Biodiversity and ecosystem functioning across structural strata in subtropical forests in China – the interplay of herbaceous and woody species richness

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Summary

The role of biodiversity on ecosystem functioning and the mechanisms leading to observed relationships have been well established for temperate grassland ecosystems, but so far they are poorly understood in forest ecosystems. Forests are characterized by a complex structure, in particular by a variety of species organized in different structural strata as well as by changes in species composition and environmental factors in the course of succession. The interplay of structural strata, understorey herb layer and overstorey tree layer, might be driven by different mechanisms which likely vary during succession.

In this PhD thesis I analysed one aspect of biodiversity-ecosystem functioning relationships in a species-rich forest with a main focus on the species richness of the herb layer, its productivity and community invasibility in a subtropical forest in China. The interactions between tree and herb layer diversity and productivity and invasibility of the herb layer as key processes were studied with regard to their temporal dynamics.

The present investigations are based on the assumption that bottom-up effects from the herb to the tree layer prevail in early successional communities, while top-down effects become the dominant mechanism in mature forest stands. These temporal dynamics of structural complexity were addressed by extensive species monitoring in natural forests as well as by experiments which focus on plant-plant interactions that in the field are obscured by extrinsic environmental factors.

An inventory of understorey species in mature forest stands revealed that the herb layer species richness was high, ranging between 25 to 71 vascular plant species per 100 m^2, but was unrelated to the tree layer diversity. Environmental variables had only minor effects on the diversity and the relationship between tree and herb layer richness.

In a second study, a common garden experiment that mimicked a simplified early-successional forest ecosystem with herb layer and tree saplings, I could show that the success of invading herbaceous species across structural strata was controlled by tree species identity only to a small degree, while within-stratum effects in the herb layer were more important to repress exotic species. The mechanisms behind such plant-plant interactions within the herb layer were analysed in a third study, a glasshouse experiment with herb species communities of different diversity levels. Different diversity level resulted in altered species performances as observed in a change of relative yield of some species, with a decrease in competitive ability with increasing diversity. This points out the importance of particular species identity effects, and thus, a prevalent significance of community composition instead of a universal diversity-induced increase of community productivity.

This PhD thesis shed light on the complexity of structural and temporal interdependencies of a species-rich forest ecosystem. In contrast to the majority of comparable investigations, I analysed these relationships from the herb layer perspective. Contrary to prior expectations, diversity-diversity and diversity-ecosystem function relationships were not coupled across structural strata in general. Rather, species identity effects caused correlations and gave evidence for the interplay of structural strata. The results of the three different studies highlighted the appropriateness of the approach of experimental simplification. Nevertheless, the outstanding species diversity and complexity in this subtropical forest needs further investigations to evaluate the interplay of structural strata.

Zusammenfassung

Die Bedeutung von Biodiversität für Ökosystem-Funktionen und die Mechanismen, welche die beobachteten Beziehungen hervorrufen, sind in temperaten Graslandsystemen gut untersucht, in Waldökosystemen allerdings bisher weniger verstanden. Wälder sind durch eine komplexe Struktur charakterisiert und vor allem weisen sie eine Vielzahl von Arten auf, die in strukturellen Schichten angeordnet sind. Während der Sukzession sind sowohl die Artzusammensetzung als auch verschiedene Umweltfaktoren gewissen Änderungen unterworfen. Das Zusammenspiel der strukturellen Schichten, die unten wachsende Krautschicht und darüber wachsende Baumschicht, könnte durch verschiedene Mechanismen gesteuert sein, welche sich während der Sukzession ändern könnten.

In der vorliegenden Doktorarbeit habe ich einen Aspekt der Beziehung zwischen Biodiversität und Ökosystemfunktionen in artenreichen Wäldern im subtropischen China untersucht, wobei der Schwerpunkt auf dem Artenreichtum in der Krautschicht, ihrer Produktivität und ihrer Empfänglichkeit gegenüber exotischen Arten lag. Die Interaktionen zwischen der Baum- und Krautschichtdiversität sowie den Prozessen der Produktivität und der Invasibilität wurden im Hinblick auf ihre zeitliche Dynamik untersucht.

Die vorliegenden Untersuchungen basieren auf der Annahme, dass sogenannte „bottom-up“ Effekte (etwa „von unten nach oben“) in früh-sukzessionalen Pflanzengesellschaften vorherrschend sind, während „top-down“ Effekte (etwa „von oben nach unten“) die dominierenden Mechanismen in alten Wäldern sind. Die zeitliche Dynamik der strukturellen Schichten wurde sowohl mithilfe ausgedehnter Artenmonitorings in natürlichen Wäldern untersucht, als auch durch Experimente, die Pflanzeninteraktionen hervorheben, die im Gelände durch extrinsische Umweltfaktoren verdeckt werden könnten.

Eine Artenaufnahme in vollentwickelten Waldbeständen zeigte einen hohen Artenreichtum in der Krautschicht (25 bis 71 Gefäßpflanzen pro 100 m^2), der jedoch nicht mit der Baumschichtdiversität korrelierte. Umweltvariablen hatten dagegen nur geringe Auswirkungen auf die Krautschichtdiversität und die Beziehung zwischen Baum- und Krautschicht.

In einem zweiten Untersuchungsansatz, einem sogenannten „common garden experiment“ welches ein vereinfachtes früh-sukzessionales System mit krautigen Arten und jungen Bäumen simulierte, konnte ich zeigen, dass nur die Baumartenidentität den Erfolg von eindringenden krautigen Arten zu einem gewissen Anteil über die strukturellen Schichten hinweg kontrollierte. Allerdings waren die Effekte innerhalb der Krautschicht bedeutender für die Unterdrückung exotischer Arten als Effekte zwischen den Schichten. Die Mechanismen, die zu derartigen Pflanzeninteraktionen führen, wurden in einer dritten Studie untersucht, einem Gewächshausexperiment mit Gemeinschaften krautiger Pflanzen in unterschiedlichen Diversitätsstufen.

Unterschiedliche Diversitätsstufen riefen veränderte Leistungen bezogen auf die relative Produktivität einiger Arten und eine Verminderung ihrer Konkurrenzstärke mit steigender Diversität hervor. Dies zeigt die Bedeutung von bestimmten Artidentitätseffekten und dem daraus resultierendem vorherrschenden Einfluss von Artzusammensetzung anstelle einer generell erhöhten Produktivität mit steigender Diversität.

Die vorliegende Doktorarbeit gibt Aufschluss über die Komplexität von strukturellen und zeitlichen Wechselwirkungen in artenreichen Wäldern. Im Gegensatz zu vielen anderen vergleichbaren Untersuchungen, habe ich diesen Zusammenhang aus der Perspektive der Krautschicht analysiert. Entgegen der Erwartung, konnte ich keine generelle Verknüpfung zwischen den Diversitäten der Baum- und Krautschicht bzw. Diversität und Ökosystemfunktionen feststellen. Stattdessen verursachten Artidentitätseffekte Korrelationen zwischen den strukturellen Schichten und wiesen auf die Wechselbeziehung dieser hin. Die Ergebnisse der drei angewendeten Methoden zeigten, dass die experimentelle Vereinfachung angemessen ist. Nichtsdestotrotz erfordern der hohe Artenreichtum und die Komplexität dieses subtropischen Waldes weitere Untersuchungen um den Umfang der Wechselbeziehung der strukturellen Schichten beurteilen zu können.

Chapter 1 - Introduction

1.1 General introduction

During the last decades studies about the impact of biodiversity on ecosystem functioning became a fundamental topic in ecological research and many highly sophisticated investigations contributed to the growing body of knowledge (Hooper et al. 2005; Balvanera et al. 2006; Quijas et al. 2010). The value of biodiversity and its protection have provoked observational and experimental studies worldwide and have boosted the activities for the 'International Year of Biodiversity' in 2010 (proclaimed by the United Nations).

Biodiversity, defined as the number of entities with regard to species, functional and trophic groups as well as genotypes, has been shown to be intrinsically linked to ecosystem functioning (Hodgson et al. 2002; Hooper et al. 2005; Hughes et al. 2008; Reiss et al. 2009) where ecosystem functioning is a surrogate for ecosystem goods, services and properties (Christensen et al. 1996; Hooper et al. 2005). In very general terms, ecosystem functioning, thus, describes the performance of an ecosystem (Fig. 1.1). Against this background, the interest in biodiversity research has derived from the current threat of species loss and the anticipated irreversible depletion in ecosystem functioning with open consequences for human life and well-being (Tilman 1999; Chapin et al. 2000; Hector et al. 2001; Srivastava & Vellend 2005; Naeem et al. 2009).

The relationship between biodiversity and ecosystem functioning has been found to be predominantly positive (Schläpfer & Schmid 1999; Hooper et al. 2005; van Ruijven & Berendse 2009). In the context of plant community research, many investigations have focused on the effects of species richness on community biomass (Tilman et al. 1997; Hector et al. 1999; Dukes 2001; Fridley 2001; Spehn et al. 2005; Roscher et al. 2005; Lanta & Leps 2007; Marquard et al. 2009) and invasion resistance (Moore et al. 2001; Prieur-Richard et al. 2002; Fargione & Tilman 2005; Pokorny et al. 2005). Resistance of a plant community against exotic species invasions can be considered a crucial characteristic of ecosystems since exotic species have been found to alter ecosystem properties and, thus, functioning. (Vitousek & Walker 1989; D'Antonio & Vitousek 1992; D'Antonio et al. 1998; Mack et al. 2000; Flory & Clay 2010a; Flory & Clay 2010b; Simao et al. 2010; Vila et al. 2010).

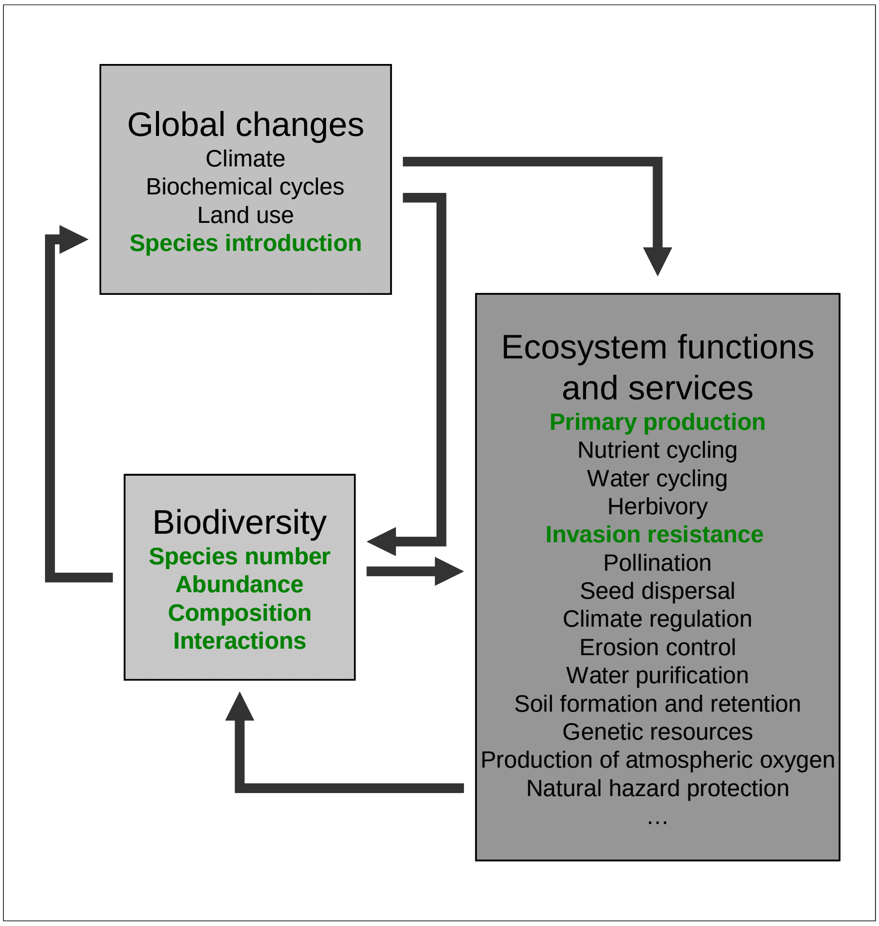

Figure 1.1: Components of biodiversity, effects of global changes and the impacts on ecosystem functions and services. In the present studies, mainly species number as the unit of diversity was emphasized, hence, in the following I refer to biodiversity as a synonym for species richness. Variables relevant in the following investigations are given in green colour (modified after the Millennium Ecosystem Assessment 2005).

Ecosystem functions like productivity and susceptibility to exotic invaders are dynamic in time, the strength of correlation with species richness was shown to be variable as well (Cleland et al. 2004; van Ruijven & Berendse 2005; Roscher et al. 2008). Besides that, diversity-ecosystem functioning relationships have been altered with regard to the environmental context of the ecosystem (Pfisterer & Schmid 2002; Tylianakis et al. 2008, Wacker et al. 2008; Wardle et al. 2008).

Consensus has emerged that the complexity of real world ecosystem functioning can be understood only by focusing on the biotic and abiotic components of the ecosystem at the same time (Gamfeldt et al. 2008; Hillebrand & Matthiessen 2009; Olff et al. 2009). With regard to biotic components, ecosystem attributes depend not only on species richness but also on species identity (Symstad et al. 1998; Temperton et al. 2007; Lorentzen et al. 2008;

Bell et al. 2009). The interplay of species is dynamic and complex since species form various trophic and functional groups acting in concert with abiotic characteristics of the respective habitat, and thus, species effects might differ at spatial scales, but also in response to temporal changes (Weis et al. 2007; Hillebrand et al. 2008; Roscher et al. 2008; Reiss et al. 2009; Scherber et al. 2010).

The challenge of incorporating several orders of complexity involving temporal, spatial and multidimensional species linkages in biodiversity research without causing obscured diversity-ecosystem functioning relationships needs to be faced.

Forest ecosystems

Research on diversity-ecosystem functioning relationships has been preferentially conducted in temperate grasslands (Tilman 1997a; Hector et al. 1999; Roscher et al. 2004) as well as in aquatic microcosms (McGrady-Steed et al. 1997; Cardinale et al. 2002; Cardinale et al. 2006; Weis et al. 2007). This preference might have been derived from both, the global importance of these ecosystems and the comparatively simple feasibility of experimental manipulations. However, the outstanding hotspots of biodiversity are forest ecosystems where species richness was found to be remarkably high (Fig. 1.2), especially in forests of the tropical zones (Whitmore et al. 1985; Gentry & Dodson 1987; Gentry 1988; Duivenvoorden 1994; Galeano et al. 1998; Langenberger et al. 2006).

The high species richness of forest ecosystems is promoted by the structural complexity of forest strata, also termed structural layers, which features a three-dimensional mosaic comprising a variety of species and life forms. The herb layer, by definition, including all vascular plants below 1 meter height (Siccama et al. 1970; Rogers 1981; Gilliam & Christensen 1986), contributes significantly to overall species diversity, comprising life forms differing phenologically, morphologically and ontogenetically. Although tree species composition and diversity are the most striking features of forest ecosystems and, thus, studies predominantly focused on woody species inventory and attributes, the impact of non-woody species is non-negligible. Investigations in temperate forests (Ingerpuu et al. 2003; Gilliam 2007) as well as in tropical forests (Gentry & Dodson 1987; Linares-Palomino et al. 2009) demonstrated that high species richness is mainly attributable to non-tree species such as herbs, climbers and epiphytes. In particular, the results of species monitoring in lowland tropical rain forests of Ecuador (Gentry & Dodson 1987) have demonstrated that tree species richness can contribute surprisingly little to overall plant diversity.

Although subtropical regions of Southeast Asia do not lag behind in terms of vascular plant species richness (Barthlott et al. 2005; Barthlott et al. 2007; Legendre et al. 2009; Fig. 1.2) information about these ecosystems is scarce. This circumstance is unfortunate since particularly China as a country with aspiring economy and an immense population of more than 1.3 billion citizens still has a nature conservation system that lags behind China's increasing environmental problems (Lopez-Pujol et al. 2006; Wang et al. 2007a; Ma et al. 2009; Fu et al. 2010). Negative impact of human activities on natural ecosystems also are critical for the process of plant invasions and have led to an increasing number of naturalized exotic species within China (Liu et al. 2005; Weber & Li 2008; Weber et al. 2008; Feng & Zhu 2010), thus bearing the risk of accelerating the loss of native species (Mack et al. 2000; Meiners et al. 2001; Hejda et al. 2009). Especially in afforested areas, diversity loss by habitat degradation and detrimental human disturbance urge a further understanding of the effects of biodiversity on ecosystem functioning in subtropical forests (Wang et al. 2007b; Lu et al. 2010).

Literature research revealed that subtropical forests are underrepresented with regard to species inventories or experimental investigations and only few insights into ecosystem functioning of these forests exist (Barik et al. 1992; Cornelissen et al. 1994; Legendre et al. 2009; Wang et al. 2009). Furthermore, most of these studies preferentially focus on tree species and, thus, gives only minor information about the significance of the herb layer or rather herbaceous species. To my knowledge the present study is the first which shifts the focus to herb layer species, regardless of life form, and highlight their impact on forest ecosystem functioning in the subtropics.

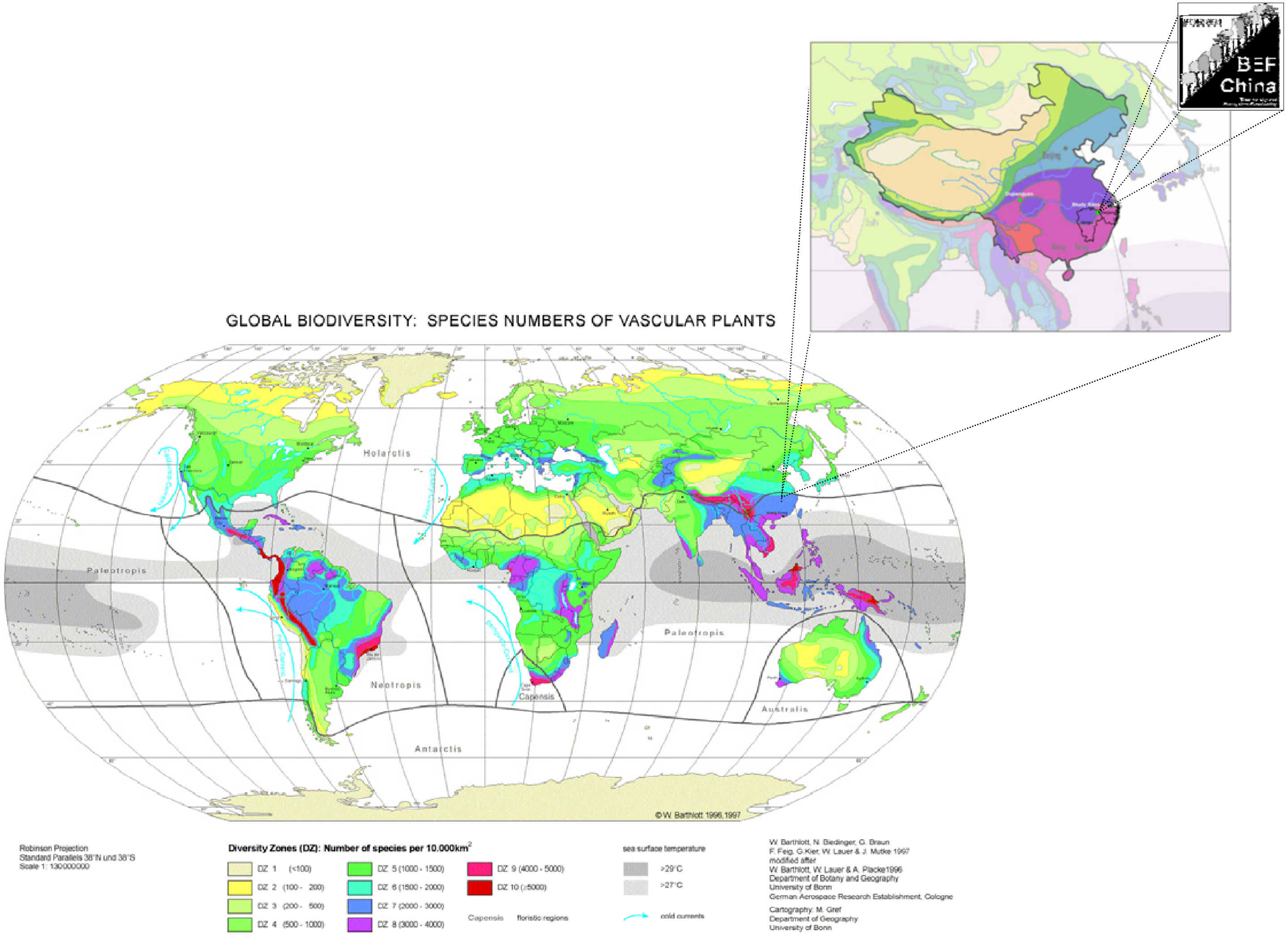

Figure 1.2: Distribution of global biodiversity in vascular plant species and the location of the BEF-China project (modified after http://www.biologie.uni-hamburg.de/b-online/)

Diversity-ecosystem functioning relationships in forest ecosystems

Tree layer-herb layer interactions

Information concerning the functioning of forests has been mainly derived from the tree layer perspective so far (Augusto et al. 2002; Scherer-Lorenzen et al. 2007; Geißler et al. 2010; Lang et al. 2010; Bruelheide et al. 2011 but see Barbier et al. 2008). The importance of the herb layer to overall ecosystem functions such as net primary productivity and nutrient cycling, has been demonstrated in investigations of temperate forests (Muller 2003; Gilliam 2007) as well as tropical ones (Chandrashekara & Ramakrishnan 1994). The contributions of herb and tree layer to ecosystem functions are not mutually exclusive, instead, linkage of the forests' structural layers is realized via various multidimensional interdependencies. Tree layer characteristics such as tree species richness, species composition and forest stand age have the potential to affect herb layer vegetation.

Although being more prominent, the link between tree and herb layer is not only a 'top-down' effect (in the sense of the hierarchical order of structural layers rather than in a tropic meaning). The significance of the herb layer is particularly evident when considering that every recruiting tree individual has to pass through and compete with plants of the herb layer (George & Bazzaz 1999; George & Bazzaz 2003; Taverna et al. 2005; Denslow et al. 2006; Marshall et al. 2009). Mechanisms of interference between resident herb layer species and recruiting tree individuals determine the extent of 'bottom-up' effects on tree layer composition and include competition for resources, allelopathy or mechanical interference (Royo & Carson 2006). Such bottom-up effects depend on the species composition and further characteristics of the herb layer (George & Bazzaz 1999; Coomes et al. 2005; Benitez-Malvido 2006; Marshall et al. 2009). Most relevant herb layer properties for implementing bottom-up effects might be its productivity, which potentially illustrate competition intensity (Fraser & Keddy 2005; Dormann 2007; Engel & Weltzin 2008; Lamb et al. 2009), but also resistance against exotic species. The presence of exotics intensifies the impact of the herb layer on regenerating tree individuals in a detrimental way (Flory & Clay 2010a) and was demonstrated to change environmental conditions (Ehrenfeld 2003; Niu et al. 2007), and, consequently, might alter strata interactions. So far, only a few attempts have been made to experimentally disentangle the factors driving the invasibility of forest ecosystem with respect to structural layer (Knight et al. 2008).

Course of succession

Tree layer as well as herb layer properties are both variable in space and time (Christensen & Gilliam 2003; Jules et al. 2008) and, thus, the strength of the relationship between tree and herb layer might be variable as well. Accordingly, linkages observed between strata in mature forest stands might be absent in young forests (Gilliam et al. 1995). It is unclear how and to which extent the linkage between strata and the strength of this correlation is altered in the course of succession. It can be assumed that young, and, thus, less complex forests with a prominent herb layer are predominantly driven by bottom-up effects (Benitez-Malvido 2006; Royo & Carson 2008), while in older forests the tree layer and, consequently, top-down effects dominate (Gilliam & Roberts 2003; Barbier et al. 2008) as illustrated in Figure 1.3. The predominant direction of influence, bottom-up effects from herb layer to tree layer versus top-down effects from tree to herb layer with regard to time, i.e. forest succession, are not yet understood comprehensively.

Successional development results in alteration of environmental conditions and usually involves changes in species composition (Jules et al. 2008). Success of introducing exotic species is often associated with species turn-over, e.g. due to disturbances or changes in environmental conditions. Studies of old-field succession revealed that the abundance and impact of exotic species decreased in the course of succession (Robertson et al. 1994; Meiners et al. 2002), thus, early-successional forests are more susceptible to exotic species. As a consequence, invading species are able to alter recruitment patterns of native tree species (Woods 1993), change strata characteristics and, hence, influence the interplay between structural layers (Wyckoff & Webb 1996; Luken 2003; Flory & Clay 2010a). In this regard, I assume that susceptibility to species invasion might be most pronounced in early successional forest systems (Eschtruth & Battles 2009; Flory & Clay 2006; Thiele & Otte 2006) and might then be associated with intensified strength of bottom-up effects on the tree layer (Fig. 1.3).

In summary, the forest structural layers interact in various ways which defies investigating a particular stratum separately from other strata within biodiversity-ecosystem functioning research.

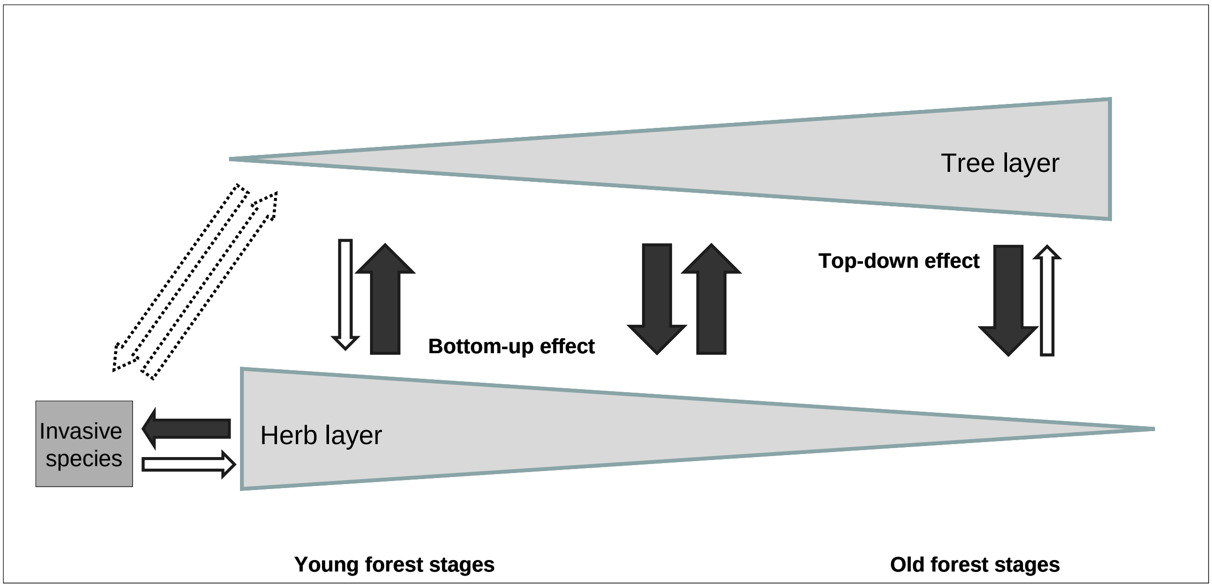

Figure 1.3: Scheme of interdependencies of hierarchical layers during forest succession with a prominent herb layer in early successional stages and an assumed predominant bottom-up effect on the tree layer. The decreasing impact of the herb layer in the course of succession leads to a shift to top-down effects of the overstorey tree layer. Dominant effects are visualised by dark arrows, unclear relationships are shown by dashed lines. Modified after Alexandra Erfmeier.

Mechanisms of diversity-ecosystem functioning relationships

Plant species richness does not inevitably enhance ecosystem processes (Mulder et al. 2001) which can be explained by the type of mechanistic link between species richness and ecosystem functioning (Loreau 1998a; Aarssen 2001; Loreau & Hector 2001). Therefore, information about the underlying mechanisms is essential to predict species richness effects. The mechanistic link has been primarily analysed for grassland ecosystems where three focal mechanisms have become apparent to drive positive diversity-ecosystem functioning correlations, which I will summarize briefly in the following: complementarity, facilitation and sampling effect.

Based on the niche concept of community assembly, investigations revealed niche complementarity in species-rich communities as the mechanism enhancing ecosystem processes (Hooper et al. 2005). Several forms of differentiation between species can lead to complementarity, like rooting pattern (Dimitrakopoulos & Schmid 2004; Fargione & Tilman 2005; von Felten & Schmid 2008), plant height (Gross et al. 2007; Lorentzen et al. 2008) or nutrient use (Spehn et al. 2002; Palmborg et al. 2005; Kahmen et al. 2006; Ashton et al. 2010). In addition, diversity effects emerge when species not only tolerate but facilitate neighbouring species via specific characteristics. Facilitation frequently occurs when nitrogen fixing species provide enriched nitrogen conditions also for adjacent heterospecific individuals. These positive interactions among species have been demonstrated to promote ecosystem processes (Hooper & Vitousek 1997; Cardinale et al. 2002; Prieur-Richard et al. 2002; Temperton et al. 2007).

Finally, ecosystem functioning might be enhanced by the sampling effect, which describes the stochastic phenomenon of increasing probability with increasing species richness to include species with particular characteristics. Although some scientists consider the sampling effect simply a statistical artefact (Aarssen 1997, Huston 1997), others tend to comprehend it a real-world effect of biodiversity (Tilman et al. 1997; Tilman 1997b; Loreau 1998a; Loreau & Hector 2001).

Negative relationships between species richness and ecosystem processes emerge when effects of interspecific competition exceed effects of positive species interactions (Stoll & Prati 2001; Weigelt et al. 2007). As the balance between these interactions determines ecosystem processes, a current presumption includes that it might be not only species richness per se but species identities which determine the ecosystem functioning (Symstad et al. 1998; Crawley et al. 1999; Hillebrand et al. 2008).

Observational studies that assess near-natural community composition reflect the result of natural processes but impede conclusions on causal relationships (Schmid & Hector 2004). Thus, experiments at the community scale provide the opportunity to reveal biotic interaction because the link between species diversity and ecosystem functioning is less confounded by changes in abiotic conditions (Loreau 1998b; Pfisterer & Schmid 2002; Tylianakis et al. 2008; Wacker et al. 2008; Wardle et al. 2008). The interaction between species was demonstrated to change with environment (Mulder et al. 2001, Partzsch & Bachmann 2011) which emphasizes the consideration of the abiotic environment.

In most systems we have only limited knowledge about the exact contributions of individual species to ecosystem functioning (Schmid & Hector 2004) for that reason I further zoomed into the level of organisation from near-natural forests with a variety of life forms and species to small patches of two distinct types of species to plant communities comprised of species classified as one functional group. Species- or rather individual-based experiments in controlled environment are required to disentangle the impact of specific species and mechanisms to diversity-ecosystem functioning relationships.

Brief summary

The preceding introduction identified certain gaps of knowledge in current biodiversity-ecosystem functioning research in forest ecosystems:

- The contribution of the herb layer to species richness in subtropical forest ecosystems and its interaction with the overstorey tree layer attributes.
- The relevance of strata-overarching effects of species richness on ecosystem functions and the strength of relationship with regard to forest succession.
- The importance of covarying environmental factors relative to biotic interactions and their effects on tree layer-herb layer relationships.
- Underlying mechanisms leading to observed species richness-ecosystem functioning relationships.

1.2 Objectives and aims of this thesis

The present PhD thesis focuses on biodiversity-ecosystem functioning relationships in subtropical forest ecosystems in southeast China and highlights those relationships from different point of views and with several approaches. Within the framework of the BEF-China project (DFG Forschergruppe 891) "*The role of tree and shrub diversity for production, erosion control, element cycling, and species conservation in Chinese subtropical forest ecosystems*" and in the context of subproject 11 "*Invasion-diversity interactions in subtropical forests: the interplay of herbaceous and woody species richness*" I conducted a downscaling of ecosystem functioning in a near-natural forest to an experimental early-successional forest system to within-stratum experimental plant communities.

The mutual support of a several different projects within the BEF-China, both European and Chinese enabled this thesis to benefit from logistics which were achieved jointly.

Diversity-diversity and diversity-productivity relationships across structural strata

In the framework of this thesis, an observational approach was conducted in near-natural subtropical forest stands that differ with regard to their successional stage and investigate whether a species-rich overstorey promotes a species-rich understorey, i.e. whether species richness is positively correlated across strata.

In chapter 2, I present the mutual relationships between tree and herb layer, taking species richness, species composition and herb layer productivity into account while also considering abiotic environmental conditions. I hypothesized that the species richness of the herb layer is positively related to species richness in the tree layer. In line with this, I assumed that herb layer productivity is positively correlated with tree layer species richness. Both hypotheses point at a positive diversity-ecosystem functioning relationship not only within but also across structural strata. In addition, this study aimed at quantifying the temporal course of tree layer-herb layer interactions by observing forest stands in relation to successional age. I tested the hypothesis that the strength of top-down effects of tree layer species richness on herb layer properties increases in the course of succession. Accordingly, I expected a decreasing impact of herb layer species and, thus, a decreasing strength of bottom-up effects. This study attempts to fill the gap of knowledge regarding the interactions of species richness across structural strata and their importance relative to succession and environment.

Diversity-invasibility and diversity-productivity relationships across and within structural strata

Contrary to grasslands, forest ecosystems are rarely mimicked in experiments that focus on herb layer properties. In the context of a joint effort to establish a common garden experiment within the BEF-China research group, I established a controlled environment study simulating a simplified early-successional forest ecosystem to disentangle the influence of species richness and abiotic environment on herb layer attributes. Experimental plant communities were established consisting of tree saplings presenting a tree layer that varied in species richness and composition. The analyses focused on the dynamics of the herb layer community consisting of spontaneously appearing native herbs and introduced exotic herbs. Soil nutrients were manipulated as additional treatment factor, while further abiotic conditions were held constant.

Chapter 3 presents the result of this common garden experiment and addresses the impact of tree layer attributes on the herb layer. I assessed the influence of the tree layer on the self-assembled native herb layer species as well as herb layer invasibility caused by exotic seed addition. In addition, I determined the role of soil nutrient enrichment on native and exotic herbaceous species.

This investigation elucidates the relevance of strata-overarching effects of tree richness on herb layer productivity and invasibility with respect to covarying environmental factors.

Diversity-productivity relationships under controlled conditions

Covarying environmental factors might mask biodiversity-ecosystem functioning relationships if not appropriately disentangled experimentally, thus, controlled abiotic conditions can be essential for detecting mechanisms that may underlie positive biodiversity effects.

With regard to community productivity, niche differences were considered to lead to overyielding and thus positive relationship between species richness and species biomass. Overyielding is assumed to happen in functionally divergent species, however, the extent of variance between species was not estimated so far. I suggest that down-scaling to species specific interactions may lead to detailed resolution for analysing the mechanisms that bring about positive diversity-ecosystem functioning relationships.

Chapter 4 focuses on species richness effects on community productivity at a fine scale, while in addition analysing individual species responses to community diversity. The experiment was carried out in a glasshouse, allowing to keep abiotic factors constant to the largest possible degree. I hypothesized that not only species with highly contrasting traits lead to niche complementarity and accordingly overyielding but that even in communities comprised of similar species with regard to life form and life cycle there are positive small-scale diversity-productivity relationships.

This experiment accounts for the species specific contribution to community productivity and seeks to detect the underlying mechanisms leading to observed species richness-ecosystem functioning relationships.

Figure 1.4: Experimental communities of the glasshouse experiment. Monoculture of *Pterocypsela formosana* (A) and *Siegesbeckia glaberescens* (B) and the 8-species mixture (C) at the beginning of the experiment and impression of one glasshouse chamber at the end of the experiment (D).

1.3 Study area

Gutianshan National Nature Reserve

History of Gutianshan Reserve

The observational study (Chapter 2) was conducted in the Gutianshan National Nature Reserve (GNNR) in Zhejiang Province, southeast China (29º8'18"–29º17'29" N, 118º2'14"–118º11'12" E). The Reserve was initially established as a National Forest Reserve in 1975 and became a National Nature Reserve in 2001. The GNNR consists of broad-leaved forests of advanced successional stages as well as early-successional stages. The younger forest stands indicate that within and adjacent to the reserve extensive deforestation occurred in the 1950s. As a consequence, the majority of stands are secondary forests with maximum tree ages of about 180 years. Under natural conditions, maximum tree ages can be assumed to be exceeded by several decades and even centuries (Teng Fang, personal communication). The GNNR and its surrounding are influenced by tree plantations, or rather their remnants, of the economically important conifer species *Cunninghamia lanceolata* and *Pinus massoniana.* Although Gutianshan is a nationally protected nature reserve, there still occur a few human activities, even some detrimental ones. Because of the steep terrain of the entire reserve, the GNNR area was only marginally usable for agricultural activities, and thus, an exceptionally intact forest cover has been preserved especially on the steep slopes.

Topography and climate

The GNNR covers an area of about 81 km^2, with elevations ranging from 300 to 1260 meters. The topography is characterized by high steepness with slopes frequently exceeding 30°. The climate at GNNR is warm-temperate with an annual average temperature of 15.1 °C. The mean minimum and maximum temperatures are -6.8 °C (January) and 38.1 °C (July), respectively. The mean annual precipitation sums up to approximately 2000 mm with most rainfall occurring from March to September and a short dry season in November and December.

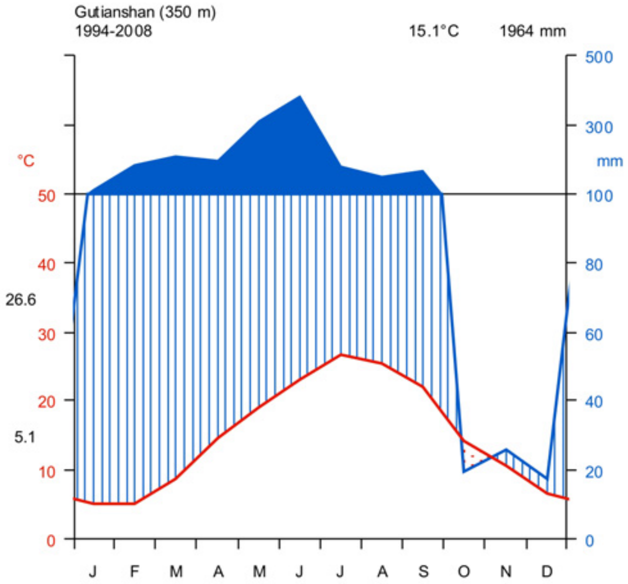

Figure 1.5: Climate of GNNR illustrated as a Walter and Lieth climate diagram. Blue solid line shows monthly precipitation, red solid line indicates average temperature at GNNR. Vertical area specifies moist season, dotted area indicates dry season (from Geißler et al. 2010).

Vegetation

The vegetation is characterized by broad-leaved mixed forest, a total of 1426 seed-plants species of 648 genera and 149 families occur naturally in the GNNR (Lou & Jin 2000). Within the tree layer, evergreen species dominate in abundance of individuals (Yu et al. 2001) but in species numbers the ratio of evergreen and deciduous tree species is well-balanced (Lou & Jin 2000). In the course of succession the proportion of deciduous trees decreases significantly with regard to both species and individuals (Bruelheide et al. 2011).

The type of forest in GNNR is characteristic of this subtropical region (Wu 1980; Hu & Yu 2008; Legendre et al. 2009).

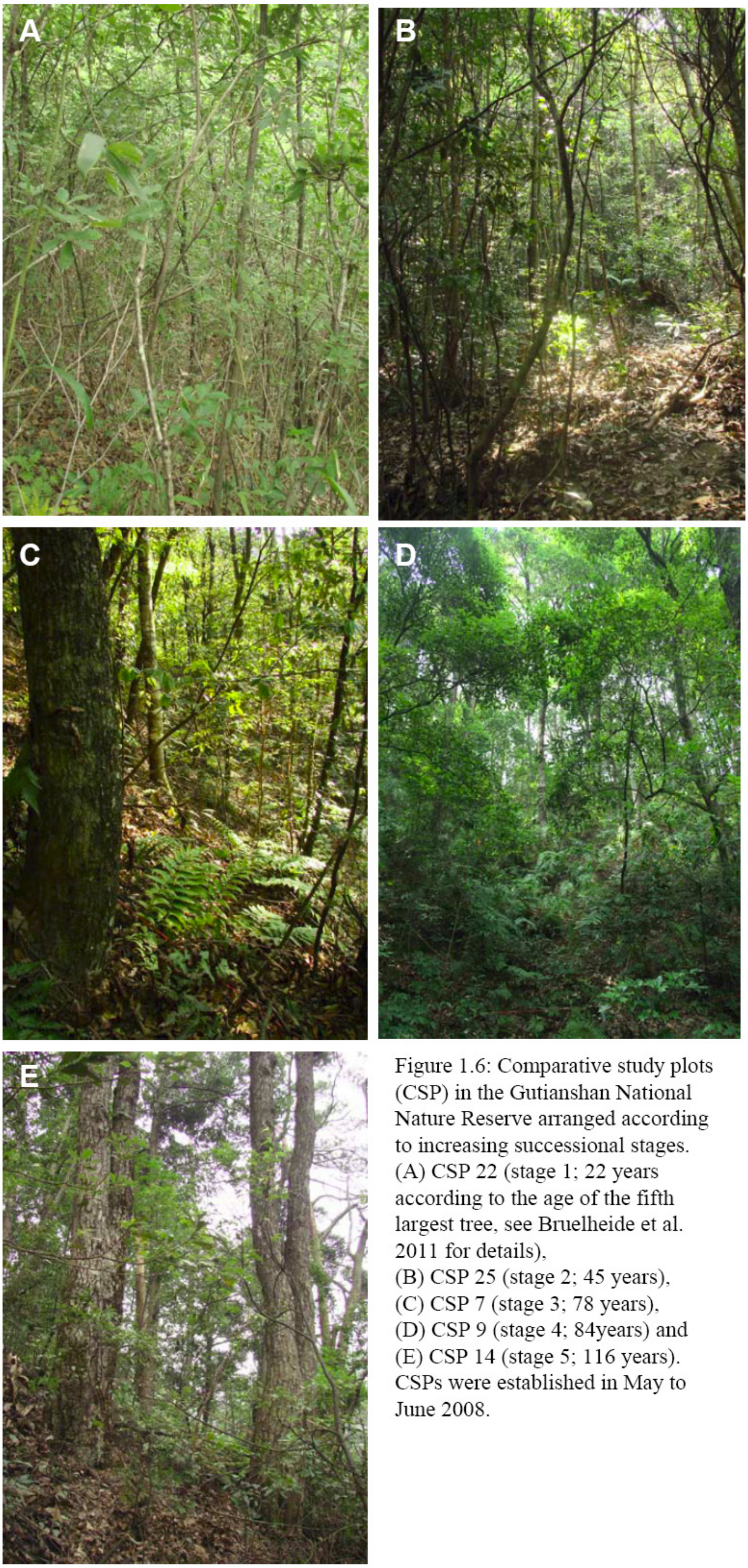

Figure 1.6: Comparative study plots (CSP) in the Gutianshan National Nature Reserve arranged according to increasing successional stages. (A) CSP 22 (stage 1; 22 years according to the age of the fifth largest tree, see Bruelheide et al. 2011 for details), (B) CSP 25 (stage 2; 45 years), (C) CSP 7 (stage 3; 78 years), (D) CSP 9 (stage 4; 84years) and (E) CSP 14 (stage 5; 116 years). CSPs were established in May to June 2008.

Pilot Experiment

Study site

The experimental study site for the common garden experiment is situated near Xingangshan, Jiangxi Province, southeast China in approximately 25 km linear distance to GNNR (N29° 06.293 E117° 55.286, Fig. 1.8 C). The common garden experiment has been established in a former agricultural field, used for the cultivation of rice, wheat and other crops. The location is in the flood plain of a river, i.e. a flat area.

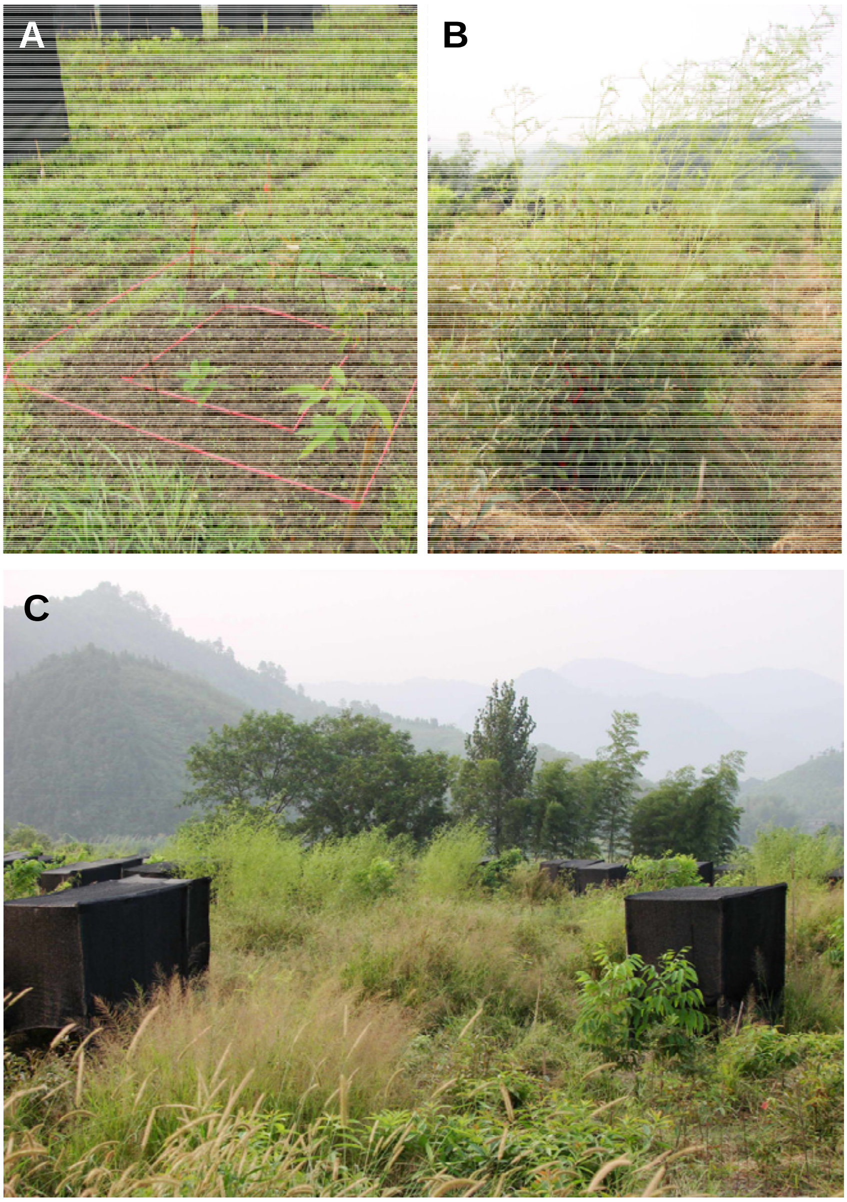

Figure 1.7: Common garden experiment in Xingangshan, Jiangxi Province. Experimental plots at the beginning of the experiment in May 2009 (A) and at the end before the harvest in September 2009 (B). The impression of the experimental site (C) with shading houses belonging to additional experimental approaches of other projects.

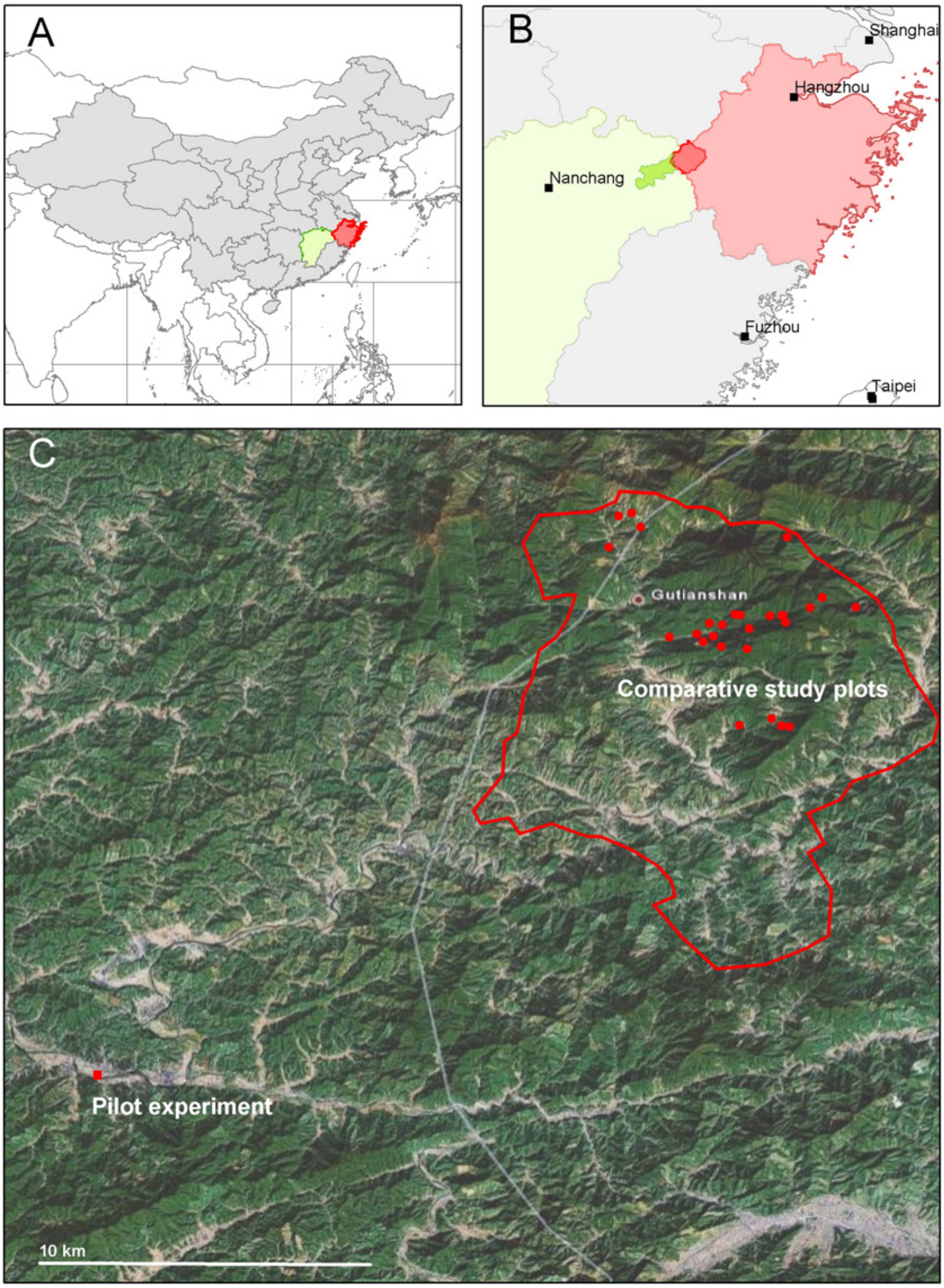

Figure 1.8: Location of the study sites in southeast China (A, B) and position of the common garden experiment (“BEF-China Pilot experiment”) in relation to the Gutianshan National Nature Reserve (maps by Erik Welk).

Chapter 2 - Lack of tree layer control on herb layer characteristics in a subtropical forest, China

Sabine Both, Teng Fang, Martin Böhnke, Helge Bruelheide, Christian Geißler, Peter Kühn, Thomas Scholten, Stefan Trogisch, & Alexandra Erfmeier

Journal of Vegetation Science (in press)

2.1 Abstract

Question: Knowledge of the interaction between understorey herb and overstorey tree layer diversity is mostly restricted to temperate forests. How do tree layer diversity and environmental variables affect herb layer attributes in subtropical forests and do these relationships change in the course of succession? Do abundance and diversity of woody saplings within the herb layer shift during succession?

Location: Subtropical broad-leaved forests in southeast China (29º8'18"–29º17'29" N, 118º2'14"–118º11'12" E).

Methods: A full inventory of the herb layer including all plants below 1-m height was done in 27 plots (10 x 10 m) from five successional stages (< 20, < 40, < 60, < 80 and ≥ 80 yr).We quantified the contribution of different life forms (herbaceous, woody and climber species) to herb layer diversity and productivity and analysed effects of environmental variables and tree layer diversity on these attributes.

Results: Herb layer composition followed a successional gradient, as revealed by non-metric multidimensional scaling (NMDS), but diversity was not correlated to the successional gradient. There was no correlation of diversity across layers. Herb layer productivity was neither affected by tree layer diversity nor by herb layer diversity. Although abundance of woody species in the herb layer decreased significantly during succession, woody species contributed extraordinarily to herb layer species diversity in all successional stages. All environmental factors considered had little impact on herb layer attributes.

Conclusions: The subtropical forest investigated displays an immense richness of woody species in the herb layer while herbaceous species are less prominent. Species composition of the herb layer shows a clear successional pattern, however, the presence or absence of certain species appears to be random.

Keywords: BEF-China; Chronosequence; Comparative study plot (CSP); Forest understorey; Gutianshan National Nature Reserve (GNNR); Indicator species analysis; Non-metric multidimensional scaling (NMDS); Secondary forest succession; Zhejiang Province

Nomenclature: Flora of China (http://flora.huh.harvard.edu/china)

Chapter 3 - Impact of tree diversity on herb layer invasibility in young experimental communities of subtropical species

Sabine Both, Teng Fang, Martin Baruffol, Bernhard Schmid, Helge Bruelheide & Alexandra Erfmeier

Ecological Research (under review)

3.1 Abstract

Knowledge about diversity-invasibility relationships is mainly based on experiences in grasslands. Little is known about these relationships in forests, where tree species interact with herbaceous species especially in the early phases of succession. We addressed this issue experimentally by quantifying the impact of trees on herb layer attributes and invasibility. We established a common garden experiment in southeast China using four broad-leaved tree species (*Elaeocarpus decipiens, Schima superba, Castanea henryi* and *Quercus serrata*) to study effects of tree diversity on herb layer productivity and invasibility.

Tree saplings were planted in monocultures, 2- and 4-species mixtures. A full-factorial design was applied in which the species compositions were crossed with fertilizer- and seed-addition treatments. For the latter, mixtures of seeds from eight exotic herb species were used. Herb community attributes were assessed after 4-month growing season. Tree layer diversity had only small effects on herb layer invasibility. However, presence of *Elaeocarpus decipiens* negatively affected native herb layer species but also negatively influenced abundance and species richness of invading exotic species. Significant tree diversity × fertilizer interactions emphasized the impact of nutrient supply. The exotics were more strongly controlled by a high productivity of native herbs than by tree layer attributes. These results show that there was only a low impact of tree diversity on herb layer invasibility with effects being most evident under nutrient addition. However, the effects from one particular tree species supported strata-overarching effects. We suggest that during the earliest phases of forest succession, herb layer invasibility depends more on resource supply than on tree layer attributes.

Keywords: BEF-China; early-successional forest ecosystem; exotic seed addition; fertilizer application; structural strata

Chapter 4 - Productivity and species interactions in plant communities composed of one functional group

Sabine Both, Helge Bruelheide & Alexandra Erfmeier

Acta Oecologica (under review)

4.1 Abstract

Biodiversity experiments have detected positive effects of diversity on ecosystem functioning, these positive effects are thought to be caused mainly by complementarity and facilitation of coexisting species. Coexistence driven by complementary resource use or by mutual beneficial effects of different species requires functional differences among the species present. Such functional differences are commonly assumed to be higher among than within functional groups and, thus, accordingly niche differences are supposed to be more pronounced among but not within groups. However, several studies found that species diversity within functional groups also affects ecosystem functioning, suggesting that species of one functional group are not functionally redundant. The present study focused on diversity-productivity relationships in experimental communities composed of plant species representing one functional group only.

We established a glasshouse experiment by choosing frequently occurring species from subtropical southeast China, all comprising fast growing tall annuals of different plant families, and established a total of 160 communities, representing 25 different species compositions, with diversity levels of 1, 2, 4 and 8 species. We measured individual growth and biomass as well as community productivity after a growing period of 12 weeks. While some of the species displayed significant overyielding, others showed no such trend. We found a prevalent importance of community composition confirmed by particular species identity effects. Our investigation demonstrated that small-scale species differences are capable to increase ecosystem functioning to a certain extent via species identity effects. In mixed communities, the relative performance of species was increased for species performing weakly in monoculture and was mitigated for strong performers in monoculture. These findings let us assume that altered species performances were derived from shifts in competitive ability as a function of diversity level. As a conclusion, there is some evidence that small-scale complementarity occurs even within a single functional group.

Keywords: annual species; BEF-China; functional group; glasshouse experiment; overyielding; relative yield total

Chapter 5 - Synthesis

5.1 Main results

The present study provides insights into forest diversity-ecosystem functioning relationships by downscaling approaches from the whole-ecosystem level of a near-natural subtropical forest to simplified experimental systems of early-successional tree-herb communities to fine scale mechanisms that induce diversity-ecosystem functioning relationships in particular plant communities. The studies presented in the preceding chapters provided the following main results:

Monitoring approach: The monitoring approach in the GNNR revealed a high species richness along the succession series. I found a high contribution of herb layer species richness to overall diversity. However, herb layer diversity was independent of overstorey species richness, in addition herb layer productivity was not affected significantly by overstorey tree layer richness in the investigated forest stands Herb species richness, as well as herbaceous and woody species abundance, decreased significantly as a function of forest successional age. I could not investigate objectives regarding exotic herb species due to insignificant numbers.

Common garden experiment: The experimental early-successional forest system revealed few strata-overarching links of tree layer attributes and herb layer properties. But tree layer effects were exclusively reflected in species identity and not in ubiquitous species richness effects. I could show that effects of the tree layer increased when interaction effects with the environmental context were taken into account since the impact of tree diversity on herb layer invasibility was most evident under nutrient addition. Invasibility of the herb layer was predominantly controlled by within-stratum attributes as well as by nutrient supply.

Glasshouse experiment: Within herb layer communities which were comprised of only one functional group, no positive diversity-productivity relationship was found. While several species revealed a shift in competition ability as a function of community diversity and displayed higher biomass gain in diverse mixtures, competitively strong species were inhibited in species-rich communities. These effects compensated each other and, thus, did not generate overall increased community productivity with increasing species richness.

5.2 Overall discussion

My study reveals new insights into the interaction of overstorey tree layer and understorey herb layer and I gained baseline information about herb layer composition from species inventories in a subtropical forest. The conceptual framework presented in the introduction of this thesis (Fig. 1.3) is based on the assumption that structural strata are linked by the interplay of bottom-up and top-down effects, which are dynamic in the course of succession. I expected to disclose relationships between strata in GNNR like those described from observations of temperate forests (Gilliam 2007; Jules et al. 2007; Mölder et al. 2008). Following Hooper et al. (2005), I further expected positive effects of species richness on ecosystem functioning within and across structural strata. By implementing three different approaches I confirmed some of my assumptions while others were not supported.

In the following overall discussion I pay attention to the most important findings with regard to the main outline of species richness effects across structural strata.

Strata-overarching effects of diversity

Species numbers were high in both tree and herb layer, similar to forests in the tropics (Whitmore et al. 1985; Gentry & Dodson 1987; Gentry 1988; Duivenvoorden 1994; Galeano et al. 1998; Langenberger et al. 2006), but species richness was uncorrelated across the two strata which is in contrast to investigations from temperate forests (Auclair & Goff 1971; Gilliam 2007). No relationship was found between diversity of the tree layer and species richness or productivity of the herb layer in the forest stands investigated in the GNNR. The temporal dynamics, as reflected in the successional stages, did not result in altered correlations or correlation strengths (Chapter 2). Herb layer species richness was strongly controlled by structural variables of the forest stands, such as cover of the shrub layer and height of the first tree layer as well as by extrinsic environmental factors, i.e. soil pH, CN ratio and litter, rather than by the diversity of the tree layer. Productivity of the herb layer was not related to species richness, neither within, nor across structural strata, environmental conditions only slightly influenced herb layer biomass.

The observations in the GNNR were not appropriate to investigate tree layer effects on herb layer invasibility, since only one exotic species (*Crassocephalum crepidioides*) was encountered in the study plots and only with very low abundances. The absence of other exotic species may depend on the lack of shade-tolerant exotics (Von Holle et al. 2003; Martin et al. 2009). Although it is likely that forests like GNNR will be troubled by exotics in the future (Liu et al. 2005; Niu et al. 2007; Weber & Li 2008; Weber et al. 2008; Feng & Zhu 2010).

Information about the influence of the overstorey tree layer on potential invasion in the herb layer could be investigated in the common garden experiment (Chapter 3). The results of the experiment gave valuable insights into species effects across strata due to controlled extrinsic factors. By including different levels of tree diversity and simulated exotic species invasion, the study design allowed the analyses of herb layer-tree layer interactions and native-exotic relationships at the same time. I could show that one keystone tree species was able to compete, and thus, negatively affect certain herb species across structural strata (Chapter 3). However, this inhibiting effect was rather widespread and not strong enough to provoke a general negative species richness effect from the tree to the herb layer. I conclude that in these very young successional forest communities the strata-overarching effects are induced only by species identity effects of keystone species in the tree layer. *Elaeocarpus decipiens* acted as such a keystone species in the experiment and had a measurable impact on abundance of herb layer species and the number of exotic species that could establish.

Follow the assumptions given in Figure 5.1, ongoing investigations might detect increased influence of the tree layer which could lead to competition-induces declines of herb layer species performance with proceeding succession. Alteration in herb layer attributes might later on result from negative shading effects and light competition of the overstorey (Kabakoff & Chazdon 1996; Kochy & Wilson 2000; Knight et al. 2008) and intensified competition for soil resources (Coomes & Grubb 2000). In addition, litter quality or accumulation (Schimpf & Danz 1999; Sariyildiz et al. 2005) and allelopathic effects (Gilliam & Roberts 2003; Härdtle et al. 2003) caused by tree species have been found to affect herb layer species.

The current data does not proof that species richness of the tree layer negatively affects invasibility of the herb layer per se, instead, species identity effects demonstrate a strata-overarching impact. This simplified experiment with only a very small species pool and controlled environmental conditions provided evidence for interactions between species across the structural strata.

In accordance with the hypothesis illustrated in Figure 1.3, bottom-up effects from the herb layer affected tree individuals, negative feedback mechanisms were particularly driven from exotic herbs. In the common garden experiment, the bottom-up effect was evident in significantly decreased tree individual height in the presence of exotic herbs. However, it can be assume that a longer study time will promote effects on other characteristics of the tree layer (Woods 1993; Wyckoff & Webb 1996; Marshall et al. 2009).

The results are summarized in Figure 5.1 and underline that exotic species in the herb layer might not only have effects within the same stratum (Woods 1993; Verheyen et al. 2007) but also negatively affect the tree layer (Fagan & Peart 2004; Flory & Clay 2010a).

In the system investigated, exotic herbaceous species did not negatively affect native herb species, instead, a suppressing control from native herb productivity could be detected.

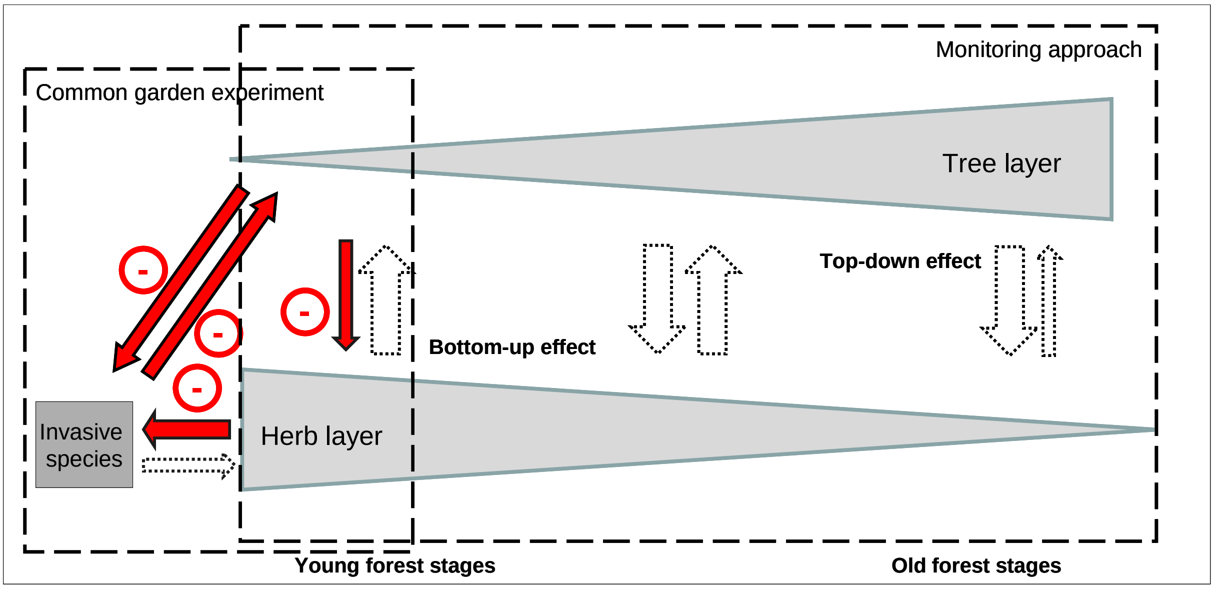

Figure 5.1: Interrelationship of herb and tree layer in subtropical forest systems. Red arrows indicate a negative relationship, dashed arrows specify the absence of correlation. The results are attributed to the respective investigations.

My results support that bottom-up effects predominantly occur in early successional forest ecosystems, in contrast, the expected reverse top-down control in mature forest stands was not confirmed by the observational study (Chapter 2). The lack of measurable top-down effects might be explained by obscured relationships in the species-rich forest stands in the GNNR due to environmental factors. Comparable studies often detected interactions with extrinsic factors, and diversity patterns are correlated with such factors (Naeem et al. 2000; Foster et al. 2002). In the context of invasion ecology, there is fundamental evidence that diversity-ecosystem functioning relationships depend on the scale of the study (Shea & Chesson 2002; Davis et al. 2005) with the prevalent importance of environmental variables (at large scale) or species interactions (at small scale). Moreover, such scale-shaped mechanisms might similarly apply to community productivity since no effect from tree diversity to herb layer productivity could be revealed in the GNNR study plots.

The high number of species in the tree layer, ranging from 25 to 69 species per 900 m^2 in the study plots in GNNR, might lead to compensations with regard to species specific identity effects. While positive correlations between tree and herb layer diversity were observed in subalpine forests (Bradfield & Scagel 1984), in temperate (Ingerpuu et al. 2003; Gilliam 2007) and boreal forests (Benayas 1995) those forest stands display lower tree species richness. Top-down impact depending on tree species was shown in relatively species poor systems (Härdtle et al. 2003; Knight et al. 2008; Mölder et al. 2008), however, the species identity effects detected in the common garden experiment might not be directly transferable to near-natural forest stands. The effect of *Elaeocarpus decipiens* on herb layer species (Chapter 3) can be different in natural forests, with regard to its local neighbourhood where species identity effects might be compensated by contrasting effects of adjacent species.

There was a remarkable dominance of woody species in the herb layer which is in contrast to findings from some tropical forests (Gentry & Dodson 1987; Linares-Palomino et al. 2009) but was revealed in China before (Lu et al. 2010). Their predominant occurrence might have caused shifts in competitive ability of species within the herb layer, and thus, alter the interplay with the overstorey. The dominance of woody saplings implies that recruitment of trees is not hampered by properties of the herb layer (George & Bazzaz 1999; George & Bazzaz 2003; Harms et al. 2004; Royo & Carson 2008). Drawing conclusions about forest regeneration was beyond the scope of this study and would require repeated monitoring of tree saplings (e.g. Bustamante-Sanchez et al. 2011). However, the present data support the assumption that constant numbers of tree saplings during the course of succession reflect continuous random immigration (Bruelheide et al. 2011). Hill & Hill (2001) discussed that tropical rain forests provide pronounced mosaics of recruitment conditions which leads to higher species richness than in temperate forests. The present study complements this feature for subtropical forests by its frequent occurrence of tree species that dominate the understorey herb layer.

Those woody saplings will undergo strong shifts in ontogeny, manifested in size plasticity and age-related changes in responses to environmental conditions (Clark & Clark 1992; Cavender-Bares & Bazzaz 2000; Lusk 2004) while growing from herb layer to the overstorey tree layer. Experimental approaches, like the common garden experiment presented in Chapter 3, are suitable to give insights into the developments of individuals and communities over time.

Experiments at the community scale provide the opportunity to reveal biotic interactions which are likely obscured in observational studies. The outcomes of diversity-ecosystem functioning relationships strongly depend on the underlying mechanisms, which are extensively investigated for grassland species (Hector et al. 2010, Marquard et al. 2009, van Ruijven & Berendse 2005). However, there is a paucity of studies using species as contrasting as tree and herb species in one community while focusing on the patterns of species richness effects.

The correlation between keystone species and particular ecosystem properties, invasibility in the common garden experiment, gave evidence that biodiversity affects ecosystems because certain organisms interact (Schläpfer & Schmid 1999), also across hierarchical structures. In most systems, we have limited knowledge about the exact contributions of individual species to ecosystem functioning (Schmid & Hector 2004). The experiments conducted in the present PhD thesis give insight into the individual contribution of particular species. I demonstrated that the very fine scale resolution of species-specific interactions can lead to compensation of effects on the community level. The glasshouse experiment (Chapter 4) detected species that responded positively to community diversity, thus, highlighting the importance of facilitation among species (Tilman et al. 1996; Hooper & Vitousek 1997; Prieur-Richard et al. 2002; Temperton et al. 2007). In contrast, other species showed decreased performance with increasing diversity level, which pointed at prevailing mechanism of competition (Hooper 1998 Ecol; Leger & Espeland 2010). Overall, the compensation of these contrasting species-specific correlations resulted in equalized relationships on the community level. Likewise, Compagnoni & Halpern (2009) demonstrated that competitive interactions between certain exotic and native species can be compensated by positive relationships among other pairs of species within the stratum.

The experiment revealed that, at community scale, diversity induced fitness differences of species and thus, ‘diversity winners’ and ‘diversity losers’. The relevance of these findings for ‘real-world’ ecosystems is not easy to assess regarding the simplicity and environmental homogeneity of the experiment (Chapter 4). The common garden experiment emphasized the importance of the environmental context (Fig. 3.1), likewise, interactions of tree layer richness and stand age with soil pH significantly influence ecosystem functions of the herb layer (Chapter 2). Nonetheless, the glasshouse experiment demonstrated that mechanisms of species interactions depend not only on the abiotic context (Mulder et al. 2001; Partzsch & Bachmann 2011) but might also change as a function of community diversity. Regarding the absence of correlations in the observational study, compensating species effects as a function of environmental conditions are conceivable.

Both experimental approaches emphasized the relevance of species identity effects and community composition on ecosystem functioning, a result complementing other investigations (Symstad et al. 1998; Emery & Gross 2006; Roscher et al. 2009).

Possible reasons for the lack of interplay

The absence of strata-relationships in the GNNR might have been provoked by hidden or rather unmeasured conditions. Management practices have been shown to strongly influence herb layer composition in temperate forests (Brunet et al. 1996; Van Calster et al. 2007; Van Calster et al. 2008; Baeten et al. 2009; Takafumi & Hiura 2009; Plue et al. 2010). Several forest stands in the GNNR might have been shaped by agricultural impacts, evidenced by relicts of agricultural terraces as well as charcoal in the soil profiles in some plots (Bruelheide et al. 2011, Christian Geißer personal communication). The GNNR exclusively contains secondary forest that might still reflect former management practices. Consequently, species assembly have been influenced anthropogenically, which could have led to factors other than overstorey tree composition to influence herb layer species richness and performance.

Summary

Concluding the results of the presented investigations, no strong relationships between structural layers could be revealed (Chapter 2). However, by scaling down to experimental systems strata-overarching effects became evident (Chapter 3). Moreover biotic interactions within strata could compensate each other without leading to diversity-induced correlations at the community level (Chapter 4). While early successional forest communities were strongly influenced by bottom-up effects, the expected top-down influences in mature forest stands were not confirmed. In the mixed broad-leaved subtropical forest, species richness and productivity of the herb layer was only poorly governed by tree layer diversity.

My results indicate that small-scale mechanisms decouple relationships between hierarchical layers in the GNNR, either because of species interactions or due to environmental heterogeneity, which might have obscured correlations between structural strata.

5.3 Outlook

The present PhD thesis illustrated that the complexity of species and structural richness provoke difficulties to detect clear patterns in the interplay of herbaceous and woody species richness. Instead, relationships between diversity and ecosystem functioning across structural strata could be demonstrated through manipulation of biotic and abiotic variables.

I suggest to record additional variables in the near-natural forest stands of the GNNR. Synthesis on functional diversity of tree and herb layers as a continuous measure of diversity and fine scale information of soil conditions with consideration of microbial communities should be conducted to give a realistic understanding of the relationship between the different components of this highly diverse subtropical forest ecosystem. Complexity will increase, but also become more realistic, if structural strata will be considered in detail. The investigations in the GNNR revealed several effects of shrub layer cover and height, emphasizing that further analyses should unravel the components of the overstorey.

The absence of invasive species does not guarantee that the GNNR will remain free of them, since many exotic species (e.g. *Crassocephalum crepidioides, Conyza Canadensis, Erigeron annuus, Phytolacca americana*) are already established in its close proximity (personal observation, Fig. 5.2) and might evolve to become a serious threat of the rare near-natural forest stands of the GNNR.

Experimental approaches were demonstrated to be an adequate simplification of the study system. However, it will be appropriate to conduct the experiments for longer time periods and analyse the development of impacts induced by individual trees. Attention should be paid to detect asymmetric effects of species specific size, especially apparent when studying tree and herb species simultaneously.

Future experiments need to extend the species pool and analyse all possible species combinations to reveal keystone species, as well as species identity effects as a function of community diversity. Additional focus must be placed on the relative importance of tree identity effects in the course of forest succession which will be possible in the ongoing BEF-China experiments.

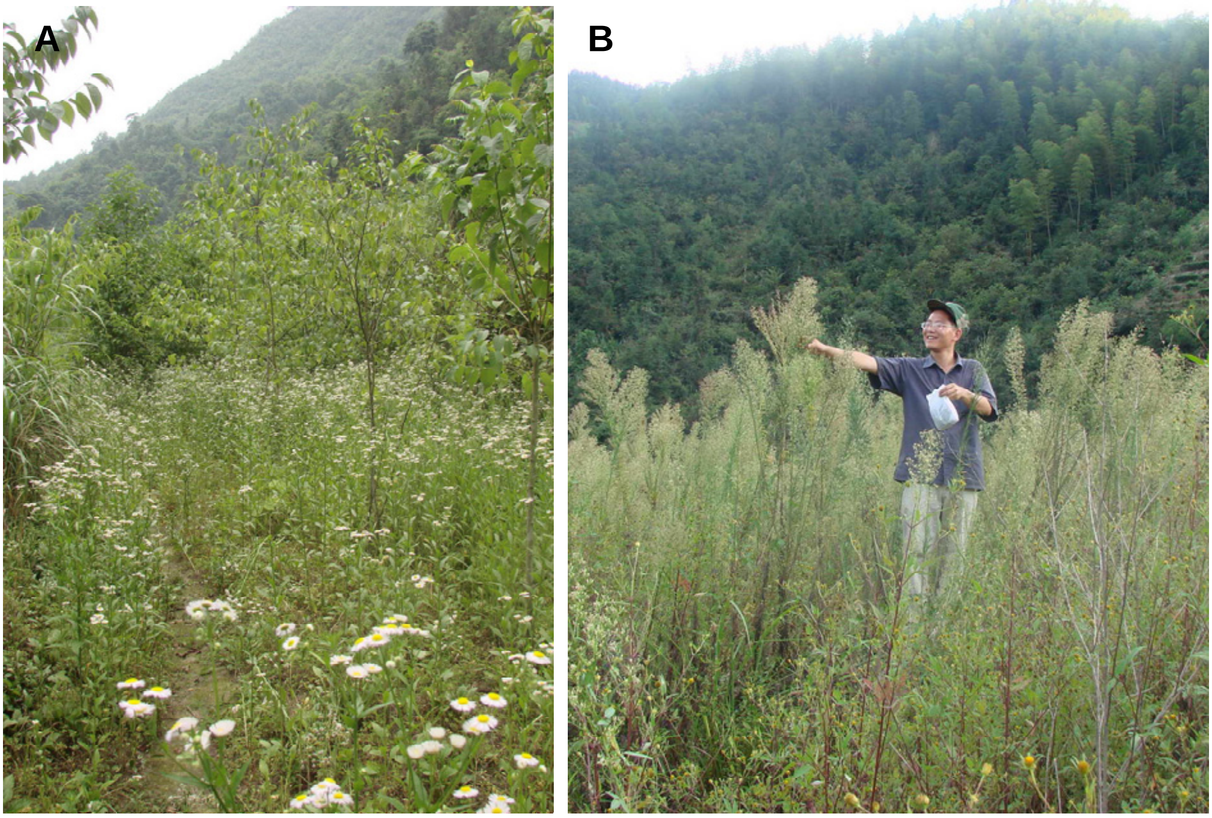

Figure 5.2: (A) *Erigeron annuus* population in farm land near CSP 11, (B) local expert Teng Fang in a *Conyza canadensis* population which is an omnipresent invader in farm and waste land near villages and tea plantations.

The 'Year of Biodiversity 2010' has strengthened biodiversity-ecosystem functioning research and ongoing research should follow the plea for complex, and consequently highly sophisticated studies to give further insights into the prevalence and importance of biodiversity effects on ecosystem processes (Hillebrand & Matthiessen 2009; Harvey et al. 2010). The ongoing BEF-China project will further aim to fill the gaps after establishing a large scale and long term biodiversity experiment which will offer the opportunity to further disentangle the impact of species richness on ecosystem functioning (www.bef-china.de).

References

Aarssen, L. W. (1997). High productivity in grassland ecosystems: effected by species diversity or productive species? *Oikos* 80: 183-184.

Aarssen, L. W. (2001). On correlations and causations between productivity and species richness in vegetation: predictions from habitat attributes. *Basic Appl. Ecol.* 2: 105-114.

Ashton, I. W., Miller, A. E., Bowman, W. D., Suding, K. N. (2010). Niche complementarity due to plasticity in resource use: plant partitioning of chemical N forms. *Ecology* 91: 3252-3260

Auclair, A. N., Goff, F. G. (1971). Diversity Relations Of Upland Forests In Western Great Lakes Area. *Am. Nat.* 105: 499-528.

Augusto, L., Ranger, J., Binkley, D., Rothe, A. (2002). Impact of several common tree species of European temperate forests on soil fertility. *Ann. For. Sci.* 59: 823-831.

Baeten, L., Bauwens, B., De Schrijver, A., De Keersmaeker, L., Van Calster, H., Vandekerkhove, K., Roelandt, B., Beeckman, H., Verheyen, K. (2009). Herb layer changes (1954-2000) related to the conversion of coppice-with-standards forest and soil acidification. *Applied Vegetation Science* 12: 187-197.

Balvanera, P., Pfisterer, A. B., Buchmann, N., He, J. S., Nakashizuka, T., Raffaelli, D., Schmid, B. (2006). Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecol. Lett.* 9: 1146-1156.

Barbier, S., Gosselin, F., Balandier, P. (2008). Influence of tree species on understory vegetation diversity and mechanisms involved - A critical review for temperate and boreal forests. *Forest Ecol. Manag.* 254: 1-15.

Barik, S. K., Pandey, H. N., Tripathi, R. S., Rao, P. (1992). Microenvironmental Variability And Species-Diversity In Treefall Gaps In A Subtropical Broadleaved Forest. *Vegetatio* 103: 31-40.

Barthlott, W., Mutke, J., Rafiqpoor, M. D., Kier, G., Kreft, H. (2005). Global centres of vascular plant diversity. *Nova Acta Leopoldina* 92: 61-83.

Barthlott, W., Hostert, A., Kier, G., Küper, W., Kreft, H., Mutke, J., Rafiqpoor, M. D., Sommer, J. H. (2007): Geographic patterns of vascular plant diversity at continental to global scales. *Erdkunde* 61: 305-315.

Bell, T., Lilley, A. K., Hector, A., Schmid, B., King, L., Newman, J. A. (2009). A Linear Model Method for Biodiversity-Ecosystem Functioning Experiments. *Am. Nat.* 174: 836-849.

Benayas, J. M. R. (1995). Patterns of diversity in the strata of boreal montane forest in British-Columbia. *J. Veg. Sci.* 6: 95-98.

Benitez-Malvido, J. (2006). Effect of low vegetation on the recruitment of plants in successional habitat types. *Biotropica* 38: 171-182.

Bradfield, G. E., Scagel, A. (1984). Correlations among vegetation strata and environmental variables in subalpine spruce-fir forests, southeastern British Columbia. *Vegetatio* 55: 105-114.

Bruelheide, H., Böhnke, M., Both, S., Fang, T., Assmann, T., Baruffol, M., Bauhus, J., Buscot, F., Chen, X. Y., Ding, B. Y., Durka, W., Erfmeier, A., Fischer, M., Geißler, C., Guo, D., Guo, L.D., Härdtle, W., He, J. S., Hector, A., Kröber, W., Kühn, P., Lang, A. C., Nadrowski, K., Pei, K., Scherer-Lorenzen, M., Shi, X., Scholten, T., Schuldt, A., Trogisch, S., von Oheimb, G., Welk, E., Wirth, C., Wu, Y. T., Yang, X., Zeng, X., Zhang, S., Zhou, H., Ma, K., Schmid, B. (2011). Community assembly during secondary forest succession in a Chinese subtropical forest. *Ecol. Monogr.* 81: 25-41.

Brunet, J., Falkengren-Grerup, U., Tyler, G. (1996). Herb layer vegetation of south Swedish beech and oak forests-effects of management and soil acidity during one decade. *Forest Ecol. Manag.* 88: 259-272.

Bustamante-Sanchez, M. A., Armesto, J. J., Halpern, C. B. (2011). Biotic and abiotic controls on tree colonization in three early successional communities of Chiloe Island, Chile. *J. Ecol.* 99: 288-299.

Cardinale, B. J., Palmer, M. A., Collins, S. L. (2002). Species diversity enhances ecosystem functioning through interspecific facilitation. *Nature* 415: 426-429.

Cardinale, B. J., Srivastava, D. S., Duffy, J. E., Wright, J. P., Downing, A. L., Sankaran, M., Jouseau, C. (2006). Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature* 443: 989-992.

Cavender-Bares, J.; Bazzaz, F. A. (2000). Changes in drought response strategies with ontogeny in *Quercus rubra*: implications for scaling from seedlings to mature trees. *Oecologia* 124: 8-18.

Chandrashekara, U. M., Ramakrishnan, P. S. (1994). Successional Patterns And Gap Phase Dynamics Of A Humid Tropical Forest Of The Western Ghats Of Kerala, India - Ground Vegetation, Biomass, Productivity And Nutrient Cycling. *Forest Ecol. Manag.* 70: 23-40.

Chapin, F. S., Zavaleta, E. S., Eviner, V. T., Naylor, R. L., Vitousek, P. M., Reynolds, H. L., Hooper, D. U., Lavorel, S., Sala, O. E., Hobbie, S. E., Mack, M. C., Diaz, S. (2000). Consequences of changing biodiversity. *Nature* 405: 234-242.

Christensen, N. L., Bartuska, A. M., Brown, J. H., Carpenter, S., Dantonio, C., Francis, R., Franklin, J. F., MacMahon, J. A., Noss, R. F., Parsons, D. J., Peterson, C. H., Turner, M. G., Woodmansee, R. G. (1996). The report of the ecological society of America committee on the scientific basis for ecosystem management. *Ecol. Appl.* 6: 665-691.

Christensen, N. L., Gilliam, F.S. (2003). Temporal and spatial patterns of herbaceous layer communities in the north Carolina Piedmont. In: Gilliam, F. S. and Roberts, M. R. (eds.) The herbaceous layer in forests of Eastern North America, pp. 224-237. Oxford University Press, USA.

Clark, D. A., Clark, D. B. (1992). Life-History Diversity Of Canopy And Emergent Trees In A Neotropical Rain-Forest. *Ecol. Monogr.* 62: 315-344.

Cleland, E. E., Smith, M. D., Andelman, S. J., Bowles, C., Carney, K. M., Horner-Devine, M. C., Drake, J. M., Emery, S. M., Gramling, J. M., Vandermast, D. B. (2004). Invasion in space and time: non-native species richness and relative abundance respond to interannual variation in productivity and diversity. *Ecol. Lett.* 7: 947-957.

Compagnoni, A., Halpern, C. B. (2009). Properties of native plant communities do not determine exotic success during early forest succession. *Ecography* 32: 449-458.

Coomes, D. A., Grubb, P. J. (2000). Impacts of root competition in forests and woodlands: a theoretical framework and review of experiments. *Ecol. Monogr.* 70: 171-207.

Coomes, D. A., Allen, R. B., Bentley, W. A., Burrows, L. E., Canham, C. D., Fagan, L., Forsyth, D. M., Gaxiola-Alcantar, A., Parfitt, R. L., Ruscoe, W. A., Wardle, D. A., Wilson, D. J., Wright, E. F. (2005). The hare, the tortoise and the crocodile: the ecology of angiosperm dominance, conifer persistence and fern filtering. *J. Ecol.* 93: 918-935.

Cornelissen, J. H. C., Werger, M. J. A., Zhong, Z. C. (1994). Effects Of Canopy Gaps On The Growth Of Tree Seedlings From Subtropical Broad-Leaved Evergreen Forests Of Southern China. *Vegetatio* 110: 43-54.

Crawley, M. J., Brown, S. L., Heard, M. S., Edwards, G. R. (1999). Invasion-resistance in experimental grassland communities: species richness or species identity? *Ecol. Lett.* 2: 140-148.

D'Antonio, C. M., Vitousek, P. M. (1992). Biological Invasions By Exotic Grasses, The Grass Fire Cycle, And Global Change. *Annu. Rev. Ecol. Syst.* 23: 63-87.

D'Antonio, C. M., Hughes, R. F., Mack, M., Hitchcock, D., Vitousek, P. M. (1998). The response of native species to removal of invasive exotic grasses in a seasonally dry Hawaiian woodland. *J. Veg. Sci.* 9: 699-712.

Denslow, J. S., Uowolo, A. L., Hughes, R. F. (2006). Limitations to seedling establishment in a mesic Hawaiian forest. *Oecologia* 148: 118-128.

Dimitrakopoulos, P. G., Schmid, B. (2004). Positive biodiversity effects increase linearly with biotope space. *Ecol. Lett.* 7: 574-583.

Dukes, J. S. (2001). Biodiversity and invasibility in grassland microcosms. *Oecologia* 126: 563-568.

Dormann, C. F. (2007). Competition hierarchy, transitivity and additivity: investigating the effect of fertilisation on plant-plant interactions using three common bryophytes. *Plant Ecol.* 191: 171-184.

Duivenvoorden, J. F. (1994). Vascular plant-species counts in the rain-forests of the middle Caqueta area, Colombian Amazonia. *Biodivers. Conserv.* 3: 685-715.

Ehrenfeld, J. G. (2003). Effects of exotic plant invasions on soil nutrient cycling processes. *Ecosystems* 6: 503-523.

Emery, S. M., Gross, K. L. (2006). Dominant species identity regulates invasibility of old-field plant communities. *Oikos* 115: 549-558.

Engel, E. C., Weltzin, J. F. (2008). Can community composition be predicted from pairwise species interactions? *Plant Ecol.* 195: 77-85.

Eschtruth, A. K., Battles, J. J. (2009). Assessing the relative importance of disturbance, herbivory, diversity, and propagule pressure in exotic plant invasion. *Ecol. Monogr.* 79: 265-280.

Fagan, M. E., Peart, D. R. (2004). Impact of the invasive shrub glossy buckthorn (*Rhamnus frangula* L.) on juvenile recruitment by canopy trees. *Forest Ecol. Manag.* 194: 95-107.

Fargione, J. E., Tilman, D. (2005). Diversity decreases invasion via both sampling and complementarity effects. Ecol. Lett. 8: 604-611.

Feng, J. M., Zhu, Y. Y. (2010). Alien invasive plants in China: risk assessment and spatial patterns. *Biodivers. Conserv.* 19: 3489-3497.

Flory, S. L., Clay, K. (2006). Invasive shrub distribution varies with distance to roads and stand age in eastern deciduous forests in Indiana, USA. *Plant Ecol.* 184: 131-141.

Flory, S. L., Clay, K. (2010a). Non-native grass invasion suppresses forest succession. *Oecologia* 164: 1029-1038.

Flory, S. L., Clay, K. (2010b). Non-native grass invasion alters native plant composition in experimental communities. *Biol. Invasions 12*: 1285-1294.

Foster, B. L., Smith, V. H., Dickson, T. L., Hildebrand, T. (2002). Invasibility and compositional stability in a grassland community: relationships to diversity and extrinsic factors. *Oikos* 99: 300-307.

Fraser, L. H., Keddy, P. A. (2005). Can competitive ability predict structure in experimental plant communities? *J. Veg. Sci.* 16: 571-578.

Fridley, J. D. (2001). The influence of species diversity on ecosystem productivity: how, where, and why? *Oikos* 93: 514-526.

Fu, Y., Chen, J., Guo, H., Hu, H., Chen, A., Cui, J. (2010). Agrobiodiversity Loss And Livelihood Vulnerability As A Consequence Of Converting From Subsistence Farming Systems To Commercial Plantation-Dominated Systems In Xishuangbanna, Yunnan, China: A Household Level Analysis. *Land Degrad. Dev.* 21: 274-284.

Galeano, G., Cediel, J., Pardo, M. (1998). Structure and floristic composition of a one-hectare plot of wet forest at the Pacific Coast of Choco, Colombia. *Biodivers. Conserv.* 7: 1563-1575.

Gamfeldt, L., Hillebrand, H., Jonsson, P. R. (2008). Multiple functions increase the importance of biodiversity for overall ecosystem functioning. *Ecology* 89: 1223-1231.

Geißler, C., Kühn, P., Böhnke, M., Bruelheide, H., Shi, X., Scholten, T. (2010). Splash erosion potential under tree canopies in subtropical SE China. *Catena* doi:10.1016/j.catena.2010.10.009.

Gentry, A. H., Dodson, C. (1987). Contribution of nontrees to species richness of a tropical rain forest. *Biotropica* 19: 149-156.

Gentry, A. H. (1988). Tree species richness of upper Amazonian forests. *Proc. Natl Acad. Sci. USA* 85: 156-159.

George, L. O., Bazzaz, F. A. (1999). The fern understory as an ecological filter: Emergence and establishment of canopy-tree seedlings. *Ecology* 80: 833-845.

George, L. O., Bazzaz, F. A. (2003). The herbaceous layer as a filter determining spatial pattern in forest tree regeneration. In: Gilliam, F. S. and Roberts, M. R. (eds.) The herbaceous layer in forests of Eastern North America, pp. 265-282. Oxford University Press, USA.

Gilliam, F. S., Christensen, N. L. (1986). Herb-Layer Response To Burning In Pine Flatwoods Of The Lower Coastal-Plain Of South-Carolina. *B. Torrey Bot. Club* 113: 42-45.

Gilliam, F. S., Turrill, N. L., Adams, M. B. (1995). Herbaceous-layer and overstory species in clear-cut and mature central Appalachian hardwood forests. *Ecol. Appl.* 5: 947-955.

Gilliam, F. S., Roberts, M. R. (2003). Interactions between the herbaceous layer and overstory canopy of Eastern forests. In: Gilliam, F. S. and Roberts, M. R. (eds.) The herbaceous layer in forests of Eastern North America, pp. 198-223. Oxford University Press, USA.

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

Gross, N., Suding, K. N., Lavorel, S., Roumet, C (2007). Complementarity as a mechanism of coexistence between functional groups of grasses. *J. Ecol.* 95: 1296-1305.

Härdtle, W., von Oheimb, G., Westphal, C. (2003). The effects of light and soil conditions on the species richness of the ground vegetation of deciduous forests in northern Germany (Schleswig-Holstein). *Forest Ecol. Manag.* 182: 327-338.

Harms, K. E., Powers, J. S., Montgomery, R. A. (2004). Variation in small sapling density, understory cover, and resource availability in four Neotropical forests. *Biotropica* 36: 40-51.

Harvey, J. A., Bukovinszky, T., van der Putten, W. H. (2010). Interactions between invasive plants and insect herbivores: A plea for a multitrophic perspective. *Biol. Conserv.* 143: 2251-2259.

Hector, A., Schmid, B., Beierkuhnlein, C., Caldeira, M. C., Diemer, M., Dimitrakopoulos, P. G., Finn, J. A., Freitas, H., Giller, P. S., Good, J., Harris, R., Hogberg, P., Huss-Danell, K., Joshi, J., Jumpponen, A., Korner, C., Leadley, P. W., Loreau, M., Minns, A., Mulder, C. P. H., O'Donovan, G., Otway, S. J., Pereira, J. S., Prinz, A., Read, D. J., Scherer-Lorenzen, M., Schulze, E. D., Siamantziouras, A. S. D., Spehn, E. M., Terry, A. C., Troumbis, A. Y., Woodward, F. I., Yachi, S., Lawton, J. H. (1999). Plant diversity and productivity experiments in European grasslands. *Science* 286: 1123-1127.

Hector, A., Dobson, K., Minns, A., Bazeley-White, E., Lawton, J. H. (2001). Community diversity and invasion resistance: An experimental test in a grassland ecosystem and a review of comparable studies. *Ecol. Res.* 16: 819-831.

Hector, A., Hautier, Y., Saner, P., Wacker, L., Bagchi, R., Joshi, J., Scherer-Lorenzen, M., Spehn, E. M., Bazeley-White, E., Weilenmann, M., Caldeira, M. C., Dimitrakopoulos, P. G., Finn, J. A., Huss-Danell, K., Jumpponen, A., Mulder, C. P. H., Palmborg, C., Pereira, J. S., Siamantziouras, A. S. D., Terry, A. C., Troumbis, A. Y., Schmid, B., Loreau, M. (2010). General stabilizing effects of plant diversity on grassland productivity through population asynchrony and overyielding. *Ecology* 91: 2213-2220.

Hejda, M., Pysek, P., Jarosik, V. (2009). Impact of invasive plants on the species richness, diversity and composition of invaded communities. *J. Ecol.* 97: 393-403

Hill, J. L., Hill, R. A. (2001). Why are tropical rain forests so species rich? Classifying, reviewing and evaluating theories. *Prog. Phys. Geog.* 25: 326-354.

Hillebrand, H., Bennett, D. M., Cadotte, M. W. (2008). Consequences of dominance: A review of evenness effects on local and regional ecosystem processes. *Ecology* 89: 1510-1520.

Hillebrand, H., Matthiessen, B. (2009). Biodiversity in a complex world: consolidation and progress in functional biodiversity research. *Ecol. Lett.* 12: 1405-1419.

Hodgson, D. J., Rainey, P. B., Buckling, A. (2002). Mechanisms linking diversity, productivity and invasibility in experimental bacterial communities. *Proc. Natl Acad. Sci. USA* 269: 2277-2283.

Hooper, D. U. (1998). The role of complementarity and competition in ecosystem responses to variation in plant diversity. *Ecology* 79: 704-719.

Hooper, D. U., Vitousek, P. M. (1997). The effects of plant composition and diversity on ecosystem processes. *Science* 277: 1302-1305.

Hooper, D. U., Chapin, F. S., Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J. H., Lodge, D. M., Loreau, M., Naeem, S., Schmid, B., Setala, H., Symstad, A. J., Vandermeer, J., Wardle, D. A. (2005). Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecol. Monogr.* 75: 3-35.

Hu, Z. G., Yu, M. J. (2008). Study on successions sequence of evergreen broad-leaved forest in Gutian Mountain of Zhejiang, Eastern China: species diversity. *Frontiers in Biology in China* 3: 45-49.

Hughes, A. R., Inouye, B. D., Johnson, M. T. J., Underwood, N., Vellend, M. (2008). Ecological consequences of genetic diversity. *Ecol. Lett.* 11: 609-623.

Huston, M. A. (1997). Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia* 110: 449-460.

Ingerpuu, N., Vellak, K., Liira, J., Pärtel, M. (2003). Relationships between species richness patterns in deciduous forests at the north Estonian limestone escarpment. *J. Veg. Sci.* 14: 773-780.

Jules, M. J., Sawyer, J. O., Jules, E. S. (2008). Assessing the relationships between stand development and understory vegetation using a 420-year chronosequence. *Forest Ecol. Manag.* 255: 2384-2393.

Kabakoff, R. P., Chazdon, R. L. (1996). Effects of canopy species dominance on understorey light availability in low-elevation secondary forest stands in Costa Rica. *Journal Of Tropical Ecology* 12: 779-788.

Kahmen, A., Renker, C., Unsicker, S. B., Buchmann, N. (2006). Niche complementarity for nitrogen: An explanation for the biodiversity and ecosystem functioning relationship? *Ecology* 87: 1244-1255.

Knight, K. S., Oleksyn, J., Jagodzinski, A. M., Reich, P. B., Kasprowicz, M. (2008). Overstorey tree species regulate colonization by native and exotic plants: a source of positive relationships between understorey diversity and invasibility. *Diversity and Distributions* 14: 666-675.

Kochy, M., Wilson, S. D. (2000). Competitive effects of shrubs and grasses in prairie. *Oikos* 91: 385-395.

Lang, A. C., Härdtle, W., Bruelheide, H., Geißler, C., Nadrowski, K., Schuldt, A., Yu, M. J., von Oheimb, G. (2010). Tree morphology responds to neighbourhood competition and slope in species-rich forests of subtropical China. *Forest Ecol. Manag.* 260: 1708-1715.

Langenberger, G., Martin, K., Sauerborn, J. (2006). Vascular plant species inventory of a Philippine lowland rain forest and its conservation value. *Biodivers. Conserv.* 15: 1271-1301.

Lanta, V., Leps, J. (2007). Effects of species and functional group richness on production in two fertility environments: an experiment with communities of perennial plants. *Acta Oecol.* 32: 93-103.

Lamb, E. G., Kembel, S. W., Cahill, J. F. (2009). Shoot, but not root, competition reduces community diversity in experimental mesocosms. *J. Ecol.* 97: 155-163

Legendre, P., Mi, X. C., Ren, H. B., Ma, K. P., Yu, M. J., Sun, I. F., He, F. L. (2009). Partitioning beta diversity in a subtropical broad-leaved forest of China. *Ecology* 90: 663-674.

Leger, E. A., Espeland, E. K. (2010). The shifting balance of facilitation and competition affects the outcome of intra- and interspecific interactions over the life history of California grassland annuals. *Plant Ecol.* 208: 333-345.

Linares-Palomino, R., Cardona, V., Hennig, E. I., Hensen, I., Hoffmann, D., Lendzion, J., Soto, D., Herzog, S. K., Kessler, M. (2009). Non-woody life-form contribution to vascular plant species richness in a tropical American forest. *Plant Ecol.* 201: 87-99.

Liu, J., Liang, S. C., Liu, F. H., Wang, R. Q., Dong, M. (2005). Invasive alien plant species in China: regional distribution patterns. *Diversity And Distributions* 11: 341-347.

Lopez-Pujol, J., Zhang, F. M., Ge, S. (2006). Plant biodiversity in China: richly varied, endangered, and in need of conservation. *Biodivers. Conserv.* 15: 3983-4026.

Loreau, M. (1998a). Biodiversity and ecosystem functioning: recent theoretical advances. *Oikos* 91: 3-17.

Loreau, M. (1998b). Biodiversity and ecosystem functioning: A mechanistic model. *Proc. Natl Acad. Sci. USA* 95: 5632-5636.

Loreau, M., Hector, A. (2001). Partitioning selection and complementarity in biodiversity experiments. *Nature* 412: 72-76.

Lorentzen, S., Roscher, C., Schumacher, J., Schulze, E. D., Schmid, B. (2008). Species richness and identity affect the use of aboveground space in experimental grasslands. *Perspect. Plant Ecol.* 10: 73-87.

Lou, L., Jin, S. (2000). Spermatophyta flora of Gutianshan Nature Reserve in Zhejiang. *Journal of Beijing Forestry University* 22: 33-39. (In Chinese)

Lu, X. K., Mo, J. M., Gilliam, F. S., Zhou, G. Y., Fang, Y. T. (2010). Effects of experimetnal nitrogen addition in an old-growth tropical forest. Global Change Biology 16: 2688-2700.

Luken, J. O. (2003). Invasions of Forests in the Eastern United States. In: Gilliam, F. S. and Roberts, M. R. (eds.) The herbaceous layer in forests of Eastern North America, pp. 283-301. Oxford University Press, USA.

Lusk, C. H. (2004). Leaf area and growth of juvenile temperate evergreens in low light: species of contrasting shade tolerance change rank during ontogeny. *Funct. Ecol.* 16: 820-828.

Ma, Z. J., Li, B., Li, W. J., Han, N. Y., Chen, J. K., Watkinson, A. R. (2009). Conflicts between biodiversity conservation and development in a biosphere reserve. *Journal Of Applied Ecology* 46: 527-535.

Mack, R. N., Simberloff, D., Lonsdale, W. M., Evans, H., Clout, M., Bazzaz, F. A. (2000). Biotic invasions: Causes, epidemiology, global consequences, and control. *Ecol. Appl.* 10: 689-710.

Marquard, E., Weigelt, A., Temperton, V. M., Roscher, C., Schumacher, J., Buchmann, N., Fischer, M., Weisser, W. W., Schmid, B. (2009). Plant species richness and functional composition drive overyielding in a six-year grassland experiment. *Ecology* 90: 3290-3302.

Marshall, J. M., Buckley, D. S., Franklin, J. A. (2009). Competitive interaction between Microstegium vimineum and first-year seedlings of three central hardwoods. *Journal Of The Torrey Botanical Society* 136: 342-349.

Martin, P. H., Canham, C. D., Marks, P. L. (2009). Why forests appear resistant to exotic plant invasions: intentional introductions, stand dynamics, and the role of shade tolerance. *Frontiers In Ecology And The Environment* 7: 142-149.

McGrady-Steed, J., Harris, P. M., Morin, P. J. (1997). Biodiversity regulates ecosystem predictability. *Nature* 390: 162-165.

Meiners, S. J., Pickett, S. T. A., Cadenasso, M. L. (2001). Effects of plant invasions on the species richness of abandoned agricultural land. *Ecography* 24: 633-644.

Meiners, S. J., Pickett, S. T. A., Cadenasso, M. L. (2002). Exotic plant invasions over 40 years of old field successions: community patterns and associations. *Ecography* 25: 215-223.

Millennium Ecosystem Assessment (2005). Ecosystems and Human Well-Being: Biodiversity Synthesis Report. Island Press, Washington, DC.

Mölder, A., Bernhardt-Römermann, M., Schmidt, W. (2008). Herb-layer diversity in deciduous forests: Raised by tree richness or beaten by beech? *Forest Ecol. Manag.* 256: 272-281.

Moore, J. L., Mouquet, N., Lawton, J. H., Loreau, M. (2001). Coexistence, saturation and invasion resistance in simulated plant assemblages. *Oikos* 94: 303-314.

Mulder, C. P. H., Uliassi, D. D., Doak, D. F. (2001). Physical stress and diversity-productivity relationships: The role of positive interactions. *Proc. Natl Acad. Sci. USA* 98: 6704-6708.

Muller, R.N. (2003). Nutrient Relations of the Herbaceous Layer in Deciduous Forest Ecosystems. In: Gilliam, F. S. and Roberts, M. R. (eds.) The herbaceous layer in forests of Eastern North America, pp. 15-37. Oxford University Press, USA.

Naeem, S., Knops, J. M. H., Tilman, D., Howe, K. M., Kennedy, T., Gale, S. (2000). Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. *Oikos* 91: 97-108.

Naeem, S., Bunker, D. E., Hector, H., Loreau, L., Perrings, C. (2009). Biodiversity, Ecosystem Functioning, and Human Wellbeing An Ecological and Economic Perspective. Oxford University Press, USA.

Niu, H. B., Liu, W. X., Wan, F. H., Liu, B. (2007). An invasive aster (Ageratina adenophora) invades and dominates forest understories in China: altered soil microbial communities facilitate the invader and inhibit natives. *Plant And Soil* 294: 73-85.

Olff, H., Alonso, D., Berg, M. P., Eriksson, B. K., Loreau, M., Piersma, T., Rooney, N. (2009). Parallel ecological networks in ecosystems. *Philos. T. Roy. Soc. B.* 364: 1755-1779.

Palmborg, C., Scherer-Lorenzen, M., Jumpponen, A., Carlsson, G., Huss-Danell, K., Hogberg, P. (2005). Inorganic soil nitrogen under grassland plant communities of different species composition and diversity. *Oikos* 110: 271-282.

Partzsch, M., Bachmann, U. (2011). Is *Campanula glomerata* threatened by competition from expanding grasses? Results from a 5-year pot-experiment. *Plant Ecol.* 212: 251-261.

Pfisterer, A. B., Schmid, B. (2002). Diversity-dependent production can decrease the stability of ecosystem functioning. *Nature* 416: 84-86.

Plue, J., Verheyen, K., Van Calster, H., Marage, D., Thompson, K., Kalamees, R., Jankowska-Blaszczuk, M., Bossuyt, B., Hermy, M. (2010). Seed banks of temperate deciduous forests during secondary succession. *J. Veg. Sci.* 21: 965-978.

Pokorny, M. L., Sheley, R. L., Zabinski, C. A., Engel, R. E., Svejcar, T. J., Borkowski, J. J. (2005). Plant functional group diversity as a mechanism for invasion resistance. *Restor. Ecol.* 13: 448-459.

Prieur-Richard, A. H., Lavorel, S., Dos Santos, A., Grigulis, K. (2002). Mechanisms of resistance of Mediterranean annual communities to invasion by *Conyza bonariensis*: effects of native functional composition. *Oikos* 99: 338-346.

Quijas, S., Schmid, B., Balvanera, P. (2010). Plant diversity enhances provision of ecosystem services: A new synthesis. *Basic Appl. Ecol.* 11: 582-593.

Reiss, J., Bridle, J. R., Montoya, J. M., Woodward, G. (2009). Emerging horizons in biodiversity and ecosystem functioning research. *Trends Ecol. Evol.* 24: 505-514.

Robertson, D. J., Robertson, M. C., Tague, T. (1994). Colonization Dynamics Of 4 Exotic Plants In A Northern Piedmont Natural Area. *B. Torrey Bot. Club* 121: 107-118.

Rogers, R. S. (1981). Mature Mesophytic Hardwood Forest - Community Transitions, By Layer, From East-Central Minnesota To Southeastern Michigan. *Ecology* 62: 1634-1647.

Roscher, C., Schumacher, J., Baade, J., Wilcke, W., Gleixner, G., Weisser, W. W., Schmid, B., Schulze, E. D. (2004). The role of biodiversity for element cycling and trophic interactions: an experimental approach in a grassland community. *Basic Appl. Ecol.* 5: 107-121.

Roscher, C., Temperton, V. M., Scherer-Lorenzen, M., Schmitz, M., Schumacher, J., Schmid, B., Buchmann, N., Weisser, W. W., Schulze, E. (2005). Overyielding in experimental grassland communities – irrespective of species pool or spatial scale. *Ecol. Lett.* 9: 419-429.

Roscher, C., Thein, S., Schmid, B., Scherer-Lorenzen, M. (2008). Complementary nitrogen use among potentially dominant species in a biodiversity experiment varies between two years. *J. Ecol.* 96: 477-488.

Roscher, C., Bessler, H., Oelmann, Y., Engels, C., Wilcke, W., Schulze, E. D. (2009). Resources, recruitment limitation and invader species identity determine pattern of spontaneous invasion in experimental grasslands. *J. Ecol.* 97: 32-47.

Royo, A. A., Carson, W. P. (2006). On the formation of dense understory layers in forests worldwide: consequences and implications for forest dynamics, biodiversity, and succession. *Can. J. Forest Res.* 36: 1345-1362.

Royo, A. A., Carson, W. P. (2008). Direct and indirect effects of a dense understory on tree seedling recruitment in temperate forests: habitat-mediated predation versus competition. *Can. J. Forest Res.* 38: 1634-1645.

Sariyildiz, T., Anderson, J. M., Kucuk, M. (2005). Effects of tree species and topography on soil chemistry, litter quality, and decomposition in Northeast Turkey. *Soil Biol. Biochem.* 37: 1695-1706.

Scherber, C., Eisenhauer, N., Weisser, W. W., Schmid, B., Voigt, W., Fischer, M., Schulze, E. D., Roscher, C., Weigelt, A., Allan, E., Bessler, H., Bonkowski, M., Buchmann, N., Buscot, F., Clement, L. W., Ebeling, A., Engels, C., Halle, S., Kertscher, I., Klein, A. M., Koller, R., Konig, S., Kowalski, E., Kummer, V., Kuu, A., Lange, M., Lauterbach, D., Middelhoff, C., Migunova, V. D., Milcu, A., Muller, R., Partsch, S., Petermann, J. S., Renker, C., Rottstock, T., Sabais, A., Scheu, S., Schumacher, J., Temperton, V. M., Tscharntke, T. (2010). Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. *Nature* 468: 553-556.

Scherer-Lorenzen, M., Bonilla, J. L., Potvin, C. (2007). Tree species richness affects litter production and decomposition rates in a tropical biodiversity experiment. *Oikos* 116: 2108-2124.

Schimpf, D. J., Danz, N. P. (1999). Light passage through leaf litter: variation among northern hardwood trees. *Agr. Forest Meteorol.* 97: 103-111.

Schläpfer, F., Schmid, B. (1999). Ecosystem effects of biodiversity: A classification of hypotheses and exploration of empirical results. *Ecol. Appl.* 9: 893-912.

Schmid, B., Hector, A. (2004). The value of biodiversity experiments. *Basic Appl. Ecol.* 5: 535-542.

Shea, K., Chesson, P. (2002). Community ecology theory as a framework for biological invasions. *Trends Ecol. Evol.* 17: 170-176.

Siccama, T. G., Bormann, F. H., Likens, G. E. (1970). Hubbard Brook Ecosystem Study - Productivity, Nutrients, And Phytosociology Of Herbaceous Layer. *Ecol. Monog.* 40: 389-402.

Simao, M. C. M., Flory, S. L., Rudgers, J. A. (2010). Experimental plant invasion reduces arthropod abundance and richness across multiple trophic levels. *Oikos* 119: 1553-1562.

Spehn, E. M., Scherer-Lorenzen, M., Schmid, B., Hector, A., Caldeira, M. C., Dimitrakopoulos, P. G., Finn, J. A., Jumpponen, A., O'Donnovan, G., Pereira, J. S., Schulze, E. D., Troumbis, A. Y., Korner, C. (2002). The role of legumes as a component of biodiversity in a cross-European study of grassland biomass nitrogen. *Oikos* 98: 205-218.

Spehn, E. M., Hector, A., Joshi, J., Scherer-Lorenzen, M., Schmid, B., Bazeley-White, E., Beierkuhnlein, C., Caldeira, M. C., Diemer, M., Dimitrakopoulos, P. G., Finn, J. A., Freitas, H., Giller, P. S., Good, J., Harris, R., Hogberg, P., Huss-Danell, K., Jumpponen, A., Koricheva, J., Leadley, P. W., Loreau, M., Minns, A., Mulder, C. P. H., O'Donovan, G., Otway, S. J., Palmborg, C., Pereira, J. S., Pfisterer, A. B., Prinz, A., Read, D. J., Schulze, E. D., Siamantziouras, A. S. D., Terry, A. C., Troumbis, A. Y., Woodward, F. I., Yachi, S., Lawton, J. H. (2005). Ecosystem effects of biodiversity manipulations in European grasslands. *Ecol. Monogr.* 75: 37-63.

Stoll, P., Prati, D. (2001). Intraspecific aggregation alters competitive interactions in experimental plant communities. *Ecology* 82: 319-327.

Srivastava, D. S., Vellend, M. (2005). Biodiversity-ecosystem function research: Is it relevant to conservation? *Annual Review Of Ecology Evolution And Systematics* 36: 267-294.

Symstad, A. J., Tilman, D., Willson, J., Knops, J. M. H. (1998). Species loss and ecosystem functioning: effects of species identity and community composition. *Oikos* 81: 389-397.

Takafumi, H., Hiura, T. (2009). Effects of disturbance history and environmental factors on the diversity and productivity of understory vegetation in a cool-temperate forest in Japan. *Forest Ecol. Manag.* 257: 843-857.

Taverna, K., Peet, R. K., Phillips, L. C. (2005). Long-term change in ground-layer vegetation of deciduous forests of the North Carolina Piedmont, USA. *J. Ecol.* 93: 202-213

Temperton, V. M., Mwangi, P. N., Scherer-Lorenzen, M., Schmid, B., Buchmann, N. (2007). Positive interactions between nitrogen-fixing legumes and four different neighbouring species in a biodiversity experiment. *Oecologia* 151: 190-205.

Thiele, J., Otte, A. (2006). Analysis of habitats and communities invaded by *Heracleum mantegazzianum* Somm. et Lev. (Giant Hogweed) in Germany. *Phytocoenologia* 36: 281-320.

Tilman, D., Wedin, D., Knops, J. (1996). Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature* 379: 718-720.

Tilman, D. (1997a). Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology* 78: 81-92.

Tilman, D. (1997b). Distinguishing between the effects of species diversity and species composition. *Oikos* 80: 185-185.

Tilman, D., Lehman, C. L., Thomson, K. T. (1997). Plant diversity and ecosystem productivity: Theoretical considerations. *Proc. Natl Acad. Sci. USA* 94: 1857-1861.

Tilman, D. (1999). The ecological consequences of changes in biodiversity: A search for general principles. *Ecology* 80: 1455-1474.

Tylianakis, J. M., Rand, T. A., Kahmen, A., Klein, A. M., Buchmann, N., Perner, J., Tscharntke, T. (2008). Resource heterogeneity moderates the biodiversity-function relationship in real world ecosystems. *Plos Biology* 6: 947-956.

Van Calster, H., Baeten, L., De Schrijver, A., De Keersmaeker, L., Rogister, J. E., Verheyen, K., Hermy, M. (2007). Management driven changes (1967-2005) in soil acidity and the understorey plant community following conversion of a coppice-with-standards forest. *Forest Ecol. Manag.* 241: 258-271.

Van Calster, H., Baeten, L., Verheyen, K., De Keersmaeker, L., Dekeyser, S., Rogister, J. E., Hermy, M. (2008). Diverging effects of overstorey conversion scenarios on the understorey vegetation in a former coppice-with-standards forest. *Forest Ecol. Manag.* 256: 519-528.

van Ruijven, J., Berendse, F. (2005). Diversity-productivity relationships: Initial effects, long-term patterns, and underlying mechanisms. *Proc. Natl Acad. Sci. USA* 102: 695-700.

van Ruijven, J., Berendse, F. (2009). Long-term persistence of a positive plant diversity-productivity relationship in the absence of legumes. *Oikos* 118: 101-106.

Verheyen, K., Vanhellemont, M., Stock, T., Hermy, M. (2007). Predicting patterns of invasion by black cherry (*Prunus serotina* Ehrh.) in Flanders (Belgium) and its impact on the forest understorey community. *Diversity And Distributions* 13: 487-497.

Vila, M., Basnou, C., Pysek, P., Josefsson, M., Genovesi, P., Gollasch, S., Nentwig, W., Olenin, S., Roques, A., Roy, D., Hulme, P. E. (2010). How well do we understand the impacts of alien species on ecosystem services? A pan-European, cross-taxa assessment. *Frontiers In Ecology And The Environment* 8: 135-144.

Vitousek, P. M., Walker, L. R. (1989). Biological Invasion By *Myrica Faya* In Hawaii - Plant Demography, Nitrogen-Fixation, Ecosystem Effects. *Ecol. Monogr.* 59: 247-265.

von Felten, S., Schmid, B. (2008). Complementarity among species in horizontal versus vertical rooting space. *J. Plant Ecol. - UK* 1: 33-41.

Von Holle, B., Delacourt, H. R., Simberloff, D. (2003). The importance of biological inertia in plant community resistance to invasion. *J. Veg. Sci.* 14: 425-32.

Wacker, L., Baudois, O., Eichenberger-Glinz, S., Schmid, B. (2008). Environmental heterogeneity increases complementarity in experimental grassland communities. *Basic Appl. Ecol.* 9: 467-474.

Wang, G. M., Jiang, G. M., Zhou, Y. L., Liu, Q. R., Ji, Y. S., Wang, S. X., Chen, S. B., Liu, H. (2007a). Biodiversity conservation in a fast-growing metropolitan area in China: a case study of plant diversity in Beijing. *Biodivers. Conserv.* 16: 4025-4038.

Wang, X. H., Kent, M., Fang, X. F. (2007b). Evergreen broad-leaved forest in Eastern China: Its ecology and conservation and the importance of resprouting in forest restoration. *Forest Ecol. Manag.* 245: 76-87.

Wang, Z. G., Ye, W. H., Cao, H. L., Huang, Z. G., Lian, J. Y., Li, L., Wei, S. G., Sun, I.-F. (2009). Species–topography association in a species-rich subtropical forest of China. *Basic Appl. Ecol.* 10: 648-655.

Wardle, D. A., Lagerstrom, A., Nilsson, M. C. (2008). Context dependent effects of plant species and functional group loss on vegetation invasibility across an island area gradient. *J. Ecol.* 96: 1174-1186

Weber, E., Li, B. (2008). Plant invasions in China: What is to be expected in the wake of economic development? *BioScience* 58: 437-444.

Weber, E., Sun, S. G., Li, B. (2008). Invasive alien plants in China: diversity and ecological insights. *Biol. Invasions* 10: 1411-1429.

Weigelt, A., Schumacher, J., Walther, T., Bartelheimer, M., Steinlein, T., Beyschlag, W. (2007). Identifying mechanisms of competition in multi-species communities. *J. Ecol.* 95: 53-64.

Weis, J. J., Cardinale, B. J., Forshay, K. J., Ives, A. R. (2007). Effects of species diversity on community biomass production change over the course of succession. *Ecology* 88: 929-939.

Whitmore, T. C., Peralta, R., Brown, K. (1985). Total species count in a Costa Rican tropical rain forest. *Journal of Tropical Ecology* 1: 375-378.

Woods, K. D. (1993). Effects Of Invasion By Lonicera Tatarica L On Herbs And Tree Seedlings In 4 New-England Forests. *Am. Midl. Nat.* 130: 62-74.

Wu, Z. Y. (1980). Vegetation of China. Science Press, Beijing, China. (In Chinese)

Wyckoff, P. H., Webb, S. L. (1996). Understory influence of the invasive Norway maple (Acer platanoides). *B. Torrey Bot. Club* 123: 197-205.

Yu, M. J., Hu, Z. H., Yu, J. P., Ding, B. Y., Fang, T. (2001). Forest vegetation types in Gutianshan Natural Reserve in Zhejiang. *Journal of Zhejiang University* (Agriculture and Life Science) 27: 375–380. (In Chinese)

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Appendix

Curriculum vitae

Contact information

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Personal data

Date and place of birth	22.10.1982, Halle (Saale)
Nationality	German

Education

05/2008 - present	PhD thesis, Martin Luther University Halle-Wittenberg Topic: *Biodiversity and ecosystem functioning across structural strata in subtropical forests in China – the interplay of herbaceous and woody species richness*. Supervisors: Dr. Alexandra Erfmeier, Prof. Dr. Helge Bruelheide
2002 - 2008	Studies of Biology, Martin Luther Universität Halle-Wittenberg Major subjects: geobotany, minor subjects: molecular ecology, nature conservation and soil sciences Topic diploma thesis: *Trait diversity in woody species in a subtropical forest in Dujiangyan (Sichuan, China).* Supervisor: Prof. Dr. Helge Bruelheide
06/2002	Abitur, Gymnasium „Hanns-Eisler“ in Halle (Saale)

Work experiences

05/2011 - present	Scientific coordinator in the BEF-China project
2006 – 2007	Student assistant in various projects related to germination biology and ecological experiments supervised by Dipl.-Biol. Heike Zimmermann

10.04. – 19.05.2006	Internship in the Helmholtz Centre for Environmental Research supervised by Dr. Marten Winter Topic: *Analyses regarding homogenisation of plant traits in Germany.*
18.07. – 26.08.2005	Internship in the Middle Elbe Biosphere Reserve Topic: *Data acquisition and evaluation of management arrangements for beaver, vegetation survey and evaluation of habitat types of the FFH habitat „Untere Muldeaue“.*
1.10. – 03.12.2004	Internship in the Leibniz Institute of Plant Biochemistry Halle (Saale) supervised by Dr. Thomas Fester Topic: *Establishment of transformation vectors for root transformation in the model plant Medicago truncatula.*
03.09. – 24.09.2002	Internship in an international project for the protection of ocean turtles in Mexiko, organized by ijgd – Internationale Jugendgemeinschaftsdienste
01.07. - 30.08.2002	Internship in the Department of Zoology, Martin Luther University Halle-Wittenberg, supervised by Prof. Dr. Rolf Gattermann Topic: *Analyses of body weight development and mating behaviour of Phodopus campbelli.*

Field trips related to scientific work

2011	One month field work in Xingangshan (China)
2010	One month field work in Xingangshan (China) within the framework of the PhD thesis
2009	Three and another two months field work in Gutianshan and Xingangshan (China) within the framework of the PhD thesis
2008	Three and another two months field work in Gutianshan (China) within the framework of the PhD thesis
2007	One month field work in Dujiangyan (China) within the framework of the diploma thesis
2006	Two months field work in Dujiangyan and data acquisition in the herbarium of the Chinese Academy of Sciences Beijing (China) within the framework of the diploma thesis

List of publications

Publications in peer review journals

Both, S., Fang, T., Böhnke, M., Bruelheide, H., Geißler, C., Kühn, P., Scholten, T., Trogisch, S., Erfmeier, A. Lack of tree layer control on herb layer characteristics in a subtropical forest, China. *Journal of Vegetation Science* (doi: 10.1111/j.1654-1103.2011.01324.x).

Both, S., Fang, T., Baruffol, M., Schmid, B., Bruelheide, H., Erfmeier, A. Impact of tree diversity on herb layer invasibility in young experimental communities of subtropical species. *Ecological Research* (under review).

Both, S., Bruelheide, H., Erfmeier, A. Productivity and species interactions in plant communities composed of one functional group. *Acta Oecologica* (under review).

Bruelheide, H., Böhnke, M., **Both, S.**, Fang, T., Assmann, T., Baruffol, M., Bauhus, J., Buscot, F., Chen, X.-Y., Ding, B.-Y., Durka, W., Erfmeier, A., Fischer, M., Geißler, C., Guo, D., Guo, L.-D., Härdtle, W., He, J.-S., Hector, A., Kröber, W., Kühn, P., Lang, A. C., Nadrowski, K., Pei, K. Q., Scherer-Lorenzen, M., Shi, X. Z., Scholten, T., Schuldt, A., Trogisch, S., von Oheimb, G., Welk, E., Wirth, C., Wu, Y.-T., Yang, X. F., Yu, M. J., Zeng, X. Q , Zhang, S. R., Zhou, H. Z., Ma, K. P., Schmid, B. (2011). Community assembly during secondary forest succession in a Chinese subtropical forest. - *Ecological Monographs* 81: 25-41.

Schuldt, A., **Both, S.,** Bruelheide, H., Härdtle, W., Schmid, B., Zhou, H.Z., Assmann, T. (2011). Predator diversity and abundance provide little support for the enemies hypothesis in forests of high tree diversity. *PLoS ONE* 6(7): e22905. doi:10.1371/journal.pone.0022905

Bachmann, D., **Both, S.,** Bruelheide, H., Ding, B. Y., Gao, M., Härdtle, W., Scherer-Lorenzen, M., Erfmeier, A. Functional trait similarity of native and invasive herb species in subtropical China – environment-specific differences are the key. *Oecologia* (under review after major revision).

Wu, Y. T., Gutknecht, J., Nadrowski, K., Geißler, C., Kühn, P., Scholten, T., **Both, S.**, Erfmeier, A., Böhnke, M., Bruelheide, H., Wubet, T., Buscot, F. Relationships between soil microorganisms, plant communities, and soil characteristics in Chinese subtropical forests. Plant and Soil (under review after major revision).

Symposia contributions

Both, S., Bruelheide, H., Erfmeier, A. (2010). Low impact of tree diversity on herb layer productivity and invasion resistance in experimental communities in subtropical China - Verhandlungen der Gesellschaft für Ökologie 40. *Oral presentation.*

Bachmann, D., **Both, S**., Bruelheide, H., Erfmeier, A. (2009). Effects of light and nutrients on native and invasive herb species in subtropical China - Implications for forest ecosystem invasibility? - World conference on Biological Invasions and Ecosystem Functioning (BIOLIEF), Porto (Portugal). *Poster.*

Both, S., Kröber, W., von Hagen, K. B., Welk, E., Bruelheide, H. (2008). Inter-relationships of traits of woody species in a subtropical forest in Dujiangyan, Sichuan, China - Verhandlungen der Gesellschaft für Ökologie 38. *Poster.*

Both, S., Welk., E., Bruelheide, H. (2007). Functional diversity of species traits in a subtropical forest in Dujiangyan, Sichuan, China - Verhandlungen der Gesellschaft für Ökologie 37. *Poster.*

Eigenständigkeitserklärung

Hiermit erkläre ich, dass die Arbeit mit dem Titel “*Biodiversity and ecosystem functioning across structural strata in subtropical forests in China – the interplay of herbaceous and woody species richness*“ bisher weder der Naturwissenschaftlichen Fakultät I Biowissenschaften der Martin-Luther-Universität Halle-Wittenberg noch einer anderen wissenschaftlichen Einrichtung zum Zweck der Promotion vorgelegt wurde.

Ferner erkläre ich, dass ich die vorliegende Arbeit selbstständig und ohne fremde Hilfe verfasst sowie keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe. Die den benutzten Werken wörtlich oder inhaltlich entnommenen Stellen wurden als solche von mir kenntlich gemacht.

Ich erkläre weiterhin, dass ich mich bisher noch nie um einen Doktorgrad beworben habe.

Halle, den 17. August 2011

Sabine Both