $\pm$ 0.2)	2.0 ( $\pm$ 4.5)	
3	D	4.8 ( $\pm$ 0.3)	26.0 ( $\pm$ 20.7)	58.0 ( $\pm$ 40.9)	16.0 ( $\pm$ 21.9)	0.37 ( $\pm$ 0.78)	0.1 ( $\pm$ 0.2)	10.0 ( $\pm$ 22.4)	
4	S	3.9 ( $\pm$ 0.3)	12.0 ( $\pm$ 8.4)	56.0 ( $\pm$ 19.5)	32.0 ( $\pm$ 21.7)	0.34 ( $\pm$ 0.1)	0.0 ( $\pm$ 0.0)	0.0 ( $\pm$ 0.0)	
5	BO	2.7 ( $\pm$ 0.4)	20.0 ( $\pm$ 25.5)	2.0 ( $\pm$ 4.5)	78.0 ( $\pm$ 26.8)	0.5 ( $\pm$ 0.1)	0.0 ( $\pm$ 0.0)	0.0 ( $\pm$ 0.0)	
6	BD	3.4 ( $\pm$ 0.7)	16.0 ( $\pm$ 30.5)	4.0 ( $\pm$ 8.9)	80.0 ( $\pm$ 39.4)	0.8 ( $\pm$ 0.4)	0.0 ( $\pm$ 0.0)	0.0 ( $\pm$ 0.0)	
7	BS	3.4 ( $\pm$ 1.2)	10.0 ( $\pm$ 10.0)	38.0 ( $\pm$ 26.8)	52.0 ( $\pm$ 26.8)	0.36 ( $\pm$ 0.1)	0.3 ( $\pm$ 0.3)	14 ( $\pm$ 16.7)	
8	OD	4.4 ( $\pm$ 1.3)	42.0 ( $\pm$ 14.8)	8.0 ( $\pm$ 8.4)	46.0 ( $\pm$ 29.7)	0.112 ( $\pm$ 0.5)	0.1 ( $\pm$ 0.2)	8.0 ( $\pm$ 17.9)	
9	OS	3.5 ( $\pm$ 0.8)	0.0 ( $\pm$ 0.0)	20.0 ( $\pm$ 21.2)	80.0 ( $\pm$ 21.2)	0.52 ( $\pm$ 0.1)	0.1 ( $\pm$ 0.2)	4.0 ( $\pm$ 8.9)	
10	DS	5.1 ( $\pm$ 0.9)	18.0 ( $\pm$ 18.9)	60.0 ( $\pm$ 20)	22.0 ( $\pm$ 14.4)	0.42 ( $\pm$ 0.2)	0.002 ( $\pm$ 0.0)	12 ( $\pm$ 26.8)	
11	BOD	3.2 ( $\pm$ 0.8)	15.0 ( $\pm$ 14.1)	18.0 ( $\pm$ 4.5)	67.0 ( $\pm$ 15.7)	0.84 ( $\pm$ 0.1)	0.1 ( $\pm$ 0.2)	2.0 ( $\pm$ 4.5)	
12	BOS	3.2 ( $\pm$ 0.7)	4.0 ( $\pm$ 8.9)	26.0 ( $\pm$ 15.2)	69.0 ( $\pm$ 15.2)	0.72 ( $\pm$ 0.2)	0.1 ( $\pm$ 0.2)	2.0 ( $\pm$ 4.5)	
13	BDS	3.7 ( $\pm$ 1.2)	6.0 ( $\pm$ 2.2)	13.0 ( $\pm$ 9.7)	79.0 ( $\pm$ 13.9)	0.82 ( $\pm$ 0.3)	0.5 ( $\pm$ 0.6)	10 ( $\pm$ 12.2)	
14	ODS	4.2 ( $\pm$ 1.1)	10.0 ( $\pm$ 12.2)	24.0 ( $\pm$ 18.2)	66.0 ( $\pm$ 18.2)	0.38 ( $\pm$ 0.1)	0.0 ( $\pm$ 0.0)	0.0 ( $\pm$ 0.0)	
15	BODS	3.5 ( $\pm$ 1.0)	12.0 ( $\pm$ 16.0)	10.0 ( $\pm$ 14.1)	78.0 ( $\pm$ 28.4)	0.78 ( $\pm$ 0.78)	0.1 ( $\pm$ 0.2)	2.0 ( $\pm$ 4.5)	
16	BODS	4.2 ( $\pm$ 0.7)	19.0 ( $\pm$ 26.1)	11.0 ( $\pm$ 21.9)	70.0 ( $\pm$ 25.5)	0.54 ( $\pm$ 0.1)	0.0 ( $\pm$ 0.0)	0.0 ( $\pm$ 0.0)	

<sup>a</sup>B = beech, O = oak, S = spruce, D = Douglas fir

**Table S13.2.** Component loadings and eigenvalues of principal components (PC) selected from PCA reduction analysis on environmental plot characteristics (most influential variables in bold)

	PC1	PC2	PC3
Mean tree height	<b>-0.47</b>	0.10	-0.13
% herb layer cover	-0.05	0.03	<b>-0.79</b>
% moss cover	<b>-0.53</b>	-0.19	0.17
% grass cover	<b>0.52</b>	0.14	0.25
Herb layer height	0.24	<b>0.50</b>	-0.41
Litter depth	-0.07	<b>0.68</b>	0.32
% litter cover	-0.41	<b>0.47</b>	0.04
Standard deviation	1.76	1.28	1.19
Proportion of variance explained	0.44	0.23	0.20
Cumulative proportion of variance explained	0.44	0.68	0.88

**Table S13.3.** Linear model results for the relationships between environmental plot characteristics and spider abundance, biomass and diversity across the 16 experimental study plots of the BIOTREE tree diversity experiment after accounting for the effects of tree species richness and tree species identity

Plot effects	Abundance			Biomass			Rarefied richness			Rao's Q		
	Std. Est. ( $\pm$ SE)	<i>t</i>	<i>P</i>	Std. Est. ( $\pm$ SE)	<i>t</i>	<i>P</i>	Std. Est. ( $\pm$ SE)	<i>t</i>	<i>P</i>	Std. Est. ( $\pm$ SE)	<i>t</i>	<i>P</i>
PC1	0.10 ( $\pm$ 0.08)	1.2	0.252	0.04 ( $\pm$ 0.07)	0.5	0.617	-0.001 ( $\pm$ 0.02)	-0.1	0.953	-0.18 ( $\pm$ 0.12)	-1.5	0.165
PC2	-0.03 ( $\pm$ 0.08)	-0.4	0.694	-0.04 ( $\pm$ 0.07)	-0.6	0.541	0.007 ( $\pm$ 0.02)	0.3	0.757	0.08 ( $\pm$ 0.12)	0.7	0.508
PC3	0.07 ( $\pm$ 0.08)	0.9	0.386	0.08 ( $\pm$ 0.07)	1.1	0.283	-0.010 ( $\pm$ 0.02)	-0.5	0.642	-0.08 ( $\pm$ 0.12)	-0.6	0.539
<i>F</i> -value	0.81			0.64			0.11			1.02		
DF (n,d)	3, 12			3, 12			3, 12			3, 12		
<i>P</i>	0.514			0.603			0.952			0.419		
R <sup>2</sup> adj.	-0.04			-0.08			-0.21			0.004		

**Table S13.4.** Linear mixed model results for the relationships of spider abundance, biomass and diversity (response variables) and tree species richness, tree species identity and environmental plot characteristics (predictors) across the 16 experimental study plots of the BIOTREE tree diversity experiment

	Abundance				Biomass				Rarefied richness				Rao's Q			
	Std. Est. ( $\pm$ SE)	DF	<i>t</i>	<i>P</i>	Std. Est. ( $\pm$ SE)	DF	<i>t</i>	<i>P</i>	Std. Est. ( $\pm$ SE)	DF	<i>t</i>	<i>P</i>	Std. Est. ( $\pm$ SE)	DF	<i>t</i>	<i>P</i>
Fixed effects <sup>a</sup>																
Beech	-	-	-	-	-	-	-	-	-	-	-	-	-0.30 ( $\pm$ 0.14)	14	2.1	0.051
Fir	-0.35 ( $\pm$ 0.08)	14	4.6	<b>&lt;0.001</b>	-0.39 ( $\pm$ 0.09)	13	4.3	<b>&lt;0.001</b>	-	-	-	-	-	-	-	
Spruce	-	-	-	-	-0.19 ( $\pm$ 0.09)	13	2.1	0.056	-	-	-	-	-	-	-	
PC1	-0.12 ( $\pm$ 0.04)	63	2.6	<b>0.010</b>	-0.11 ( $\pm$ 0.05)	63	2.2	<b>0.032</b>	-	-	-	-	-	-	-	
AICc full model <sup>b</sup>	107.7				126.6				-				173.4			
AICc minimal model	96.5				116.7				-				166.9			
Marginal R <sup>2</sup> <sup>c</sup>	0.40				0.36				-				0.13			
Conditional R <sup>2</sup>	0.59				0.56				-				0.50			

<sup>a</sup>Terms dropped during model simplification are marked “-“. Tree species richness, oak presence, PC2 and PC3, as well as interactions between tree species richness and tree species identity (non-significant and excluded in all cases during model simplification) not shown.

<sup>b</sup>Full model: fitted with the full set of fixed effects; minimal model: simplified model with lowest AIC<sub>c</sub>

<sup>c</sup>Marginal R<sup>2</sup>: explained by fixed factors; Conditional R<sup>2</sup>: explained by fixed and random factors (see Nakagawa S, Schielzeth H (2013) A general and simple method for obtaining R<sup>2</sup> from generalized linear mixed-effects models. *Methods in Ecology and Evolution* 4: 133-142)

**Table S13.5.** Correlation coefficients, explained variation ( $R^2$ ) and probabilities (based on 1000 permutations, significant relationships in bold) for the relationships between tree species richness, tree species identity and the NMDS axes scores, a) for the analysis excluding spider species with < 4 individuals in the total catch, and b) for all spider species

Variable	NMDS1	NMDS2	$R^2$	$P$
<i>a) Without spider species &lt; 4 individuals</i>				
Tree species richness	0.36	-0.93	0.37	<b>0.038</b>
Beech	1.00	0.04	0.38	<b>0.027</b>
Oak	0.42	-0.91	0.09	0.540
Spruce	0.58	-0.81	0.06	0.684
Douglas fir	-0.29	-0.96	0.50	<b>0.009</b>
PC1	0.94	-0.35	0.62	<b>0.006</b>
PC2	0.06	-1.00	0.13	0.421
PC3	0.75	0.66	0.34	0.070
<i>b) All spider species</i>				
Tree species richness	0.35	-0.94	0.38	<b>0.038</b>
Beech	1.00	0.05	0.37	<b>0.034</b>
Oak	0.41	-0.91	0.10	0.539
Spruce	0.56	-0.83	0.06	0.691
Douglas fir	-0.29	-0.96	0.50	<b>0.010</b>
PC1	0.94	-0.35	0.63	<b>0.005</b>
PC2	0.04	-1.00	0.13	0.403
PC3	0.75	0.66	0.34	0.060



# CHAPTER 14

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# General discussion and conclusions

## 14.1 General discussion

Primary and secondary consumers have been shown to strongly influence the functioning of ecosystems (Weisser and Siemann 2004; Schmitz 2006; Schowalter 2012). However, we only have insufficient knowledge of how higher trophic levels and their trophic interaction effects are affected by plant diversity and the potential loss of this diversity. This applies particularly to complex and species-rich ecosystems, such as many forests in subtropical and tropical regions. The 12 research chapters of this thesis address important knowledge gaps and provide insight into the relationships, and the potential mechanisms underlying the relationships, between plant diversity, herbivores and herbivory, and predators—with a primary focus on highly diverse subtropical forest ecosystems. These studies show that results from the less diverse or less complex ecosystems primarily studied so far cannot necessarily be scaled up to these biodiverse forest systems and that an in-depth understanding of biodiversity effects in these ecosystems across trophic levels requires considering the functional trait composition, and potential nonrandom associations among the species of producer and consumer communities. In the following, the main findings of the three thematic sections into which the 12 chapters can be grouped, and which were outlined together with the main hypotheses in Chapter 1, will be discussed. Chapter 14.2 then sums up the general conclusions that can be drawn from this thesis and provides an outlook on further research needs.

**Plant functional and phylogenetic diversity determine plant species-level and community-level herbivore damage as well as herbivore assemblage patterns in species-rich forests**

The chapters of Section I focused on herbivore damage and the structure of herbivore assemblages in relation to plant

diversity—analyzed with different metrics of species, functional, and phylogenetic diversity—in species-rich subtropical forests. Species-specific mean levels of herbivore damage on tree and shrub saplings in these forests can be clearly attributed to a complex of multiple plant traits that are related to palatability and defense mechanisms. Several previous studies have likewise highlighted that multiple-trait complexes are important in determining the susceptibility of plants to herbivory (Agrawal 2007; Loranger et al. 2012; Carmona and Fornoni 2013). However, the results presented here show that biogeographical characteristics of the distribution and climatic niche of plant species—characteristics that reflect the large-scale breadth, diversity, and temporal stability of herbivore-plant associations and that have rarely been considered so far in the analysis of interspecific herbivory patterns at local scales—and the plants' local visibility to herbivores are equally important. Considering that herbivory increased with the plant species' local apparency and regional availability, these characteristics might potentially contribute to maintaining patterns of coexistence among plant species in species-rich forest ecosystems.

At the same time, the strong influence of specific plant traits on herbivory indicates that the extent to which the distribution and diversity of key palatability and defense traits in plant communities are affected by changes in plant diversity will strongly determine the strength of plant diversity effects on herbivory (see also Loranger et al. 2013). Accordingly, the results reported in this thesis show that the functional trait and phylogenetic composition and diversity of species-rich woody plant communities have a strong impact on herbivory (with phylogenetic effects reflecting evolutionarily conserved trait effects and associations among plants and their herbivores). The effects of plant species richness were much less pronounced. Similar results have been reported in studies on other ecosystem processes and properties (e.g.

Mason et al. 2008; Mouillot et al. 2011), emphasizing that the inclusion of additional biodiversity metrics can be required to uncover the actual extent of (potentially nonrandom) biodiversity effects and to obtain a mechanistic understanding of these effects. For herbivory, community-level and multivariate plant trait diversity and composition emerge as important predictors also of intraspecific damage levels, revealing non-additive effects that arise from interactions among species and traits (see also Mouillot et al. 2011; Dias et al. 2013). Similar effects on herbivory that might be related to trade-offs in the traits relevant for resource use were also observed in species-rich grasslands (Loranger et al. 2013), which indicates that the relationships reported in this thesis might be more general and not limited to the studied subtropical forests.

Interestingly, most of the observed effects of plant functional and phylogenetic diversity, but also of plant species richness, on herbivory in the studied forest stands were positive and promoted higher damage. This result was rather unexpected, considering that the repeated findings of negative density dependent effects of herbivores on tree recruit mortality in such species-rich forests point to a strong resource-dependent impact of specialized herbivores (e.g. Metz et al. 2010; Swamy and Terborgh 2010; Bagchi et al. 2014). Such an impact of specialists would be expected to result in a reduction of herbivore damage with increasing plant diversity and the concomitant reduction in the availability of resources for specialized herbivores (Root 1973). And yet, the finding of increasing herbivore damage with increasing plant diversity is not a local phenomenon and has been reported recently in other studies as well, for instance in a species-rich grassland experiment (Loranger et al. 2014). Moreover, the positive herbivory-plant diversity relationship, initially found in the observational study of (near)natural forest stands (Chapter 3), is confirmed by the results of the study using the experimental setup of the large-scale BEF-China tree diversity experiment (Chapter 4). The latter study additionally makes clear that effects of herbivory on the producer level may arise

early on in secondary forest succession, i.e. herbivory and its variation due to plant species richness may be important for the structure and functioning of forest ecosystems right from the start of their development. The results of these studies and the structure of the herbivore communities in these systems point to a strong impact of generalist herbivores, which can benefit from dietary mixing of different plant species to balance the intake of nutrients and defensive compounds (Bernays et al. 1994; Pfisterer et al. 2003). This is in line with the finding that herbivore communities in similarly species-rich tropical forests often show a less narrow specialization than traditionally assumed (e.g. Basset and Novotny 1999; Novotny et al. 2002; Novotny and Basset 2005).

Overall, the observed relationships between herbivory and tree species richness, and deviating results in other forest systems with more specialized herbivore assemblages, support the view that the degree of trophic specialization of dominant herbivores strongly affects the outcome of plant-herbivore interactions under biodiversity loss (Jactel and Brockerhoff 2007; Castagneyrol et al. 2014). For the species-rich subtropical and tropical forests, this is of particular relevance as these different effects point to different mechanisms of how herbivores might contribute to the maintenance of the high plant diversity observed in these forests. While specialist herbivores have been shown to cause negative density or distance dependent seed or seedling mortality that may lead to an increase in local plant diversity (Metz et al. 2010; Swamy and Terborgh 2010; Visser et al. 2011; Bagchi et al. 2014), generalist herbivores as well can contribute to promoting plant diversity. In this case, strong negative impacts of herbivory on the most common and potentially dominant plant species (rather than a generally negative distance or density dependent impact on all species, see Terborgh 2012) could lead to increased performance of, and a promotion of coexistence with, rare or less dominant plant species. The results of this thesis indicate that the latter mechanism could play an important role in the studied subtropical forests (see Chapter 1), and results from other studies show that such

mechanisms could be widespread in many species-rich forest systems (Dyer et al. 2010; Sedio and Ostling 2013; Fricke et al. 2014).

Consistent with the results of the herbivory analyses, positive effects of plant diversity were also found for the biomass and abundance patterns of important herbivore guilds. Again, diversity metrics that go beyond mere plant species richness, in this case plant phylogenetic diversity, emerged as particularly important in uncovering biodiversity effects and the potential causes of these effects. The strong impact of plant phylogenetic diversity and, at the same time, the lack of effect of plant species richness on herbivores indicate that the diversity-dependence of herbivore-mediated ecosystem processes may fundamentally depend on nonrandom associations among plant and herbivore species (which are not restricted to specialist herbivores, as most generalist herbivores as well show some degree of host selection; see e.g. Ødegaard et al. 2005). Scenarios of random species loss may thus underestimate the consequences for ecosystem functions if they do not reflect the driving forces of community assembly (see also Dinnage et al. 2012). However, as the results of Chapter 5 show, this is not necessarily the case under all circumstances, and additional factors such as succession-related changes in plant and herbivore community structure might influence the importance of such nonrandom associations. Importantly, the study of herbivores makes clear, and thus supports the findings of the herbivory studies, that the relationships between plant diversity and (the functional effects of) herbivores in the studied subtropical forest systems are strongly shaped by bottom-up control. At the same time, however, the pronounced increase in herbivore biomass and damage with increasing plant diversity indicates important herbivore feedbacks on the structure and functioning, and potentially also on the diversity, of the producer level.

It should be noted that the studies on herbivory and herbivores presented in this thesis focus on the seedling and sapling stage of trees and shrubs, i.e. the results are representative of the forest understory. While the canopy region will have a higher share in

the overall rates of many ecosystem processes than the forest understory, the seedling and sapling cohorts are critically important for the long-term maintenance of plant diversity in these forests. Out of these cohorts the future canopy region will develop, and the impact of herbivores on these cohorts, which are particularly vulnerable to damage (Terborgh 2012), thus plays a crucial role in influencing the structure and diversity, and thus the functioning, of these forests in the long term. Moreover, results from the canopy region of the studied forests show that patterns of herbivory and herbivore abundance are very similar to those reported in this thesis (M. Brezzi et al., in preparation), which means that the general findings of this thesis are highly relevant for our understanding of ecosystem-level patterns and processes in these forests.

### **Plant diversity does not promote overall predator abundance and diversity, suggesting weak plant-diversity dependent effects of predator top-down control in species-rich forests**

Section II of this thesis united studies on the effects of plant diversity on predator abundance, species richness and functional diversity in species-rich subtropical forests. Overall, the results of these studies indicate that predator top-down control is not necessarily promoted by higher plant diversity. Abundance patterns of spiders and ants as well as different aspects of predator diversity were not related to, or even decreased, with increasing plant diversity, and only specific aspects of spider functional diversity and the species richness of strictly predatory ants showed a positive response to increasing plant diversity. While these patterns are in contrast to common ecological theory (e.g. the ‘enemies’ and ‘more individuals’ hypotheses; Root 1973; Srivastava and Lawton 1998) and the findings of recent studies in a temperate grassland biodiversity experiment (Haddad et al. 2009; Dinnage et al. 2012), they are in line with the findings of Section I, where neither herbivore abundance and biomass nor herbivore damage seemed to be restricted by a potentially increasing predator pressure along the gradients of increasing plant diversity. On the contrary, increasing damage and herbivore

abundance suggest that either overall predator top-down control did not change or even declined with increasing plant diversity.

Several reasons come to mind that could help to explain the different findings of previous studies and the studies reported in this thesis. First of all, the plant diversity gradients of the subtropical forest system started at moderate diversity levels and did not include low-diverse plant communities. Diversity effects on individual ecosystem processes are often hypothesized to become weaker at higher levels of diversity due to an increase in the probability of functionally redundant species being added to a community (Schmid et al. 2009). While the comparatively high diversity of even the least diverse plant communities of the subtropical forest system might thus have potentially obscured stronger relationships at lower diversity levels, studies of less diverse forest ecosystems also found no evidence of the effects predicted by the enemies hypothesis (e.g. Schuldt et al. 2008; Vehviläinen et al. 2008; see also the discussion of Section III below). More likely, plant diversity effects on higher trophic levels might differ among different types of ecosystems due to differences in the structural characteristics and scale-dependent patterns of species composition of the constituent plant communities (Zhang and Adams 2011). Latitudinal differences in the strength of biotic interactions might add to this, but differences in the strength of herbivore-predator interactions are an unlikely explanation as theory would have predicted a more pronounced pattern in the subtropical forests than in the above-mentioned temperate grassland system (Schemske et al. 2009). However, it might be conceivable that stronger intraguild interactions among predators could contribute to the patterns observed in the subtropical forest stands (Chapter 11). The positive effects of plant diversity on individual metrics of spider functional diversity and on the species richness of strictly predatory ants indicates the complexity of diversity patterns even within individual trophic levels, with patterns depending on taxon identity or even the functional subgroup within a specific taxon.

The results of Chapter 11 further suggest that the interactions between ants and spiders can lead to plant diversity-mediated shifts in the functional structure of spiders that could potentially affect the overall strength of predator top-down effects. Such intraguild interactions could thus contribute to an apparent lack of an overall positive plant diversity effect on predators.

Although most of the results reported in the chapters of this section are based on epigeic predators hunting on the forest floor and in the lower vegetation, these predators are important for several reasons. The forest floor has been found to harbor a significant part of the overall consumer diversity in forests of high plant diversity (Stork and Grimbacher 2006) and predator effects in this stratum can thus have a notable impact on overall biodiversity patterns. More importantly, these predators forage in the direct vicinity of, and many of these predators include in their hunting range, the young recruits of tree and shrub species that were the focus of the studies in Section I of this thesis. The potential impact of these predators may thus extend to the seedling and lower sapling stratum, in particular as many herbivores feeding on seedlings and saplings spend part of their life cycle in the forest floor compartment and thus further increase their encounter rates with epigeic predators (Tanhuanpää et al. 1999; Riihimäki et al. 2005). Importantly, the results of Chapters 5 and 10, which are based on the assessments of arthropods on tree and shrub saplings, confirm the general findings of a lack of plant diversity effects on overall predator performance directly for the higher vegetation strata (as do first results from the canopy region; M. Brezzi et al., unpublished). It also needs to be noted that this thesis focuses on generalist predators. While these generalist predators have been shown to play an important functional role in many ecosystems (Symondson et al. 2002), the impact of potentially more specialized predators, such as sphecid wasps, might be important as well. More specialized predators could show responses to plant diversity that differ from those observed in this thesis (but see e.g. Veddeler et al. 2010). However, the results of

Section I make a strong plant diversity-dependent impact of such predators on herbivores rather unlikely. Considering the complexity of interactions among predators indicated by the results of Section II and the fact that many wasp species also prey on spiders, however, it would be interesting to study the potential effects of such predatory taxa on the performance (and maybe the regulation) of the highly abundant spiders in species-rich forests.

### Temperate forest results confirm that relationships between plant diversity and predators are not necessarily different at low levels of plant diversity

The two chapters of Section III were intended as an outlook on less diverse temperate forests. While being located in regions much more easily accessible to many researchers, these forests nevertheless still lack sufficient research on many aspects of the relationships between biodiversity and ecosystem functioning. An advanced knowledge of the role that plant diversity plays in promoting the ecosystem functions and services provided by forests can inform sustainable forest management approaches that are being developed in many regions with a long history of intensive forest management, such as in Europe (Rametsteiner and Mayer 2004; Wolfslehner et al. 2005). In the context of such sustainable and multifunctional management practices, promoting the natural enemies of pests as a way to enhance pest control is a relevant research topic.

Interestingly, the comparison with the subtropical study site indicated that, although the species and family richness of spiders was lower, the functional diversity of spiders in the forest stands of the semi-natural temperate study site was similar to that of the subtropical site at a very fine spatial scale (whereas at larger spatial scales the higher  $\beta$ -richness of spiders at the subtropical site lead to significant differences in overall functional diversity). This shows that even simpler environments can exhibit similar local variability and a resulting similar local-scale diversity than more complex environments (see also the extensive latitudinal comparison of spider functional diversity of Cardoso et al.

2011). These similarities in the functional diversity of important predators between the study sites at a scale where many direct interactions between predators and their prey occur could mean that predator-related processes are similarly effective at smaller scales in these very different forests. Again, this points to the possibility raised in the discussion of Section II that differences in the general type of ecosystem (e.g. forests vs. grasslands) might have stronger effects on some of the relationships between plant diversity and higher trophic levels than potential latitudinal differences within a specific type of ecosystem (e.g. forests; see also Cardoso et al. 2011; Zhang and Adams 2011). Similarly, the lack of a tree species richness effect on spiders in the temperate BIOTREE tree diversity experiment (Chapter 13) adds to the increasing evidence that plant diversity effects on predators in forests, whether in rather species-poor or species-rich forests, are often not the positive effects suggested by theory and findings from grasslands (Schuldt et al. 2008; Vehviläinen et al. 2008; Schuldt et al. 2011; Zhang and Adams 2011; Zou et al. 2013).

Moreover, the BIOTREE results confirm what many studies in rather species-poor systems have found: that plant species identity often affects predator assemblages more strongly than plant species richness (see Vehviläinen et al. 2008 for a detailed example). Analogous patterns may be found in the effects of plant species composition on predators in more diverse plant communities (see e.g. Chapter 7 of this thesis). While such identity effects can translate into diversity effects via sampling/selection-based probability effects (Loreau and Hector 2001; Hooper et al. 2005), such a scenario is most likely under random species assembly and random extinction processes (Wardle 1999). That plant species identity and compositional effects on predators often do not result in pronounced plant diversity effects may thus reflect that random assembly and extinction processes are not necessarily the main drivers of species assembly and extinction in many natural systems (Srivastava and Vellend 2005).

However, the results of this section also make clear that in order for

generalizations to be made, more studies are needed also in temperate forests, as studies that explicitly test for biodiversity effects across trophic levels are relatively scarce even in these forests.

### 14.1 Conclusions and outlook

Altogether the results of this thesis point to an important role of plant diversity in regulating particularly herbivore assemblage patterns and in mediating plant-herbivore interactions at the levels of both individual plant species and entire plant communities in species-rich subtropical forests. Herbivores and their functional effects in these forests appear to be strongly affected by bottom-up effects of plant diversity, whereas generalist predators show an overall weak relationship with plant diversity. While intraguild interactions among predators might complicate the analysis of this relationship, the general findings of this thesis challenge the commonly held view that, at least for many forest systems, plant diversity promotes predator top-down effects on dominant herbivores. Rather, the results are in line with the expectation that plant diversity effects become weaker with increasing trophic level (Scherber et al. 2010). This, in turn, means that the positive effects of plant diversity on herbivores and herbivore damage can be expected to cause direct feedbacks on the producer level. Higher damage on more common than rare plant species might lead to a positive feedback loop of bottom-up controlled herbivores on plant diversity maintenance, and increasing damage levels with increasing plant diversity at the community-level are likely to affect the way plant diversity impacts on processes such as primary production and nutrient cycling. The identification of key plant functional traits and multivariate trait complexes in determining herbivory levels within and among species, the impact of the phylogenetic composition of the plant communities on herbivores, and differential responses of predator functional diversity and species richness to changes in plant diversity highlight the importance of striving to—where feasible—include metrics of biodiversity that go beyond species richness in order to unveil the mechanisms that may underlie biodiversity effects. This thesis thus

makes important contributions to better understanding biodiversity and ecosystem function (BEF) relationships in forests and across trophic levels—aspects that are still underrepresented in BEF research compared to insights from grassland systems and exclusive producer-level studies.

The results may be used to develop studies that follow up on key issues raised in this thesis. In particular, it will be interesting to directly manipulate the abundance, diversity, trait-composition, or host-specificity of herbivore and predator assemblages along diversity gradients of natural and experimentally assembled plant communities in forest systems. This will allow further teasing apart the relative influence of different facets of higher trophic level functional composition and diversity, and potential interaction effects among different functional groups, on BEF relationships. In this respect, more research on consumer-plant trait relationships and the identification of key functional traits of consumers will be required to advance our mechanistic understanding of diversity-dependent trophic interaction patterns (see Ibanez et al. 2013). Equally important as the manipulation of consumers, however, is the direct manipulation of the functional and phylogenetic diversity of plant communities. Whereas most BEF experiments have varied only levels of plant species richness (but see Scherer-Lorenzen et al. 2007; Ebeling et al. 2014), a clear demonstration of plant functional effects requires the direct manipulation of relevant plant traits and trait diversity (or of phylogenetic diversity if evolutionary effects of plant lineage relatedness are the research focus) (e.g. Dias et al. 2013). Finally, integrating the results of biodiversity effects across trophic levels in the framework of ecosystem multifunctionality and biodiversity conservation can be used to improve predictions of the degree to which biodiversity effects can be generalized across different ecosystem processes and taxa, and to inform strategies of sustainable forest management.

### References

Agrawal AA (2007) Macroevolution of plant defense strategies. *Trends in Ecology &*



- Evolution 22:103-109
- Bagchi R et al. (2014) Pathogens and insect herbivores drive rainforest plant diversity and composition. *Nature* 506:85-88
- Basset Y, Novotny V (1999) Species richness of insect herbivore communities on *Ficus* in Papua New Guinea. *Biological Journal of the Linnean Society* 67:477-499
- Bernays EA, Bright KL, Gonzalez N, Angel J (1994) Dietary Mixing in a Generalist Herbivore: Tests of Two Hypotheses. *Ecology* 75:1997-2006
- Cardoso P, Pekar S, Jocque R, Coddington JA (2011) Global patterns of guild composition and functional diversity of spiders. *Plos ONE* 6:e21710
- Carmona D, Fornoni J (2013) Herbivores can select for mixed defensive strategies in plants. *New Phytologist* 197:576-585
- Castagneyrol B, Jactel H, Vacher C, Brockerhoff EG (2014) Effects of plant phylogenetic diversity on herbivory depend on herbivore specialization. *Journal of Applied Ecology* 51:134-141
- Dias ATC, Berg MP, de Bello F, Van Oosten AR, Bila K, Moretti M (2013) An experimental framework to identify community functional components driving ecosystem processes and services delivery. *Journal of Ecology* 101:29-37
- Dinnage R, Cadotte MW, Haddad NM, Crutsinger GM, Tilman D (2012) Diversity of plant evolutionary lineages promotes arthropod diversity. *Ecology Letters* 15:1308-1317
- Dyer LA, Letourneau DK, Chavarria GV, Amoretti DS (2010) Herbivores on a dominant understory shrub increase local plant diversity in rain forest communities. *Ecology* 91:3707-3718
- Ebeling A et al. (2014) A trait-based experimental approach to understand the mechanisms underlying biodiversity–ecosystem functioning relationships. *Basic and Applied Ecology* 15:229-240
- Fricke EC, Tewksbury JJ, Rogers HS (2014) Multiple natural enemies cause distance-dependent mortality at the seed-to-seedling transition. *Ecology Letters* 17:593-598
- Haddad NM, Crutsinger GM, Gross K, Haarstad J, Knops JMH, Tilman D (2009) Plant species loss decreases arthropod diversity and shifts trophic structure. *Ecology Letters* 12:1029-1039
- Hooper DU et al. (2005) Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecological Monographs* 75:3-35
- Ibanez S, Lavorel S, Puijalon S, Moretti M (2013) Herbivory mediated by coupling between biomechanical traits of plants and grasshoppers. *Functional Ecology* 27:479-489
- Jactel H, Brockerhoff EG (2007) Tree diversity reduces herbivory by forest insects. *Ecology Letters* 10:835-848
- Loranger H et al. (2014) Invertebrate herbivory increases along an experimental gradient of grassland plant diversity. *Oecologia* 174:183-193
- Loranger J et al. (2012) Predicting invertebrate herbivory from plant traits: evidence from 51 grassland species in experimental monocultures. *Ecology* 93:2674-2682
- Loranger J et al. (2013) Predicting invertebrate herbivory from plant traits: Polycultures show strong nonadditive effects. *Ecology* 94:1499-1509
- Loreau M, Hector A (2001) Partitioning selection and complementarity in biodiversity experiments. *Nature* 412:72-76
- Mason NWH, Irz P, Lanoiselee C, Mouillot D, Argillier C (2008) Evidence that niche specialization explains species-energy relationships in lake fish communities. *Journal of Animal Ecology* 77:285-296
- Metz MR, Sousa WP, Valencia R (2010) Widespread density-dependent seedling mortality promotes species coexistence in a highly diverse Amazonian rain forest. *Ecology* 91:3675-3685
- Mouillot D, Villéger S, Scherer-Lorenzen M, Mason NWH (2011) Functional structure of biological communities predicts ecosystem multifunctionality. *PLoS ONE* 6
- Novotny V, Basset Y (2005) Review - Host specificity of insect herbivores in tropical forests. *Proceedings of the Royal Society B-Biological Sciences* 272:1083-1090
- Novotny V, Basset Y, Miller SE, Drozd P, Cizek L (2002) Host specialization of leaf-chewing insects in a New Guinea rainforest. *Journal of Animal Ecology* 71:400-412
- Ødegaard F, Diserud OH, Østbye K (2005) The importance of plant relatedness for host utilization among phytophagous insects. *Ecology Letters* 8:612-617
- Pfisterer AB, Diemer M, Schmid B (2003) Dietary shift and lowered biomass gain of a generalist herbivore in species-poor experimental plant communities. *Oecologia* 135:234-241
- Rametsteiner E, Mayer P (2004) Sustainable forest management and Pan-European forest policy. *Ecological Bulletins* 51:51-57
- Riihimäki J, Kaitaniemi P, Koricheva J, Vehviläinen H (2005) Testing the enemies hypothesis in forest stands: the important role of tree species composition. *Oecologia* 142:90-

- Root RB (1973) Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). *Ecological Monographs* 43:95-124
- Schemske DW, Mittelbach GG, Cornell HV, Sobel JM, Roy K (2009) Is there a latitudinal gradient in the importance of biotic interactions? *Annual Review of Ecology Evolution and Systematics* 40:245-269
- Scherber C et al. (2010) Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. *Nature* 468:553-556
- Scherer-Lorenzen M, Schulze ED, Don A, Schumacher J, Weller E (2007) Exploring the functional significance of forest diversity: A new long-term experiment with temperate tree species (BIOTREE). *Perspectives in Plant Ecology Evolution and Systematics* 9:53-70
- Schmid B et al. (2009) Consequences of species loss for ecosystem functioning: meta-analyses of data from biodiversity experiments. In: Naeem S, Bunker DE, Hector A, Loreau M, Perrings C (eds) *Biodiversity, ecosystem functioning, and human wellbeing. An ecological and economic perspective*. Oxford Univ. Press, Oxford, pp 14-29
- Schmitz OJ (2006) Predators have large effects on ecosystem properties by changing plant diversity, not plant biomass. *Ecology* 87:1432-1437
- Schowalter TD (2012) Insect herbivore effects on forest ecosystem services. *Journal of Sustainable Forestry* 31:518-536
- Schuldt A et al. (2011) Predator diversity and abundance provide little support for the enemies hypothesis in forests of high tree diversity. *PLoS ONE* 6:e22905
- Schuldt A, Fahrenholz N, Brauns M, Migge-Kleian S, Platner C, Schaefer M (2008) Communities of ground-living spiders in deciduous forests: Does tree species diversity matter? *Biodiversity and Conservation* 17:1267-1284
- Sedio BE, Ostling AM (2013) How specialised must natural enemies be to facilitate coexistence among plants? *Ecology Letters* 16:995-1003
- Srivastava DS, Lawton JH (1998) Why more productive sites have more species: An experimental test of theory using tree-hole communities. *American Naturalist* 152:510-529
- Srivastava DS, Vellend M (2005) Biodiversity-ecosystem function research: Is it relevant to conservation? *Annual Review of Ecology Evolution and Systematics* 36:267-294
- Stork NE, Grimbacher PS (2006) Beetle assemblages from an Australian tropical rainforest show that the canopy and the ground strata contribute equally to biodiversity. *Proceedings of the Royal Society B* 273:1969-1975
- Swamy V, Terborgh JW (2010) Distance-responsive natural enemies strongly influence seedling establishment patterns of multiple species in an Amazonian rain forest. *Journal of Ecology* 98:1096-1107
- Symondson WOC, Sunderland KD, Greenstone MH (2002) Can generalist predators be effective biocontrol agents? *Annual Review of Entomology* 47:561-594
- Tanhuanpää M, Ruohomäki K, Kaitaniemi P, Klemola T (1999) Different impact of pupal predation on populations of *Epirrita autumnata* (Lepidoptera; Geometridae) within and outside the outbreak range. *Journal of Animal Ecology* 68:562-570
- Terborgh J (2012) Enemies maintain hyperdiverse tropical forests. *American Naturalist* 179:303-314
- Veddeler D, Tylianakis J, Tscharncke T, Klein A-M (2010) Natural enemy diversity reduces temporal variability in wasp but not bee parasitism. *Oecologia* 162:755-762
- Vehviläinen H, Koricheva J, Ruohomäki K (2008) Effects of stand tree species composition and diversity on abundance of predatory arthropods. *Oikos* 117:935-943
- Visser MD, Muller-Landau HC, Wright SJ, Rutten G, Jansen PA (2011) Tri-trophic interactions affect density dependence of seed fate in a tropical forest palm. *Ecology Letters* 14:1093-1100
- Wardle DA (1999) Is "sampling effect" a problem for experiments investigating biodiversity-ecosystem function relationships? *Oikos*:403-407
- Weisser WW, Siemann E (2004) The various effects of insects on ecosystem functioning. In: Weisser WW, Siemann E (eds) *Insects and ecosystem function*. Springer, Berlin, Heidelberg, pp 3-24
- Wolfslehner B, Vacik H, Lexer MJ (2005) Application of the analytic network process in multi-criteria analysis of sustainable forest management. *Forest Ecology and Management* 207:157-170
- Zhang Y, Adams J (2011) Top-down control of herbivores varies with ecosystem types. *Journal of Ecology* 99:370-372
- Zou Y et al. (2013) Relationships between plant diversity and the abundance and  $\alpha$ -diversity of predatory ground beetles (Coleoptera: Carabidae) in a mature Asian temperate forest ecosystem. *PLoS ONE* 8:e82792





## Authors' contributions to manuscripts with multiple authors

Chapter	Conceived and designed the study	Performed the study	Analyzed the data	Contributed reagents/materials/analysis tools	Wrote the paper	Commented on previous versions of the manuscript
2	AS, TA, HB, MF, WH, KM, BS	AS	AS	WK, EW, WUP, WD, SM, DE, HZ	AS	HB, TA, BS, WH, WD, MF, EW, DE, WK, KM, SM, WUP, HZ
3	AS, HB, WH, TA	AS	AS	OP, WK, WD, SM, DE	AS	OP, HB, WH, WD, DE, WK, SM, TA
4	AS, HB, KM, TA	AS	AS	YL, WH, GvO, JZ	AS	HB, WH, GvO, YL, KM, JZ, TA
5	AS, HB, TA	AS, SC, MW	AS	MB, XC	AS	HB, MB, SC, XC, MW, TA
6	AS, TA, HB, WH, BS, HZ	AS	AS	SB, HB, WH, BS	AS	TA, HB, WH, BS, SB, HZ
7	AS, TA, HB, WH	AS	AS		AS	TA, HB, WH
8	AS, HB, TA	AS	AS	OP, WD, SM	AS	OP, HB, WD, SM, TA
9	MSt, AS, TA, AM	MSt, AS	MSt		MSt	AM, AS, TA
10	MSt, AS, TA, AM, HB	MSt, AS	MSt		MSt	AM, AS, HB, TA
11	AS	AS	AS	MSt	AS	MSt
12	AS, TA, MSc	AS	AS		AS	MSc, TA
13	AS, MSL	AS	AS		AS	MSL

### Abbreviations:

AS: Andreas Schuldt; AM: Alexandra-Maria Klein, BS: Bernhard Schmid, DE: David Eichenberg, EW: Erik Welk, GvO: Godder von Oheimb, HB: Helge Bruelheide, HZ: Hongzhan Zhou, JZ: Jiayong Zhang, KM: Keping Ma, MB: Martin Baruffol, MF: Markus Fischer, MSc: Matthias Schaefer, MSL: Michael Scherer-Lorenzen, MSt: Michael Staab, MW: Marcus Wall, OP: Oliver Purschke, SB: Sabine Both, SC: Simon Chen, SM: Stefan Michalski, TA: Thorsten Aßmann, WD: Walter Durka, WH: Werner Härdtle, WK: Wenzel Kröber, WUP: Wolf-Ulrich Palm, XC: Xiulian Chi, YL: Ying Li



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## List of publications

### Peer reviewed journal articles and book chapters

- Schuldt A, Assmann T, Bruelheide H, Härdtle W, Li Y, Ma K, von Oheimb G, Zhang J (submitted) Early positive effects of tree species richness on herbivory in the world's largest forest biodiversity experiment.
- Seitz S, Goebes P, Zumstein P, Assmann T, Kühn P, Niklaus P, Schuldt A, Scholten T (submitted) The influence of leaf litter diversity and soil fauna on initial soil erosion in subtropical forests
- Schuldt A, Staab M (submitted) Effects of ants on the functional composition of spider assemblages increase with tree species richness in a highly diverse forest
- Staab M, Schuldt A, Assmann T, Bruelheide H, Klein AM (submitted) Ant community composition but not overall diversity changes during forest succession in a subtropical forest
- Schuldt A, Baruffol M, Bruelheide H, Chen S, Chi X, Wall M, Assmann T (2014) Woody plant phylogenetic diversity mediates bottom-up control of arthropod biomass in species-rich forests. *Oecologia*. 176: 171-182
- Staab M, Schuldt A, Assmann T, Klein AM (2014) Tree diversity promotes predator but not omnivore ants in a subtropical Chinese forest. *Ecological Entomology*. DOI: 10.1111/een.12143
- Härdtle W, Niemeyer T, Fichtner A, Li Y, Ries C, Schuldt A, Walmsley D, von Oheimb G (2014) Climate imprints on tree-ring  $\delta^{15}\text{N}$  signatures of sessile oak (*Quercus petraea* Liebl.) on soils with contrasting water availability. *Ecological Indicators* 45: 45-50
- Homburg K, Homburg N, Schäfer F, Schuldt A, Assmann T (2014) Carabids.org – A dynamic online database of ground beetle species traits (Coleoptera, Carabidae). *Insect Conservation and Diversity* 7: 195-205
- Schuldt A, Scherer-Lorenzen M (2014) Non-native tree species (*Pseudotsuga menziesii*) strongly decreases predator biomass and abundance in mixed-species plantations of a tree diversity experiment. *Forest Ecology and Management* 327: 10-17
- Schuldt A, Assmann T, Bruelheide H, Durka W, Eichenberg D, Härdtle W, Kröber W, Michalski SG, Purschke O (2014) Functional and phylogenetic diversity of woody plants drive herbivory in a highly diverse forest. *New Phytologist* 202: 864-873
- Bruelheide H, Assmann T, Bauhus J, Both S, Buscot F, Chen XY, Durka W, Erfmeier A, Gutknecht JLM, Guo D, Guo LD, Härdtle W, He JS, Klein AM, Kühn P, Michalski S, Nadrowski K, Niklaus P, Pei K, Scherer-Lorenzen M, Scholten T, Schuldt A, Seidler G, Trogisch S, von Oheimb G, Welk E, Wirth C, Wubet T, Yang X, Yu M, Zhang S, Zhou H, Fischer M, Ma K, Schmid B (2014) Designing forest biodiversity experiments: general considerations illustrated by a new large experiment in subtropical China. *Methods in Ecology and Evolution* 5: 74-89
- Schuldt A, Bruelheide H, Durka W, Michalski SG, Purschke O, Assmann T (2014) Tree diversity promotes functional dissimilarity and maintains functional richness despite species loss in predator assemblages. *Oecologia* 174: 533-543
- Krause RH, von Wehrden H, Härdtle W, Schuldt A, Assmann T (2013) Stenotopy and eurytopy – distribution models as a tool for estimating niche overlap in two spider species, *Trochosa terricola* and *Eresus kollari* (Araneae: Lycosidae / Eresidae). *Entomologia Generalis* 34: 169-180
- Härdtle W, Niemeyer T, Assmann T, Baiboks S, Fichtner A, Friedrich U, Lang A, Neuwirth B, Pfister L, Ries C, Schuldt A, Simon N, von Oheimb G (2013) Long-term trends in tree-ring width and isotope signatures ( $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ ) of *Fagus sylvatica* L. on soils with contrasting water supply. *Ecosystems* 16: 1413-1428
- Härdtle W, Niemeyer T, Assmann T, Aulinger A, Fichtner A, Lang A, Leuschner C, Neuwirth B, Pfister L, Quante M, Ries C, Schuldt A, von Oheimb G (2013) Climatic responses of tree-ring width and  $\delta^{13}\text{C}$

- signatures of sessile oak (*Quercus petraea* Liebl.) on soils with contrasting water supply. *Plant Ecology* 214: 1147-1156
- Schuldt A, Assmann T, Schaefer M (2013) Scale-dependent diversity patterns affect spider assemblages of two contrasting forest ecosystems. *Acta Oecologica* 49: 17-22
- Homburg K, Schuldt A, Drees C, Assmann T (2013) Broad-scale geographic patterns in body size and hind wing development of western Palaearctic ground beetles (Coleoptera: Carabidae). *Ecography* 36: 166-177
- Schuldt A, Bruelheide H, Härdtle W, Assmann T (2012) Predator assemblage structure and temporal variability of species richness and abundance in forests of high tree diversity. *Biotropica* 44: 793-800
- Schuldt A, Bruelheide H, Durka W, Eichenberg D, Fischer M, Kröber W, Härdtle W, Ma K, Michalski S, Palm WU, Schmid B, Welk E, Zhou H, Assmann T (2012) Plant traits affecting herbivory on tree recruits in highly diverse subtropical forests. *Ecology Letters* 15: 732-739
- Schuldt A, Both S, Bruelheide H, Härdtle W, Schmid B, Zhou H, Assmann T (2011) Predator diversity and abundance provide little support for the enemies hypothesis in forests of high tree diversity. *PLoS ONE* 6: e22905
- Schuldt A, Assmann T (2011) Patterns and hotspots of carabid beetle diversity in the Palaearctic – insights from a hyperdiverse invertebrate taxon. In Zachos F, Habel JC (eds) *Biodiversity Hotspots*. Springer, Heidelberg
- Bruelheide H, Böhnke M, Both S, Fang T, Assmann T, Baruffol M, Bauhus J, Buscot F, Chen XY, Ding BY, Durka W, Erfmeier A, Fischer M, Geißler C, Guo D, Guo LD, Härdtle W, He JS, Hector A, Kröber W, Kühn P, Lang AC, Nadrowski K, Pei K, Scherer-Lorenzen M, Shi X, Scholten T, Schuldt A, Trogisch S, von Oheimb G, Welk E, Wirth C, Wu YT, Yang X, Zeng X, Zhang S, Zhou H, Ma K, Schmid B (2011) Community assembly during secondary forest succession in a Chinese subtropical forest. *Ecological Monographs* 81: 25-41
- Schuldt A, Assmann T (2011) Belowground carabid beetle diversity in the western Palaearctic – effects of history and climate on range-restricted taxa (Coleoptera: Carabidae). *ZooKeys* 100: 461-474
- Drees C, Brandmayr P, Buse J, Dieker P, Gürlich S, Habel J, Harry I, Härdtle W, Matern A, Meyer H, Pizzolotto R, Quante M, Schäfer K, Schuldt A, Taboada A, Assmann T (2011) Poleward range expansion without a southern contraction in the ground beetle *Agonum viridicupreum* (Coleoptera, Carabidae). *ZooKeys* 100: 333-352
- Assmann T, Drees C, Matern A, Schuldt A (2011) *Eucamaragnathus desenderi*, a new ground beetle species from Africa (Coleoptera, Carabidae). *ZooKeys* 100: 37-46
- Lang AC, Härdtle W, Bruelheide H, Geißler C, Nadrowski K, Schuldt A, Yu M, von Oheimb G (2010) Growth responses of tree individuals to neighbourhood competition in a species rich slope forest of subtropical China. *Forest Ecology and Management* 260: 1708-1715
- Schuldt A, Assmann T (2010) Invertebrate diversity and national responsibility for species conservation across Europe – A multi-taxon approach. *Biological Conservation* 143: 2747-2756
- Schuldt A, Baruffol M, Böhnke M, Bruelheide H, Härdtle W, Lang AC, Nadrowski K, von Oheimb G, Voigt W, Zhou, H, Assmann T (2010) Tree diversity promotes insect herbivory in subtropical forests of southeast China. *Journal of Ecology* 98: 917-926
- Assmann T, Casale A, Drees C, Habel JC, Matern A, Schuldt A (2010) The dark side of relict species biology. Cave animals as ancient lineages. In: Habel JC, Assmann T (eds) *Relict species – Phylogeography and conservation biology*. Springer, Heidelberg
- Schuldt A, Wang Z, Zhou H, Assmann T (2009) Integrating highly diverse invertebrates into broad-scale analyses of cross-taxon congruence across the Palaearctic. *Ecography* 32: 1019-1030
- Schuldt A, Assmann T (2009) Environmental and historical effects on richness and endemism patterns of carabid beetles in the

- Western Palaearctic. *Ecography* 32: 705-714
- Finch OD, Blick T, Schuldt A (2008) Macroecological patterns of spider species richness across Europe. *Biodiversity and Conservation* 17: 2849-2868
- Assmann T, Buse J, Drees C, Habel J, Härdtle W, Matern A, von Oheimb G, Schuldt A, Wrase DW (2008). From Latreille to DNA systematics - towards a modern synthesis for carabidology. In: Penev L, Erwin T, Assmann T (eds) Back to the roots and back to the future. Towards a new synthesis between taxonomic, ecological and biogeographical approaches in carabidology. Pensoft, Sofia, Moscow
- Schuldt A, Fahrenholz N, Brauns M, Migge-Kleian S, Platner C, Schaefer M (2008) Communities of ground-living spiders in deciduous forests: Does tree species diversity matter? *Biodiversity and Conservation* 17: 1267-1284

### Further publications

- Assmann T, Drees C, Härdtle W., Klein A, Schuldt A, von Oheimb G (2014) Ökosystem und Biodiversität. In: Heinrichs H, Michelsen G (eds) Nachhaltigkeitswissenschaften. Springer, Berlin, Heidelberg: 147-174
- Assmann T, Buse J, Dieker P, Eggers B, Drees C, Harry I, Homburg K, Krause H, Matern A, Schuldt A, Taboada A (2013). Historisch alte Waldstandorte: Bedeutung und Wert von Lebensraumtradition für Tiere. In: "Natura 2000 und Wald - Lebensraumtypen, Erhaltungszustand, Management", Naturschutz und Biologische Vielfalt 131: 65-81.



**Erklärung**

Ich versichere, dass ich die vorliegende Habilitationsschrift 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 den Schriften anderer Autorinnen oder Autoren entnommenen Stellen habe ich kenntlich gemacht.

Ich verpflichte mich hiermit des Weiteren zur Einhaltung der „Richtlinie zur Sicherung guter wissenschaftlicher Praxis und zum Verfahren zum Umgang mit wissenschaftlichem Fehlverhalten der Leuphana Universität Lüneburg“ (Leuphana Gazette Nr. 10/09; 8. Juni 2009) und der Grundsätze guter wissenschaftlicher Praxis

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