

The role of tree species richness and identity for herb layer characteristics and next generation tree species establishment in a subtropical forest in China







The role of tree species richness and identity for herb  
layer characteristics and next generation tree species  
establishment in a subtropical forest in China

Kumulative Dissertation

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*"I had the temerity to inquire about the identification of a particular forest herb.  
'Oh, that's just a step-over,' the professor replied, with a bit of humor..."*

Gilliam, F. S. 2007. The ecological significance of the herbaceous layer in temperate forest ecosystems. *AIBS Bulletin* 57:845-858.



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## Summary

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In recent years, research on Biodiversity ecosystem functioning (BEF) relationships has extended its scope towards long-lived tree diversity experiments, with their large contribution to ecosystem functions at the global scale. The herbaceous understorey contributes an impressive part to the overall diversity in forests and plays an important role for tree regeneration as well as for ecosystem functioning in general. Vice versa, trees in the overstorey control understorey herb and shrub growth such as through competition for resources. However, despite its importance, our understanding of the interactions between the herbaceous understorey and tree layer diversity is still limited. In the context of the Biodiversity-Ecosystem Functioning project in subtropical China (BEF-China), this thesis investigates the role of tree species richness and identity for herb layer characteristics and next generation tree species establishment. This thesis combines the outcome of three different experimental approaches, including one study on the effect of tree species richness and identity on herb layer composition, richness and productivity and how these relationships across strata change with abiotic environmental conditions and competition intensity. The second study focuses on the temporal aspect and studies the effect of tree species richness and identity on understorey productivity over a period of three years. The third study examines the influence of Janzen-Connell effects on next generation tree species establishment. Results obtained in all three different approaches support light transmittance as major limiting factor at the current state of forest development. While we did encounter additional effects for tree species identities, a similar effect with variations in tree species richness could not be found yet. Moreover, we were able to demonstrate conspecific negative distance-dependent seedling establishment and intraspecific competition being already effective at this early stage of forest development. While the subsequent interplay of the different identified and prospective mechanisms remains to be tested, this thesis adds to our understanding of the current and later phases of forest development and highlights the need to account for confounding effects.



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## Zusammenfassung

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In den letzten Jahren hat die Forschung der Beziehung zwischen Biodiversität und Ökosystemfunktionen (BEF) ihren Schwerpunkt um langlebige Experimente zur Baumvielfalt erweitert. Die Krautschicht trägt einen hohen Teil zur Artenvielfalt in Wäldern bei und nimmt eine wichtige Rolle für die Regeneration der Baumbestände sowie für Ökosystemfunktionen im Allgemeinen ein. Die Baumschicht wiederum kontrolliert das Wachstum von Kräutern und Sträuchern. Dennoch ist unser Verständnis der Wechselwirkungen zwischen Krautschicht und Baumartenvielfalt begrenzt. Im Rahmen des Projekts Biodiversity-Ecosystem Functioning im subtropischen China (BEF-China) untersucht diese Arbeit die Rolle von Baumartenvielfalt und -identität für die Krautschicht und die Etablierung von Baumarten der nächsten Generation. Diese Arbeit kombiniert die Ergebnisse dreier experimenteller Ansätze, darunter eine Studie über die Effekte der Baumartenvielfalt und -identität auf Zusammensetzung, Vielfalt und Produktivität der Krautschicht und wie sich diese Beziehungen mit abiotischen Bedingungen und Konkurrenzintensität verändert. Die zweite Studie fokussiert sich auf den zeitlichen Aspekt und untersucht den Einfluss von Baumartenvielfalt und -identität auf die Produktivität der Krautschicht über einen Zeitraum von drei Jahren. Die dritte Studie behandelt den Einfluss von Janzen-Connell Effekten auf die Etablierung von Baumarten der nächsten Generation. Allen drei Studien unterstützen Lichtdurchlässigkeit als wesentlichen limitierenden Faktor in der derzeitigen Phase der Sukzession. Während wir zusätzliche Effekte für die Identitäten der vorhandenen Baumarten feststellen konnten, ist ein ähnlicher Effekt mit Variationen der Baumartenvielfalt noch nicht zu finden. Darüber hinaus konnten wir jedoch bereits einen negativen Effekt zwischen der Etablierung von Keimlingen und Distanz zum adulten Individuum sowie Effekte der intraspezifischer Konkurrenz nachweisen. Während das weitere Zusammenwirken der vorhandenen sowie perspektivischen Mechanismen noch getestet werden muss, trägt diese Arbeit zum besseren Verständnis der Sukzession bei und unterstreicht die Notwendigkeit Störeinfluss zu berücksichtigen.



# CHAPTER 1

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## General introduction

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## 1.1 Research motivation and terminology

Increasing species extinction rates (Pimm et al. 2014) and the forecasted consequences for human well being (Díaz et al. 2006, Cardinale et al. 2012) stimulated researches worldwide studying on the links between biodiversity and ecosystem functioning (BEF) over the past decades (e.g. Loreau and Hector 2001, Hooper et al. 2005, Balvanera et al. 2006, Duffy 2009, Tilman et al. 2014, Naeem et al. 2016). Despite the effort, the role of biodiversity on the world's ecosystems remains controversial (Wardle et al. 2000, Srivastava and Vellend 2005), which is largely the result of an ongoing debate about the appropriate methods to study such a relationship (i.e. observational vs. experimental studies; Huston 1997, Wardle 2016) and the reproducibility of the experimental results in nature (Lepš 2004). However, in light of the present exceptionally high species extinction rates an improved understanding of the underlying processes and its potential consequences is much needed to call for swift and more effective conservation policy decisions in this matter (Balmford et al. 2005, Collen and Nicholson 2014, Duffy et al. 2017).

Biodiversity is multidimensional and encompasses genetic-, species- and ecosystem-diversity (Harper and Hawksworth 1994) and can be either described in terms of numbers of entities (i.e. number of genotypes, species and ecosystems), their evenness, their differences in functional traits or their interactions (Hooper et al. 2005). This implies that biodiversity loss is not limited to increasing species extinction rates only (Naeem et al. 1999) although it has often been used synonymously (Hooper et al. 2005). Among the different facets of ecosystem functions (i.e. goods, services and processes; Christensen et al. 1996, Hooper et al. 2005), ecosystem processes describe matter and energy dynamics (e.g. productivity and decomposition) which are the most fundamental aspects of the functioning. Yet, ecosystem processes also encompass those which have a direct impact on the maintenance of biological diversity and thus fulfil a unique position in both directions (i.e. is controlled by and contributes to biological diversity; Christensen et al. 1996).

## 1.2 Comparing the different concepts and approaches

Biodiversity ecosystem functioning relationships, have been widely studied in observational approaches (e.g. Gamfeldt et al. 2013, Chisholm et al. 2013, Plas et al. 2016, Zhang et al. 2017a) or in short-lived and small-scale experiments such as grassland experiments, yielding both, negative and positive BEF relationships (e.g. Hector et al. 1999, Hector and

Bagchi 2007, Roscher et al. 2012). Over the past years, there was an increasing need for testing BEF relationships experimentally also in forest ecosystems – with their large contribution to ecosystem functions at the global scale (Durieux et al. 2003, Bala et al. 2007, Quijas et al. 2013), such as carbon storage and climate regulation. When comparing and interpreting the outcomes amongst the different approaches (i.e. observational vs. experimental, grassland vs. forest ecosystems), it is thus essential to understand their respective strengths and shortcomings (Hooper et al. 2005, Leuschner et al. 2009, Duffy 2009, Trogisch et al. 2017).

In particular, the use of experimental designs caused some controversy about the transferability of the obtained results (e.g. Huston 1997, Wardle 1999, Huston et al. 2000, Thompson and Starzomski 2007). The first main criticism is that, if applied, selective reduction of diversity (e.g. along trait gradients) may lead to 'hidden treatments' (i.e. ignoring confounding species characteristics with high impact on ecosystem functions; Huston 1997), which then can cause to misleading interpretations of biodiversity effect. Consequently, experiments utilize randomized species extinction scenarios have become a popular alternative (Bruehlheide et al. 2014). However, the second criticism is that such randomized-extinction scenarios may not resemble the way real communities are disassembled (Wardle et al. 2000) and since extinction might be biased towards species with particular characteristics (e.g. Grime 2002), this might lead to under- (Zavaleta and Hulvey 2004) or overestimated (Schläpfer et al. 2005) biodiversity impacts.

In contrast, applying experimental designs is the easiest way to separate species diversity effects from additional confounding effects such as species identity and environmental heterogeneity effects (Vockenhuber et al. 2011). In particular, they allow to separate between sampling and niche complementary effects (Loreau and Hector 2001, Nadrowski et al. 2010), thereby two major mechanisms through which biodiversity can be linked to ecosystem functions (Hooper et al. 2005). Hereby sampling or selection effect refers to only a few species that have a large effect on ecosystem functions and the likelihood of such species being present may increase at higher species richness levels (Loreau and Hector 2001). In contrast, niche complementarity (i.e. species specialisation along niche axes) and/or facilitation effects among species (i.e. acquisition of new resources through symbiotic interactions) emphasises an increase in average performance across all species at higher diversity levels (Loreau and Hector 2001, Reich et al. 2012). Separating between these mechanisms and accounting for any additional effects requires orthogonal designs (Nadrowski et al. 2010). In this context, orthogonality means to ensure gradients in



which every species is equally represented at each richness level which allows separating species richness from identity effects. To find such gradients in natural ecosystems is rather difficult, if possible at all (Hooper et al. 2005).

### **1.3 Long-lived tree diversity experiments**

Given the huge spatial dimension forest plantations require in comparison to grassland field experiments, ensuring spatial and temporal homogeneity in long-lived tree diversity experiments is a demanding challenge (Trogisch et al. 2017). However, the sizes of tree individuals allows to capture spatial and temporal variations in microclimatic conditions in great detail. This not only enables to account for varying environmental effects, when studying the effect diversity has on ecosystem functions, it also allows to test for interactive diversity effects with different abiotic and biotic environments at the subplot level (Bruehlheide et al. 2014, Trogisch et al. 2017). Moreover, previous studies in grassland experiments (e.g. Reich et al. 2012) could show accumulative biodiversity effects on ecosystem function with time. For multi-layered forests and the therein contained long-lasting trees such accumulative biodiversity effects might be especially relevant as interactive effects between species become more pronounced with time (Forrester 2014, Huang et al. 2018). Finally, long-lived tree diversity experiments offer the possibility of studying at the level of single individuals (Scherer-Lorenzen et al. 2007). Individual-based approaches, for example allow to determine the survival of tree recruits in response to host species-specific antagonists at lower distance to or at higher density of conspecific adult plants as predicted by the Janzen-Connell theory (Janzen 1970, Connell 1971).

### **1.4 Introduction into herb layer in forests**

High species richness levels in forest ecosystems is formed by its structural complexity forming a mosaic of various species and species interactions within and across the strata (Gentry and Dodson 1987). Among these layers is the herb layer, comprising all vascular plants (i.e. resident and transient species) with one meter or less in height and thereby often exceeding the species numbers found in any other forest stratum (Gilliam and Roberts 2003, Gilliam 2007, Linares-Palomino et al. 2009). However, despite this impressive contribution to the overall diversity in forests, its high influence on tree species regeneration and its documented importance for ecosystem functioning,

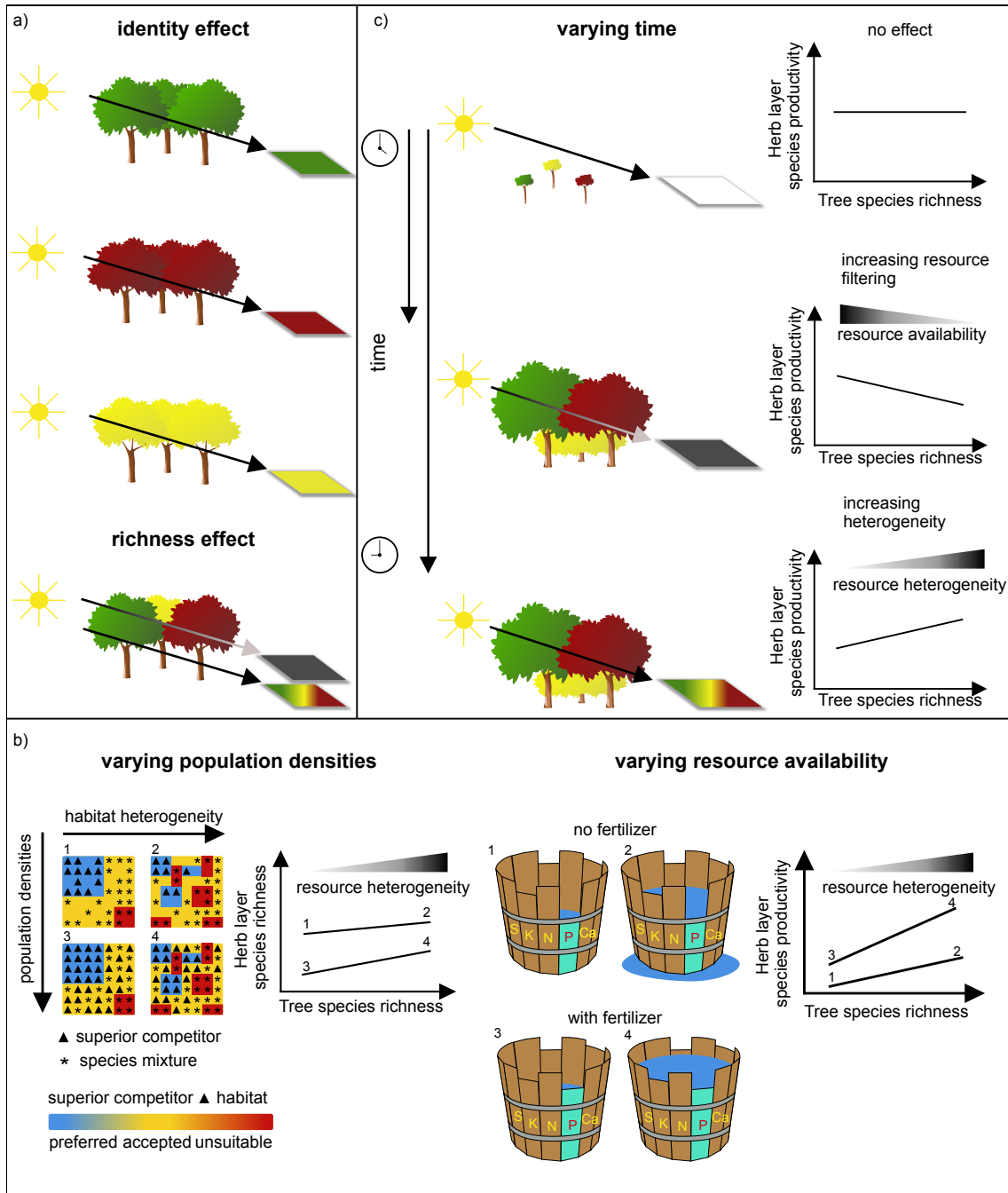
particularly, through influencing soil microbes and nutrient dynamics, our understanding of the interactions between the herb and tree layer is still limited (George and Bazzaz 2003, Taverna et al. 2005, Gilliam 2007, Mölder et al. 2008, Rein et al. 2016, Landuyt et al. 2019).

By altering above- and below-ground resource availability and heterogeneity, tree species identity and richness have been shown to impose competitive constraints to the herb layer (Barbier et al. 2008, Chávez and Macdonald 2010, Zhang et al. 2016, 2017b). For example, species-specific differences among tree species have been reported to modify canopy structure and light transmission as well as light interception, thereby altering the availability and variability of light for the herb layer (Neufeld and Young 2003, Porté et al. 2004). In addition to such species identity effects, forest stands composed of multiple tree species have also been reported to cause facilitating (i.e. higher resource availability and heterogeneity) and/or competition (i.e. lower resource availability and heterogeneity) effects on the herb layer (Fig. 1a). For instance, while forest stands composed of multiple tree species, have been reported to increase microsite availability for the herb layer (Beatty 2003, Yankelevich et al. 2006, Bartels and Chen 2010, Holmgren et al. 2015), a more efficient resource use (i.e. higher niche complementarity) at higher richness levels might also result in the overstorey to consume additional site resources, thereby reducing the amount of available resources in the herb layer (Anderson et al. 1969, Bartels and Chen 2010, Sun et al. 2017).

However, the relative dominance of such tree species richness effects (i.e. as a combination of facilitating and competition effects) on herb layer composition, richness and productivity vary with the environmental context (Weigelt et al. 2009, Schnitzer et al. 2011, Cardinale et al. 2012). For instance, Huston (1979) introduced the idea that population densities might mediate the effect of environmental heterogeneity. Following, we would expect that with increasing population densities in the herb layer, species would respond more strongly to facilitating tree species richness effects (Fig. 1b). Moreover, the effect of tree species richness may also be mediated through different levels of resource availability.

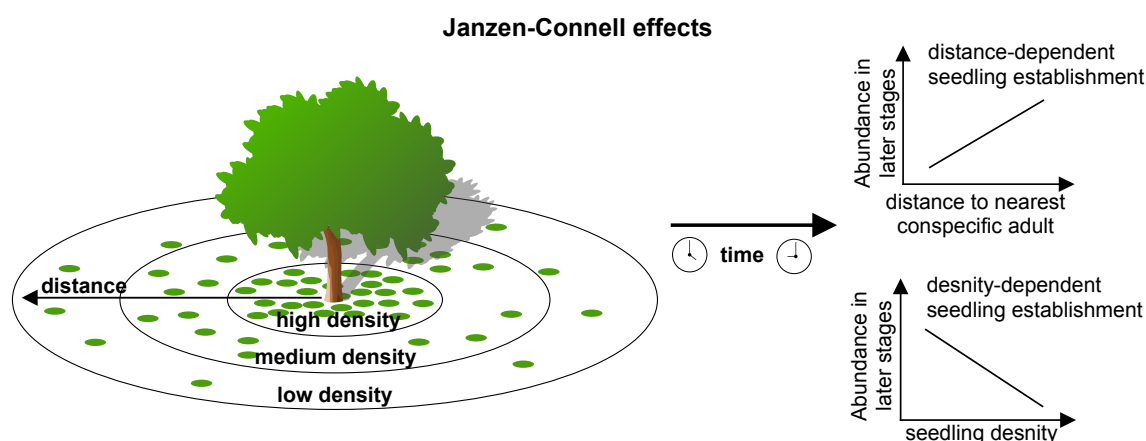
Beside such variation in the environmental context, stand development and temporal changes in species interactions have also been reported to alter the dominance of tree species richness and identity effects (Cardinale et al. 2000, Forrester 2014, Huang et al. 2018). With regard to light interception, studies have reported light niche differentiation in the tree layer to become more efficient in mixed-species forests due to complementary

crowns architectures among species in canopy space (Jucker et al. 2015, Williams et al. 2017). Yet, such an increase in crown filling has also been reported to occur as a result of stand development and increasing canopy closing over time (Lang et al. 2012, Sapijanskas et al. 2014). Moreover, while resource heterogeneity is a more important driver of herb layer species diversity particularly in old-growth stands, resource availability has been reported to act in both young and mature stands (Bartels and Chen 2010). Accordingly, we might expect tree species richness effects on the herb layer, as a combination of facilitating and competition effects, to alter over time as stands develop and competition for light and/or other resources increases (Fig. 1c).



**Figure 1.1:** Conceptual diagram summarizing the effect of tree species identity and richness (a) as well as the additional varying factors hypothesized to alter the degree as to which tree species richness and identity affects the herb layer (b,c).

Via competitive and facilitative interactive effects with woody recruits, the herbaceous understorey exert a strong direct influence on the woody species regeneration and can act as a selecting filter during the juvenile stage when each individual has to pass through the herb layer filter (Taverna et al. 2005, Gilliam 2007). However, in addition to such competitive and facilitative interactive effects within the herbaceous understorey, woody recruits may also be subjected to additional stabilizing forces which result in an increase in recruit's mortality with increasing population densities (Chesson 2000). The Janzen-Connell hypothesis (Janzen 1970, Connell 1971) refers to such stabilizing forces and is among the most important theories to explain the maintenance of diversity in species-rich plant communities, in particular in tropical forest ecosystems. Central components of the Janzen-Connell hypothesis are non-competitive effects of accumulative host species-specific antagonists at lower distance to or at higher density of conspecific plants (Fig. 2).



**Figure 1.2:** Conceptual diagram summarizing the effect of accumulative host species-specific antagonists at lower distance to or at higher density of conspecific plants as predicted by the Janzen-Connell hypothesis. Small green circles represent conspecific tree recruits. Black circles represent the density levels of tree recruit emergence in its initial phase.

The resulting decreased recruit's survival rates then can prevent dominant species from outcompeting less dominant ones, thus promoting juvenile plant diversity (see also: Terborgh 2012, Bever et al. 2015). However, while distance and density effects have been reported to contribute independently to species coexistence, in the field they often act in concert, as seedling density tends to be higher at lower distance to the mother tree, and vice versa (Hubbell 1980, Clark et al. 2005, Muller-Landau et al. 2008). Which is why, the neat separation of distance- and density dependent effects requires a full-factorial design in which both dependencies are varied independently. In addition, experimental approaches also allow for testing interactive effects of distance and density, which can be expected to occur if one mechanism alone does induce sufficient pathogen/herbivore

pressure to result in fitness constraints. Finally, since tree seedlings are not only subjected to Janzen-Connell effects a causal interpretation of density-dependent Janzen-Connell effects can be even more difficult (Terborgh 2012). For example, seedling survival may be generally favoured when the species' preferential conditions (e.g. light) are met and thus potentially can mask the presence of Janzen-Connell effects (Comita 2017). In conclusion, experimental platforms can help to separate between the different effects as well as between any additional varying mechanism.

## 1.5 The platform of BEF-China

Among the large-scale tree diversity experiments, is the BEF-China experiment. Located in a mountainous subtropical region near Xingangshan Township, Dexing County, Jiangxi Province, (China 29°60'12.91'N, 117°55'44.608'E) the platform is the first tree diversity experiment in the humid subtropics and comprises two sites established in 2009 (site A) and 2010 (site B), at a distance of 4 km and situated on 100-300 m a. s. l.. With a mean annual temperature of 16.7°C and a mean annual precipitation of 1821 mm the region can be characterized by seasonal subtropical monsoon climate with warm and humid summers and a short dry winter season between November and December. The soils are formed by Cambisols and Cambisols derivatives, interfused with Regosols on ridges and crests as well as Anthrosols from Colluvial deposits on valley floors and slope foot (Yang et al. 2013, Bruelheide et al. 2014).

Prior to the experiment, the sites had been mostly planted with the two economically important conifers, *Pinus massoniana* Lamb. and *Cunninghamia lanceolata* (Lamb.) Hook.. However, natural forests in this region are dominated by evergreen tree species mixed with deciduous species which contribute to about half of the total tree species richness (Bruelheide et al. 2011). In the nearby forests part of the Gutianshan National Nature Reserve, average species richness values of 42 woody species per 900 m<sup>2</sup> (Bruelheide et al. 2011) and 43 herb layer species per 100 m<sup>2</sup> (Both et al. 2011) have been reported.

The experiment comprises a total area of approximately 50 ha, where 566 experimental plots, with a plot size of 25.8 × 25.8 m<sup>2</sup> (corresponding to the traditional Chinese measurement unit of one mu) in horizontal projection, have been established. Each plot comprises 400 tree individuals, planted in a grid of 20 × 20 regularly arranged columns and rows and a distance of 1.29 m between trees (Yang et al. 2013, Bruelheide et al. 2014). Of the total species pool of 40 different native broad-leaved tree species, 24

species were assigned to site A and site B, respectively, which corresponds to an overlap of 8 species that have been planted on site A and site B. Within each site the species were assigned to tree richness levels of 0, 1, 2, 4, 8, 16 and 24 tree species. Understory vegetation in all plots was weeded twice a year since 2009 (site A) and 2010 (site B) which has been reduced to once a year since 2014 (with the exception of the 'no weeding' treatment described in Chapter 2 and 3; Yang et al. 2013, Bruelheide et al. 2014).

As a distinctive feature the BEF-China platform provides two different extinction scenarios (i.e. random and non-random). In the random extinction scenario, referred to in this thesis, tree species richness levels and tree species combinations were randomly allocated to the plots and followed a broken-stick design, ensuring that all species are equally represented at each richness level (Yang et al. 2013, Bruelheide et al. 2014). Through the mutual support of the different subprojects associated with the BEF-China experiment, environmental heterogeneity can be deliberately taken into account by characterizing the local topographic, microclimatic and edaphic environment of plots, for which the term 'ecoscape' was coined (Bruelheide et al. 2014). Moreover, additional integrated subplots (BEFmod experiment), on the northern edge of each of 70 very intensively studied plots, manipulation of resource supply and biotic interactions allow to explicitly test for further, interactive, diversity effects with different abiotic and biotic environments. For a more detailed description see Yang et al. (2013), Bruelheide et al. (2014) and Trogisch et al. (2017).

## 1.6 Structure and objectives of this thesis

In the context of the forest Biodiversity-Ecosystem Functioning project in southeast China (BEF-China) and the subproject 11 'The role of herb layer characteristics and productivity for forest ecosystem functioning' this thesis addresses herb layer characteristics and their feedback effects in response to tree species richness and identity as well as the interactive effects with the environmental context and time. Finally, this thesis addresses the role of stabilizing forces as predicted by the Janzen-Connell hypothesis (Janzen 1970, Connell 1971) for tree recruitment.

Chapter 2 asks to which degree tree species richness and identity affect herb layer composition, richness and productivity in 70 very intensively studied plots. Integrated manipulation of resource supply and biotic impact (i.e. BEFmod experiment) along a tree species richness gradient were then used to investigate how a modified environmental

setting interacts with tree species richness effects on herb layer composition, richness and productivity. In particular, it is hypothesized that (1) tree species richness and tree identity affect herb layer composition, richness and productivity and that (2) a modified environmental setting as assessed by the 'ecoscape' or provided by additional treatments interacts with tree richness and thus modifies tree species richness effects on herb layer composition, richness and productivity.

Based on the previous chapter, Chapter 3 investigate whether tree species richness is about to increase herb layer productivity (via increasing facilitation effects) or to reduce resource availability (by means of an even stronger increase in competition) in the current state of forest development and how these dynamics might change with time. In addition, this chapter also investigate the interactive role of different environmental settings for tree species richness effects on herb layer productivity. By making use of understorey biomass samples collected over a time period of three years along a tree species richness gradient at both sites (i.e. 70 very intensively studied plots) as well as additional subplot treatments (i.e. BEFmod experiment) it is hypothesized that (1) that tree species richness effects will decrease understorey species productivity as a result of lower resource availability over time and that (2) a modified beneficial environmental setting may counteract such detrimental effects thereby resulting in an increase in understorey species productivity. Finally, (3) it is expected that the relative importance of species identity and richness effects change over time as trees will grow higher and interactions will rise.

Chapter 4 investigates to which degree negative distance and density dependencies, as proposed by the Janzen Conell hypothesis, might be involved in establishing future tree species-rich forest systems. Juveniles plantations of eleven different tree species in their own and in foreign monocultures and at three different levels of planting densities, were used to separate between both negative distance and density dependencies. Additional plantations in a nearby Common Garden Experiment with different planting densities and 'shadow' treatments (i.e. simulating the effects of canopy shading) allowed to test for the amount as to which negative density dependencies were brought about by differences in light conditions. In particular, it is hypothesized that (1) performance, productivity, escape from herbivore attack (i.e. leaf damage) and ultimately survival is reduced when juveniles were planted in close distance to conspecific adults and (2) decrease with increasing densities of conspecific recruits, as predicted by Janzen-Connell. Further it is expected (3) that intraspecific competition for resources result in similar density-dependent pattern as predicted by the Janzen-Connell theory. Finally, it is hypothesized (4) that distance- and



density- dependencies interact with each other, with high densities being more detrimental at close distance to conspecific adults.

In conclusion, the present thesis aims at contributing to the understanding about the mechanisms behind tree layer  $\times$  herb layer interactions in forests ecosystem. The combined outcome of these studies can then provide new insights into the role of tree species richness and identity for herb layer characteristics (i.e. composition, richness and productivity) and tree recruitment.

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### Limited tree richness effects on herb layer composition, richness and productivity in experimental forest stands

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# Limited tree richness effects on herb layer composition, richness and productivity in experimental forest stands

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## Abstract

### Aims

In forests, the herbaceous understory vegetation plays an important role for ecosystem functioning as it represents a significant component of total aboveground productivity. In addition, the herb layer contributes to overall forest species richness and controls tree species regeneration. Vice versa, trees in the overstorey control understory herb and shrub growth through competition for resources. Using an experimental forest plantation with manipulated tree richness, we asked to which degree tree species richness and identity affect herb layer composition, richness and productivity and how these relationships across strata change with abiotic environmental conditions and competition intensity.

### Methods

In the context of the Biodiversity-Ecosystem Functioning project in subtropical China (BEF-China), we made use of the integrated BEFmod experiment arranged along a tree species richness gradient at two sites, with additional subplot treatments of phosphorus addition, herb layer weeding and no weeding. We recorded the understory vegetation and determined herb layer biomass production on a total of 201 subplots.

### Important Findings

We found only minor effects of tree layer richness on herb layer species composition and no significant effect on herb layer richness or productivity yet. However, there were strong tree layer identity effects on all response variables, which were partly explained by differences in leaf area index and by a high share of woody species both in total herb layer species richness and biomass. There were strong treatment effects, which were largest in the 'no weeding' treatment but we did not find any treatment × tree layer richness interaction in herb layer responses. Thus, these effects are mainly explained by increased competition intensity within the herb layer in the absence of weeding. Despite the young age of the experiment, the interactions between tree species identity, tree richness and the herb layer did already emerge and can be expected to become stronger with ongoing runtime of the experiment.

**Keywords:** experimental research platform of BEF-China, functional biodiversity research, forest understory, biomass, Jiangxi Province

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## INTRODUCTION

In forest ecosystem, the herbaceous understory vegetation is known to play an important role for ecosystem functioning (Gilliam 2007). Besides contributing an impressive part to the overall forest plant species richness, the herb layer controls tree species regeneration due to competitive and facilitative

interactions with tree recruits (George and Bazzaz 2003; Gilliam 2007; Taverna *et al.* 2005). In addition, the herb layer contributes to overall forest productivity, which is an important ecosystem function, since the herb layer biomass then enters food webs and affects nutrient storage and cycling (Mölder *et al.* 2008).

However, owing to the dominant position of trees in forests, the tree layer strongly affects the herb layer composition,

richness and biomass (Barbier *et al.* 2008; Chávez and Macdonald 2010; Mölder *et al.* 2008). A main mechanism of this tree dominance is through light interception, reducing the availability and variability of light for the forest understory and also affecting temperature and air humidity (Barbier *et al.* 2008). These effects vary strongly among tree species (Neufeld and Young 2003; Porté *et al.* 2004; Li *et al.* 2017b). Moreover, the identity of resident tree species was also shown to have a strong impact on water (Barbier *et al.* 2009) and nutrient availability (Prescott 2002; Neufeld and Young 2003; Li *et al.* 2017a) of the herb layer, for example through species specific fine-root traits (Sun *et al.* 2017). Even herbivory and pathogen load of the herb layer species may also change with tree species identity through differences among trees in attractiveness for arthropods, herbivores and pathogens (Augusto *et al.* 2002; Hahn *et al.* 2017; Staab *et al.* 2017). Finally, allelopathic compounds in the litter of certain tree species and litter accumulation affect germination and performance of herb layer species (Bertin *et al.* 2003; Ellsworth *et al.* 2004; Facelli and Pickett 1991; Rodríguez-Calcerrada *et al.* 2011).

Beside such species identity effects in the tree layer tree species diversity may also increase the variation in ecological conditions. More diverse stands of mixed forests have been shown to be more structured both horizontally and vertically than forests with lower diversity or monocultures (Morin *et al.* 2011), leading to a higher level of habitat heterogeneity in the understory and thus increased microsite availability for herb layer species. Thus, niche overlap of herb layer species might be reduced in high tree species richness stands, resulting in a higher level of resource partitioning as well as decreased population densities and reduced competition in the herb layer (Beatty 2003; Hutchinson 1959; Huston *et al.* 1979). In consequence, a more diverse tree layer would be expected to ensure a more diverse forest understory. In contrast, a higher niche complementarity among tree species at higher tree richness might also result in a more efficient resource use of the overstory components (Loreau and Hector 2001; Bu *et al.* 2017; Sun *et al.* 2017; Peng *et al.* 2017), reducing the amount of available resources for the understory. Moreover, the effect of environmental heterogeneity is not a constant and is mediated through population densities in the herb layer and disturbance intensities (Huston *et al.* 1979). However, while complementarity in resource use along species richness gradients has been intensively studied in grasslands (e.g. Fornara and Tilman 2008; von Felten *et al.* 2009; Roscher *et al.* 2012), in forests, the focus has been almost exclusively confined to the overstory components, i.e. tree species, only (e.g. Coomes *et al.* 2009; Forrester *et al.* 2006). In contrast, knowledge on mechanistic relationships among tree layer richness and herb layer composition, richness as well as productivity experimentally addressed in more complex vertically structured forest ecosystems is limited so far. While there is some evidence from observational studies from boreal (e.g. Cavard *et al.* 2011), temperate (e.g. Mölder *et al.* 2008; Vockenhuber *et al.* 2011) and subtropical forests

(e.g. Both *et al.* 2011), there are less studies using established tree richness gradients (but see Ampoorter *et al.* 2015) and there is none working on established gradients in the tropics or subtropics.

Observational studies on the relationship between tree layer and herb layer richness in natural forest ecosystems are confounded by environmental factors that affect both tree and herb layer and thus hamper a causal interpretation. In the majority of cases, observational studies do also not allow distinguishing between tree species identity and tree layer richness effects (Vockenhuber *et al.* 2011). If at all, separating the effect of a specific tree species identity from richness effects in observational studies can only be achieved by a well-balanced design, as it must be ensured that all species are equally represented at each richness level (Baeten *et al.* 2013; Nadrowski *et al.* 2010). Here, we make use of the forest Biodiversity-Ecosystem Functioning project in subtropical China (BEF-China), where tree species richness has been manipulated experimentally following a broken-stick design (Bruelheide *et al.* 2014). In this design, a set of 16 different tree species is subsequently divided into mixtures of 8, 4, 2 and 1 species, with the lower richness levels being nested subsets of the higher richness levels. The broken-stick design makes sure that all species are equally represented at every richness level, which allows separating tree richness effects from species identity effects (Bruelheide *et al.* 2014). Still, in BEF experiments with trees environmental variation cannot be fully controlled for. While in BEF grassland studies, experimental plots can often be established in homogeneous environments with uniform topography and soil properties, forest plots require larger areas to mimic realistic stands (see Bruelheide *et al.* 2014). Moreover, even a comparatively low environmental heterogeneity can strongly affect BEF relationships, as was demonstrated in the ‘Sardinilla’ forest experiment in Panama (Healy *et al.* 2008). When implementing BEF-China, environmental heterogeneity had been deliberately taken into account by characterizing the local topographic, microclimatic and edaphic environment of plots, for which the term ‘ecoscape’ was coined (Bruelheide *et al.* 2014). Thus, these variables can be used as co-drivers in tree layer–herb layer relationships addressed in the present study. In addition, we manipulated the environmental setting also at a subplot level (subsequently addressed as BEFmod subplots) to introduce variation not covered by the given ecoscape variation. While the herb layer in all plots in BEF-China has been continuously weeded regularly to increase the establishment of planted trees (Yang *et al.* 2013), free herb layer succession was allowed in one treatment of the BEFmod subplots. The general aim of the BEFmod experiment was to analyze whether BEF relationships become more pronounced in the presence of negative biotic feedback mechanisms (Schnitzer *et al.* 2011) which in this treatment are competitive effects among herb layer species. Similarly, BEF relationships should be steeper in more resource-rich environments (Reich *et al.* 2001; Weigelt *et al.* 2009). Accordingly, we additionally included a phosphorus fertilization subplot treatment of the BEFmod experiment.



In the present study, we asked how manipulated tree species richness and tree species identity affect the herb layer and to what extent tree layer–herb layer relationships change with abiotic environmental conditions and manipulated competition intensity and resource supply. In particular, we hypothesized that (i) tree layer richness and tree identity affect herb layer composition, richness and productivity and (ii) a modified environmental setting as assessed by the ecoscape or provided by the additional BEFmod treatments interacts with tree richness and thus modifies tree layer richness effects on herb layer composition, richness and productivity.

## METHODS

### Site information and experimental setup

The study was carried out on the experimental research platform of BEF-China, located in subtropical China near Xingangshan, Dexing, Jiangxi Province (117°55'E, 29°60'N). The platform was established in 2008 to answer the question to which degree plant richness maintains ecosystem functioning in subtropical forest ecosystems. The study area is located on 100–300 m above sea level and comprises two sites established in 2009 (site A) and 2010 (site B), at a distance of 4 km. The terrain is hilly ground with an average slope of 27.5° and 31° for site A and B, respectively (Bruehlheide *et al.* 2014). The climate is characterized by warm and humid summers and a short dry season between November and December. The mean annual temperature is 16.7°C and the mean annual precipitation 1821 mm (Yang *et al.* 2013).

Prior to the experiment, the sites had been planted with conifers, mostly *Pinus massoniana* Lamb. and *Cunninghamia lanceolata* (Lamb.) Hook. In contrast, natural forests in this region are dominated by evergreen tree species mixed with deciduous species which contribute to about half of the total tree species richness (Bruehlheide *et al.* 2011). The most abundant canopy tree species in old growth forests are *Castanopsis eyrei* (Champion ex Bentham) Tutcher, *Cyclobalanopsis glauca* (Thunberg) Oerst. and *Schima superba* Gardner and Champion, whereas the shrub layer is rich in *Rhododendron* and *Camellia* species (Bruehlheide *et al.* 2011). The high richness in woody species with on average 42 species per 900 m<sup>2</sup> (Bruehlheide *et al.* 2011), as identified in comparative study plots in near natural forests in the Gutianshan National Nature Reserve, is complemented by a further 43 herb layer species per 100 m<sup>2</sup> (Both *et al.* 2011).

The BEF experiment comprises 566 experimental plots on a total area of approximately 50 ha (Bruehlheide *et al.* 2014). In horizontal projection, each plot has the size of one mu (traditional Chinese measurement unit), which corresponds to 25.8 × 25.8 m<sup>2</sup>. In total, 40 different native broad-leaved tree species were planted at tree richness levels of 0, 1, 2, 4, 8, 16 to 24 tree species. Each plot comprises 400 tree individuals, planted in a grid of 20 × 20 regularly arranged columns and rows, with a distance of 1.29 m among trees. At the time of sampling, the species' mean height across subplots ranged

from 139 to 205 cm at site A and from 123 to 251 cm at site B with mean maximum height from 210 to 900 cm and 136 to 650 cm, respectively. In the random extinction scenario referred to in this study, tree species richness levels and tree species combinations were randomly allocated to the plots and followed a broken-stick design, ensuring that all species occur the same number of times and have the same number of individuals at each richness level (Bruehlheide *et al.* 2014; Yang *et al.* 2013). At each of the two sites, the research was carried out on the 35 very intensively studied plots (VIPs; see supplementary Table S1 for a detailed description of VIPs' richness levels, composition and replicates). In all plots, the understory vegetation was weeded twice a year since 2009 (site A) and 2010 (site B) and once in 2014 except for the 'no weeding' treatment described below.

In each VIP, subplots were subjected to a manipulation of resource supply and biotic interactions (BEFmod experiment), which started in 2014. On the northern edge of each VIP, 5 subplots were established, each measuring 5.16 × 5.16 m and containing 4 × 4 trees. Subplots were randomly assigned to five different treatments: 'No weeding' (NW, i.e. admitting all types of weeds, already established in 2011), 'Phosphorus fertilization' (P, i.e. applying 40 g triple super phosphate (H<sub>2</sub>PO<sub>4</sub>)<sub>2</sub> per tree, corresponding to 100 kg P/ha once in April 2014) and 'Control' (C, i.e. weeding as on the total plot level together with monthly H<sub>2</sub>O application). The BEFmod comprises two further treatments (F, i.e. Fungicide application, and I, i.e. Insecticide application), which we do not refer to in the present study. Herb layer data were collected in the NW, P and C treatments.

### Data collection

Between August 2014 and September 2014, herb layer species composition was recorded in 33 and 34 VIPs at site A and B, respectively, (three plots had to be omitted for accidental weeding and due to missing environmental data leading to 201 subplots in total). All herb layer species were identified and cover was estimated separately for each species. The herb layer was defined as all vascular plants including herbaceous species, climbers, ferns as well as all woody seedlings and saplings with <1.0 m height. The nomenclature of vascular plants follows the Flora of China (eFloras 2016). In each subplot, aboveground herb layer biomass was sampled from three patches, each 0.5 m × 0.5 m in size, located at randomly selected positions between planted trees and used as a proxy of herb layer productivity. The three biomass samples were pooled by subplot and sorted by life forms of woody species, ferns, grasses and herbs. Each sample was oven dried for 48 h at 70°C.

In order to get a measure of canopy-induced shading and understory light availability, hemispherical canopy photographs were taken at 1.2 m above the ground at the center of each subplot. Photographs were taken with a NIKON D5000 digital camera using a Nikon 10.5 mm f/2.8G ED AF DX Fisheye Nikkor Lens. Leaf Area Index (LAI) was calculated using HemiView V8 (Delta-T).

Species identity of planted trees was recorded in all subplots in 2013. Environmental data describing the ecoscape at the plot level were provided by the BEF-China database (Nadrowski *et al.* 2013). Topsoil samples were taken at 0–5 cm, sieved (<2 mm) and air-dried. Soil pH was measured using Sentix 81 electrodes and WTW pH-meter in a 1:2.5 soil:H<sub>2</sub>O suspension. Soil organic C and total soil N were measured using Elemental Analyzer (Scholten *et al.* 2017). Altitude, northness calculated as cosine of aspect in radians, slope, incident solar radiation, profile curvature (i.e. curvature in the direction of the slope) and plan curvature (i.e. curvature perpendicular to the direction of the slope) were derived from a geographic information system based on a 5 m digital elevation model (Bruehlheide *et al.* 2013a, 2013b).

### Statistical analyses

All analyses were performed separately by site. Predictors (pH, C:N ratio, LAI, altitude, northness, slope, incident solar radiation, profile curvature, plane curvature, tree layer richness, identity, treatments) were standardized which allows comparing relative effect sizes of parameter estimates.

Analyses referring to herb layer composition as response variable were done with multivariate approaches. Prior to all multivariate analyses, all species with five or less occurrences were removed. This procedure of downsizing was applied to facilitate the detection of the main gradients.

We applied Detrended Correspondence Analysis (DCA; Hill 1979) to determine gradient lengths as a measure of site homogeneity. Constrained correspondence analysis (CCA; Ter Braak 1986) using cover values for herb layer species was then used to analyze relationships between tree richness, weighted tree identities (i.e. using the number of times a tree species occurred in a subplot as weight), subplot treatments (NW, P, C), environmental variables and understory species composition separately. Regarding the effects of tree identities and environmental variables, all those variables were tested that were significant in a prior permutation test ( $N = 999$ ), reducing potential multicollinearity between variables. Effects of subplot treatments were analyzed using partial CCA (i.e. partial out plot effects) in order to test for subplot treatment effects within plot. Overall significance and significance of constraints was tested with permutation tests ( $N = 999$ ).

Data of herb layer richness and biomass were analyzed using general linear mixed models. Biomass data at the subplot level (i.e. by treatment) was log-transformed to obtain normal distribution. In the full model, tree richness, treatments and their interaction were considered fixed effects while plot was considered random. Tree richness was included as a continuous variable. We tested for effects of environmental variables and tree identities by implementing them as covariates in subsequent covariance analyses with general linear mixed models and comparing the Akaike's information criterion (AIC; Akaike 1973) using maximum likelihood. Models that differed <1 in AIC were considered equivalent. Less complex models were preferred. Final models were analyzed using restricted maximum likelihood.

All data analyses were performed within R v.3.2.0. DCA and CCA were performed using the vegan package v. 2.3 (Oksanen *et al.* 2015). Mixed effect models were conducted with lme4 v.1.1–8 and lmerTest v. 2.0–25 package.

## RESULTS

### Differences between sites

In total, 202 vascular plant species were recorded in the herb layer across the two sites. Among those, 121 species were common to both sites, leading to a species overlap of 59.9%. In the DCA, the gradient length was larger at site A than at site B (4.5 SD vs. 2.9 SD), thus showing a higher species turnover across all plots at site A (Table 1). Herb layer species richness was higher at site A, in terms of both total species richness of the site (169 vs. 154 species at site A and site B, respectively) and mean species richness per plot (31 vs. 27 species at site A and site B, respectively). In subplots at both sites, woody species contributed most to total herb layer species richness (66.16% vs. 70.85% at site A and site B, respectively; Table 1).

Mean herb layer biomass was higher at site B than at site A with mean dry weights of 625 g m<sup>-2</sup> and 352 g m<sup>-2</sup>, respectively. The two sites also differed in the relative biomass proportion of functional groups per subplot. While in subplots at both sites, ferns had the highest mean proportion of total herb layer biomass (38.69% vs. 40.54% at site A and site B, respectively), woody species tended to have a higher share

**Table 1:** Summary statistics for site A and site B including DCA gradient lengths as a measure of variation in species composition, total species richness values at the site level as well as at the subplot level: mean species richness, mean biomass as a measure of productivity and biomass proportions of functional groups

	Site A	Site B
First DCA axis length values	4.5	2.9
Total number of herb layer vascular plant species	169	154
Mean proportion of herb layer species richness by functional group and per subplot (%)		
Grasses	8.41	8.46
Ferns	11.78	13.47
Herbs	13.65	7.22
Woody species	66.16	70.85
Mean number of herb layer vascular plant species per 5 × 5 m subplot	31	27
Herb layer biomass	351.87	625.34
Mean proportion of herb layer biomass by functional group and per subplot (%)		
Grasses	21.50	37.43
Ferns	38.69	40.54
Herbs	4.22	1.06
Woody species	35.57	20.97

Herb layer biomass = mean oven-dried aboveground biomass per subplot (g m<sup>-2</sup>).

on the biomass at site A (35.57% compared to 20.97% at site B), whereas at site B grasses had a higher mean proportion (37.43% compared to 21.50% at site A; Table 1).

### Constrained correspondence analysis

While the CCA revealed that tree layer richness did not affect understory species composition at site A, there was a significant effect at site B. Species composition was significantly associated with tree identities at both sites, with five and one significant effects of single species on herb layer species composition at site A and B, respectively. (Fig. 1a and b; Table 2). While at site A, there were significant relationships identified between herb layer composition and *Koelreuteria bipinnata* Franchet, *Castanea henryi* (Skan) Rehder and E. H. Wilson, *Cyclobalanopsis myrsinifolia* (Blume) Oersted *Choerospondias axillaris* (Roxburgh) B. L. Burtt and A. W. Hill, and *Nyssa sinensis* Oliver, there were fewer relationships at site B, as displayed only for *Machilus thunbergii* Siebold and Zuccarini.

Both sites showed highly significant differences in the herb layer species composition between the C and NW treatments across subplots within plots. In contrast, herb layer species composition was significantly affected by P addition at B only (Table 2).

At both sites, CCA indicated a strong relationship of the floristic gradient to the C:N ratio in the topsoil, ranging from 10.51 to 20.47 at site A and 12.98 to 17.91 at site B, respectively. In addition, at both sites, there were opposing effects, with on the one hand of altitude and solar and with pH and LAI on the other hand. While at site A, pH ranged from 4.24 to 5.39, the values were slightly lower at site B ranging from 4.22 to 4.99. In addition, at both sites, lower levels of understory light (LAI) and, for site B, less exposed plots (i.e. stronger concave curvature in the direction of the slope) coincided with plots of high pH values, narrow C:N ratios and lower incident solar radiations values (Fig. 1a and b).

### Linear mixed effect models

In the final linear mixed effect models for both sites, the subplot treatments were retained as significant factor for predicting herb layer species richness and biomass. While in the NW treatment herb layer richness was decreased, P addition showed no effect. Similarly, herb layer biomass was higher in the NW treatment than in the control but did not significantly increase with P addition (Table 3). In contrast, tree richness had only marginally significant effects on herb layer richness at site A and no significant effect on herb layer richness at site B; however, including tree richness in the model improved model quality for both sites. Herb layer biomass was neither affected by tree richness as main factor nor by its interaction with the subplot treatments. Additional environmental variables that explained herb layer species richness differed between sites. At site A, herb layer species richness decreased with increasing incident solar radiation and C:N ratio. At site B, herb layer species richness increased similarly with narrower C:N ratio (Table 3). Herb layer biomass decreased with

LAI at site A, but decreased with wider C:N ratio at site B. At site A and B herb layer biomass decreased with plot exposure (i.e. stronger convex curvature perpendicular to the slope; Table 3).

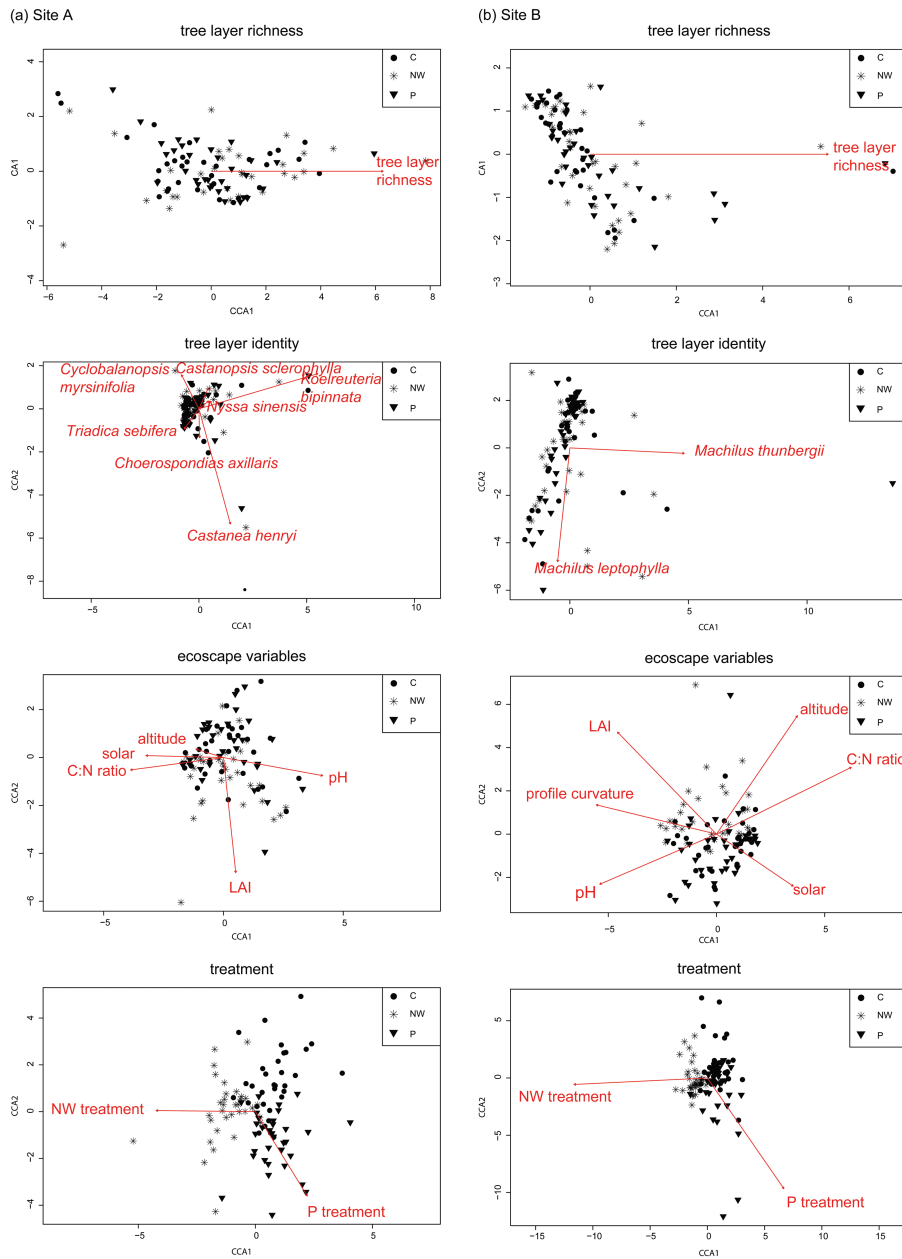
In all final models at both sites, tree species identity was retained to predict herb layer richness or biomass (Table 3). Here, presence of species significantly influenced herb layer species biomass (*Choerospondias axillaris*, *Castanopsis fargesii* Franchet, *Elaeocarpus japonicus* Siebold and Zuccarini).

## DISCUSSION

Four to five years after establishing the plantation (2009 at site A, 2010 at site B), herb layer species composition, richness and biomass showed strong responses to some predictors of environment, subplot treatment and tree identity, while the effects of tree species richness was not yet clearly visible which is in accordance to Yang *et al.* 2017 who have found similar results for the shrub layer. Nevertheless, our study contributed to the current knowledge of tree and herb layer relationships in several aspects.

Although both sites were considered comparable with respect to site conditions, they differed in herb layer richness, composition and biomass. When setting up the experiment, two sites were mainly chosen to evaluate the impact of different tree species pools on BEF relationships (Bruehlheide *et al.* 2014). Our results show that associated communities, such as those of the herb layer, respond to different environmental variables such as pH, solar radiation and altitude that were not controlled by the experimenter. Although some differences in response variables between both sites might be partly explained by the difference in runtime of the experiment after establishment, the differences in predictor variables point to other confounding factors. While ferns had the highest share in herb layer biomass at both sites, at site B, the biomass proportion of grasses was even higher. A similar pattern was already found in 2012, i.e. early after establishment of the BEFmod experiment, for the NW subplots only, with high biomass proportions of ferns, however, even a higher share of grasses at site B and a higher share of woody species at site A (unpublished data). In accordance to our findings, Both *et al.* (2011) reported that tree recruits contributed to a large part of the herb layer species richness and biomass in observational plots of different successional stage, corresponding to the high proportions of woody species we found at both sites.

Significant effects of tree richness on herb layer composition were only found for site B and there was no such effect on herb layer richness or productivity. Thus, we did not encounter much support for our first hypothesis. The expected effect of higher structural richness in more diverse stands of tree species (Morin *et al.* 2011) did not involve a higher herb layer species richness or biomass. Thus, if a higher level of habitat heterogeneity resulted in a higher level of resource partitioning in the tree layer and a decreased competition



**Figure 1:** Constrained correspondence analysis (CCA) of all herb layer species occurring (a) more than five times in the subplots of site A (96 cases out of 99), (b) occurring more than five times in the subplots of site B (78 cases out of 102). Subplots are separated by treatments and displayed by circles (control), stars (no weeding) and triangles (phosphorus addition). Species names refer to the tree species planted in the plots. Influence of tree layer richness, species identity, ecoscape and treatment was tested separately, using individual ordinations. Prior to the analysis, the constrained variables (i.e. tree layer identity and ecoscape variables) were selected using permutation tests ( $n = 999$ ) and keeping all significant predictors.

intensity within the herb layer (Beatty 2003; Hutchinson 1959; Huston et al. 1979), this effect is not yet visible. The absence of tree richness effects on the herb layer

corresponds to results of Both et al. (2011) for the observational plots in the Gutianshan National Nature Reserve (CSPs), which also showed no relationships between herb and

**Table 2:** Permutation test ( $n = 999$ ) for the joint effect of the constraining variables in the Canonical correspondence analysis (CCA)

	DF	Chi-square	<i>F</i>	Pr(> <i>F</i> )	
<b>Site A</b>					
Treatment	2	0.141	1.825	<0.001	***
P vs. C	1	0.053	1.379	0.087	.
NW vs. C	1	0.088	2.271	0.001	***
Residual	64	2.473			
Proportion of explained variation (%)					2.56
Tree layer richness	1	0.030	0.539	0.948	
Tree layer richness	1	0.030	0.539	0.965	
Residual	97	5.471			
Proportion of explained variation (%)					0.55
Tree layer identity	7	1.217	3.692	<0.001	***
<i>Koelreuteria bipinnata</i>	1	0.321	6.817	<0.001	***
<i>Castanea henryi</i>	1	0.245	5.208	<0.001	***
<i>Cyclobalanopsis myrsinifolia</i>	1	0.181	3.852	<0.001	***
<i>Choerospondias axillaris</i>	1	0.134	2.849	0.023	*
<i>Nyssa sinensis</i>	1	0.136	2.896	0.037	*
<i>Castanopsis sclerophylla</i>	1	0.108	2.293	0.065	.
<i>Triadica sebifera</i>	1	0.091	1.929	0.063	.
Residual	91	4.285			
Proportion of explained variation (%)					22.12
Ecoscape	5	0.757	2.967	<0.001	***
pH	1	0.238	4.666	<0.001	***
Solar	1	0.172	3.371	<0.001	***
C:N ratio	1	0.105	2.052	0.009	**
LAI	1	0.149	2.923	0.009	**
Altitude	1	0.093	1.821	0.02	*
Residual	93	4.745			
Proportion of explained variation (%)					13.76
<b>Site B</b>					
Treatment	2	0.139	2.808	<0.001	***
P vs. C	1	0.053	2.127	0.002	**
NW vs. C	1	0.087	3.490	<0.001	***
Residual	66	1.637			
Proportion of explained variation (%)					4.21
Tree layer richness	1	0.146	4.625	<0.001	***
Tree layer richness	1	0.146	4.625	<0.001	***
Residual	100	3.162			
Proportion of explained variation (%)					4.42
Tree layer identity	2	0.159	2.503	0.005	**
<i>Machilus thunbergii</i>	1	0.093	2.935	0.012	*
<i>Machilus leptophylla</i>	1	0.066	2.072	0.052	.
Residual	99	3.149			
Proportion of explained variation (%)					4.81
Ecoscape	6	0.580	3.363	<0.001	***
C:N ratio	1	0.191	6.635	<0.001	***
LAI	1	0.128	4.442	<0.001	***
Profile curvature	1	0.074	2.566	0.003	**

**Table 2:** *Continued*

	DF	Chi-square	<i>F</i>	Pr(> <i>F</i> )	
Solar	1	0.078	2.730	<0.001	***
pH	1	0.059	2.054	0.007	**
Altitude	1	0.050	1.752	0.034	*
Residual	95	2.729			
Proportion of explained variation (%)					17.52

Prior to the analysis, the constrained variables (i.e. tree layer identity and ecoscape variables) were selected using permutation tests ( $n = 999$ ) and keeping all significant predictors. Significance levels are \*\*\*<0.001; \*\*<0.01; \*<0.05; .<0.1.

tree layer richness. Nevertheless, owing to the broken-stick design of the BEF-China experiment, we were able to detect tree species identity effects on herb layer composition and biomass, thus confirming this part of the first hypothesis. In this respect, our results fully conform to those of [Ampoorter \*et al.\* \(2015\)](#) who described the absence of tree richness effects on total aboveground herb layer biomass for temperate forest stands in the BIOTREE experiment in Kaltenborn (Germany).

As hypothesized, we encountered significant effects of the ecoscape and of the BEFmod treatments on herb layer composition, richness and productivity, i.e. providing evidence that the environmental setting strongly affects BEF relationships. There were strong effects of the non-weeding treatment on species composition as well as an increase in herb layer biomass and a decrease in herb layer species richness. These findings suggest that the decrease in species richness results from increased competition with increasing biomass in the herb layer. [Huston \*et al.\* \(1979\)](#) introduced the idea that species richness is at maximum when disturbance counteracts competitive exclusion. In accordance, the absence of disturbance in the NW treatment favored fast growing grasses and woody species with high biomass production, i.e. competitors in the sense of [Grime \(1973\)](#), that outcompeted other herb layer species. We found a significant effect of the phosphorus addition treatment only at site B. This shows that the nutrient manipulation had an effect on the floristic composition, however, strongly depending on the site. Although phosphorus is probably a limiting resource, a direct impact on herb layer biomass or an indirect impact on the herb layer through the tree layer was not consistently visible. This might be due to the differences in runtime of the plantings, given that site B was established 1 year later with thus a less developed overstory than at site A. Whereas the overstory species composition is largely determined by the species' ability to exploit light, the understory is driven by water and nutrient availability ([Gilliam \*et al.\* 1995](#)), and the latter can thus assumed to be more responsive to phosphorus addition. Moderate effects of fertilization might also be due to the short runtime of the treatment given that the fertilization application had just started in the same year. However, for grassland ecosystems it has been shown that although P fertilization might be associated with shifts in plant community composition in the long run, these shifts do not necessarily have to translate into shifts in community diversity ([Avolio \*et al.\* 2014](#)).

There were other environmental effects on species composition such as incipient light conditions, as quantified by the LAI measurements. Availability and variability of light is known to affect understory species compositions ([Ampoorter \*et al.\* 2015](#); [Augusto \*et al.\* 2003](#)) and to vary largely among tree species identities ([Neufeld and Young 2003](#); [Porté \*et al.\* 2004](#)). For a subset of our experimental tree species, e.g. [Lang \*et al.\* \(2012\)](#) could demonstrate that the competition for light among tree species affects their crown architecture and foliage distribution, indicating niche separation with regard to light harvesting. Thus, the significant effect of LAI on herb layer species composition at both sites as well as on biomass at site A might be an indirect effect of tree species identities.

Beside LAI, C:N ratio and pH values were found to significantly affect herb layer species composition. We found less exposed plots (i.e. lower altitude and solar radiation as well as stronger concave curvature in the direction of the slope for site B) to be related to higher pH values and lower C:N ratios. In particular, there were negative relationships between the C:N ratio and herb layer richness, with lower species numbers at wider C:N ratios, which points to a positive dependence of herb layer richness on nutrient supply. Such differences in the topsoil C:N ratio can be a legacy of the preceding land use by conifer plantations. However, they might also be affected already by the planted trees, and then, would also be an indirect effect of species identity. Tree species having litter with a narrow C:N ratio might already have modified their site conditions.

[Gilliam \*et al.\* \(1995\)](#) stated that a linkage between overstory and understory vegetation cannot be expected earlier than approximately 20 year after clear-cutting because the species composition of both layers is governed by different main environmental factors (see above). This was also confirmed on the basis of broad scale forest inventory data in temperate Canadian forests, where the influence of local site conditions on plant diversity patterns strongly differed between strata ([Zhang \*et al.\* 2014](#)). Therefore, with an increasing number of woody species within the herb layer during succession overstory and understory begin to respond more similarly to environmental gradients ([Gilliam \*et al.\* 1995](#)). However, this finding holds for temperate forests and these processes might be accelerated in tropical and subtropical forests. In accordance to [Both \*et al.\* \(2011\)](#) who studied Comparative Study

**Table 3:** Optimal general linear mixed effects model for predicting herb layer biomass and richness

	Estimate	Standard error	df	<i>t</i> value	Pr (>  <i>t</i>  )	
<b>Site A</b>						
<b>Biomass</b>						
(Intercept)	4.833	0.130	85.65	37.097	<0.001	***
NW treatment	0.783	0.187	69.41	4.182	<0.001	***
P treatment	0.046	0.174	61.80	0.263	0.793	
LAI	-0.331	0.090	84.01	-3.668	<0.001	***
pH	0.001	0.117	26.61	0.012	0.991	
Plan curvature	0.309	0.123	29.58	2.513	0.018	*
<i>Quercus fabri</i>	0.141	0.086	28.33	1.636	0.113	
<i>Choerospondias axillaris</i>	-0.184	0.083	27.00	-2.212	0.036	*
<i>Castanopsis eyrei</i>	0.161	0.087	25.24	1.855	0.075	.
<b>Richness</b>						
(Intercept)	32.777	0.949	75.50	34.547	<0.001	***
Tree layer richness	-1.218	0.680	26.00	-1.790	0.085	.
NW treatment	-4.052	1.177	64.00	-3.444	0.001	**
P treatment	-1.078	1.177	64.09	-0.916	0.363	
pH	0.156	1.001	26.07	0.156	0.877	
C:N ratio	-4.196	1.084	26.01	-3.871	<0.001	***
Slope	0.688	0.883	25.99	0.779	0.443	
Solar	-2.768	0.769	26.09	-3.598	0.001	**
<i>Schima superba</i>	-1.300	0.713	27.67	-1.823	0.079	.
<b>Site B</b>						
<b>Biomass</b>						
(Intercept)	5.610	0.103	86.64	54.633	<0.001	***
NW treatment	0.665	0.134	65.88	4.960	<0.001	***
P treatment	-0.018	0.134	65.94	-0.133	0.895	
C:N ratio	-0.180	0.082	28.06	-2.195	0.037	*
Altitude	-0.080	0.086	28.15	-0.938	0.356	
Plan curvature	0.193	0.072	28.08	2.657	0.013	*
<i>Castanopsis fargesii</i>	-0.168	0.068	30.13	-2.480	0.019	*
<i>Elaeocarpus japonicus</i>	-0.169	0.071	30.41	-2.400	0.023	*
<b>Richness</b>						
(Intercept)	27.733	1.146	80.53	24.206	<0.001	***
Tree layer richness	1.715	1.089	76.52	1.575	0.119	
NW treatment	-4.773	1.632	75.76	-2.925	0.005	**
P treatment	1.378	1.289	63.16	1.069	0.289	
LAI	1.326	0.810	91.56	1.637	0.105	
C:N ratio	-2.571	0.815	30.64	-3.155	0.004	**
<i>Phoebe bournei</i>	1.562	0.777	32.14	2.010	0.053	.
Tree layer richness:NW	-2.000	1.300	63.93	-1.538	0.129	
Tree layer richness:P	1.111	1.288	63.31	0.862	0.392	

Significance levels are \*\*\*<0.001; \*\*<0.01; \*<0.05; .<0.1.

Plots along gradients of diversity and succession, we found woody samplings already contributing significantly to herb layer species richness and biomass in the present study. This might explain the LAI effects detected and thus indicate that, in the subtropics, presumably less time is needed until

a linkage between overstory and understory vegetation may emerge. Considering the early phase of the project, we expect stronger and clearer relationships between tree and herb layer through time as trees will grow higher and interactions will rise.

## SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Plant Ecology* online.

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**Understorey aboveground biomass production decreases with overstorey tree species identities and time**

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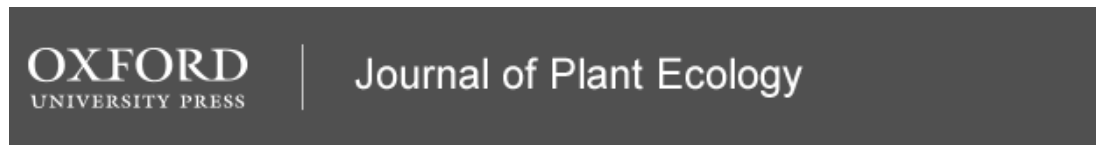
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1 **Running title:** Tree identity effects on understorey productivity

2 **Understorey aboveground biomass production decreases with overstorey tree**  
3 **species identities and time**

4 Markus S. Germany<sup>1,2,3</sup>, Helge Bruelheide<sup>2,3</sup> & Alexandra Erfmeier<sup>1,3</sup>

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## 18 **Abstract**

### 19 **Aims**

20 Positive biodiversity ecosystem functioning relationships have been widely reported and  
21 predominating for grassland ecosystems. However, this does not necessarily have to  
22 apply accordingly in more complex situations such as across different vertical strata in  
23 forests, e.g., where overstorey tree species richness have been shown to be associated  
24 with a lower understorey productivity. Whether or not tree species richness effects add  
25 to understorey productivity by increasing (e.g., due to habitat heterogeneity) or reducing  
26 resource availability (i.e. through increasing competition) and whether understorey  
27 productivity is indeed being governed more strongly by tree species identity is likely to  
28 change over time. Moreover, studies also suggested that richness-productivity  
29 relationships change with the environmental context. Using an experimental forest  
30 plantation with manipulated tree species richness, this study examines these temporal  
31 and environmental dynamics across strata.

### 32 **Methods**

33 In the context of the Biodiversity-Ecosystem Functioning project in subtropical China  
34 (BEF-China), we made use of understorey biomass samples repeatedly collected over a  
35 time period of three years along a tree species richness gradient. In the context of  
36 experimentally manipulated richness-productivity relationships at two sites, the effects  
37 of phosphorus addition, herb layer weeding and no weeding were studied on subplots  
38 for their impact on understorey biomass

### 39 **Important Findings**

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40 While we found significant and consistent tree layer identity effects on understorey  
41 biomass, for tree species richness no such an effect could be found. However, our  
42 results also indicate that among structural layers in forests, there might not be a single,  
43 generalizable species richness-productivity relationship and that the extent as to which  
44 overstorey-related environmental factors such as light transmittance contribute to  
45 understorey productivity change with time. Overall, we could demonstrate that temporal  
46 dynamics should be considered when studying relationship among structural layers in  
47 forests.

For Peer Review



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48 **Keywords**

- 49 BEF-China, subtropical forests, species diversity and richness, productivity, horizontal  
50 forest strata, facilitation, competition

For Peer Review

## 51 **Introduction**

52 In recent years, positive biodiversity ecosystem functioning (BEF) relationships, in  
53 particular, productivity, have been widely reported in near-natural forests (e.g. Vilà *et*  
54 *al.*, 2007, 2013; Paquette and Messier, 2011; Barrufol *et al.*, 2013; Jucker *et al.*, 2014)  
55 as well as in experimentally controlled forest ecosystems (e.g. Erskine *et al.*, 2006;  
56 Scherer-Lorenzen *et al.*, 2007; Grossman *et al.*, 2017; Fichtner *et al.*, 2018). On a global  
57 scale, empirical assessment of BEF-(biodiversity-ecosystem functioning) relationships  
58 predict an average 3% decrease in productivity given a 10% decrease in species richness  
59 (Liang *et al.*, 2016). However, while most studies in forest ecosystems have focussed on  
60 the relationships between overstorey species diversity and productivity, little work has  
61 been done on the associations between the structural forest layers, in particular on the  
62 effects of the overstorey on the understorey (e.g. Vockenhuber *et al.*, 2011; Cavard *et*  
63 *al.*, 2011; Ampoorter *et al.*, 2015; Zhang *et al.*, 2016, 2017). This is surprising given  
64 that the understorey vegetation has been shown to play an important role for ecosystem  
65 functioning, particularly, through influencing soil microbes and nutrient dynamics  
66 (Gilliam, 2007; Mölder *et al.*, 2008; Rein *et al.*, 2016).

67 Owing to the dominant role of trees, the overstorey stratum may impose competitive  
68 constraints to understorey vegetation by altering above- and belowground resource  
69 availability and heterogeneity (Gilliam *et al.*, 1995; Gilliam, 2007; Barbier *et al.*, 2008).  
70 For example, species-specific differences among tree species modify canopy structure  
71 and light transmission as well as light interception, thereby altering the availability and  
72 variability of light for the forest understorey (Neufeld and Young, 2003; Porté *et al.*,  
73 2004). Such direct impacts on understorey resource availability may translate into  
74 effects on understorey species composition, productivity (Ampoorter *et al.*, 2015;

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3 75 Germany *et al.*, 2017; De Groot *et al.*, 2017) and tree recruitment (Germany *et al.*,  
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5 76 2019). In addition to tree species identity effects on the understorey, forest understorey  
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7 77 vegetation may also be subjected to facilitating (i.e. higher resource availability and  
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9 78 heterogeneity; Beatty, 2003; Yankelevich *et al.*, 2006; Bartels and Chen, 2010;  
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11 79 Holmgren *et al.*, 2015) and/or competition (i.e. lower resource availability and  
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13 80 heterogeneity; Anderson *et al.*, 1969; Bartels and Chen, 2010) when stands are  
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15 81 composed of multiple tree species. In consequence, we may expect overstorey effects,  
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17 82 including both, signals of tree species identity and tree species richness, as a  
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19 83 combination of facilitation and competition effects, to alter understorey species  
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21 84 productivity (Fridley, 2002; Ampoorter *et al.*, 2015; Wright *et al.*, 2017; De Groot *et*  
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23 85 *al.*, 2017).

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29 86 Moreover, tree species richness and identity effects as well as the relative dominance of  
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31 87 particular identities vary with stand development and temporal changes in species  
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33 88 interactions, as reported in modelling approaches (Cardinale *et al.*, 2000), literature  
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35 89 review on mixed forest stands (Forrester, 2014), and in outcomes of forest biodiversity  
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37 90 ecosystem functioning experiments (Potvin and Gotelli, 2008; Huang *et al.*, 2018).  
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39 91 Intuitively an increase in crown filling usually takes place on the basis of stand  
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41 92 development and increasing canopy closing (Lang *et al.*, 2012; Sapjanskas *et al.*,  
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43 93 2014). Yet, in addition, light niche differentiation in the overstorey can become more  
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45 94 efficient in mixed-species forests due to complementary crowns architectures among  
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47 95 species in canopy space (Jucker *et al.*, 2015; Williams *et al.*, 2017). In consequence, we  
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49 96 might expect tree species richness effects on the herb layer to become more pronounced  
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51 97 over time as stands develop and competition for light and/or other resources increases.  
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53 98 Therefore, we hypothesize that the amount as to which understorey productivity is  
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3 99 predominantly being governed by tree species identity as well as facilitative and  
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5 100 competitive richness effects changes over time (Germany *et al.*, 2017).  
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9 101 In the present study, we make use of the forest Biodiversity-Ecosystem Functioning  
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11 102 Main Experiment plantation in subtropical China (BEF-China) with tree species  
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13 103 richness gradients established from 1 to 24 specie following a broken-stick design.  
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15 104 Using this design ensures that all species are equally represented at every richness level  
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17 105 (Bruehlheide *et al.*, 2014), which allows to separate between tree species identity and tree  
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19 106 species richness effects also on the understorey characteristics. While studies on BEF  
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21 107 conducted in forest ecosystems have often been criticized for failing to account for  
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23 108 environmental drivers (Flombaum and Sala, 2008; Duffy, 2009; Willig, 2011), BEF-  
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25 109 China, in addition, takes this circumstance particularly into account (Bruehlheide *et al.*  
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27 110 2014). We manipulated the environmental setting at a subplot level (subsequently  
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29 111 addressed as BEFmod subplots) to answer to what extent the relative contributions of  
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31 112 species richness and identity to ecological processes will change in different  
32  
33 113 environmental settings (Cardinale *et al.*, 2000). In a previous study, using this platform,  
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35 114 Germany *et al.* (2017) experimentally tested to which degree tree species richness and  
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37 115 identity affect understorey species composition, richness and productivity and how  
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39 116 these relationships across strata vary with altered abiotic environmental conditions (as  
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41 117 induced by phosphorus addition) and competition intensity. The present study focuses  
42  
43 118 on understorey productivity of repeated measurements taken over 3 years. By referring  
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45 119 to this time series, we can test to what extent effects of tree species identity and thus of  
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47 120 the net effect from facilitating and competing tree species richness changes over time  
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49 121 due to enhanced interaction among tree individuals and species. In particular, increased  
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51 122 complementarity over time have shown to improve resource use efficiency in the  
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53 123 overstorey. More specifically, we thus hypothesize: (i) that tree species richness effects  
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3 124 will decrease understorey species productivity as a result of lower resource availability  
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5 125 over time. Further, (ii) we expect that a modified beneficial environmental setting may  
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7 126 counteract such detrimental effects thereby resulting in an increase in understorey  
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9 127 species productivity. Finally, (iii) we expect the relative importance of species identity  
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11 128 and richness effects to change over time as trees will grow higher and interactions will  
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## 130 **Methods**

### 131 **Site information**

132 The study was carried out on the experimental research platform of BEF-China. Located  
133 in subtropical China near Xingangshan, Dexing County, Jiangxi Province (117°55'E,  
134 29°60'N) and situated on 100–300 m a. s. l. the platform comprises two sites as forest  
135 plantations established in 2009 (site A) and 2010 (site B), at a distance of 4 km. The  
136 region can be described as hilly ground with an average slope of 27.5° and 31° for site  
137 A and B, respectively (Bruelheide *et al.*, 2014). The climate is a seasonal subtropical  
138 monsoon climate with warm and humid summers and a short dry winter season between  
139 November and December. The mean annual temperature is 16.7°C and the mean annual  
140 precipitation 1821 mm (Yang *et al.*, 2013).

141 The potential natural vegetation is a species-rich deciduous forest with evergreen tree  
142 species dominating in total number, while deciduous species contribute to about half of  
143 the total tree species richness. Inventories in the nearby Gutianshan National Nature  
144 Reserve revealed an average of 42 woody species per 900 m<sup>2</sup>, and an average of 43  
145 understorey species per 100 m<sup>2</sup> (Bruelheide *et al.*, 2011; Both *et al.*, 2011). In old  
146 growth forests, the most abundant canopy tree species are *Castanopsis eyrei* (Champion  
147 ex Bentham) Tutchter, *Cyclobalanopsis glauca* (Thunberg) Oerst. and *Schima superba*  
148 Gardner and Champion, whereas the shrub layer is rich in *Rhododendron* and *Camellia*  
149 *species* (Bruelheide *et al.*, 2011). However, prior to the experiment both sites were  
150 covered with plantations of conifers, mostly *Pinus massoniana* Lamb. and  
151 *Cunninghamia lanceolata* (Lamb.) Hook.

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3 152 With the plot size of 25.8 x 25.8 m<sup>2</sup> (corresponding to the traditional Chinese  
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5 153 measurement unit of one mu) in horizontal projection and a total area of approximately  
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7 154 50 ha distributed across both sites, the experimental research platform comprises 566  
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9 155 experimental plots representing the BEF-China Main Experiment (Bruehlheide *et al.*,  
10  
11 156 2014). The total species pool used for this experiment consists of 40 different native  
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13 157 broad-leaved tree species, of which 24 each were used in site A and site B including an  
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15 158 overlap of 8 species. Within site, species were assigned to tree species richness levels of  
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17 159 0, 1, 2, 4, 8, 16 to 24 tree species following a broken-stick design (for details of species  
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19 160 composition and levels of tree species richness diversity see Bruehlheide *et al.* (2014).  
20  
21 161 Planted in a grid of 20 × 20 regularly arranged columns and rows and at distance of 1.29  
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23 162 m among trees, each plot comprises 400 tree individuals (Yang *et al.*, 2013; Bruehlheide  
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25 163 *et al.*, 2014). While, in the beginning, the understorey vegetation of all plots was  
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27 164 weeded twice a year since (since 2009 at site A and 2010 at site B), weeding has been  
28  
29 165 applied once a year since 2014; with the exception of the ‘no weeding’ treatment  
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31 166 described below.  
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### 39 **Experimental setup**

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43 168 The study was carried out on Site A and Site B, each comprising 35 plots, covering the  
44  
45 169 full tree species richness gradient and labelled as very intensively studied plots (VIPs).  
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47 170 The nomenclature of vascular plants follows the Flora of China (eFloras 2020). On the  
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49 171 northern edge of each of the 70 VIPs a strip subdivided in 5 subplots in total was  
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51 172 implemented, with each subplot containing 4 × 4 trees and therefore measuring 5.16 ×  
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53 173 5.16 m<sup>2</sup> in size. These subplots were subjected to the BEFmod experiment, a  
54  
55 174 manipulation of resource supply and biotic interactions (BEFmod experiment), which  
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57 175 started in 2014. Each subplot was randomly assigned to one of the following different  
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59 176 treatments: i) ‘No weeding’ (NW, i.e. admitting all types of weeds, already established  
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3 177 in 2011), ii) ‘Phosphorus fertilization’ (P, i.e. applying 40 g triple super phosphate  
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5 178  $(\text{H}_2\text{PO}_4)_2$  per tree, corresponding to 100 kg P/ha once in April 2014), iii) ‘Control’ (C,  
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8 179 i.e. weeding as on the total plot level together with monthly  $\text{H}_2\text{O}$  application), iv)  
9  
10 180 ‘Fungicide application’ and v) ‘Insecticide application’. In the present study, we refer to  
11  
12 181 the “No weeding”, “Phosphorous fertilization” and “Control” treatments (in the  
13  
14 182 following: NW, P and C, respectively) only.

### 183 **Data collection**

184 In 2014, 2015 and 2016, understorey aboveground biomass, was harvested in each of  
185 these three treatments once a year during the time period from August to September and  
186 served as a proxy of understorey productivity across years. Samples were harvested in  
187 subplots as replicates at three out of nine randomly selected grid positions, each  $0.5 \text{ m} \times$   
188  $0.5 \text{ m}$  in size, in between the planted trees. The three biomass samples then were pooled  
189 by plot and treatment to account for within-understorey heterogeneity by treatment (see  
190 Germany et al. 2017 for a more detailed description).

191 In 2014, hemispherical photographs were taken at 1.2 m above soil surface at the center  
192 of each subplot to get a measure of light transmission and more specifically information  
193 about canopy-induced shading. Canopy was fully foliated at that time of the  
194 measurements. Photographs were taken with a NIKON D5000 digital camera using a  
195 Nikon 10.5 mm f/2.8G ED AF DX Fisheye Nikkor Lens. Leaf Area Index (LAI) was  
196 calculated using HemiView V8 (Delta-T) and varied from 0 to 6.1.

### 197 **Statistical analyses**

198 Data of understorey biomass was analysed by fitting mixed effects models with  
199 Gaussian error distribution. Biomass data at the subplot level (i.e. by treatment) was



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200 log-transformed prior to analysis. A minimum skewness was determined by adding a  
201 value of twelve. Continuous predictors (i.e. time and tree species richness) and covariate  
202 (i.e. LAI) were standardized (by subtracting the mean and dividing by two standard  
203 deviations), which allows comparing relative effect sizes of parameter estimates  
204 (Gelman, 2008). The relative abundance of each tree species identity was determined by  
205 dividing the number of occurrences by the maximum number of occurrences possible  
206 for each species within a single Treatment (N = 16). During the model selection, tree  
207 species richness, tree species identity, time, treatment, their interactions (i.e.  
208 treatment:tree species richness, time:tree species richness, time:tree species identity and  
209 time:treatment) and LAI were considered fixed effects, while site and plot (i.e.  
210 1|site/plot) and their interaction with treatment (1|site:plot:treatment) were considered  
211 random factors. Tree identities were subsequently added to the model using forward  
212 selection based on the Akaike's information criterion (AIC; Akaike, 1973). Models that  
213 differed <1 in AIC were considered equivalent. Less complex models were preferred.  
214 Final models were analysed using restricted maximum likelihood. Moreover, to  
215 investigate whether understorey productivity is being governed more strongly by LAI,  
216 tree species identity or tree species richness and whether this is likely to change over  
217 time, we estimated the explained variance (marginal R<sup>2</sup>) for Linear Mixed-effects  
218 Models (Nakagawa and Schielzeth, 2013; Johnson, 2014) by separated models for each  
219 predictor (i.e. LAI, tree species identity and richness) and time (i.e. no. weeks). All data  
220 analyses were performed within R v.3.5.3 (R Core Team, 2019). Mixed effect models  
221 were conducted with lme4 v.1.1-2.1 (Bates *et al.*, 2015) and lmerTest v. 3.1  
222 (Kuznetsova *et al.*, 2017) package. Estimating the marginal R<sup>2</sup> was performed using the  
223 MuMIn v. 1.42.1 package (Bartoń, 2018).

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## 224 **Results**

225 Tree species richness had no significant effect on herb layer biomass: understory  
226 biomass was neither significantly affected by trees species richness alone, nor as an  
227 additional interactive effect with subplot treatment or with time (Tab. 1, Fig. 1a). There  
228 was an overall significant effect of time, indicating that understory biomass  
229 significantly decreased across years (Tab. 1, Fig. 1c). Similar, LAI displayed a  
230 significantly negative effect on understory biomass (Tab. 1, Fig. 1d) and even gained  
231 in explanatory variance over the course of this study.

232 Treatment displayed highly significant effects: Understorey biomass in the NW  
233 treatment was higher compared to the control and the P addition treatment (Tab. 1, Fig.  
234 1b). These differences between the treatments decreased in the course of the study  
235 period as indicated by a significant interaction effect with time (Tab. 1, Fig. 4).

236 The presence of individual tree species (i.e. *Castanea henryi* (Skan) Rehder and E. H.  
237 Wilson, *Nyssa sinensis* Oliver, *Choerospondias axillaris* (Roxburgh) B. L. Burtt and A.  
238 W. Hill, and *Schima superba*) significantly contributed to a decrease in understory  
239 biomass (Tab. 1, Fig. 2). An increasing abundance of *Schima superba* and *Castanea*  
240 *henryi* had the strongest negative effects on understory biomass. For *Choerospondias*  
241 *axillaris* and *Elaeocarpus japonicus* Siebold and Zuccarini the negative tree identity  
242 effects decreased in the course of the study, whereas for *Manglietia yuyuanensis* Law,  
243 the effect increased with time (Tab. 1, Fig. 3).

244 However, while temporal dynamics for tree species richness effects were less clear, the  
245 most of the variance could be explained by tree identities throughout this study (Fig. 5).  
246 Variance partitioning among LAI, tree identity and tree species richness over the time

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247 show that the relative importance of tree species richness increased from year one to  
248 year two and then decreased again while LAI and tree species identity tended to  
249 increase their relative importance across the years.

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## 250 **Discussion**

251 Over a period of three years, we found lower understorey biomass potentially associated  
252 with the presence of certain tree layer species identities. Moreover, we found tree  
253 identities to explain the most variance throughout this study. The expected contrary  
254 effect of tree species richness becoming a more effective driver of understorey  
255 performance over the course of this study was not found. Nevertheless, increasing  
256 negative effects on biomass with time, jointly with an overall negative effect of LAI as  
257 well as an increase in explanatory variance, indicate initials of successional processes as  
258 induced by closing canopies in the experimental study area.

### 259 **The explanatory value of tree species richness and identity**

260 Four to seven years after establishing the plantation (2009 at site A, 2010 at site B), we  
261 encountered a significantly lower understorey biomass with greater proportion of  
262 individual tree species identity (i.e. *Castanea henryi*, *Nyssa sinensis*, *Choerospondias*  
263 *axillaris* and *Schima superba*). However, while it has been shown that overstorey tree  
264 species richness has positive effects for overall tree productivity that intensify with time  
265 (Huang *et al.*, 2018) and for an array of different other ecosystem functions (Gamfeldt  
266 *et al.*, 2013), we were unable to find a similar, consistent effect on understorey biomass.  
267 The absence of tree species richness effects is consistent with our previous findings  
268 made in the same experiment (Germany *et al.*, 2017) and also corresponds to results of  
269 Both *et al.* (2011) for observational plots in the nearby Gutianshan National Nature  
270 Reserve. The amount as to which understorey plant species performance is driven by  
271 resource heterogeneity (i.e. brought about by facilitating tree species richness effects) or  
272 resource availability (i.e. brought about by increasing competition as a result of higher  
273 tree species richness and/or species-specific differences among tree identities) and

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3 274 whether the relationship between over- and understorey is indeed being governed more  
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5 275 strongly by tree species identity instead of tree species richness is likely to change the  
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8 276 with successional stage of a forest. In the present setting of experimental plantation, we  
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10 277 still are studying effects in young successional stages, while many theories referenced  
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12 278 refer to mechanisms prevailing in mature forest stands. Admittedly, resource  
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14 279 heterogeneity is a more important driver of understorey plant species diversity  
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17 280 particularly in old-growth stands, whereas resource availability can act in both young  
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19 281 and mature stands (Bartels and Chen, 2010). This might be an explanation for the  
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21 282 absence of any positive tree species richness effects on understorey biomass. Overall,  
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23 283 we did not encounter much support for our first hypothesis. The expected effect of a  
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25 284 decreased understorey species productivity as a result of a lower resource availability  
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27 285 under higher tree species richness levels was not yet visible. However, considering the  
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29 286 early phase of the project, we might expect tree species richness effects to become a  
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31 287 more reliable predictor of understorey biomass on the basis of stand development and  
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33 288 increasing canopy closing.  
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### 39 **The importance of the environmental context**

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43 290 Although phosphorus is probably a limiting resource, we neither found a direct impact  
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45 291 of phosphorous fertilization on understorey biomass nor an indirect impact through tree  
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47 292 species richness. There are two options that might serve as explanations: 1)  
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49 293 phosphorous limitation is not of major importance in the forest system studied.  
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51 294 However, for grassland ecosystems it has been shown that P fertilization might be  
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53 295 associated with shifts in plant community composition, thereby having large impact on  
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55 296 ecosystem productivity (Avolio *et al.*, 2014). 2) Alternatively, methodological  
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57 297 challenges might have hampered the outcomes: Additional leaf samples taken from the  
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59 298 understorey have shown, that the absence of effects might be caused by a lack of  
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3 299 absorption of phosphorus from the understorey (unpublished data), thus indicating that  
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5 300 fertilization application was not working as expected.  
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9 301 In contrast, we found a higher understorey biomass within the NW treatment compared  
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11 302 to the biomass in the C treatment. This result conform to those of Germany et al. (2017)  
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13 303 in which we described a significant NW treatment effect on understorey species  
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15 304 composition, richness as well as productivity and concluded that the absence of  
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17 305 disturbance (i.e. in comparison to regular weeding in the C treatment) favoured fast  
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19 306 growing functional groups, such as grasses, and woody species with high biomass  
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21 307 production, i.e. competitors in the sense of Grime (1973). Following, these functional  
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23 308 groups might gain a competitive advantage over less productive and competitive  
24  
25 309 functional groups (Huston, 1979). However, we did not find any support for a change in  
26  
27 310 the strength of tree species richness-understorey productivity relationships when  
28  
29 311 comparing NW to the C treatment (Cardinale *et al.*, 2000). This relative insensitivity  
30  
31 312 might be explained by the absence of tree species richness effects at the current state of  
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33 313 forest development thereby preventing interactive overstorey species richness x  
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35 314 treatment effects to be involved. The effect of environmental heterogeneity is not a  
36  
37 315 constant and might be mediated through varying population densities Huston (1979).  
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39 316 Accordingly, we would have expected that lower population densities in the  
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41 317 understorey, as apparent in subplots of the C compared to the NW treatment,  
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43 318 understorey species would respond more strongly to facilitating tree species richness  
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45 319 effects (i.e. stronger relationships of understorey biomass-environmental heterogeneity).  
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47 320 However, with understorey productivity being governed more effectively by tree  
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49 321 identities than by tree species richness such interactive effects apparently did (yet) not  
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51 322 appear. We, thus, have to reject our second hypothesis in which we expect that a  
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53 323 modified environmental setting interacts with the strength of species richness effects, at  
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3 324 least for this short period of early stage-succession. Later-stage analyses are needed to  
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5 325 corroborate whether this finding holds when forest stands reach maturity.  
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9 326 **Effects of time and its interaction with tree diversity and identity**

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12 327 Owing to the dominant position of trees in forests, overstorey trees have been shown to  
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14 328 impose competitive constraints on understorey vegetation by altering above- and  
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16 329 belowground resource availability and heterogeneity (e.g. Gilliam *et al.*, 1995; Muller,  
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18 330 2003; Neufeld and Young, 2003). In the present analysis, such competitive constraints  
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20 331 were evident by strong negative effects of reduced light conditions, as quantified by the  
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22 332 LAI measurements, we found for the understorey biomass. Light transmittance through  
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24 333 canopy is generally considered to be the major limiting factor for forest understorey  
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26 334 vegetation (Kirby, 1988; Jennings *et al.*, 1999; Bartemucci *et al.*, 2006), however, it is  
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28 335 mediated through different components, i.e., tree species properties (Barbier *et al.*,  
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30 336 2008; Niinemets, 2010), tree species richness (Pretzsch, 2014; Sapijanskas *et al.*, 2014;  
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32 337 Jucker *et al.*, 2015; Williams *et al.*, 2017; Niklaus *et al.*, 2017) and with successional  
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34 338 stages (Tilman, 1985; Bartels and Chen, 2010). In accordance, we found overall  
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36 339 understorey biomass to become significantly reduced in the course of our experiment  
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38 340 which is remarkable considering that these effects appear after three years only.  
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40 341 Following Christensen and Gilliam (2003), the thinning phase (i.e. approximately 10  
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42 342 years after forest establishment) can be described as a period in which canopy closure  
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44 343 marks the initiation of intense competition for limited light and soil resources and strong  
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46 344 implications for vegetation patterns and composition of woody species in the  
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48 345 understorey. Following, the negative association of time with understorey biomass we  
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50 346 found might indicate a rapid increase in competitive constraints in the given forest  
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52 347 plantation in subtropical China. This is in accordance with the increase explanatory  
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54 348 variance of LAI over the course of this study.  
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3 349 While corresponding to the first part of our last hypothesis, we found negative  
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5 350 overstorey species identity effects in the majority of the cases (i.e. two identities vs. one  
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7 351 identity) to diminish over time, we also found that throughout this study most of the  
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9 352 variance could still be explained by tree identities. Moreover, the contrary effect of tree  
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11 353 species richness to become a more effective driver was not confirmed in the current  
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13 354 observation period. Thus, while according to the last hypothesis where we expected the  
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15 355 relative importance of species identity and richness effects to change over time in  
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17 356 opposite direction, we can only partially confirm the expected dynamics. Nevertheless,  
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19 357 considering that, only four to seven years after establishing the plantation, we already  
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21 358 being able to report negative effects for tree species identities, time and LAI on  
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23 359 understorey productivity, we might predict stronger and clearer relationships between  
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25 360 over- and understorey through time as trees will grow higher and interactions will  
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27 361 further rise.  
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34 362 In spite of the short time of only three years and four to seven years after establishing  
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36 363 the plantation, we could already demonstrate clear tree layer effects brought about by  
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38 364 species identities on the understorey production. Contrasting to a widespread agreement  
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40 365 on facilitating tree species richness effects for an array of different ecosystem functions  
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42 366 in forests, we were unable to find a similar effect on understorey biomass. Nevertheless,  
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44 367 our results indicate that there may be no single, generalizable species richness-  
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46 368 productivity relationship among structural layers in forests and that the extent as to  
47  
48 369 which overstorey related environmental factors, such as light transmittance, contributes  
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50 370 to understorey productivity change with time. Thereby, this study clearly underscores  
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52 371 the importance of considering temporal dynamics when studying species richness x  
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54 372 productivity relationships among structural layers in forests and advocates making use  
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373 of time-series analysis in future BEF studies to enlighten the role of tree species  
374 richness x herb layer interactions for forest succession.

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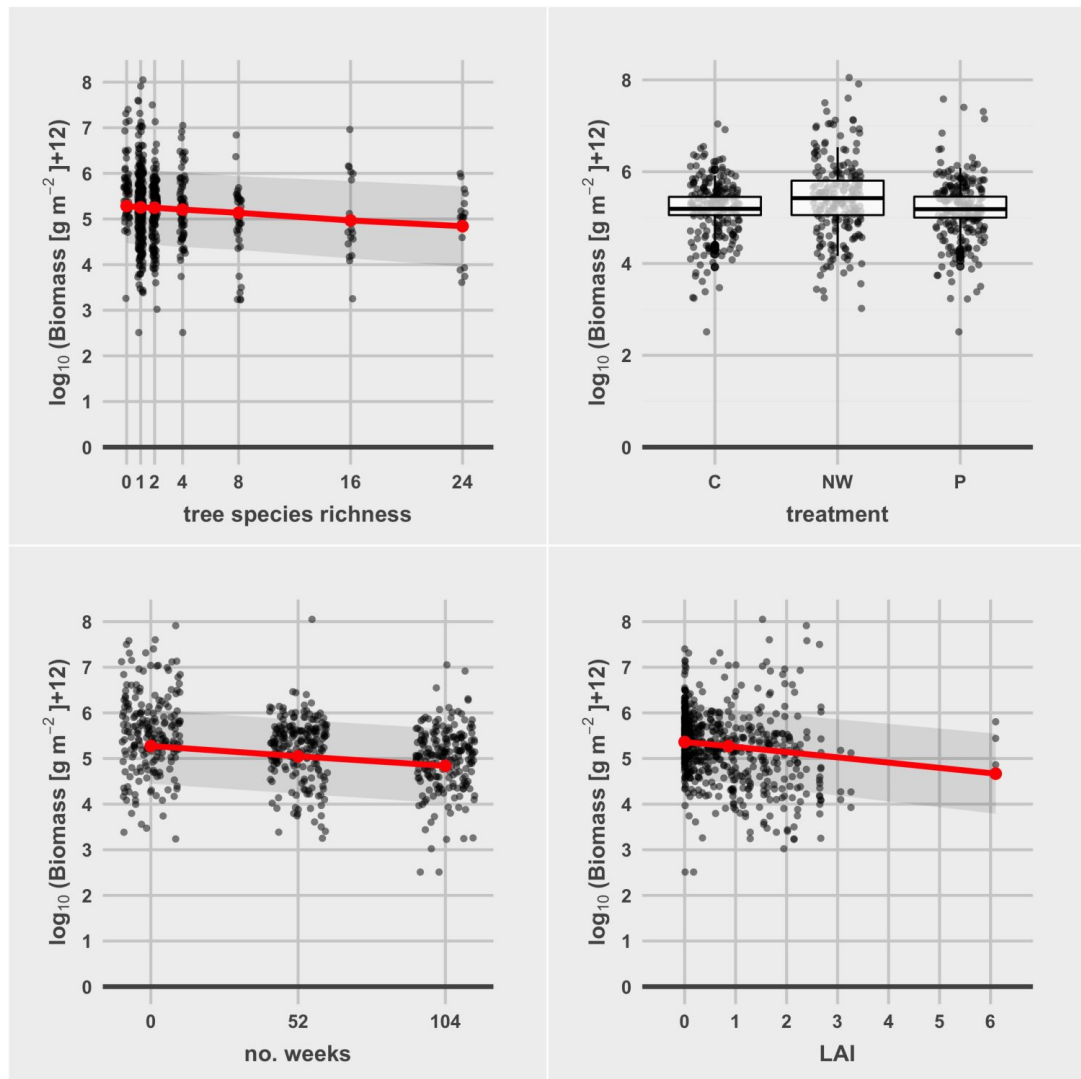
570 **Table 1:** Linear mixed effects model for predicting understorey biomass over the course of the  
 571 experiment. Significance levels are \*\*\*<0.001; \*\*<0.01; \*<0.05; .<0.1.

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	Estimate	Std. Error	df	t value	Pr(> t )	
(Intercept)	5.244	0.135	1.202	38.920	0.008	**
Tree species richness	-0.161	0.108	143.763	-1.486	0.139	
Treatment						
NW	0.297	0.071	148.146	4.190	<0.001	***
P	-0.020	0.061	132.475	-0.319	0.751	
Time	-0.357	0.085	402.000	-4.196	0.000	***
LAI	-0.208	0.075	186.357	-2.785	0.006	**
Tree layer identity						
<i>Castanea henryi</i>	-0.883	0.318	65.894	-2.773	0.007	**
<i>Nyssa sinensis</i>	-0.638	0.315	65.306	-2.025	0.047	*
<i>Choerospondias axillaris</i>	-0.795	0.302	69.214	-2.631	0.010	*
<i>Schima superba</i>	-0.926	0.316	69.510	-2.930	0.005	**
<i>Castanopsis eyrei</i>	0.408	0.318	62.375	1.281	0.205	
<i>Cyclobalanopsis myrsinifolia</i>	0.357	0.302	63.194	1.180	0.243	
<i>Manglietia yuyuanensis</i>	-0.308	0.301	61.073	-1.021	0.311	
<i>Elaeocarpus japonicus</i>	-0.224	0.277	65.255	-0.809	0.422	
Tree species richness:NW-Treatment	-0.025	0.123	133.259	-0.206	0.837	
Tree species richness:P-Treatment	-0.084	0.123	134.242	-0.678	0.499	
Time:Tree species richness	0.018	0.092	402.000	0.195	0.846	
Time:NW-Treatment	-0.430	0.113	402.000	-3.808	<0.001	***
Time:P-Treatment	-0.060	0.113	402.000	-0.527	0.598	
Time:Castanea henryi	0.436	0.356	402.000	1.223	0.222	
Time:Nyssa sinensis	-0.166	0.353	402.000	-0.471	0.638	
Time:Choerospondias axillaris	1.112	0.335	402.000	3.318	<0.001	***
Time:Schima superba	0.303	0.343	402.000	0.883	0.378	
Time:Castanopsis eyrei	-0.083	0.360	402.000	-0.231	0.817	
Time:Cyclobalanopsis myrsinifolia	0.606	0.340	402.000	1.784	0.075	.
Time:Manglietia yuyuanensis	-1.041	0.341	402.000	-3.054	0.002	**
Time:Elaeocarpus japonicus	0.830	0.315	402.000	2.637	0.009	**

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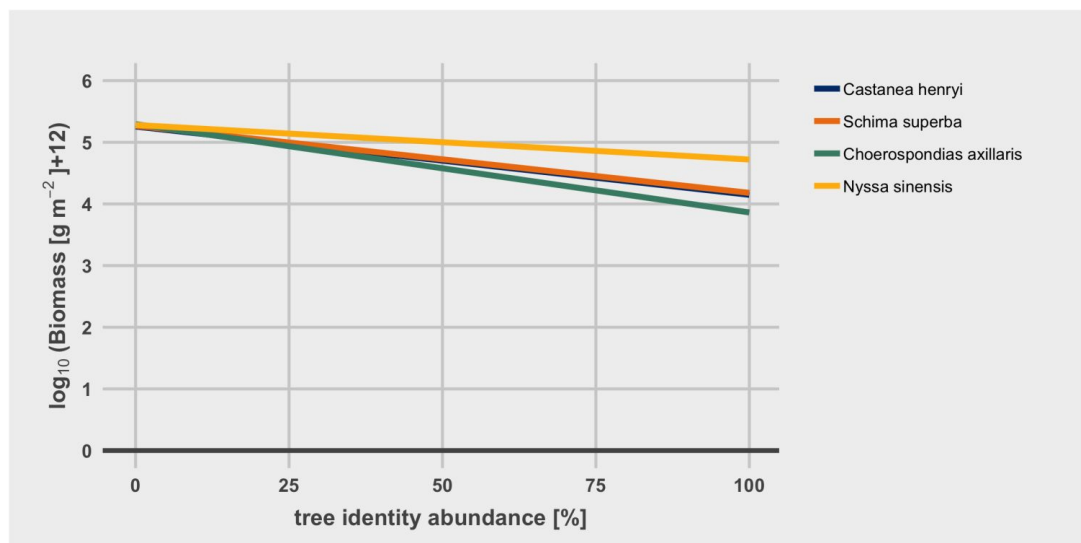
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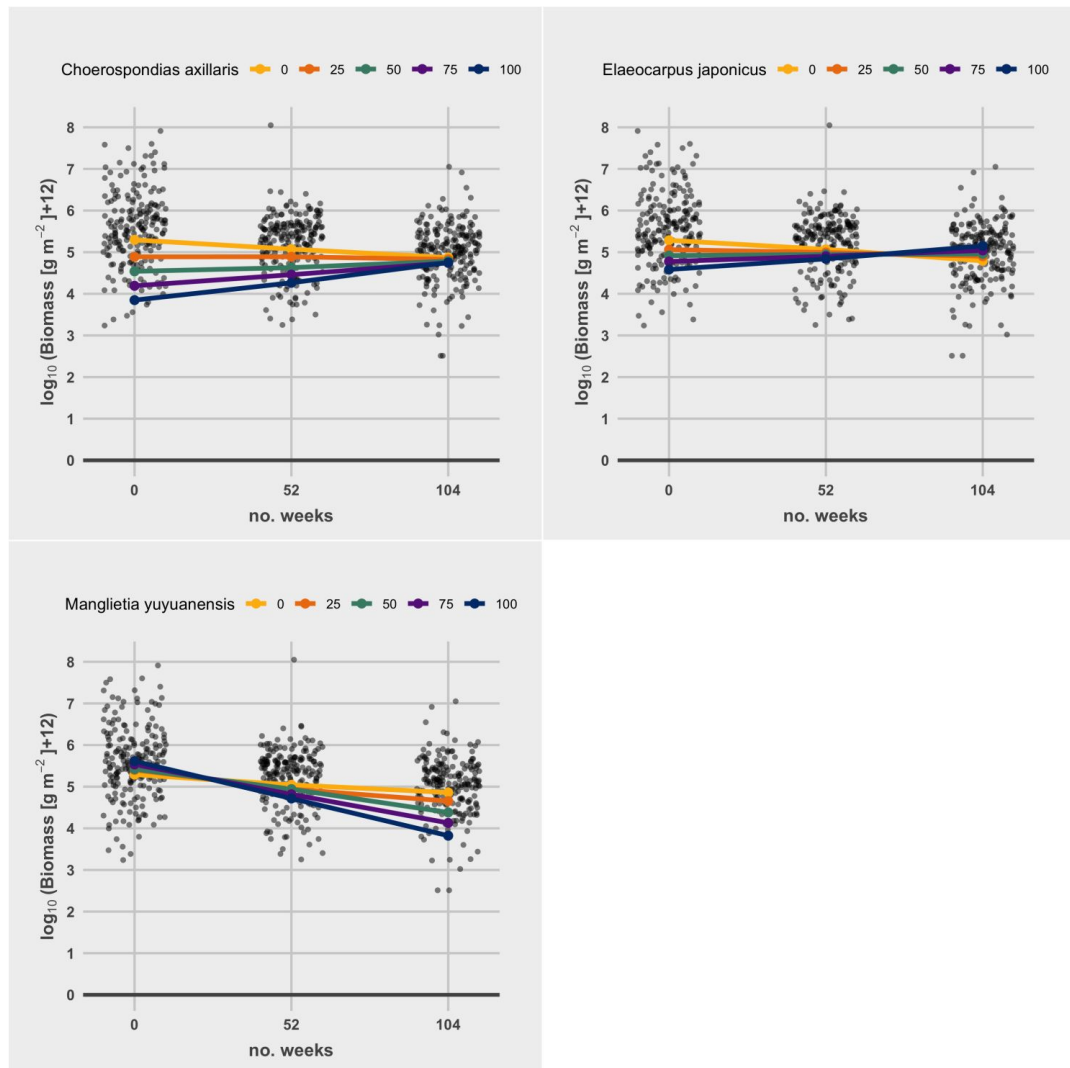
576 **Fig. 1:** Understorey productivity as a function of tree species richness (a), treatment (b), time (c) and leaf  
 577 area index (LAI; d). Continuous predictors (i.e tree species richness and time) and covariate (i.e. LAI) are  
 578 given on the original scale by making use of the inverse-scale function. Black circles represent the  
 579 measured biomass.

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581 **Fig. 2:** Understorey productivity as a function of tree layer identities. Please note that, for the purposes of  
582 clarity, confidence intervals are not shown. Note that the graph for *Castanea henryi* is in parallel to the  
583 graph for *Schima superba* and therefore hidden behind. For the purposes of clarity, confidence intervals  
584 are not shown.

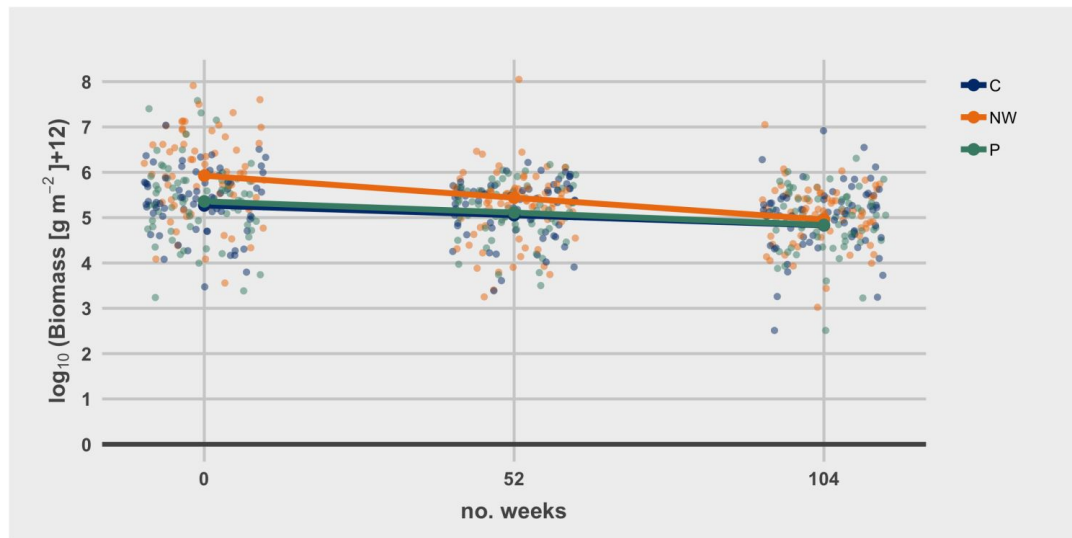


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586 **Fig. 3:** Understorey productivity as a function of interactive time:tree layer identity effects. Time is  
 587 printed on the original scale by making use of the inverse-scale function. Colours represent different  
 588 classes of relative abundances of the respective tree species. Black circles represent the measured  
 589 biomass. Note that, for the purposes of clarity, confidence intervals are not shown.

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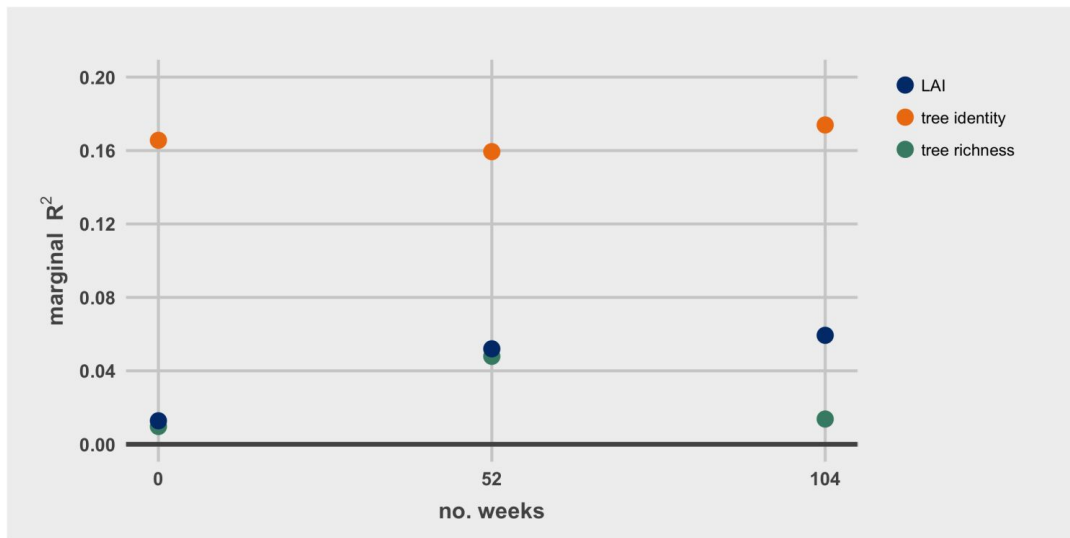


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591 **Fig. 4:** Understorey productivity as a function of interactive time:treatment effects. Time is printed on the  
592 original scale by making use of the inverse-scale function. Circles represent the measured biomass.  
593 Colors represent different treatments. Note that, for the purposes of clarity, confidence intervals are not  
594 shown.

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596 **Fig. 5** Explained variance (marginal  $R^2$ ) by separated models ( $N=9$ ) for each predictor (i.e. LAI, tree  
597 species identity and -richness) and time (i.e. no. weeks).





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**Janzen-Connell effects in a forest BEF experiment: Strong distance-dependent seedling establishment of multiple species**

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## Janzen-Connell effects in a forest BEF experiment: Strong distance-dependent seedling establishment of multiple species

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**Abstract.** The Janzen-Connell (JC) hypothesis is a major ecological explanation for high species richness, in particular in tropical forest ecosystems. Central components of the JC hypothesis are noncompetitive effects of distance and density dependence, two drivers that contribute independently to species coexistence, but are ultimately linked in the field. However, although numerous studies provide evidence for either distance- or density-dependent effects based on observational data, experimental testing of simultaneous and interactive effects of distance and density has rarely been conducted, especially in a comprehensive multispecies approach. Here, we make use of the forest Biodiversity-Ecosystem Functioning project (BEF) – China to estimate distance- and density-dependent effects in a reciprocal tree seedling transplant experiment of 11 tree species. We deployed 13,490 juveniles of all 11 species in their own (home) and in all foreign monocultures (away), as well as at three different levels of planting density, thereby testing for distance and density effects, respectively. In addition, to quantify the amount to which density effects were brought about by potential additional effects of intraspecific competition, we set up a common garden experiment with different levels of planting density, where an additional “shadow” treatment controlled for effects of canopy shading. Although the “away” and “high-density” treatments significantly impaired the performance and productivity of seedlings, leaf damage and survival was exclusively affected by either the home/away or the density treatment, respectively. Negative density-dependent effects on leaf damage were less pronounced in the “home” treatment, showing that the effects were not additive. In addition, results obtained in the Common Garden Experiment showed that negative effects of high density may be also brought about by intraspecific competition as an alternative density-responsive mechanism and less by true JC effects. Overall, our results provide strong support on a multispecies basis for the influence of host-specific effects already operating in early stages of a forest plantation. However, they also emphasize the need to account appropriately for potential additional density-responsive mechanisms such as intraspecific competition or microenvironmental conditions when addressing the role of JC effects for species coexistence.

**Key words:** BEF-China; competitive exclusion; herbivory; natural enemies; plant population and community dynamics; seedling mortality; species diversity and richness; subtropical forests; tree recruitment; understory.

### INTRODUCTION

Identifying the mechanisms that allow evading competitive exclusion and ensure long-term coexistence of species has long been a focal objective of community ecology (Hutchinson 1959, Huston 1979). Mechanisms identified to date that promote biodiversity can be categorized in two major ways that are not necessarily exclusive. Although equalizing forces reduce fitness

differences among species, stabilizing forces increase mortality with increasing population densities within a single species (Chesson 2000). The Janzen-Connell (JC) hypothesis (Janzen 1970, Connell 1971) refers to such stabilizing forces and states that seed and juvenile (i.e., seedling and sapling) survival rates decrease with increasing effects of accumulating host species-specific antagonists at lower distance to or at higher density of conspecific plants. As a consequence, dominant species are prevented from outcompeting less-dominant ones, thus promoting juvenile plant diversity (see also Terborgh 2012, Bever et al. 2015).

Since first proposed, the JC hypothesis has been frequently tested in temperate to tropical situations with

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studies finding either support for JC effects with respect to distance (Norghauer et al. 2009, Reinhart and Clay 2009, Swamy et al. 2011) or density (Johnson et al. 2012, Zhu et al. 2015a, b). However, there are a number of studies that report no such effects, or even contradictory ones (Reinhart et al. 2012, Zhu et al. 2013). In addition, distance and density effects in the field often act in concert, as seedling density tends to be higher at lower distance to the mother tree, and vice versa (Hubbell 1980, Clark et al. 2005, Muller-Landau et al. 2008). Thus, the neat separation of distance- and density-dependent effects requires experimental approaches with a full-factorial design in which both dependencies are varied independently. Yet there are only few studies that experimentally tested for both dependencies simultaneously (Comita et al. 2014). Packer and Clay (2000) found seedling survival of *Prunus serotina* to display more distance than density dependence. These findings have been confirmed by Li et al. (2009) on seedlings of *Ormosia semicastrata* and by Xu et al. (2015) on seedlings of *Engelhardtia fenzelii*. In addition, JC effects are hypothesized to vary among species with their relative abundances (i.e., common versus rare species; Comita et al. 2010, Johnson et al. 2012) and differing life-history strategies (Janzen 1970, Connell 1971). Thus, multi-species approaches should be more likely to detect general trends compared to single-species ones (Comita et al. 2014). Yet, there is only one single study so far that explicitly manipulated distance and density dependency at the same time in multiple species of the same forest community. Yamazaki et al. (2009) exposed seedlings from eight species near or distant from conspecific adult trees at different density levels and identified either distance- and/or density-dependent effects for six species. Moreover, experimental manipulation also allows for testing interactive effects of distance and density, which can be expected to occur if one mechanism alone does induce sufficient pathogen/herbivore pressure to evoke fitness constraints. Thus, density effects of seedlings may only play out close to conspecific adults where pathogen/herbivore pressure is already high. Alternatively, sufficient escape from pathogens or herbivores might be only provided at low density of seedlings growing at larger distance to adult conspecifics. So far, evidence for these effects is controversial, with single examples for both types of interactions (*Cornus controversa* and *Prunus grayana* in Yamazaki et al. 2009).

In addition, in the forest understory, tree seedlings are not only subjected to JC effects but may also compete for resources, which makes a causal interpretation of density-dependent JC effects even more difficult (Terborgh 2012). Moreover, while in a recent study LaManna et al. (2017) proposed that the strength of conspecific negative density-dependence increases from temperate to tropical forests as a result of more intense biotic interactions, Comita (2017) pointed out the possibility that stronger effects of abiotic factors at temperate latitudes might mask existing negative density

dependence derived by biotic interactions (such as herbivory and competition). Light interception, reducing the availability and transmittance of light, water, and nutrient availability (Barbier et al. 2008), is a key factor influencing resource availability in forests. However, light interception as well as species-specific preferences are known to vary strongly among tree species (Neufeld and Young 2003, Porté et al. 2004, Li et al. 2017). Thus, seedling survival may be generally favored when the species' preferential light conditions are met, irrespective of JC effects, and thus potentially mask the presence of additional JC effects (Comita 2017). As a consequence, light supply to seedlings should be considered and quantified in JC experiments (Yamazaki et al. 2009).

In the present study, we aimed at assessing density- and distance-dependency effects just as their interactions. Making use of the forest Biodiversity-Ecosystem Functioning Experiment in subtropical China (BEF-China), we used monoculture plots to test for differences between "home" and "away" treatments with respect to large conspecifics (i.e., distance dependence). In addition, each species was planted at different density levels of 4, 9, and 25 individuals in 0.25-m<sup>2</sup> subplots (i.e., density dependence). As an additional *ex situ* experimental approach, we repeated a similar setup in a nearby common garden. The general aim of the Common Garden Experiment was to test for density-dependent effects brought about by intraspecific competition as an alternative mechanism. Density-dependent patterns that are prevalent in the Main Experiment, although not appearing in the Common Garden Experiment, can be considered as true JC effects. In addition, we added a shading treatment to simulate reduced light conditions induced by the canopy. In particular, we hypothesized that performance, productivity, escape from herbivore attack (i.e., leaf damage), and ultimately survival (1) is reduced when growing at home (i.e., under a conspecific adult canopy) compared to away (i.e., under a heterospecific adult canopy) and (2) decreases with increasing densities of conspecific recruits, as predicted by JC. We expected (3) that intraspecific competition for resources result in similar density-dependent pattern as predicted by the JC theory. Finally, we (4) hypothesized that distance and density dependencies interact with each other, with high densities being more detrimental at home than at away sites.

## METHODS

### *Site information*

The study was carried out on the experimental research platform of BEF-China located in subtropical China near Xingangshan, Dexing County, Jiangxi Province (117°55' E, 29°60' N). The platform comprises two sites as forest plantations established in 2009 (site A) and 2010 (site B), at a distance of 4 km and situated on 100–300 m above sea level. The region is



characterized by hilly terrain with an average slope of 27.5° and 31° for site A and site B, respectively (Bruehlheide et al. 2014), and a seasonal subtropical monsoon climate with warm and humid summers and a short dry winter season between November and December. The mean annual temperature is 16.7°C and the mean annual precipitation is 1,821 mm (Yang et al. 2013).

On a total area of ~50 ha, 566 experimental plots had been established with a plot size of 25.8 × 25.8 m<sup>2</sup> (corresponding to the traditional Chinese measurement unit of 1 mu) in horizontal projection, representing the platform of the BEF-China Main Experiment (Bruehlheide et al. 2014). The total species pool used for the Main Experiment consists of 40 different native broad-leaved tree species, 24 of which each were assigned to site A and site B, respectively, with an overlap of eight species. Within site, species were assigned to tree richness levels of 0, 1, 2, 4, 8, 16, and 24 tree species (for details of species composition and levels of tree diversity, see Bruehlheide et al. 2014). Planted in a grid of 20 × 20 regularly arranged columns and rows and with a distance of 1.29 m between trees, each plot comprises 400 tree individuals (Yang et al. 2013, Bruehlheide et al. 2014). In the beginning, the understory vegetation was weeded twice a year in all plots (since 2009 and 2010, for site A and site B, respectively); since 2014 weeding has occurred once a year each at both sites.

#### *Reciprocal transplant experiment*

Within the BEF-China Main Experiment we implemented a reciprocal transplant experiment with juvenile plants of 11 different tree species assigned to 29 and 19 different plots on site A and site B, respectively (see Appendix S1: Table S1). The tree species represent a subset of the Main Experiment's species pool and had been selected according to their representation at the two sites. They included six evergreen and five deciduous species. The design was planned for 10 species, in total, to be studied at site A and 7 species at site B, i.e., an overlap of six species occurring at both sites. For each species, three monoculture plots at each site were used for subplot implementation, following a project-specific experimental setup. The general design of BEF-China provides two replicates of each species' monoculture at the plot level (i.e., where all 20 × 20 planted individuals belong to the same species). As an additional replicate, we used two-species mixtures including the respective target species, and in these plots, subplots were strictly established in local neighborhood monocultures; that is, they were always surrounded by four individuals of the target species. Exceptions were *Diospyros japonica* (on site A and B) and *Schima superba* (on site B), where a third replicate could not be established (see Appendix S1: Table S1 for a more detailed description of the subplot assignment and details of the reciprocal transplant design).

To test for effects of distance dependence, a home vs. away approach was used in which all site-specific target

species were planted in subplots either established in their own monocultures (home) or in monocultures of the other species within site (away; Fig. 1). In the course of the experiment, 2 out of the 10 species on site A (i.e., *Castanopsis sclerophylla* and *Schima superba*) could not be established at all. In the analyses, these species were not considered, but their monocultures were kept as additional away sites for the remaining species. One further species (i.e., *Cinnamomum camphora*) failed to become established in 10 out of 26 plots in foreign monocultures on site A and was only considered in the remaining plots.

To test for effects of density dependence, tree seedlings of all species were planted at levels of 4, 9, and 25 individuals in home and away plots, respectively. Establishment of independent subplots for all species (i.e.,  $n = 10$  at site A) at all density levels ( $n = 3$ ) in all plots, for example, at site A, would have required 30 subplots per plot. However, sharing a common platform, the plots were also used for other purposes; therefore, it was impossible to have this number of subplots available in all 48 plots (sites A and B). We thus employed a split-subplot design, by establishing subplots with each being subdivided into six split-subplots and involving seedlings of two species at three density levels (Fig. 1).

Accordingly, in target plots at site A, five subplots (hosting recruits of eight species in total) each were implemented, whereas at site B, the number of subplots per plot was lower because of the lower number of species tested. Thus, in each 29 and 19 plots (for site A and site B, respectively), five and four subplots each having a size of 1.5 × 1.0 m<sup>2</sup> were randomly assigned to suitable locations within the plot (Fig. 1). Within each subplot, the split-subplot occupied an area of 0.5 × 0.5 m<sup>2</sup>. Species were randomly allocated to subplots and species × density combinations were randomly assigned to split-subplots. In total, 8,436 and 5,054 tree seedlings were planted between April and May 2015 at site A and site B, respectively. The experiment ran for two growing seasons from June 2015 to September 2016.

#### *Common Garden Experiment*

For 8 out of the 11 tree species used in the Main Experiment juvenile plants were grown in an additional Common Garden Experiment established on a former agricultural field nearby (see Appendix S1: Table S1 for a more detailed description). The Common Garden Experiment was located at linear distances of 2.2 and 2 km away from site A and B, respectively and was surrounded by agricultural fields. By making use of a former agricultural field without exchanging the existing soil, we cannot exclude the existence of some legacy effects of former or recent agricultural usage in terms of soil conditions (e.g., higher resource availability caused by fertilization); however, we can expect a significantly reduced number of host-specific herbivores and pathogens compared to forested stands in the Main

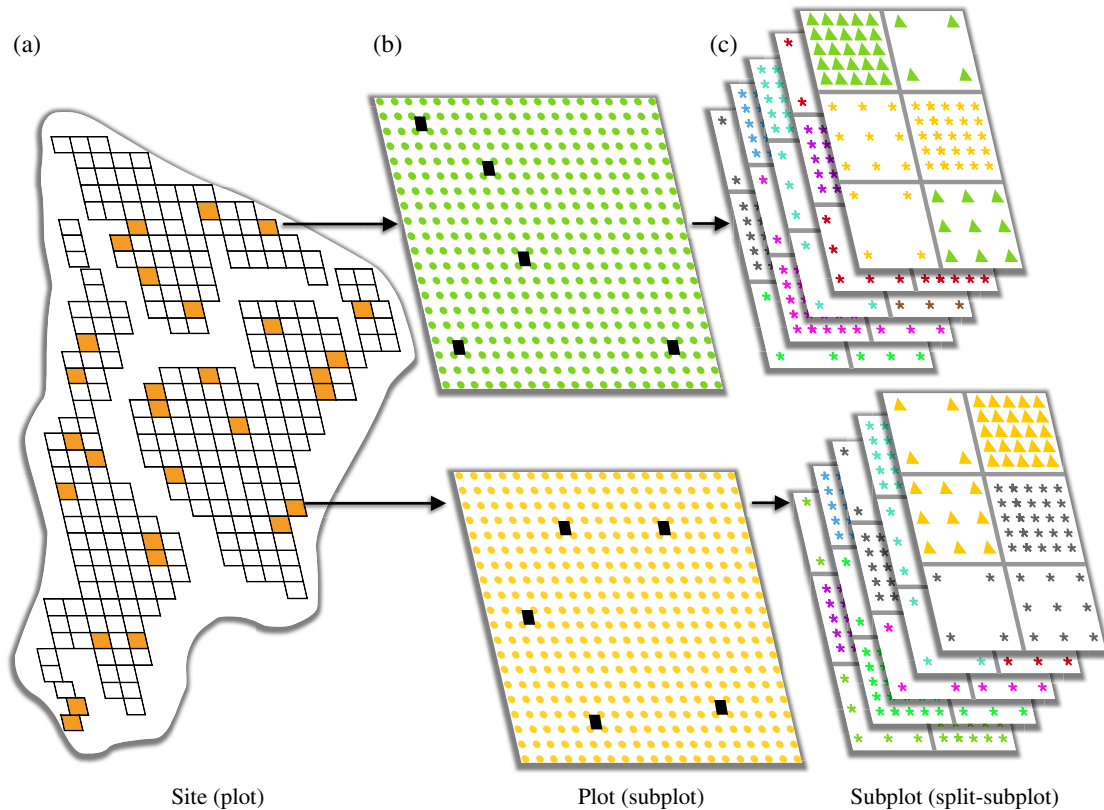


FIG. 1. (a) Conceptual diagram summarizing the hierarchical levels of the reciprocal transplant experiment on the example of site A in the Main Experiment. Orange rectangles represent the 29 different plots on site A where seedlings have been planted. (b) Each plot is composed of 400 tree individuals represented by colored dots. Different colored dots, among the plots, represent different species identities of the adult trees. On site A, each plot contained five randomly positioned subplots as represented by black rectangles in between the trees. (c) Each subplot was additionally subdivided into six split-subplots and involved seedlings of each of two species at three density levels. The coloring of the seedlings (usually given as asterisks) represent the species' identity. Colored triangles accordingly represent situations where the species identity of the seedlings conforms to the monocultures' species identity (i.e., home) while colored asterisks always represent individuals planted in monocultures of other species' identities within site (i.e., away).

Experiment as necessary for demonstrating JC effects (i.e., brought about by a high distance to the nearest forests and/or pesticide usage in the surrounding area). In the course of the experiment, one species (i.e., *Rhus chinensis*) could not be established at all. In the following, this species was not considered in the subsequent analyses. In parallel to the Main Experiment, each species was planted at density levels of 4, 9, and 25 individuals. In addition, they were planted in single individual plots without intraspecific competition (density = 1). Each species  $\times$  density combination was grown in plots either established as “shadow” or “light” treatment (with three replicates each). Shading treatments were implemented by establishing separate shadow net-wrapped containers 1.2 m in height on half of all plots. Thus, light levels in the shadow treatment were reduced to about 36% of photosynthetically active radiation compared to the light treatment. Shadow nets were opened from the bottom up to 0.5 m in height on the northern side of the

containers to facilitate natural air circulation and allow multitrophic interactions (see Appendix S6: Fig. S1). Each species  $\times$  density  $\times$  treatment combination was randomly allocated to plots with a size of  $0.5 \times 0.5 \text{ m}^2$  (corresponding to the size of one split-subplot of the Main Experiment) and assigned to random plot positions in regular rows within an area of  $135 \text{ m}^2$  in total. The experiment ran concurrently with the Main Experiment from June 2015 to September 2016.

#### Plant material

The plant material used in both experiments refers to seedlings, i.e., juveniles that had germinated in 2015 ( $n = 2$ ) and saplings, i.e., juveniles that had germinated in 2014 ( $n = 9$ ). Seedlings were grown from seed material collected from the nearby Gutianshan National Nature Reserve, Zhejiang Province, in 2013 and 2014, and were cultivated in a nursery near Dexing, Jiangxi Province.

Three species, *Schima superba*, *Cinnamomum camphora*, and *Triadica sebifera*, were purchased from a nursery near Jiujiang, Jiangxi Province. Saplings of *Cinnamomum camphora*, *Liquidambar formosana*, *Rhus chinensis*, and *Triadica sebifera* had to be trimmed to a standard height (i.e., 0.5 m) before planting to increase establishment probabilities. All seedlings and saplings were then planted into the experiment plots in April and May 2015. In the following, we use seedling as the common term for both age classes. (see Appendix S1: Table S1 for a more detailed description).

#### Data collection

As an initial census of establishment success, at each of the three study sites (site A, site B and common garden), every seedling was monitored 2 weeks after planting and seedlings that had failed to become established by then were replaced once.

Seedling survival, height (i.e., length from ground to last occurrence of leaves), and number of leaves was subsequently monitored at five census dates (i.e., June or July, August, and October 2015 as well as March and September 2016) in the Main Experiment, and three times in the Common Garden Experiment (August and September 2015 as well as September 2016). In October 2015 and September 2016, respectively, leaf damage (i.e., the proportion of leaf area damaged) was additionally estimated at all three study sites.

In September 2016, all seedlings that had survived were harvested, separated in above- and belowground fractions, oven-dried for 48 h at 70°C, and subsequently weighed to 0.01-g precision.

In early October 2015, hemispherical photographs were taken in the Main Experiment at 1.2 m above soil surface at the center of each subplot to get a measure of canopy-induced shading. Canopy was still fully foliated at that time. Photographs were taken with a Nikon D100 digital camera using a Nikon 10.5 mm f/2.8G ED AF DX Fisheye Nikkor Lens. Leaf area index (LAI) was calculated using HemiView V8 (Delta-T) and varied from 0 to 8.08 in plots of the Main Experiment. To compare light availability between the experiments, light was measured at the top of the seedlings using the LI-1500 Light Sensor Logger in combination with the LI-190 Quantum Sensor and related to reference measurements taken simultaneously outside the forest.

Mean light availability compared between reference measurements in the open and experimental sites in the Main Experiment was 29% and 40% for sites A and B, respectively, and the shadow and light treatment in the Common Garden Experiment resulted in 23% and 63%, respectively.

#### Statistical analyses

All analyses, with the exception of time series analyses, were performed separately by record date and the

presented results refer to the last measurement (i.e., September 2016) only. For results of all single date analyses see supporting information (see Appendix S2: Table S1 and Appendix S4: Table S1). In order to obtain normal distribution of residuals, height of the seedlings and biomass was log-transformed prior to analysis, whereas leaf damage was logit transformed. Height, biomass, and leaf damage were analyzed by fitting mixed-effects models with Gaussian error distribution, while the model fit for number of leaves and seedling survival was done with Poisson and binomial distribution, respectively.

Density was  $\log_2$  transformed to evenly weight all density levels. Subsequently, the continuous predictor (i.e., density) and covariate (i.e., LAI) were standardized (by subtracting the mean and dividing by two standard deviations), which allows comparing relative effect sizes of parameter estimates (Gelman 2008).

#### MAIN EXPERIMENT

To test whether the combined treatments of home/away and density affect seedling performance, productivity, escape from herbivore attack, and survival, we subjected the data of the Main Experiment to mixed-effects models. In the full model, treatments of home/away, density, and their interactions; LAI; and the interaction of density and LAI were considered fixed effects while species, site, plot, subplot, and split-subplot were considered random factors. We additionally calculated these models separately by species to examine species-specific responses (see Appendix S3: Table S1). In these analyses, the factors species and subplot were removed, and site was only retained as random factor in those cases, where species were planted on both sites. To test whether the effects of home/away, density, and LAI on seedling survival changed over the course of the experiment, we implemented an additional model using the data monitored at five census dates (i.e., June or July 2015, August 2015, October 2015, March 2016, and September 2016) and included time (i.e., weeks elapsed between the five census dates) as well as the interactions of home/away, density, and LAI with time as fixed effects.

#### COMMON GARDEN EXPERIMENT

To test whether density effects were brought about by intraspecific competition, we applied mixed-effects models with shading as well as density treatments and their interaction (i.e., density  $\times$  shading) as fixed effects, whereas species and plot were considered random effects in the full model. In addition, species-specific models were calculated using only plot as random factor (see Appendix S5: Table S1).

With the exception of the time series analysis, final models were selected by comparing all possible predictor combinations based on Akaike information criterion with correction for small sample sizes ( $AIC_c$ ; Sugiura 1978) and maximum likelihood. The final models were

recalculated using restricted maximum likelihood. High structural complexity and numbers of observations impeded a model selection in the time series analysis. For this reason, the full model (i.e., full covariance structure) was included. Residuals were visually verified (i.e., histogram, qqnorm, and residuals vs. fitted).

All analyses were performed with R v. 3.3.2 (R Core Team 2016). Mixed effect models were conducted in the lme4 v. 1.1-1.2 (Bates et al. 2015) and lmerTest v. 2.0-32 package (Kuznetsova et al. 2016). Model selection was performed using the MuMIn v. 1.15.6 package (Bartoń 2016). Predicted values were obtained using the effects v. 4.0-0 package (Fox 2003).

## RESULTS

### Main Experiment

With the exception of seedling survival, all variables tested differed significantly between home and away plots (Table 1). Seedling performance (i.e., height, number of leaves) and productivity (i.e., above-, belowground biomass) were significantly lower in home plots (i.e., in plots with conspecific adults) compared to away plots (plots with heterospecific adults, Fig. 2a–d). Leaf damage was significantly increased when seedlings were grown in their own monocultures in comparison to being planted into heterospecific monocultures (Fig. 2e), while the survival of seedlings was not affected by distance (Fig. 2f). Seedling density displayed a significant effect on all variables tested with the exception of seedling height and leaf damage (Table 1). Although height showed no significant effect (Fig. 2g), the number of leaves and seedling productivity (i.e., above-, belowground biomass) was lower at plots with high density (Fig. 2h–j). Similarly, although leaf damage showed no significant effect (Fig. 2k), seedling survival at high density was significantly lower compared to low density of conspecific recruits (Fig. 2l). In addition, LAI displayed significant effects for most of the variables tested: seedling performance (i.e., height, number of leaves), productivity (i.e., above-, belowground biomass) and survival decreased with increasing LAI (Table 1, Fig. 3a–e).

Significant interaction effects between main treatment factors were only encountered for leaf damage: seedlings experienced a higher level of leaf damage in low- as compared to high-density plots when grown at home, whereas the opposite was true in away plots, thereby indicating a significant home/away  $\times$  density interaction (Table 1, Fig. 4).

### Main Experiment—time analysis

Using data collected at five census dates, seedling survival was significantly reduced with increasing density, LAI, and time of the experiment (Table 2). Additional home/away and LAI interactions with time indicated that negative effects of home treatments and higher LAI values became more evident over time (Table 2, Fig. 5).

### Common Garden Experiment

In the Common Garden Experiment, overall seedling performance (i.e., height, number of leaves), productivity (above-, belowground biomass) and survival was higher than in the Main Experiment (Tables 1, 3, Figs. 2, 3). In addition, although seedling performance (i.e., height, number of leaves), and productivity (i.e., above-, belowground biomass) were lower at high density of conspecific recruits, leaf damage and seedling survival did not show significant differences among seedling density levels tested (Table 3, Fig. 2m–p). Seedling productivity (i.e., above-, belowground biomass) was significantly reduced in shaded compared to unshaded (i.e., light) plots, whereas there was no such effect on seedling performance (i.e., height, number of leaves). Seedling survival was significantly higher in shaded plots compared to plots exposed to full light, whereas there was no such effect for leaf damage (Table 3, Fig. 3).

Significant interaction effects between density of recruits and shading on seedling performance and productivity in the common garden were only found in number of leaves and aboveground biomass (Table 3). For both variables, responses strongly decreased with increasing density of conspecific recruits in the light treatment, while the negative slope was less steep when seedlings were exposed to shading (Table 3, Fig. 6).

TABLE 1. Main Experiment.

	(Intercept)	df	Home treatment	df	Density	df	LAI	df	Density:	df	Density: LAI	df
									Home - treatment			
Performance												
Height	3.446 $\pm$ 0.104***	10.927	-0.153 $\pm$ 0.044***	575.477	-0.036 $\pm$ 0.019	529.205	-0.123 $\pm$ 0.051*	143.946			0.078 $\pm$ 0.044	550.872
No. leaves	2.351 $\pm$ 0.203***		-0.448 $\pm$ 0.084***		-0.164 $\pm$ 0.035***		-0.504 $\pm$ 0.106***					
Productivity												
Aboveground	0.568 $\pm$ 0.298	9.509	-0.289 $\pm$ 0.087***	579.943	-0.207 $\pm$ 0.037***	508.53	-0.481 $\pm$ 0.101***	145.482				
Belowground	0.228 $\pm$ 0.267 n.s.	10.02	-0.156 $\pm$ 0.07*	567.891	-0.181 $\pm$ 0.03***	504.897	-0.473 $\pm$ 0.082***	148.222				
Leaf damage	-2.393 $\pm$ 0.296**	3.084	0.308 $\pm$ 0.128*	449.004	0.077 $\pm$ 0.059 n.s.	421.527			-0.379 $\pm$ 0.17*	460.64		
Survival	-1.22 $\pm$ 0.578*		-0.266 $\pm$ 0.165 n.s.		-0.18 $\pm$ 0.069**		-0.781 $\pm$ 0.224***					

Notes: Estimates, standard error, significance levels (i.e., \*\*\* $<$ 0.001; \*\* $<$ 0.01; \* $<$ 0.05;  $<$ 0.1), and degrees of freedom associated with *t*-test statistics for optimized (generalized) linear mixed-effects models of seedling height ( $N = 4,232$ ), number of leaves ( $N = 4,222$ ), above- ( $N = 4,233$ ) and belowground productivity ( $N = 4,228$ ), leaf damage ( $N = 4,120$ ), and survival ( $N = 13,490$ ). Analyses were performed separately by record date; results refer to the last measurement (i.e., September 2016). Blank cells indicate excluded predictors during model optimization with (1|species) + (1|site/plot/subplot/splitplot) as a random structure.

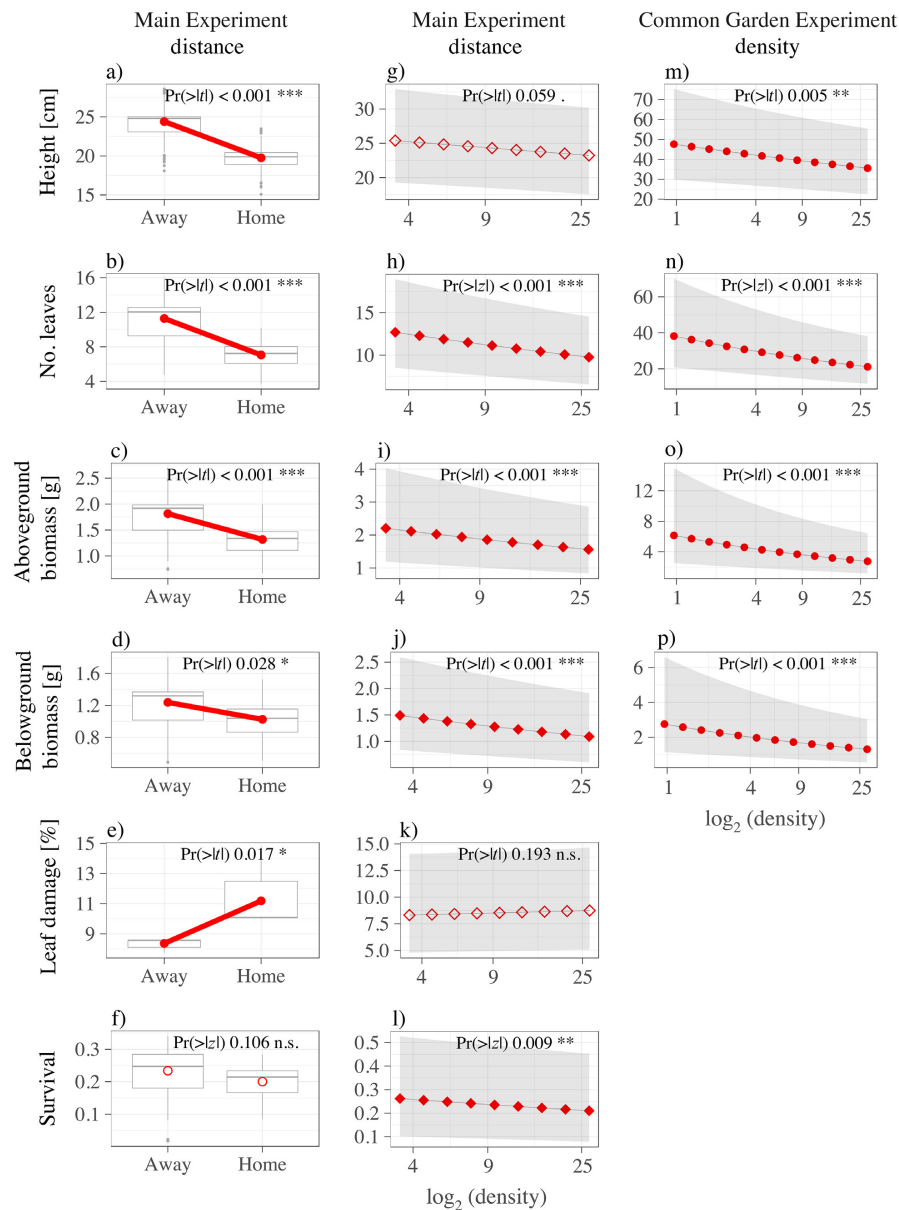


FIG. 2. Seedling performance (i.e., height, number of leaves), productivity (i.e., above-, belowground biomass), leaf damage, and survival as a function of (a)–(f) home/away in the Main Experiment, and (g)–(l) density in the Main Experiment and (m)–(p) Common Garden Experiment. Symbols (i.e., filled and unfilled for significant and nonsignificant predictors, respectively) represent predicted values from optimized (generalized) linear mixed-effects models, referring to the last measurement event (September 2016). Density as predictor for leaf damage and survival in the Common Garden Experiment was removed from the model during model optimization, and, thus, is not shown here. Predicted values are printed on the scale of the response variable by making use of the inverse-link function. Note that density is in  $\log_2$  scale, where a seedling density of 1, 4, 9, and 25 corresponds to 0, 2.0, 3.17, and 4.64.

#### DISCUSSION

After two growing seasons, we found home/away- and density-dependent patterns consistent with the Janzen-Connell (JC) hypothesis. The strongest evidence for JC

effects was provided for the responses in leaf damage and survival in the Main Experiment, which were strongly affected by the home/away and density treatments, respectively. A higher seedling performance (i.e., height, number of leaves) and productivity (above-,

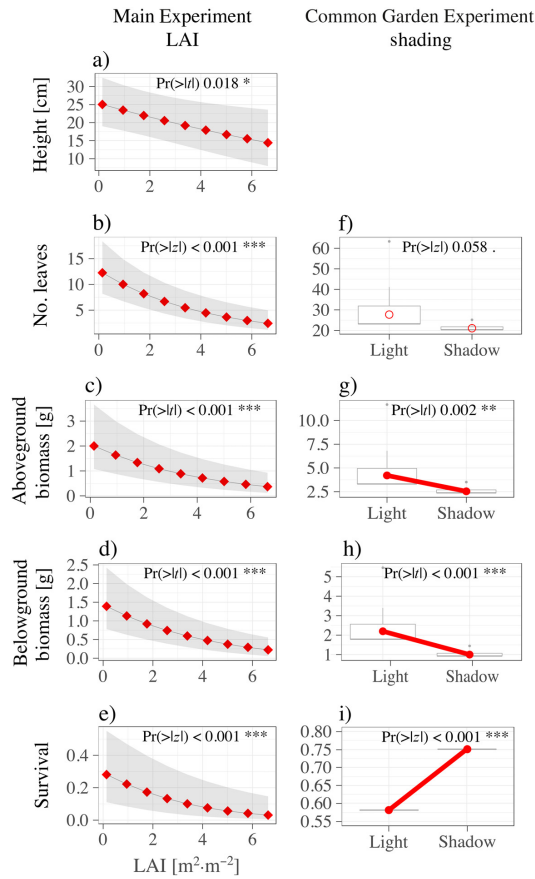


FIG. 3. Seedling performance (i.e., height, number of leaves, productivity (i.e., above-, belowground biomass), and survival) as a function of leaf area index (LAI) in (a)–(e) the Main Experiment and (f)–(i) shading in the Common Garden Experiment. Symbols (i.e., filled and unfilled for significant and nonsignificant predictors, respectively) represent predicted values from optimized (generalized) linear mixed-effects models, referring to the last measurement event (September 2016). LAI as predictor for leaf damage in the Main Experiment, as well as shading as predictor for height and leaf damage in the Common Garden Experiment, were removed from the model during model optimization and thus not shown here. Predicted values are printed on the scale of the response variable by making use of the inverse-link function.

belowground biomass) in the Common Garden Experiment compared to the Main Experiment as well as corresponding density-dependent patterns in seedling performance (i.e., number of leaves) and productivity between the experiments might be attributable to intraspecific competition acting as an additional mechanism besides the JC hypothesis in the Main Experiment. Furthermore, we identified light availability assessed by LAI in the Main Experiment and shading treatments in the Common Garden Experiment to be a strong predictor for seedling performance, productivity, and survival. There were a few interaction effects with density displaying that negative density dependence was less

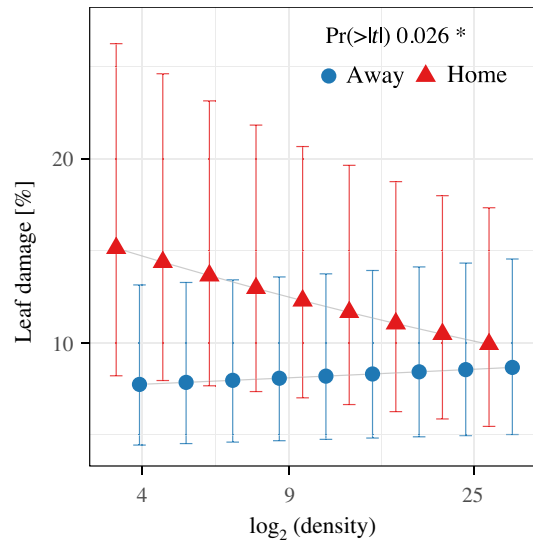


FIG. 4. Leaf damage as a function of density  $\times$  home/away interactive effects in the Main Experiment. Symbols represent predicted values from optimized linear mixed-effects models, referring to the last measurement event (September 2016). Predicted values are printed on the scale of the response variable by making use of the inverse-link function. Error bars represent lower and upper confidence intervals. Note that density is in  $\log_2$  scale, where a seedling density of 4, 9, and 25 corresponds to 2.0, 3.17, and 4.64.

TABLE 2. Main Experiment—time analysis.

	Estimate	Standard error	z value	Pr(> z )
(Intercept)	−0.067	1.268	−0.053	0.958
Density	−0.346	0.111	−3.113	0.002**
Home treatment	−0.195	0.258	−0.753	0.452
LAI	−0.871	0.313	−2.784	0.005**
Time	−2.953	0.704	−4.197	<0.001***
Density: Home treatment	−0.093	0.273	−0.340	0.734
Density: LAI	0.019	0.174	0.108	0.914
Density: Time	−0.117	0.099	−1.187	0.235
Home treatment: Time	−0.767	0.230	−3.329	<0.001***
LAI: Time	−1.119	0.291	−3.845	<0.001***

Notes: Generalized linear mixed-effects model for predicting seedling survival over the course of the experiment ( $N = 67,450$ ) with (time|species) + (time|site|plot|subplot|split-plot|individual) as a random structure. Significance levels are \*\*\*<0.001; \*\*<0.01; \*<0.05; <0.1.

pronounced when seedlings were grown beneath conspecific adult trees (in the Main Experiment) or under low light environments as provided in the shadow treatment (in the Common Garden Experiment).

#### Distance dependence

Seedlings located in plots of conspecific adults, that is, at home, experienced significantly reduced performance

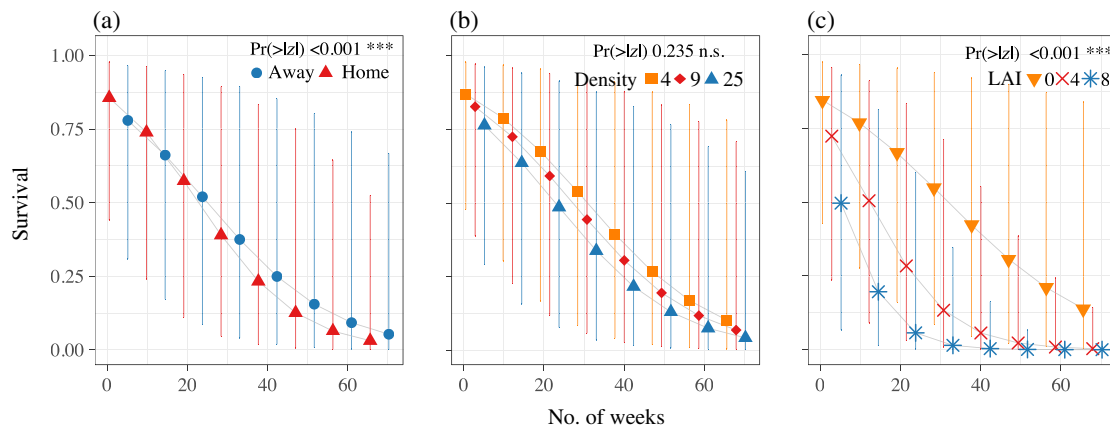


FIG. 5. Interactive (a) home/away  $\times$  time, (b) density  $\times$  time, and (c) LAI  $\times$  time predictions in the Main Experiment on seedling survival. Predicted values are printed on the scale of the response variable by making use of the inverse-link function. Error bars represent lower and upper confidence intervals. Note that density is in  $\log_2$  scale, where a seedling density of 4, 9, and 25 corresponds to 2.0, 3.17, and 4.64.

TABLE 3. Common Garden Experiment.

	(Intercept)	df	Density	df	Shading	df	Density: shadow treatment	df
Performance								
Height	$3.685 \pm 0.214^{***}$	6.033	$-0.126 \pm 0.044^{**}$	170.15				
No. leaves	$3.298 \pm 0.304^{***}$		$-0.48 \pm 0.109^{***}$		$-0.253 \pm 0.133$ .		$0.379 \pm 0.151^*$	
Productivity								
Aboveground	$1.413 \pm 0.435^*$	6.433	$-0.594 \pm 0.147^{***}$	172.788	$-0.457 \pm 0.139^{**}$	75.788	$0.412 \pm 0.201^*$	162.819
Belowground	$0.806 \pm 0.428$ n.s.	6.272	$-0.515 \pm 0.125^{***}$	193.576	$-0.711 \pm 0.111^{***}$	74.909	$0.32 \pm 0.17$ .	178.962
Leaf damage	$-2.289 \pm 0.27^{***}$	6.01						
Survival	$0.329 \pm 0.306$ n.s.				$0.775 \pm 0.225^{***}$			

Notes: Estimates, standard error, significance levels (i.e.,  $^{***}<0.001$ ;  $^{**}<0.01$ ;  $^{*}<0.05$ ;  $<0.1$ ), and degrees of freedom associated with  $t$ -test statistics for optimized (generalized) linear mixed-effects models of seedling height ( $N = 1,038$ ), number of leaves ( $N = 1,034$ ), above- ( $N = 1,004$ ) and belowground productivity ( $N = 1,001$ ), leaf damage ( $N = 1,032$ ), and survival ( $N = 1,654$ ). Analyses were performed separately by record date; results refer to the last measurement (i.e., September 2016). Blank cells indicate excluded predictors during model optimization with (1|species) + (1|plot) as a random structure.

and productivity, and suffered from higher levels of leaf damage compared to seedlings located in monocultures of foreign tree species. Accordingly, across multiple species tested here, there is consistent evidence that herbivore and pathogen attack exert a significant negative influence on seedlings in close proximity to conspecific adult trees. Moreover, although seedling survival was not significantly reduced in plots of conspecific adults at the time of the harvest, our time series analysis revealed that they experienced a significantly reduced likelihood of survival over the course of the experiment. Thus, we can accept our first hypothesis stating that agents from the adults' populations act as herbivores or pathogens on seedlings as proposed by Janzen (1970) and consider the escape from enemy attack as an important mechanism in seedling establishment at this early stage of our experimental forest. Encountering such effects as early as 7 yr after planting of forest indicates a very rapid establishment of multitrophic interactions at the

community level. Although this corresponds to earlier findings of Schuldt et al. (2015) on overall herbivory effects in the same experiment, our data clearly demonstrate the additional impact of multitrophic control on juvenile tree establishment and thus forest regeneration. Despite the multitude of published studies, such a clear pattern has rarely been shown experimentally on a multi-species basis and is remarkable considering the inter-specific variation in distance- and density-dependent effects found so far (Comita et al. 2010, Swamy and Terborgh 2010, Gripenberg et al. 2014). The absence of effects on seedling survival at single monitoring dates corresponds to earlier findings showing that effects of distance dependency intensify over time and may take several years after initiation of experimental seedling planting to become prominent (Swamy and Terborgh 2010). However, for many of the home/away effects, we found increasing effect sizes in the course of the experiment. Thus, we would expect that lower performance

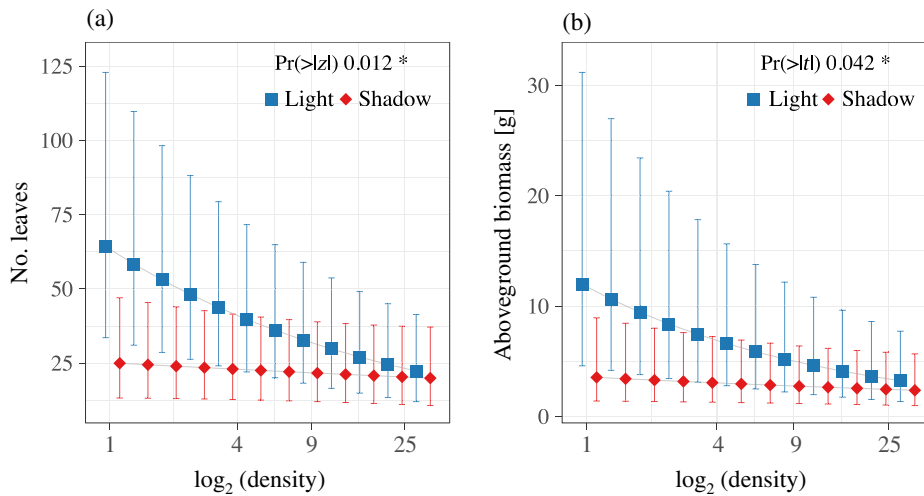


FIG. 6. (a) Number of leaves and (b) aboveground biomass as a function of density  $\times$  shading interactive effects in the Common Garden Experiment. Symbols represent predicted values from optimized (generalized) linear mixed-effects models, referring to the last measurement event (September 2016). Predicted values are printed on the scale of the response variable by making use of the inverse-link function. Error bars represent lower and upper confidence intervals. Note that density is in  $\log_2$  scale, where a seedling density of 1, 4, 9, and 25 corresponds to 0, 2.0, 3.17, and 4.64.

and productivity as well as higher levels of leaf damage ultimately result in a lower seedling survival in home monocultures at later developmental stages and with increasing forest maturity (Comita et al. 2014).

#### Density dependence

Increasing density of conspecific recruits significantly reduced seedling performance (i.e., number of leaves), productivity, and survival in the Main Experiment. These findings are consistent with the interpretation of conspecific negative density dependence by natural enemies causing lower seedling performance, productivity, and ultimately lower seedling survival (Janzen 1970, Connell 1971). In contrast, there was no such effect on leaf damage in the Main Experiment or in the Common Garden Experiment. The absence of such an effect in the Main Experiment might be explained by two scenarios. First, one has to take into account that soil-borne organisms may act as an alternative density-dependent driver for JC effects in the present system. Several studies have provided evidence that soil-borne organisms, similar to insect herbivores and leaf fungal pathogens, are able to cause negative frequency-dependent effects (Kulmatiski et al. 2008, Swamy and Terborgh 2010, Bagchi et al. 2014). If negative density-dependent patterns in the present study were induced by soil-borne organisms, a lack of significant effects on leaf damage would not necessarily contradict the JC hypothesis. A second scenario, however, might be that density-dependent effects encountered were additionally brought about by intraspecific competition and not necessarily by JC effects only. A reduction in seedling performance,

productivity, and survival with increasing seedling density as evidenced in the Main Experiment would then at least partly be the result of competitive effects for space and other resources (Yao et al. 2016, Lin et al. 2017). In the present study, this interpretation could be particularly valid for seedling performance and productivity, for both of which we found similar effects of significant reduction with increasing density of conspecific recruits in the Main Experiment and in the Common Garden Experiment. Even though we did not explicitly test for host-specific enemy load differences between the main and Common Garden Experiment, we can expect a high distance to the nearest forest in combination with pesticide application in the surrounding area to result in a significantly reduced number of host-specific herbivores and pathogens in the Common Garden Experiment. Correspondingly, a density-dependent pattern in the Common Garden Experiment would then result from increased intraspecific competition (Comita et al. 2014, Comita 2017) for resources (e.g., water availability). Consistent with this assumption, seedlings exposed to light in the Common Garden Experiment became more susceptible to negative density dependence (i.e., stronger decline in number of leaves and aboveground biomass) than compared to those seedlings in the shadow, thus indicating strong effects of such increased intraspecific competition for light. Our results contradict the outcome of Swamy and Terborgh (2010), who did not find any evidence for intraspecific resource competition within seedlings in a lowland Amazonian rain forest experiment. However, they did not explicitly intend to disentangle density-dependent patterns brought about by intraspecific competition and herbivory. Ultimately,



seedling survival that was strongly affected by density in the Main Experiment but not at all in the common garden would provide some evidence for JC to be involved. However, although a high initial seedling density should lead to disproportionate decrease in seedling survival over time to be considered as true JC effects (Bellows 1981, Freckleton and Lewis 2006, Bagchi et al. 2010), this effect was not visible in our time series analysis for seedling survival. Combining the results from the main and the Common Garden Experiment, we cannot attribute the effects of negative density dependency found exclusively to natural enemies, as predicted by the JC theory, and thus can only partly confirm our second hypothesis of increasing negative density dependencies with increasing levels of conspecific recruits, as predicted by the JC theory. However, we did find some support for our third hypothesis showing that intraspecific competition for resources may result in similar density-dependent patterns as predicted by the JC theory. In conclusion, our findings may reflect strong interactive effects of different mechanisms (i.e., intraspecific competition and multitrophic interactions as herbivory) jointly impacting seedling survival and resulting in strong negative density dependencies in the Main Experiment. These findings experimentally support the conclusions recently reported by Johnson et al. (2017) based on long-term observational data.

#### *Distance and density interactions*

Leaf damage in plots of conspecific adults (i.e., at home) was significantly higher for seedlings at low densities compared to seedlings at high density levels, while the reverse was true for seedlings located in plots of heterospecific tree species (i.e., away). Accordingly, the detrimental effect of home situations particularly played out at low densities, whereas the lack of differences at high densities indicates a prominent role of strong negative density-dependent effects regardless of the monoculture's identity. This result differs from the study of Yamazaki et al. (2009), who found seedling survival to be lowest at high density beneath conspecific adults for one out of eight species (i.e., *Cornus controversa*). The present results could be explained by an already saturated number of insect herbivores and pathogens in close distance to conspecific adults in the experimental plots. Thus, instead of higher density levels attracting new natural enemies in the home treatment, a higher density may result in a more evenly distributed infestation and decrease the per capita infestation. Overall, we found only limited support for our fourth hypothesis of density and distance interactions. If density dependence at home compared to away has a stronger effect on seedling performance, productivity, and survival, this effect was not yet visible in our experiment. This suggests a nonadditive nature of the effects and might be explained by the strong overall negative density dependence we found. One might consider that with density levels of up to

100 individuals/m<sup>2</sup>, we explicitly applied higher densities than naturally found in mixed-species tree seedling crop in young forests. For example, from the nearby Gutianshan National Nature Reserve densities of 1.4 individuals/m<sup>2</sup> were found in an early successional secondary forest stand (<20 yr; Bruelheide et al. 2011), although densities of conspecific seedlings in seedling carpets may still be much higher (Alvarez-Loayza and Terborgh 2011). However, our results also showed a constant decline in seedling survival with time at all tested density levels.

#### *Light conditions*

In both experiments, light availability was a strong predictor for differences in performance, productivity, and survival with increasing importance (i.e., for seedling survival in the Main Experiment) over the course of the experiment. A strong influence of light availability for understory productivity was also reported for experimental plots of the Main Experiment in a previous study (Germany et al. 2017). These results are consistent with findings from Inman-Narahari et al. (2016), who demonstrated that the strength of density effects varied with light conditions in different forest situations and might be ascribed to species-specific preferences (Comita 2017). However, whereas in the Main Experiment seedling survival was significantly reduced with increasing LAI, indicating detrimental effects of closing canopy, seedlings in the Common Garden Experiment experienced a higher seedling survival with shading compared to seedlings exposed to full light. These contradictory findings between the experiments might be resolved by the possibility that other resources (e.g., water) were more limiting in the Common Garden Experiment than in the Main Experiment. Therefore, seedlings in the Common Garden Experiment would benefit from additional shading, whereas the reverse is true for the Main Experiment. Nevertheless, seedlings exposed to full light in the Common Garden Experiment still had a higher likelihood of survival compared to seedlings exposed to any light availability level in the Main Experiment. An additional explanation for our contradictory findings might be that in low light and high humidity sites, seedlings will experience a lower seedling survival because of more abundant or virulent pathogens, as demonstrated by Augspurger and Kelly (1984). Thus, under low light conditions and at reduced levels of host-specific enemies, seedlings may benefit from a higher water availability in the Common Garden Experiment, but survival was reduced in the presence of more abundant or virulent specialized pathogens in the Main Experiment.

#### CONCLUSIONS

In spite of the strong influence of light availability we could demonstrate host-specific distance effects on seedling performance, productivity, escape from herbivore

attack (i.e., leaf damage) and ultimately survival in an early-stage experimental forest plantation. Although we found similar and, in most cases, noninteractive results with increasing density of conspecific recruits, mechanisms causing such negative density dependence were less easily identifiable. The extent to which negative density dependence effects reflect the impact of different and possibly interactive mechanisms (i.e., intraspecific competition and biotic factors as herbivory) will need to be further addressed, for instance, by implementing higher-resolution density gradients. In addition, although we applied two levels of distances that finally displayed very strong main effects, we would recommend testing of gradual increment in distances in order to go beyond pure presence/absence effects. However, this study clearly underscores the importance of experimental approaches when studying mechanisms regulating tree recruitment and demonstrates that future studies should account for different and potentially coupled mechanisms of negative density dependence just as well as for micro-environmental conditions when addressing the role of JC effects for species coexistence.

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## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecy.2736/supinfo>

## DATA AVAILABILITY

Data are available on the BEFChina Data Portal: <http://china.befdata.biow.uni-leipzig.de/datasets/577>; <http://china.befdata.biow.uni-leipzig.de/datasets/580>



## CHAPTER 5

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### Synthesis

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In the context of the forest Biodiversity-Ecosystem Functioning project in southeast China (BEF-China) and the subproject 11 'The role of herb layer characteristics and productivity for forest ecosystem functioning', this thesis adds new insights into the role of tree species richness and identity for herb layer characteristics (i.e. composition, richness and productivity) and tree recruitment. Implementing three different approaches it was asked: (i) to which degree tree species richness and identity affect herb layer composition, richness and productivity in the 70 very intensively studied plots, (ii) whether tree species richness is about to increase herb layer productivity (via increasing facilitation effects) or to reduce resource availability (by means of an even stronger increase in competition) in the current state of forest development and how these dynamics might change with time, and (iii) how a modified environmental setting as provided by additional treatments at a subplot level interacts with tree species richness effects on herb layer composition, richness and productivity. Finally, it was addressed (iiii) to which degree negative distance and density dependencies, as proposed by the Janzen Conell hypothesis, might be involved in establishing future tree species-rich forest systems. In the following, I will briefly discuss the findings made to these questions before discussing the consolidated results in more detail.

## **5.1 To which degree do tree species richness and identity affect herb layer composition, richness and productivity?**

By altering above- and below-ground resource availability and heterogeneity overstorey trees have been shown to impose competitive constraints to the herb layer (e.g. Zhang et al. 2016, 2017, Ampoorter et al. 2016, Sercu et al. 2017, De Groote et al. 2017). In Germany et al. (2017; Chapter 2), such competitive constraints were mostly evident by strong effects of reduced light conditions, on herb layer species composition at both sites as well as on biomass at site A. These findings are consistent with findings made in temperate and boreal forests, showing light transmittance to be a major limiting factor for the herb layer composition and productivity (Zhang et al. 2017, Kumar et al. 2018, Hedwall et al. 2019). Variations in light transmittance have been reported to be mediated through both tree species properties (Barbier et al. 2008, Ishii and Asano 2010, Niinemets 2010) as well as species richness (Pretzsch 2014, Sapijanskas et al. 2014, Jucker et al. 2015, Williams et al. 2017, Niklaus et al. 2017). Thus, the significant effects of light transmittance might be indirect effects of tree species identities and richness. Yet, in Germany et al.

(2017; Chapter 2), we did encounter only limited support for any additional tree species richness effects on herb layer composition, richness and productivity. Significant effects of tree richness were only found on herb layer composition for site B, while there was neither such an effect on herb layer richness nor on productivity. These results correspond to earlier findings of Both et al. (2011) who studied along gradients of diversity and succession stages, using observational plots in the nearby Gutianshan National Nature Reserve (CSPs), and did not find any significant relationships between herb and tree species richness. Nevertheless, by making use of the broken-stick design as provided by the BEF-China experiment (Bruehlheide et al. 2014), we were still able to detect the corresponding effect for tree species identity on herb layer composition and biomass. In conclusion, despite the young age of the experiment, the interactions between tree species and the herb layer did already emerge. Gilliam et al. (1995) stated that a linkage between tree and herb layer can be expected to increase with an increasing number of woody species within the herb layer, since both strata will then start to respond and compete to similar sets of environmental gradients, such as light. Following, finding a linkage between both strata after such short time since plantation might be explained by the additional finding of woody juveniles already contributing significantly to herb layer species richness and biomass.

## **5.2 Whether tree species richness is about to increase herb layer productivity or to reduce resource availability in the current state of forest development and how these dynamics might change with time?**

In general, the effect of tree species richness on the herb layer can be decomposed into facilitating effects as induced by increased microsite availability (Huston 1979, Stein et al. 2014) and impeding effects, as evidenced by increased reduction in resource availability as a result of complementary effects in the overstorey (Anderson et al. 1969, Loreau and Hector 2001, Stevens and Carson 2002, Huang et al. 2018). The amount as to which these effects play out may largely vary with the developmental stage of a forest system (Kumar et al. 2018). For example, Bartels and Chen (2010) reported in their literature review, that facilitating effects of resource heterogeneity are the most determinant promoters of herb layer species diversity in old-growth stands, while complementary effects



on resource availability can be observed in both young and mature stands. Following, we might expect overstorey effects, including both, signals of tree species identity and tree species richness, as a combination of facilitating and competition effects, to alter herb layer productivity (Fridley 2002, Ampoorter et al. 2015, Wright et al. 2017, De Groote et al. 2017, Kumar et al. 2018). In addition, we might expect tree species richness effects to become more pronounced over time as stands develop and competition for light and/or other resources increases (Forrester 2014, Jucker et al. 2015, Huang et al. 2018). In Chapter 3, designed as a time-extended follow up study of Germany et al. (2017), we encountered a significantly lower herb layer biomass with greater proportion of individual tree species identities. However, we did not encounter a similar effect with variations in tree species richness. These findings are consistent with their previous made findings in Germany et al. (2017; Chapter 2) and also correspond to results of Both et al. (2011) for observational plots in the nearby Gutianshan National Nature Reserve. The absence of tree species richness effects can be explained by recognizing that whether the relationship between tree- and herb layer is indeed being governed more strongly by tree species identity instead of tree species richness is also likely to change the with successional stage of the forest (Forrester 2014, Kumar et al. 2018, Huang et al. 2018). Given that the two sites of the BEF-China project have been established in 2009 (site A) and 2010 (site B) we still are studying effects in young successional stages, while many theories referenced refer to mechanisms prevailing in mature forest stands. Christensen and Gilliam (2003) describe the thinning phase (i.e. approximately 10 years after forest establishment) as a period in which canopy closure marks the initiation of intense competition for limited light and soil resources. In accordance, we found overall herb layer biomass to become significantly reduced in the course of the experiment while we also found the significant effect of light transmittance to gain in explanatory variance over the course of this study. Nevertheless, since variations in light transmittance are mediated through both tree species properties (Barbier et al. 2008, Ishii and Asano 2010, Niinemets 2010) as well as species richness (Pretzsch 2014, Sapijanskas et al. 2014, Jucker et al. 2015, Williams et al. 2017, Niklaus et al. 2017) its effect might be, to some extent, linked to effects of tree species identities and richness. In conclusion, we might expect light transmittance as an isolated effect to further gain in explanatory variance over time until a point in time where its variations, and thus effects, can predominantly be reduced to variations in tree identities and/or species richness effects (i.e. as a combination of facilitating and complementary effects).

### **5.3 How a modified environmental setting interacts with tree species richness effects on herb layer composition, richness and productivity?**

In addition to temporal dynamics, effect sizes of species richness and species composition on ecological processes have been hypothesized to alter with the environmental context (Cardinale et al. 2000, Ratcliffe et al. 2017, Kardol et al. 2018). However, while in Germany et al. (2017; Chapter 2) and in Chapter 3 we found some variations in the herb layer species composition, richness and/or biomass as a outcome of the 'No weeding treatment', we did not find any treatment  $\times$  tree species richness interaction in herb layer responses. Huston (1979) introduced the idea that population densities might mediate the effect of environmental heterogeneity. Following, we would have expected that with increasing population densities in the herb layer (i.e. as it is the case in the 'No weeding treatment') and by eliminating resource limitations (i.e. as it is the case in the 'Phosphorus fertilization treatment'; Chapin et al. 1986, Fridley 2002), species would respond more strongly to facilitating tree species richness effects (i.e. increase in herb layer species richness and/or biomass). This relative insensitivity might be explained by the circumstance that variations in tree species richness only played a minor role in the current state of forest development thereby preventing interactive tree species richness  $\times$  treatment effects to involve (Bartels and Chen 2010). In conclusion, while we found a modified environmental setting to affect the outcome of BEF-relationships (i.e. in- /decrease in the intercept) an interactive effect with tree species richness (i.e. in- /decrease in the slope) was not visible at the current phase of forest development.

## **5.4 To which degree might negative distance and density dependencies, as proposed by the Janzen-Connell hypothesis, be involved in establishing future species-rich forest systems?**

Central components of the Janzen-Connell hypothesis are non-competitive effects of accumulative host species-specific antagonists at lower distance to or at higher density of conspecific plants, thereby two drivers that contribute independently to species coexistence, but that are ultimately linked in the field (Janzen 1970, Connell 1971). As a consequence of such processes, dominant species are prevented from outcompeting less dominant ones and therefore are important for maintaining high tree species richness levels during the later phases of forest development (see also: Terborgh 2012, Revilla et al. 2013, Bever et al. 2015). However, as tree seedlings also compete for resources and thus are not only subjected to Janzen-Connell effects a causal interpretation of density-dependent Janzen-Connell effects can be difficult (Terborgh 2012). Moreover, since light interception as well as species-specific preferences are known to vary strongly among tree species (Neufeld and Young 2003, Porté et al. 2004, Li et al. 2017), seedling survival has been proposed to be generally favoured when the species' preferential light conditions are met, irrespective of Janzen-Connell effects, thus masking the presence of any additional Janzen-Connell effects derived by biotic interactions (Comita 2017). As a consequence, light interception in forests should be considered and quantified when studying the Janzen-Connell hypothesis (Yamazaki et al. 2009). In Germany et al. (2019; Chapter 4) we were able to demonstrate conspecific negative distance dependence mechanism being already effective in early stages of a forest plantation on a multi-species basis. This finding corresponds to earlier findings of Schuldt et al. (2015) on overall herbivory effects in the same experiment which, considering the seven years after establishing the plantation, indicate a very rapid establishment of multitrophic interactions at the community level. However, results obtained in an additionally established Common Garden Experiment showed that additional negative effects of high density may also be brought about by intraspecific competition as an alternative density-responsive mechanism and less by true Janzen-Connell effects. In accordance to these findings, Johnson et al. (2017) reported seedling survival to be significantly correlated with key abiotic (i.e. topographic habitat, annual variation in water availability) and biotic (i.e. plant size, densities of conspecific seedlings as well as conspecific and heterospecific adult trees)

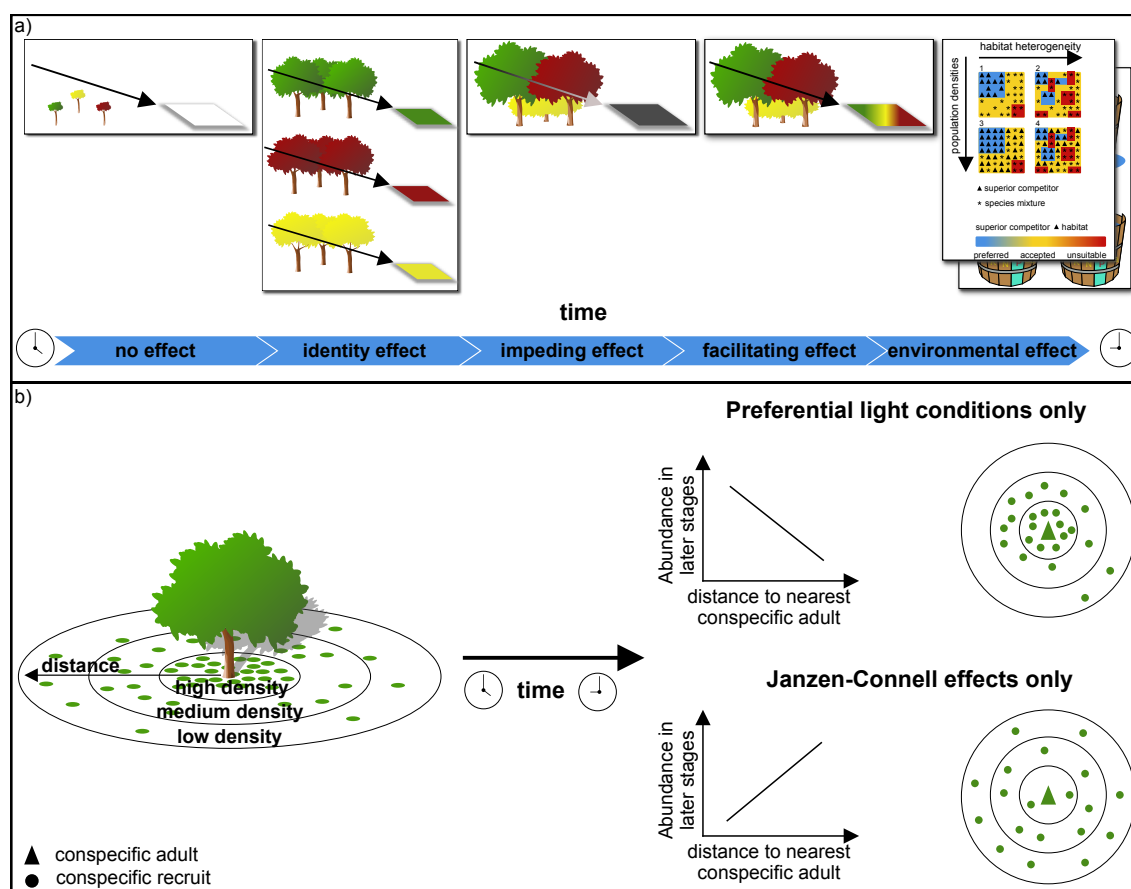
neighbourhood variables, in a long-term observational experiment. In conclusion, while these results do indicate a very rapid establishment of multitrophic interactions in the study system, they also emphasize the need to appropriately account for potential additional density-responsive mechanisms such as intraspecific competition or micro-environmental conditions when addressing the role of Janzen-Connell effects for species coexistence.

## 5.5 Consolidated findings and outlook

Results obtained in all three different experiments support that light transmittance is a major limiting factor for forest herb layer composition, richness and biomass at the current state of forest development. This finding can be explained by the additional finding of woody juveniles already contributing significantly to herb layer species richness and biomass (Gilliam et al. 1995). Moreover, we encountered significant differences in herb layer species composition and biomass with greater proportion of individual tree species identities while a similar effect with variations in tree species richness could not be found. Since light transmittance is mediated through both tree species properties (Barbier et al. 2008, Niinemets 2010) and species richness (Pretzsch 2014, Sapijanskas et al. 2014, Jucker et al. 2015, Williams et al. 2017, Niklaus et al. 2017) its effects might, in some parts, be attributed to some first indirect effects of tree species identities and richness. Moreover, effect size and quantity of light transmittance effects has been reported to alter with successional stages (Tilman 1985, Christensen and Gilliam 2003, Bartels and Chen 2010). In accordance, we found the effect of light transmittance to gain in explanatory variance over the course of forest development. In conclusion, these results indicate light transmittance to gain in explanatory variance over the beginning phase of forest development. However, we might also expect a certain point in forest development where variations in light transmittance can predominantly be reduced to variations in tree identities and/or species richness effects (i.e. as a combination of facilitating and complementary effects). At this point we may also expect interactive environmental  $\times$  tree species richness effects start to occur (Fig.1a).

Yet, already today these results indicate the effect of light transmittance to be associated with additional varying factors such as the effects predicted by the Janzen-Connell hypothesis (Janzen 1970, Connell 1971). While in general seedling density and survival tend to be high when the species' preferential conditions are met (Johnson et al. 2017), which under natural conditions can be expected to be true when conspecific adult

densities tend to be high (Comita 2017), we found accumulating host species-specific antagonists at lower distance to conspecific adults to diminish overall seedling productivity, performance and survival. Following we might expect the net outcome of both, potentially counteracting, mechanism (i.e species' preferential light conditions and accumulating host species-specific antagonists) to facilitate or impair seedling establishment in close distance to conspecific adult trees (Fig. 1b). Moreover, by identifying intraspecific competition as an alternative density-responsive mechanism we could demonstrate yet another mechanism being already effective at this early stage of a forest plantation.



**Figure 5.1:** Conceptual diagram summarizing the effect of tree species identity and richness as well as the additional varying factors over the course of forest development (a) and the potential opposing effects brought about by light transmittance and accumulating host species-specific antagonists as predicted by the Janzen-Connell hypothesis (b). Small green triangles and circles represent conspecific adults and tree recruits, accordingly. Black circles represent the density levels of tree recruit emergence in its initial phase.

Overall, by identifying a range of different mechanism such as light transmittance, accumulative host species-specific antagonists and intraspecific competition being already effective, this thesis adds to our understanding of the current and later phases of forest development and its consequences for the herb layer. While the subsequent interplay of the different identified and prospective mechanisms remains to be tested, this thesis also reveals some of the challenges in future studies when studying the herb layer, such as

the need to account for confounding variables when focusing on single mechanism. Here, experimental platforms, such as BEF-China, can help with their high comparably and their ability to establish orthogonal designs. Corresponding relationships might then be validated in natural ecosystems to increase the significance of the prediction. Experimental and natural designs both jointly considered can then ensure that future political decisions are taken in a more streamlined format.

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I would like to dedicate this work to my son Alvar in the hope that he will have the opportunity to experience the same fascinating unique aspects of nature as I have been allowed to.







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## **Supporting Information**

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**Chapter 2: Table S1:** Detailed description of Very Intensively studied Plots (VIP): richness levels, composition and replicates.

Site A	Plot	Tree layer richness	Replicates	Tree layer composition	Site B	Plot	Tree layer richness	Replicates	Tree layer composition
	C32	2	vip	<i>Castanea henryi</i> <i>Nyssa sinensis</i>		D29	1	vip	<i>Meliosma flexuosa</i>
	E23	2	viprep	<i>Rhus chinensis</i> <i>Schima superba</i>		F25	8	viprep	<i>Alniphyllum fortunei</i> <i>Betula luminifera</i> <i>Castanopsis fargesii</i> <i>Elaeocarpus chinensis</i> <i>Machilus leptophylla</i> <i>Machilus thunbergii</i> <i>Manglietia yuyuanensis</i> <i>Quercus phillyraeoides</i>
	E24	1	viprep	<i>Liquidambar formosana</i>		F26	0	vip	
	E31	1	vip	<i>Quercus fabri</i>		G28	2	vip	<i>Betula luminifera</i> <i>Castanopsis fargesii</i>
	E33	1	vip	<i>Lithocarpus glaber</i>		H29	1	viprep	<i>Alniphyllum fortunei</i>
	E34	1	vip	<i>Castanea henryi</i>		H30	4	viprep	<i>Betula luminifera</i> <i>Castanopsis fargesii</i> <i>Manglietia yuyuanensis</i> <i>Quercus phillyraeoides</i>
	F21	1	vip	<i>Quercus serrata</i>		I22	16	viprep	<i>Ailanthus altissima</i> <i>Alniphyllum fortunei</i> <i>Betula luminifera</i> <i>Castanopsis fargesii</i> <i>Celtis biondii</i> <i>Elaeocarpus chinensis</i> <i>Elaeocarpus glabripetalus</i> <i>Elaeocarpus japonicus</i> <i>Idesia polycarpa</i> <i>Machilus grijsii</i> <i>Machilus leptophylla</i> <i>Machilus thunbergii</i> <i>Manglietia yuyuanensis</i> <i>Meliosma flexuosa</i> <i>Phoebe bournei</i> <i>Quercus phillyraeoides</i>
	F22	2	viprep	<i>Castanea henryi</i> <i>Nyssa sinensis</i>		I24	2	viprep	<i>Manglietia yuyuanensis</i> <i>Quercus phillyraeoides</i>
	F27	4	vip	<i>Castanopsis sclerophylla</i> <i>Choerospondias axillaris</i> <i>Quercus serrata</i> <i>Triadica sebifera</i>		I25	1	vip	<i>Manglietia yuyuanensis</i>
	F28	4	viprep	<i>Castanopsis eyrei</i> <i>Cyclobalanopsis myrsinifolia</i> <i>Koelreuteria bipinnata</i> <i>Lithocarpus glaber</i>		J29	8	vip	<i>Ailanthus altissima</i> <i>Celtis biondii</i> <i>Elaeocarpus glabripetalus</i> <i>Elaeocarpus japonicus</i> <i>Idesia polycarpa</i> <i>Machilus grijsii</i> <i>Meliosma flexuosa</i> <i>Phoebe bournei</i>
	G17	1	viprep	<i>Castanopsis sclerophylla</i>		K27	1	viprep	<i>Castanopsis fargesii</i>
	G22	1	viprep	<i>Lithocarpus glaber</i>		K29	1	viprep	<i>Celtis biondii</i>
	G24	1	vip	<i>Koelreuteria bipinnata</i>		M07	1	vip	<i>Betula luminifera</i>
	G28	0	vip			M22	4	vip	<i>Alniphyllum fortunei</i> <i>Elaeocarpus chinensis</i> <i>Machilus leptophylla</i> <i>Machilus thunbergii</i>
	G33	1	viprep	<i>Quercus serrata</i>		M24	2	vip	<i>Celtis biondii</i> <i>Elaeocarpus glabripetalus</i>
	H25	1	viprep	<i>Nyssa sinensis</i>		M29	2	vip	<i>Elaeocarpus japonicus</i> <i>Phoebe bournei</i>
	H31	2	vip	<i>Liquidambar formosana</i> <i>Sapindus saponaria</i>		N02	1	viprep	<i>Meliosma flexuosa</i>
	I12	1	viprep	<i>Castanea henryi</i>		N05	1	vip	<i>Ailanthus altissima</i>

Site A	Plot	Tree layer richness	Replicates	Tree layer composition	Site B	Plot	Tree layer richness	Replicates	Tree layer composition
	I27	2	vip	<i>Choerospondias axillaris</i> <i>Triadica sebifera</i>		N21	1	viprep	<i>Machilus grijsii</i>
	I28	1	vip	<i>Liquidambar formosana</i>		N28	1	vip	<i>Idesia polycarpa</i>
	J21	2	vip	<i>Koelreuteria bipinnata</i> <i>Lithocarpus glaber</i>		O05	1	viprep	<i>Idesia polycarpa</i>
	J27	2	viprep	<i>Castanopsis eyrei</i> <i>Cyclobalanopsis myrsinifolia</i>		O06	2	viprep	<i>Idesia polycarpa</i> <i>Machilus grijsii</i>
	K03	2	viprep	<i>Cyclobalanopsis glauca</i> <i>Quercus fabri</i>		O27	2	vip	<i>Manglietia yuyuanensis</i> <i>Quercus phillyraeoides</i>
	K09	1	viprep	<i>Cyclobalanopsis glauca</i>		O31	4	vip	<i>Celtis biondii</i> <i>Elaeocarpus glabripetalus</i> <i>Elaeocarpus japonicus</i> <i>Phoebe bournei</i>
	K19	1	vip	<i>Schima superba</i>		P16	2	viprep	<i>Celtis biondii</i> <i>Elaeocarpus glabripetalus</i>
	L04	0	vip			P24	1	viprep	<i>Manglietia yuyuanensis</i>
	L10	1	vip	<i>Castanopsis eyrei</i>		P25	1	viprep	<i>Elaeocarpus japonicus</i>
	L11	1	vip	<i>Castanopsis sclerophylla</i>		Q06	1	viprep	<i>Elaeocarpus chinensis</i>
	L20	0	vip			Q17	8	vip	<i>Alniphyllum fortunei</i> <i>Betula luminifera</i> <i>Castanopsis fargesii</i> <i>Elaeocarpus chinensis</i> <i>Machilus leptophylla</i> <i>Machilus thunbergii</i> <i>Manglietia yuyuanensis</i> <i>Quercus phillyraeoides</i>
	L22	16	vip	<i>Castanea henryi</i> <i>Castanopsis eyrei</i> <i>Castanopsis sclerophylla</i> <i>Choerospondias axillaris</i> <i>Cyclobalanopsis glauca</i> <i>Cyclobalanopsis myrsinifolia</i> <i>Koelreuteria bipinnata</i> <i>Liquidambar formosana</i> <i>Lithocarpus glaber</i> <i>Nyssa sinensis</i> <i>Quercus fabri</i> <i>Quercus serrata</i> <i>Rhus chinensis</i> <i>Sapindus saponaria</i> <i>Triadica sebifera</i> <i>Schima superba</i>		Q23	0	vip	
	L23	1	viprep	<i>Choerospondias axillaris</i>		Q27	1	vip	<i>Alniphyllum fortunei</i>
	N08	4	vip	<i>Cyclobalanopsis glauca</i> <i>Quercus fabri</i> <i>Rhus chinensis</i> <i>Schima superba</i>		Q29	1	vip	<i>Machilus leptophylla</i>

Site A	Plot	Tree layer richness	Replicates	Tree layer composition	Site B	Plot	Tree layer richness	Replicates	Tree layer composition
				<i>Acer davidii</i> <i>Castanea henryi</i> <i>Castanopsis carlesii</i> <i>Castanopsis eyrei</i> <i>Castanopsis sclerophylla</i> <i>Choerospondias axillaris</i> <i>Cinnamomum camphora</i> <i>Cyclobalanopsis glauca</i> <i>Cyclobalanopsis myrsinaefolia</i> <i>Daphniphyllum oldhamii</i> <i>Diospyros glaucifolia</i> <i>Koelreuteria bipinnata</i> <i>Liquidambar formosana</i> <i>Lithocarpus glaber</i> <i>Melia azedarach</i> <i>Nyssa sinensis</i> <i>Quercus acutissima</i> <i>Quercus fabri</i> <i>Quercus serrata</i> <i>Rhus chinensis</i> <i>Sapindus saponaria</i> <i>Sapium discolor</i> <i>Triadica sebifera</i> <i>Schima superba</i>					
	N09	24	vip		R03	4	vip		<i>Betula luminifera</i> <i>Castanopsis fargesii</i> <i>Manglietia yuyuanensis</i> <i>Quercus phillyraeoides</i>
	N11	1	vip	<i>Sapindus saponaria</i>	R04	1	viprep		<i>Elaeocarpus glabripetalus</i>
	N13	1	vip	<i>Triadica sebifera</i>	R05	1	viprep		<i>Phoebe bournei</i>
	N17	1	vip	<i>Rhus chinensis</i>	R29	1	vip		<i>Castanopsis fargesii</i>
	N20	4	viprep	<i>Castanopsis sclerophylla</i> <i>Choerospondias axillaris</i> <i>Quercus serrata</i> <i>Triadica sebifera</i>	R30	24	viprep		<i>Ailanthus altissima</i> <i>Alniphyllum fortunei</i> <i>Betula luminifera</i> <i>Castanopsis eyrei</i> <i>Castanopsis fargesii</i> <i>Castanopsis sclerophylla</i> <i>Celtis biondii</i> <i>Cinnamomum camphora</i> <i>Cyclobalanopsis glauca</i> <i>Daphniphyllum oldhamii</i> <i>Diospyros glaucifolia</i> <i>Elaeocarpus chinensis</i> <i>Elaeocarpus glabripetalus</i> <i>Elaeocarpus japonicus</i> <i>Idesia polycarpa</i> <i>Lithocarpus glaber</i> <i>Machilus grijsii</i> <i>Machilus leptophylla</i> <i>Machilus thunbergii</i> <i>Manglietia yuyuanensis</i> <i>Meliosma flexuosa</i> <i>Phoebe bournei</i> <i>Quercus phillyraeoides</i> <i>Schima superba</i>
	N29	1	viprep	<i>Castanopsis eyrei</i>	S03	1	viprep		<i>Quercus phillyraeoides</i>
	O06	2	viprep	<i>Castanopsis sclerophylla</i> <i>Quercus serrata</i>	S11	1	viprep		<i>Betula luminifera</i>
	O22	1	vip	<i>Cyclobalanopsis myrsinifolia</i>	S18	4	vip		<i>Ailanthus altissima</i> <i>Idesia polycarpa</i> <i>Machilus grijsii</i> <i>Meliosma flexuosa</i>
	O27	1	vip	<i>Choerospondias axillaris</i>	S22	16	vip		<i>Ailanthus altissima</i> <i>Alniphyllum fortunei</i> <i>Betula luminifera</i> <i>Castanopsis fargesii</i> <i>Celtis biondii</i> <i>Elaeocarpus chinensis</i> <i>Elaeocarpus glabripetalus</i> <i>Elaeocarpus japonicus</i> <i>Idesia polycarpa</i> <i>Machilus grijsii</i> <i>Machilus leptophylla</i> <i>Machilus thunbergii</i> <i>Manglietia yuyuanensis</i> <i>Meliosma flexuosa</i> <i>Phoebe bournei</i> <i>Quercus phillyraeoides</i>

Site A	Plot	Tree layer richness	Replicates	Tree layer composition	Site B	Plot	Tree layer richness	Replicates	Tree layer composition
	P07	1	viprep	<i>Rhus chinensis</i>		T05	1	viprep	<i>Machilus leptophylla</i>
									<i>Ailanthus altissima</i> <i>Alniphyllum fortunei</i> <i>Betula luminifera</i> <i>Castanopsis eyrei</i> <i>Castanopsis fargesii</i> <i>Castanopsis sclerophylla</i> <i>Celtis biondii</i> <i>Cinnamomum camphora</i> <i>Cyclobalanopsis glauca</i> <i>Daphniphyllum oldhamii</i> <i>Diospyros glaucifolia</i> <i>Elaeocarpus chinensis</i> <i>Elaeocarpus glabripetalus</i> <i>Elaeocarpus japonicus</i> <i>Idesia polycarpa</i> <i>Lithocarpus glaber</i> <i>Machilus grijsii</i> <i>Machilus leptophylla</i> <i>Machilus thunbergii</i> <i>Manglietia yuyuanensis</i> <i>Meliosma flexuosa</i> <i>Phoebe bournei</i> <i>Quercus phillyreoides</i> <i>Schima superba</i>
	P08	1	viprep	<i>Cyclobalanopsis myrsinifolia</i>		T08	24	vip	
	P19	4	vip	<i>Castanea henryi</i> <i>Liquidambar formosana</i> <i>Nyssa sinensis</i> <i>Sapindus saponaria</i>		T10	0	vip	
	P23	2	vip	<i>Rhus chinensis</i> <i>Schima superba</i>		T13	1	vip	<i>Machilus thunbergii</i>
	P26	2	vip	<i>Castanopsis sclerophylla</i> <i>Quercus serrata</i>		T15	2	viprep	<i>Alniphyllum fortunei</i> <i>Machilus leptophylla</i>
	P27	8	viprep	<i>Castanopsis eyrei</i> <i>Cyclobalanopsis glauca</i> <i>Cyclobalanopsis myrsinifolia</i> <i>Koelreuteria bipinnata</i> <i>Lithocarpus glaber</i> <i>Quercus fabri</i> <i>Rhus chinensis</i> <i>Schima superba</i>		T25	4	viprep	<i>Celtis biondii</i> <i>Elaeocarpus glabripetalus</i> <i>Elaeocarpus japonicus</i> <i>Phoebe bournei</i>
	P29	4	viprep	<i>Castanea henryi</i> <i>Liquidambar formosana</i> <i>Nyssa sinensis</i> <i>Sapindus saponaria</i>		T29	1	vip	<i>Quercus phillyraeoides</i>
	Q07	2	viprep	<i>Koelreuteria bipinnata</i> <i>Lithocarpus glaber</i>		U06	1	viprep	<i>Machilus thunbergii</i>
	Q09	2	vip	<i>Castanopsis eyrei</i> <i>Cyclobalanopsis myrsinifolia</i>		U08	2	viprep	<i>Elaeocarpus japonicus</i> <i>Phoebe bournei</i>
	Q13	1	viprep	<i>Koelreuteria bipinnata</i>		U16	1	vip	<i>Elaeocarpus japonicus</i>
	Q16	1	viprep	<i>Quercus fabri</i>		U20	4	viprep	<i>Alniphyllum fortunei</i> <i>Elaeocarpus chinensis</i> <i>Machilus leptophylla</i> <i>Machilus thunbergii</i>
	Q21	2	vip	<i>Cyclobalanopsis glauca</i> <i>Quercus fabri</i>		U21	2	viprep	<i>Betula luminifera</i> <i>Castanopsis fargesii</i>
	R14	1	vip	<i>Cyclobalanopsis glauca</i>		U27	2	vip	<i>Idesia polycarpa</i> <i>Machilus grijsii</i>
	R16	8	viprep	<i>Castanea henryi</i> <i>Castanopsis sclerophylla</i> <i>Choerospondias axillaris</i> <i>Liquidambar formosana</i> <i>Nyssa sinensis</i> <i>Quercus serrata</i> <i>Sapindus saponaria</i> <i>Triadica sebifera</i>		V08	2	viprep	<i>Elaeocarpus chinensis</i> <i>Machilus thunbergii</i>



Site A	Plot	Tree layer richness	Replicates	Tree layer composition	Site B	Plot	Tree layer richness	Replicates	Tree layer composition
	R17	1	viprep	<i>Sapindus saponaria</i>		V15	2	vip	<i>Ailanthus altissima</i> <i>Meliosma flexuosa</i>
				<i>Acer davidii</i> <i>Castanea henryi</i> <i>Castanopsis carlesii</i> <i>Castanopsis eyrei</i> <i>Castanopsis sclerophylla</i> <i>Choerospondias axillaris</i> <i>Cinnamomum camphora</i> <i>Cyclobalanopsis glauca</i> <i>Cyclobalanopsis myrsinaefolia</i> <i>Daphniphyllum oldhamii</i> <i>Diospyros glaucifolia</i> <i>Koelreuteria bipinnata</i>					
	R18	24	viprep	<i>Liquidambar formosana</i> <i>Lithocarpus glaber</i> <i>Melia azedarach</i> <i>Nyssa sinensis</i> <i>Quercus acutissima</i> <i>Quercus fabri</i> <i>Quercus serrata</i> <i>Rhus chinensis</i> <i>Sapindus saponaria</i> <i>Sapium discolor</i> <i>Triadica sebifera</i> <i>Schima superba</i>		V19	2	vip	<i>Elaeocarpus chinensis</i> <i>Machilus thunbergii</i>
				<i>Castanea henryi</i> <i>Castanopsis sclerophylla</i> <i>Choerospondias axillaris</i> <i>Liquidambar formosana</i> <i>Nyssa sinensis</i> <i>Quercus serrata</i> <i>Sapindus saponaria</i> <i>Triadica sebifera</i>					<i>Ailanthus altissima</i> <i>Celtis biondii</i> <i>Elaeocarpus glabripetalus</i> <i>Elaeocarpus japonicus</i> <i>Idesia polycarpa</i> <i>Machilus grijsii</i> <i>Meliosma flexuosa</i> <i>Phoebe bournei</i>
	S10	8	vip	<i>Triadica sebifera</i>		V20	8	viprep	
				<i>Choerospondias axillaris</i> <i>Triadica sebifera</i>					<i>Alniphyllum fortunei</i> <i>Machilus leptophylla</i>
	S18	2	viprep			V23	2	vip	
				<i>Castanopsis eyrei</i> <i>Cyclobalanopsis glauca</i> <i>Cyclobalanopsis myrsinifolia</i> <i>Koelreuteria bipinnata</i> <i>Lithocarpus glaber</i> <i>Quercus fabri</i> <i>Rhus chinensis</i> <i>Schima superba</i>					<i>Elaeocarpus chinensis</i>
	T15	8	vip			V24	1	vip	
				<i>Liquidambar formosana</i> <i>Sapindus saponaria</i>					<i>Phoebe bournei</i>
	T17	2	viprep			W10	1	vip	
				<i>Schima superba</i>					<i>Elaeocarpus glabripetalus</i>
	T18	1	viprep			W11	1	vip	
				<i>Castanea henryi</i> <i>Castanopsis eyrei</i> <i>Castanopsis sclerophylla</i> <i>Choerospondias axillaris</i> <i>Cyclobalanopsis glauca</i> <i>Cyclobalanopsis myrsinifolia</i> <i>Koelreuteria bipinnata</i> <i>Liquidambar formosana</i> <i>Lithocarpus glaber</i> <i>Nyssa sinensis</i> <i>Quercus fabri</i> <i>Quercus serrata</i> <i>Rhus chinensis</i> <i>Sapindus saponaria</i> <i>Triadica sebifera</i> <i>Schima superba</i>					<i>Ailanthus altissima</i> <i>Idesia polycarpa</i> <i>Machilus grijsii</i> <i>Meliosma flexuosa</i>
	U10	16	viprep			X08	4	viprep	
				<i>Cyclobalanopsis glauca</i> <i>Quercus fabri</i> <i>Rhus chinensis</i> <i>Schima superba</i>					<i>Machilus grijsii</i>
	U15	4	viprep			X21	1	vip	
				<i>Castanopsis eyrei</i> <i>Cyclobalanopsis myrsinifolia</i> <i>Koelreuteria bipinnata</i> <i>Lithocarpus glaber</i>					<i>Ailanthus altissima</i> <i>Meliosma flexuosa</i>
	W12/X12	4	vip			X22	2	viprep	
				<i>Triadica sebifera</i> <i>Nyssa sinensis</i>					<i>Celtis biondii</i> <i>Ailanthus altissima</i>
	W13	1	viprep			Y09	1	vip	
	W14	1	vip			Y23	1	viprep	

**Chapter 4: Table S1:** Detailed description of species used in the reciprocal transplant experiment. Replicates (i.e. R1, R2, R3) refer to monocultures and mono-specific neighbourhoods (1), respectively, used in the Main Experiment. In six plots of site A the establishment of the home species failed (2); thus, these plots have been used as 'away'-treatment only. Age differs between species that have been germinated in the year 2014 (1) and 2015 (0). The Common Garden (i.e. CG) refers to species either also implemented within the additional ex-situ experiment. The taxonomy follows the Flora of China. Note that *Cinnamomum camphora* failed to become established in ten (i.e. B38, C37, E24, E33, F21, G22, G33, P07, S08, W13) out of 26 plots in foreign monocultures on site A

Species	Site A			Site B			CG	Age	Leaf phenology
	R1	R2	R3	R1	R2	R3			
<i>Cinnamomum camphora</i> (L.) J. Presl	L08 <sup>1</sup>	Q25	U16 <sup>1</sup>	I27	R19	U13	No	1	evergreen
<i>Castanopsis fargesii</i> Franch.				K27	R29	S25 <sup>1</sup>	Yes	1	evergreen
<i>Cyclobalanopsis glauca</i> (Thunb.) Oerst.	B38 <sup>1</sup>	K09	R14	L27 <sup>1</sup>	P08 <sup>1</sup>	Q24	Yes	1	evergreen
<i>Castanopsis sclerophylla</i> (Lindl. & Paxton) Schotky	G17 <sup>2</sup>	L11 <sup>2</sup>	S08 <sup>1,2</sup>	L07	S20 <sup>1</sup>	S27 <sup>1</sup>	Yes	0	evergreen
<i>Diospyros japonica</i> Siebold & Zucc.	K18 <sup>1</sup>	K23		O20 <sup>1</sup>	U22 <sup>1</sup>		Yes	0	deciduous
<i>Liquidambar formosana</i> Hance	E24	I28	T17 <sup>1</sup>				Yes	1	deciduous
<i>Lithocarpus glaber</i> (Thunb.) Nakai	E33	G22	O20 <sup>1</sup>	L05 <sup>1</sup>	P06 <sup>1</sup>	R08	Yes	1	evergreen
<i>Quercus serrata</i> Murray	F21	G33	P26 <sup>1</sup>				Yes	1	deciduous
<i>Rhus chinensis</i> Miller	H15 <sup>1</sup>	N17	P07				Yes	1	deciduous
<i>Schima superba</i> Gardner & Champ.	C37 <sup>1,2</sup>	K19 <sup>2</sup>	T18 <sup>2</sup>	P08 <sup>1</sup>	T20		No	1	evergreen
<i>Triadica sebifera</i> (L.) Small	I27 <sup>1</sup>	N13	W13				No	1	deciduous

**Chapter 4: Table S2: Main Experiment:** Estimates, standard error, significance levels (i.e. \*\*<0.001; \*<0.01; \*<0.05; <0.1) and degrees of freedom associated with t-test statistics for optimized (generalized) linear mixed-effects models of seedlings established. All analyses were performed separately by record date (i.e. June/July 2015, August 2015, March 2016 and September 2016). In the full model, treatments of home/away and density, LAI, and their interactions were considered fixed effects, while species, site, plot, subplot and split-subplot were considered random. In the subsequent analyses models were optimized using the AICc criterion and maximum likelihood. Blank cells indicate excluded predictors during model optimization.

	(Intercept)	df	Home - treatment	df	Density	df	LAI	df	Density: Home - treatment	df	Density:LAI	df
June 2015												
Performance												
Height	3.088 ± 0.216 ***	5.737			-0.026 ± 0.01 *	834.176						
No. leaves	1.49 ± 0.355 ***		0.15 ± 0.067 *		-0.052 ± 0.029 .		-0.111 ± 0.065 .					
Survival	1.245 ± 0.695 .				-0.179 ± 0.067 **							
August 2015												
Performance												
Height	3.11 ± 0.205 ***	6.889			-0.096 ± 0.023 ***		-0.288 ± 0.065 ***					
No. leaves	1.955 ± 0.242 ***		0.255 ± 0.149 .		-0.167 ± 0.064 **							
Survival	0.102 ± 0.706 n.s.											
October 2015												
Performance												
Height	3.304 ± 0.148 ***	9.279	-0.049 ± 0.027 .	607.542	-0.022 ± 0.013 .	637.95						
No. leaves	2.138 ± 0.211 ***		-0.195 ± 0.056 ***		-0.148 ± 0.024 ***		-0.384 ± 0.062 ***					
Leaf damage	-2.171 ± 0.335 ***	9.379	0.325 ± 0.12 **	524.246			-0.442 ± 0.109 ***	108.918				
Survival	-0.003 ± 0.438 n.s.				-0.109 ± 0.062 .		-0.383 ± 0.153 *					
March 2016												
Performance												
Height	3.227 ± 0.185 ***	8.323	-0.069 ± 0.03 *	560.76	0 ± 0.014 n.s.	605.126			-0.08 ± 0.039 *	589.032		
No. leaves	0.586 ± 0.384 n.s.		-0.503 ± 0.14 ***		-0.127 ± 0.054 *		-0.478 ± 0.175 **					
Survival	-0.265 ± 0.84 n.s.				-0.218 ± 0.073 **		-0.518 ± 0.206 *					
September 2016												
Performance												
Height	3.446 ± 0.104 ***	10.927	-0.153 ± 0.044 ***	575.477	-0.036 ± 0.019 .	529.205	-0.123 ± 0.051 *	143.946			0.078 ± 0.044 .	550.872
No. leaves	2.351 ± 0.203 ***		-0.448 ± 0.084 ***		-0.164 ± 0.035 ***		-0.504 ± 0.106 ***					
Productivity	0.568 ± 0.298 .	9.509	-0.289 ± 0.087 ***	579.943	-0.207 ± 0.037 ***	508.53	-0.481 ± 0.101 ***	145.482				
Aboveground	0.228 ± 0.267 n.s.	10.02	-0.156 ± 0.071 *	567.891	-0.181 ± 0.03 ***	504.897	-0.473 ± 0.082 ***	148.222				
Belowground	-2.393 ± 0.296 **	3.084	0.308 ± 0.128 *	449.004	0.077 ± 0.059 n.s.	421.527			-0.379 ± 0.17 *	460.64		
Leaf damage												
Survival	-1.22 ± 0.578 *		-0.266 ± 0.165 n.s.		-0.18 ± 0.069 **		-0.781 ± 0.224 ***					

**Chapter 4: Table S3: Main Experiment:** Species-specific estimates, standard error, significance levels (i.e. \*\*\*<0.001; \*\*<0.01; \* <0.05; <0.1) and degrees of freedom associated with t-test statistics for optimized (generalized) linear mixed-effects models of seedlings established. All analyses were performed separately by record date (i.e. June/July 2015, August 2015, October 2015, March 2016 and September 2016) and species. In the full model, treatments of home/away and density, LAI, and their interactions were considered fixed effects, while species, site, plot, subplot and split-subplot were considered random. In the subsequent analyses models were optimized using the AICc criterion and maximum likelihood. Blank cells indicate excluded predictors during model optimization.

		Density:				Home - treatment				Density:LAI			
	(Intercept)	df	Home	df	Density	df	LAI	df	Home - treatment	df	Density:LAI	df	
<b>Cinnamomum camphora</b>													
June 2015													
Performance													
Height	3.17 ± 0.211 *	1	0.518 ± 0.347 n.s.	69.547	-0.108 ± 0.036 **								
No. leaves	1.031 ± 0.141 ***				-0.54 ± 0.218 *								
Survival	2.622 ± 0.476 ***												
August 2015													
Performance													
Height	2.838 ± 0.172 *	1.001	0.837 ± 0.737 n.s.	47.832	-0.069 ± 0.038 .								
No. leaves	1.974 ± 0.084 ***				-0.158 ± 0.046 ***								
Survival	1.077 ± 0.292 ***				-0.271 ± 0.156 .								
October 2015													
Performance													
Height	3.021 ± 0.082 *	1.006		54.58	-0.072 ± 0.039 .								
No. leaves	2.151 ± 0.104 ***		-0.343 ± 0.173 *		-0.196 ± 0.049 ***		0.022 ± 0.088 n.s.	30.427			0.188 ± 0.084 *	55.829	
Leaf damage	-2.902 ± 0.387 .	1.048	0.806 ± 0.296 *	27.499	-0.212 ± 0.138 n.s.		-0.341 ± 0.144 *						
Survival	0.676 ± 0.278 *		0.89 ± 0.701 n.s.		-0.156 ± 0.148 n.s.		-0.716 ± 0.26 **	32.338			0.487 ± 0.295 n.s.	66.474	
March 2016													
Performance													
Height	3.113 ± 0.197 *	1.005		55.811	-0.063 ± 0.041 n.s.								
No. leaves	0.229 ± 0.508 n.s.				-0.176 ± 0.113 n.s.								
Survival	1.308 ± 0.838 n.s.												
September 2016													
Performance													
Height	3.264 ± 0.059 ***	0.059	-0.322 ± 0.138 *	0.138	-0.073 ± 0.045 n.s.								
No. leaves	2.229 ± 0.147 ***		-0.84 ± 0.256 **		-0.262 ± 0.078 ***								
Productivity													
Aboveground	0.635 ± 0.12 ***	29.121	-0.463 ± 0.278 n.s.	30.945	-0.348 ± 0.101 **								
Belowground	0.575 ± 0.088 *	1.554	-0.249 ± 0.175 n.s.	30.452	-0.271 ± 0.074 ***								
Leaf damage	-2.551 ± 0.151 ***	27.699			0.278 ± 0.128 *								
Survival	-1.273 ± 0.325 ***				-0.645 ± 0.15 ***								
Castanopsis fargesii													
June 2015													
Performance													
Height	2.776 ± 0.029 ***	15.33	-0.765 ± 0.219 ***										
No. leaves	1.736 ± 0.08 ***												
Survival	0.882 ± 0.313 **												
August 2015													
Performance													
Height	2.842 ± 0.03 ***	15.581	-1.241 ± 0.257 ***										
No. leaves	2.053 ± 0.097 ***												
Survival	-0.134 ± 0.293 n.s.												
October 2015													



	(Intercept)		Home		Density	LAI	Density - treatment		Density:LAI
	df		df		df		df		df
Belowground	1.016	-0.207 ± 0.283 n.s.	40.256	-0.507 ± 0.198 *	67.254	-0.617 ± 0.147 ***	38.15		
Leaf damage	0.997	-2.46 ± 0.236 .							
Survival		-1.036 ± 0.642 n.s.							
<i>Castanopsis sclerophylla</i>									
June 2015									
Performance									
Height	5.968	2.294 ± 0.031 ***							
No. leaves		0.851 ± 0.124 ***							
Survival		-1.286 ± 0.603 *		2.75 ± 1.483 .					
August 2015									
Performance									
Height	11.465	2.241 ± 0.032 ***	9.123	0.143 ± 0.073 .	18.644			0.137 ± 0.053 *	13.014
No. leaves		1.131 ± 0.1 ***		0.421 ± 0.208 *					
Survival		-1.524 ± 0.641 *							
October 2015									
Performance									
Height	16.498	2.619 ± 0.036 ***	12.407	0.137 ± 0.082 n.s.					
No. leaves		1.416 ± 0.102 ***		0.365 ± 0.223 n.s.					
Leaf damage	13.959	-3.449 ± 0.262 ***			11.037				
Survival		-1.726 ± 0.575 **							
March 2016									
Performance									
Height	15.54	2.322 ± 0.046 ***	12.112	0.164 ± 0.102 n.s.	193.658			-0.561 ± 0.262 *	
No. leaves		1.206 ± 0.12 ***							
Survival		-2.17 ± 0.644 ***		2.082 ± 1.582 n.s.				1.513 ± 0.714 *	
September 2016									
Performance									
Height	18.867	2.853 ± 0.073 ***							
No. leaves		1.684 ± 0.152 ***							
Productivity									
Aboveground	18.172	-0.815 ± 0.178 ***							
Belowground	17.767	-1.038 ± 0.155 ***							19.279
Leaf damage	12.684	-2.711 ± 0.257 ***							18.81
Survival		-1.965 ± 0.544 ***							
<i>Diospyros japonica</i>									
June 2015									
Performance									
Height	1	2.318 ± 0.063 *							
No. leaves		1.622 ± 0.024 ***		-0.176 ± 0.122 n.s.					
Survival		0.657 ± 0.171 ***		-2.262 ± 0.622 ***					
August 2015									
Performance									
Height	0.998	2.473 ± 0.061 *							
No. leaves		1.807 ± 0.051 ***		-0.788 ± 0.2 ***					
Survival		0.377 ± 0.193 .		-2.779 ± 0.73 ***					
October 2015									0.133 ± 0.072 .



	(Intercept)		Home		Density		L:AI		Density:L:AI		df
		df		df		df		df		df	
<b>Lithocarpus glaber</b>											
June 2015											
Belowground	1.263 ± 0.085 ***	24.536	-0.449 ± 0.285 n.s.	32.493	-0.578 ± 0.07 ***	40.76	-0.671 ± 0.183 ***	30.784	-1.341 ± 0.609 *	68.098	
Leaf damage	-2.878 ± 0.156 ***	23.184	0.497 ± 0.546 n.s.	38.954	0.086 ± 0.166 n.s.	25.804					
Survival	-0.601 ± 0.31 .				-0.577 ± 0.175 **		-1.59 ± 0.637 *				
August 2015											
Performance											
Height	2.938 ± 0.092 *	1.001	0.366 ± 0.207 .		0.028 ± 0.016 .	76.982					
No. leaves	0.543 ± 0.393 n.s.				0.083 ± 0.054 n.s.						
Survival	1.812 ± 0.947 .										
October 2015											
Performance											
Height	2.948 ± 0.073 *	1	0.292 ± 0.136 *		0.043 ± 0.015 **	61.809	0.058 ± 0.037 n.s.	39.739			
No. leaves	1.257 ± 0.188 ***				0.063 ± 0.044 n.s.		-0.212 ± 0.096 *				
Survival	0.542 ± 0.888 n.s.										
March 2016											
Performance											
Height	3.173 ± 0.063 *	1	0.74 ± 0.394 .		0.035 ± 0.014 *	58.472	-0.412 ± 0.093 ***				
No. leaves	1.731 ± 0.11 ***										
Leaf damage	-3.419 ± 0.248 *	0.999									
Survival	0.568 ± 0.4 n.s.										
September 2016											
Performance											
Height	3.023 ± 0.047 **	0.999	0.724 ± 0.401 .		0.061 ± 0.016 ***	54.344	-0.275 ± 0.115 *				
No. leaves	1.624 ± 0.118 ***										
Survival	-0.04 ± 0.872 n.s.										
October 2016											
Performance											
Height	3.324 ± 0.072 *	1			0.031 ± 0.021 n.s.	66.899	-0.092 ± 0.055 n.s.	39.479			
No. leaves	2.234 ± 0.139 ***						-0.64 ± 0.17 ***				
Productivity											
Aboveground	0.003 ± 0.239 n.s.	1									
Belowground	-0.51 ± 0.182 n.s.	1									
Leaf damage	-3.209 ± 0.215 *	1.053	0.342 ± 0.216 n.s.	28.519			0.366 ± 0.163 *	35.919			
Survival	-0.58 ± 0.946 n.s.		0.986 ± 0.411 *								
<b>Quercus serrata</b>											
June 2015											
Performance											
Height	3.224 ± 0.032 ***	29.196	0.523 ± 0.236 *		-0.049 ± 0.033 n.s.	56.357					
No. leaves	1.812 ± 0.081 ***				-0.151 ± 0.068 *						
Survival	1.517 ± 0.138 ***				-0.311 ± 0.194 n.s.						
August 2015											
Performance											
Height	3.267 ± 0.041 ***	26.907									
No. leaves	2.175 ± 0.064 ***				-0.1 ± 0.059 .						
Survival	0.104 ± 0.171 n.s.				-0.286 ± 0.16 .						
October 2015											



	(Intercept)		Home		Density		LAI		Home - treatment		Density:LAI	
		df		df		df		df		df		df
Rhus chinensis												
June 2015												
Performance												
Height	3.417 ± 0.037 ***	28.365										
No. leaves	2.382 ± 0.058 ***											
Leaf damage	-0.866 ± 0.147 ***	21.73			-0.145 ± 0.065 *		-0.388 ± 0.101 ***					
Survival	0.087 ± 0.179 n.s.		0.895 ± 0.573 n.s.		-0.368 ± 0.163 *		-0.425 ± 0.266 n.s.		48.764			
March 2016												
Performance												
Height	3.336 ± 0.036 ***	26.495										
No. leaves	-2.505 ± 0.659 ***											
Survival	-0.254 ± 0.207 n.s.				-0.329 ± 0.19 .		-0.622 ± 0.282 *					
September 2016												
Performance												
Height	3.458 ± 0.047 ***	25.064			0.032 ± 0.045 n.s.	26.409	-0.08 ± 0.12 n.s.		24.058		0.299 ± 0.113 *	23.557
No. leaves	2.685 ± 0.104 ***				0.025 ± 0.091 n.s.		-0.351 ± 0.267 n.s.				0.691 ± 0.236 **	
Productivity												
Aboveground	0.556 ± 0.09 ***	27.218			-0.154 ± 0.075 *	387.759						
Belowground	0.898 ± 0.074 ***	27.345			-0.133 ± 0.08 n.s.	45.469					0.302 ± 0.199 n.s.	41.151
Leaf damage	-1.578 ± 0.201 ***	16.446										
Survival	-0.712 ± 0.002 ***											
August 2015												
Performance												
Height	3.364 ± 0.086 ***	12.769										
No. leaves	1.993 ± 0.085 ***											
Survival	-3.427 ± 0.265 ***				-0.35 ± 0.002 ***		-1.048 ± 0.325 **					
Survival	-2 ± 0.002 ***						-1.425 ± 0.002 ***					
October 2015												
Performance												
Height	3.505 ± 0.089 ***	8.232										
No. leaves	1.859 ± 0.092 ***											
Leaf damage	-0.253 ± 0.307 n.s.	22.21										
Survival	-2.556 ± 0.216 ***											
March 2016												
Performance												
Height	3.573 ± 0.126 ***	14.381										
No. leaves	0.023 ± 0.442 n.s.				0.301 ± 0.17 .	13.598						
Survival	-4.492 ± 0.558 ***				-0.844 ± 0.56 n.s.							
September 2016												
Performance												
Height	3.502 ± 0.164 n.s.	7.86										
No. leaves	1.582 ± 0.173 ***											
Productivity												
Aboveground	1.928 ± 0.238 ***	28			-2.177 ± 0.753 **	28						



	(Intercept)	df	Home	df	Density	df	LAI	df	Home - treatment	df	Density:LAI	df
Performance												
Height	3.924 ± 0.06 ***	18.778										
No. leaves	3.525 ± 0.081 ***											
Leaf damage	-1.849 ± 0.287 ***	22.791			0.332 ± 0.217 n.s.	31.086						
Survival	-1.237 ± 0.189 ***				-0.344 ± 0.142 *		-0.876 ± 0.438 *					
March 2016												
Performance												
Height	3.867 ± 0.043 ***	18.66										
No. leaves	-8.405 ± 1.531 ***											
Survival	-1.548 ± 0.269 ***				-0.281 ± 0.151 .		-1.75 ± 0.638 **					
September 2016												
Performance												
Height	4.012 ± 0.057 ***	20.518										
No. leaves	3.356 ± 0.116 ***		-0.715 ± 0.283 *									
Productivity												
Aboveground	1.872 ± 0.082 ***	18.016										
Belowground	1.154 ± 0.087 ***	19.51	-0.343 ± 0.224 n.s.	16.995	-0.155 ± 0.098 n.s.	175.51	-0.554 ± 0.238 *	24.027	-0.356 ± 0.215 .	176.083		
Leaf damage	-2.667 ± 0.193 ***	20.548										
Survival	-2.557 ± 0.4 ***		0.715 ± 1.123 n.s.		-0.116 ± 0.197 n.s.							

**Chapter 4: Table S4: Common garden Experiment:** Estimates, standard error, significance levels (i.e. \*\*\*<0.001, \*\*<0.01, \*<0.05, <0.1.) and degrees of freedom associated with t-test statistics for optimized (generalized) linear mixed-effects models of seedlings established. All analyses were performed separately by record date (i.e. August 2015, September 2015 and September 2016). In the full model, treatments of light/shadow, density and their interactions were considered fixed effects, while species and plot were considered random. In the subsequent analyses models were optimized using the AICc criterion and maximum likelihood. Blank cells indicate excluded predictors during model optimization.

	(Intercept)	df	Density	df	Shadow - treatment	df	Density:	df
							Shadow - treatment	
August 2015								
Performance								
Height	2.863 ± 0.199 ***	6.093	-0.091 ± 0.034 **	212.781	0.037 ± 0.031 n.s.	81.866	0.096 ± 0.047 *	207.361
No. leaves	1.796 ± 0.311 ***		-0.121 ± 0.047 **					
Survival	1.577 ± 0.303 ***				0.541 ± 0.237 *			
September 2015								
Performance								
Height	2.858 ± 0.207 ***	6.223			0.078 ± 0.054 n.s.	121.348		
No. leaves	2.099 ± 0.325 ***		-0.15 ± 0.05 **					
Leaf damage	-3.248 ± 0.537 ***	6.32	0.29 ± 0.128 *	186.627	-0.698 ± 0.151 ***	104.741		
Survival	1.313 ± 0.313 ***				0.498 ± 0.228 *			
September 2016								
Performance								
Height	3.685 ± 0.214 ***	6.033	-0.126 ± 0.044 **	170.15				
No. leaves	3.298 ± 0.304 ***		-0.48 ± 0.109 ***		-0.253 ± 0.133 .		0.379 ± 0.151 *	
Productivity								
Aboveground	1.413 ± 0.435 *	6.433	-0.594 ± 0.147 ***	172.788	-0.457 ± 0.139 **	75.788	0.412 ± 0.201 *	162.819
Belowground	0.806 ± 0.428 n.s.	6.272	-0.515 ± 0.125 ***	193.576	-0.711 ± 0.111 ***	74.909	0.32 ± 0.17 .	178.962
Leaf damage	-2.289 ± 0.27 ***	6.01						
Survival	0.329 ± 0.306 n.s.				0.775 ± 0.225 ***			

**Table S5: Common garden Experiment:** Estimates, standard error, significance levels (i.e. \*\*\*<0.001; \*\*<0.01; \*<0.05; <0.1.) and degrees of freedom associated with t-test statistics for optimized (generalized) linear mixed-effects models of seedlings established. All analyses were performed separately by record date (i.e. August 2015, September 2015 and September 2016) and species. In the full model, treatments of light/shadow, density and their interactions were considered fixed effects, while species and plot were considered random. In the subsequent analyses models were optimized using the AICc criterion and maximum likelihood. Blank cells represent during the model optimization excluded predictors.

	(Intercept)	df	Density	df	Shadow - treatment	df	Density: Shadow - treatment	df
<i>Castanopsis fargesii</i>								
August 2015								
Performance								
Height	2.64 ± 0.036 ***	16.305						
No. leaves	1.529 ± 0.104 ***				0.361 ± 0.14 **			
Survival	1.297 ± 0.425 **		1.019 ± 0.545 .		2.454 ± 0.71 ***			
September 2015								
Performance								
Height	2.834 ± 0.036 ***	14.476						
No. leaves	2.002 ± 0.094 ***				0.197 ± 0.126 n.s.			
Leaf damage	-2.722 ± 0.216 ***	12.089						
Survival	0.527 ± 0.257 *				2.632 ± 0.556 ***			
September 2016								
Performance								
Height	3.423 ± 0.103 ***	13.016						
No. leaves	3.15 ± 0.166 ***		0.36 ± 0.226 n.s.					
Productivity								
Aboveground	0.765 ± 0.17 ***	16.275						
Belowground	0.389 ± 0.246 n.s.	18.402			-0.483 ± 0.309 n.s.	16.096		
Leaf damage	-2.857 ± 0.164 ***	13.542						
Survival	-0.812 ± 0.003 ***				2.852 ± 0.003 ***			
<i>Cyclobalanopsis glauca</i>								
August 2015								
Performance								
Height	2.819 ± 0.034 ***	11.849	0.157 ± 0.055 **	35.206				
No. leaves	0.734 ± 0.14 ***		0.387 ± 0.22 .					
Survival	1.247 ± 0.252 ***							
September 2015								
Performance								
Height	2.417 ± 0.104 ***	0.104	0.345 ± 0.164 *	0.164				
No. leaves	0.965 ± 0.132 ***		0.329 ± 0.221 n.s.					



	(Intercept)	df	Density	df	Shadow - treatment	df	Density:	df
							Shadow - treatment	
Height	2.841 ± 0.053 ***	18.468						
No. leaves	2.318 ± 0.04 ***							
Survival	0.752 ± 0.284 **							
September 2015								
Performance								
Height	2.983 ± 0.091 ***	18.353						
No. leaves	2.476 ± 0.055 ***							
Leaf damage	-3.765 ± 0.28 ***	12.388			-0.618 ± 0.392 n.s.	12.061		
Survival	0.737 ± 0.283 **							
September 2016								
Performance								
Height	4.383 ± 0.112 ***	17.777						
No. leaves	3.762 ± 0.2 ***							
Productivity								
Aboveground	3.203 ± 0.367 ***	17.691			-1.338 ± 0.514 *	17.196		
Belowground	2.345 ± 0.273 ***	17.832			-1.426 ± 0.38 **	17.174		
Leaf damage	-1.426 ± 0.232 ***	20.101			-0.645 ± 0.325 .	19.582		
Survival	0.586 ± 0.271 *							
Liquidambar formosana								
August 2015								
Performance								
Height	3.563 ± 0.059 ***	13.863			0.145 ± 0.079 .	17.379		
No. leaves	3.06 ± 0.096 ***							
Survival	4.435 ± 0.866 ***				-1.88 ± 0.889 *			
September 2015								
Performance								
Height	3.656 ± 0.057 ***	16.45			0.186 ± 0.077 *	20.819		
No. leaves	3.539 ± 0.117 ***							
Leaf damage	-4.705 ± 0.22 ***	18.655			-0.652 ± 0.312 .	19.028		
Survival	4.27 ± 0.827 ***				-2.187 ± 0.859 *			
September 2016								
Performance								
Height	4.572 ± 0.041 ***	7.9			-0.238 ± 0.077 **	26.112		
No. leaves	4.646 ± 0.135 ***				-0.856 ± 0.112 ***			
Productivity								
					-0.372 ± 0.167 *			

	(Intercept)	df	Density	df	Shadow - treatment	df	Density: Shadow - treatment	df
Lithocarpus glaber								
August 2015								
Performance								
Height	3.23 ± 0.133 ***	11.509	-1.064 ± 0.172 ***	29.772	-0.592 ± 0.19 **	15.566		
No. leaves	2.519 ± 0.156 ***	13.224	-1.018 ± 0.182 ***	28.846	-0.798 ± 0.214 **	16.976		
Survival	-1.935 ± 0.083 ***	10.111	0.283 ± 0.136 *	28.564	-2.489 ± 0.705 ***		-2.138 ± 1.052 *	
September 2015	3.811 ± 0.663 ***		1.058 ± 0.863 n.s.					
Performance								
Height	2.822 ± 0.017 ***	5.372			0.379 ± 0.236 n.s.			
No. leaves	0.823 ± 0.175 ***				1.196 ± 0.732 n.s.			
Survival	1.031 ± 0.491 *							
September 2016								
Performance								
Height	2.521 ± 0.124 ***	17.569			0.257 ± 0.171 n.s.	16.225		
No. leaves	1.418 ± 0.151 ***							
Leaf damage	-4.296 ± 0.155 ***	158			1.302 ± 0.674			
Survival	0.594 ± 0.444 n.s.							
September 2016								
Performance								
Height	3.517 ± 0.061 ***	14.594			-0.229 ± 0.078 *	12.776		
No. leaves	3.385 ± 0.152 ***				-0.679 ± 0.21 **			
Productivity								
Aboveground	0.804 ± 0.173 ***	12.262			-0.57 ± 0.225 *	10.857		
Belowground	-0.06 ± 0.174 n.s.	13.684			-0.749 ± 0.227 **	12.105		
Leaf damage	-3.177 ± 0.125 ***	10.109						
Survival	-0.373 ± 0.387 n.s.				1.626 ± 0.58 **			
Quercus serrata								
August 2015								
Performance								
Height	3.418 ± 0.039 ***	206	-0.154 ± 0.054 **	206	-0.096 ± 0.056	206		
No. leaves	2.609 ± 0.094 ***		-0.264 ± 0.082 **		-0.327 ± 0.119 **			
Survival	2.123 ± 0.212 ***							
September 2015								
Performance								
Height	3.456 ± 0.057 ***	213	-0.151 ± 0.078	213	-0.282 ± 0.08 ***	213		
No. leaves	2.862 ± 0.118 ***		-0.217 ± 0.099 *		-0.429 ± 0.147 **			



	(Intercept)	df	Density	df	Shadow - treatment	df	Density: Shadow - treatment	df
Leaf damage	-0.626 ± 0.305 .	18.362			-0.619 ± 0.434 n.s.	18.77		
Survival	2.37 ± 0.331 ***				-0.665 ± 0.418 n.s.			
September 2016								
Performance								
Height	3.678 ± 0.061 ***	148	-0.257 ± 0.09 **	148	-0.237 ± 0.092 *	148		
No. leaves	3.438 ± 0.182 ***		-0.26 ± 0.153 .		-0.943 ± 0.227 ***			
Productivity								
Aboveground	1.174 ± 0.103 ***	9.086	-0.46 ± 0.151 **	44.952	-0.586 ± 0.16 **	13.125		
Belowground	1.089 ± 0.098 ***	139	-0.244 ± 0.149 n.s.	139	-0.669 ± 0.154 ***	139		
Leaf damage	-1.11 ± 0.228 ***	22.573						
Survival	1.001 ± 0.255 ***				-0.752 ± 0.347 *			



**Chapter 4: Fig. S1:** Exemplary plots in the Main Experiment (a) and in the Common Garden Experiment for treatments of light (b) and shadow (c).





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## Eigenständigkeitserklärung

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Hiermit erkläre ich an Eides Statt, dass die vorliegende Dissertation - ausgenommen der Beratung durch Prof. Dr. Alexandra Erfmeier - selbständig und ausschließlich unter Zuhilfenahme der im Quellen- und Literaturverzeichnis genannten Werke und Dokumente angefertigt wurde. Die Stellen der Arbeit die anderen Werken im Wortlaut oder dem Sinn nach entnommen wurden sind durch Angaben und Quellen als solche kenntlich gemacht. Die Arbeit ist unter Einhaltung der Regeln der guten wissenschaftlichen Praxis der Deutschen Forschungsgemeinschaft entstanden. Diese Arbeit hat weder in gleicher oder ähnlicher Form einer anderen Institution oder Prüfungsbehörde vorgelegen, noch habe ich bisher erfolglose Promotionsversuche unternommen. Da es sich bei der Arbeit um eine kumulative Dissertation handelt sind einzelne Kapitel der Arbeit in wissenschaftlichen Journals veröffentlicht worden. Dies ist entsprechend gekennzeichnet. Weiterhin erkläre ich, dass mir zu keiner Zeit ein akademischer Grad entzogen wurde.

Karlsruhe, 20.02.2021



Markus Germany











