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UNRAVELING THE INTERACTIONS BETWEEN DIVERSITY, DISTURBANCES AND PRODUCTIVITY IN A TEMPERATE FOREST ECOSYSTEM

Dissertation

to obtain the doctoral degree (*Dr.nat.techn.*)

at the University of Natural Resources and Applied Life Sciences (BOKU), Vienna

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Vienna, October 2016

"The most unique feature of Earth is the existence of life,

and the most extraordinary feature of life is its diversity."

Cardinale et al., 2012

Preface

Biodiversity is one of the most extraordinary features of Earth. We all agree that biodiversity with its enormous variety of life forms and splendor enriches our lives. But does biodiversity also have an effect on the functions and services humans derive from an ecosystem? This question has motivated this work, which was part of a large collaborative European project that aimed to quantify the role of forest biodiversity for ecosystem functioning and the provisioning of services in major European forest types. The present dissertation represents a synthesis of the main findings addressed in three original, peer-reviewed scientific papers written by me under the supervision of Assoc. Prof. DI Dr. Rupert Seidl and in collaboration with DI Dr. Werner Rammer. A detailed description of all analysis and results can be found in the abovementioned papers (see Appendices 10.1 to 10.3). The following synthesis aims to deliver relevant and understandable information not only for stakeholders and policymakers, but also for students or simply curious minds that long to understand the ecological aspects of Life. Please cite this work as “Silva Pedro, 2016. Unraveling the interactions between diversity, disturbances and productivity in a temperate forest ecosystem. Dissertation, University of Natural Resources and Applied Life Sciences (BOKU) Vienna. p. 178.” or refer to the individual papers:

Silva Pedro, M., Rammer, W., Seidl, R. Disentangling the effects of compositional and structural diversity on forest productivity. J. Veg. Sci. in revision

Silva Pedro, M., Rammer, W., Seidl, R., 2016. A disturbance-induced increase in tree species diversity facilitates forest productivity. Landsc. Ecol. 31, 989–1004. doi:10.1007/s10980-015-0317-y

Silva Pedro, M., Rammer, W., Seidl, R., 2015. Tree species diversity mitigates disturbance impacts on the forest carbon cycle. Oecologia 177, 619–630. doi:10.1007/s00442-014-3150-0

Abstract

The observed global loss of biodiversity in forest ecosystems has prompted concerns on the ability of forests to function sustainably and deliver services to society also in the future. It has been suggested that diversity fosters the functioning and resilience of forest ecosystems. More diverse forests are frequently hypothesized to have higher resources use efficiency (i.e., niche complementarity) and are more likely to include highly productive tree species (i.e., selection effect). In addition, species-rich forests are suggested to buffer ecosystems against the impacts of disturbances, a proposition known as the “insurance hypothesis”. Forests in Central Europe are less diverse today than in the past, as a result of century-long management practices resulting in forests relatively simple in structure and composition. In the face of increasing disturbances in Europe, it is essential to understand how diversity (a feature of forests that can be directly altered by management) acts both on the functioning and resilience of these ecosystems. Using the process-based model iLand, a factorial simulation experiment studying 128 species combinations was conducted for a temperate forest ecosystem in Central Europe. Furthermore, different disturbance regimes (including a non-disturbed scenario) with varying severity and frequency were analyzed over a gradient of tree species richness. Overall, both diversity in species and structures were found to positively affect productivity. However, relationships between tree diversity and productivity were not constant and varied, for example, over the course of forest development or selected diversity indicator. This finding highlights the importance of considering an integrated approach which accounts for extended temporal scales and different dimensions of tree diversity when aiming to fully understand how tree diversity influences ecosystem productivity. An important outcome from this study is that more diverse forests can mitigate the impacts of predicted intensifying disturbance regimes under climate change. To increase the robustness of forest ecosystem functioning, forest managers could furthermore incorporate the diversity created by disturbances into stand development.

Keywords

Tree diversity; Forest productivity; Resilience; Disturbances; Temperate forest; Succession; iLand; Modelling

Kurzfassung

Der weltweit beobachtete Rückgang an Biodiversität in Waldökosystemen wirft die Frage auf, ob der Wald auch in Zukunft seine Funktionen und Leistungen nachhaltig erbringen kann. Vieles deutet darauf hin, dass Diversität die Funktionalität und Resilienz von Waldökosystemen fördert. Es wird oft postuliert, dass Wälder mit höherer Diversität die örtlichen Ressourcen effizienter nutzen können (Nischen-Komplementarität) und einen höheren Anteil an hochproduktiven Baumarten aufweisen (Selektionseffekt). Darüber hinaus besagt die ökologische Versicherungshypothese, dass Artenreichtum die negativen Auswirkungen von Störungen auf Ökosystemleistungen des Waldes abschwächen kann. Durch die jahrhundertelange Bewirtschaftung weisen die Wälder Zentraleuropas eine reduzierte Biodiversität auf und sind im Vergleich mit natürlichen Systemen relativ strukturarm. In Anbetracht der vermehrt auftretenden Störungen in Europa ist es wichtig zu verstehen, wie die Diversität, also eine direkt durch die Bewirtschaftung beeinflussbare Eigenschaft des Waldes, sowohl die Funktionalität als auch die Resilienz des Ökosystems beeinflusst. Um diese Hypothesen zu testen wurde für ein zentraleuropäisches Waldökosystem mithilfe des prozessbasierten Modells iLand ein faktorielles Simulationsexperiment bestehend aus 128 Artenkombinationen durchgeführt. Bei dem gewählten Ansatz wurden die Auswirkungen von Szenarien (inklusive einem Szenario ohne Störungen) mit unterschiedlicher Störungsintensität und -häufigkeit über einen Gradienten von Baumartendiversität verglichen. Sowohl für die Arten- als auch für die Strukturdiversität wurde ein positiver Effekt auf die Produktivität gefunden. Allerdings war der Zusammenhang zwischen Diversität und Produktivität nicht konstant sondern variierte, z.B. Abhängigkeit von der Bestandesentwicklungsphase und Diversitätsindikator. Die Ergebnisse zeigen deutlich, dass für ein tieferes Verständnis dieser Zusammenhänge ein integraler Ansatz nötig ist, der die zeitliche und räumliche Dynamik von Diversität ausreichend berücksichtig. Eine wichtige Erkenntnis dieser Arbeit ist, dass Wälder mit höherer Diversität die Auswirkungen eines durch den Klimawandel veränderten Störungsregimes abschwächen können. Die durch Störungen erzeugte Diversität könnte also in waldbauliche Behandlungskonzepte integriert werden um dadurch die zukünftige Resilienz und Funktionalität der Waldökosysteme zu stärken.

Stichwörter

Diversität; Zuwachsleistung; Resilienz; Störungen; temperierte Wälder; Sukzession; iLand; Modellierung

Contents

1 Introduction

Forests are among the richest biological systems on Earth (Aerts and Honnay 2011), providing habitat for the large majority of the world's known terrestrial species (Aerts and Honnay, 2011; Shvidenko et al., 2005). Biodiversity in forests has been identified as a key determinant of the functioning of ecosystems (e.g., climate regulation, carbon (C) and nutrient cycling) and the provisioning of services that support human well-being (e.g., food, clean water and timber) (Morales-Hidalgo et al., 2015). However, biodiversity in forest ecosystems has been subject to increasing pressures from changes in both anthropogenic (e.g., land-use change, soil degradation, introduction of non-native species) (Brockerhoff et al., 2008) and natural (e.g. more frequent and severe disturbances) (Seidl et al., 2014a) processes in recent decades. This observed decline of biodiversity has prompted concerns about the sustainable delivery of goods and services to society (Cardinale et al., 2012) and stimulated research to better understand the relationships between biodiversity and forest ecosystem functions and services (see Zhang et al., 2012 and Scherer-Lorenzen, 2014 for reviews).

The relationship between diversity and forest productivity – a proxy of ecosystem function and timber provision – (DFP) has been one of the most intensively studied relationships over the past ten years in this context (Seidel et al., 2013). Several approaches such as experimental studies (e.g., Pretzsch et al. 2013), observations in natural forests (e.g., Paquette and Messier 2011), and simulation models (Morin et al., 2011) have been used to study the DFP relationship. While most of these studies report a positive association between diversity and productivity (Scherer-Lorenzen, 2014; Zhang et al., 2012), others have also found negative (e.g., Potter and Woodall 2014) or non-significant (e.g., Vilà et al. 2005) relationships, with the effect of diversity on productivity thus remaining unclear. These divergent findings may arise from differences in soil fertility and climate in different studies (Scherer-Lorenzen 2014), but also from variation across successional stages and spatial scales (Lasky et al., 2014; Paquette and Messier, 2011; Thompson et al., 2009; Zhang et al., 2012). Two main mechanisms underpinning the higher growth performance of species-rich forests compared to monocultures have been suggested: niche complementarity (i.e., more diverse ecosystems are better able to exploit limited resources due to different and complementary traits of species) (Morin et al., 2011; Pretzsch and Schütze, 2009; Tilman, 1994) and selection effects (i.e., resulting from an increased likelihood of including a highly productive species as the species pool increases) (Ruiz-Benito et al., 2014; Tilman et al., 1997; Tobner et al., 2016).

In addition to negatively affecting the level of ecosystem functioning and service provisioning, biodiversity loss may also reduce ecological stability through a lowered resistance to perturbations and a lowered resilience to disturbances (e.g., Bengtsson et al. 2000; Hooper et al. 2005; Thompson et al. 2009). It has been previously hypothesized that species-rich ecosystems are more likely to contain species that are better able to cope with and recover from perturbations (i.e., ecological insurance hypothesis) (Morin et al., 2014; Naeem and Li, 1997; Yachi and Loreau, 1999). However, most studies on diversity effects to date have focused on the central tendency in ecosystem functioning and services provisioning (Zhang et al. 2012; Scherer-Lorenzen 2014), disregarding the role of natural disturbances and perturbations in the DFP relationship (Cardinale et al., 2013; Thompson et al., 2009). Disturbances are important processes of forest landscape dynamics, they alter the system state and trajectory of an ecosystem, being thus key drivers of spatial and temporal heterogeneity (Turner, 2010). In addition, disturbance damage is increasing in many ecosystems across a wide range of scales as a result of climatic and anthropogenic changes (Seidl et al., 2011; Turner, 2010).

The overall objective of this thesis was to advance our understanding of the relationship between diversity and forest productivity in a temperate forest landscape in Central Europe. It further aimed at analyzing the role of disturbances in this relationship, and investigate whether more diverse forests can mitigate the negative impacts of disturbances on ecosystem functioning. A century-long management practice favoring a small number of highly productive coniferous species has reduced biodiversity in the temperate forests of Central Europe (Spiecker et al., 2004). This loss of diversity in species and structures has prompted concerns (Spiecker, 2003) about the capacity of European temperate forests to cope with the observed disturbance increases (Schelhaas et al., 2003; Seidl et al., 2011) as well sustainably provide ecosystem services to society (Thom and Seidl, 2016). It is thus of growing importance to better understand the significance of diversity in the context of ecosystem functioning and resilience of forests in

Central Europe, in order to anticipate risks and foster robust forests in an uncertain future (Seidl, 2014).

The present thesis is divided in three main parts which specifically aimed at:

1) disentangling the relative effects of compositional and structural diversity on forest productivity at the stand scale (Fig. 1, I). While most previous studies have focused exclusively on the effects of compositional diversity or structural diversity on productivity (Hardiman et al., 2011; Jucker et al., 2015), they have rarely been analyzed jointly;

2) investigating how robust the DFP relationship is under disturbances and beyond the local scale (study II). The main questions addressed here were how disturbances affect tree species diversity at within- (α) and between-stand (β) scales (Fig. 1, II-a), and how the disturbance-mediated variation in tree species diversity further influences landscape productivity (Fig. 1, II-b). In addition, the processes and ecological mechanisms underpinning the diversity effects on forest productivity were analyzed;

3) analyzing whether tree species diversity contributes to ecosystem resilience (Fig. 1, III-b) by reducing the disturbance impact on productivity and dampening the disturbance-induced variability in forest productivity (Fig. 1, III-a).

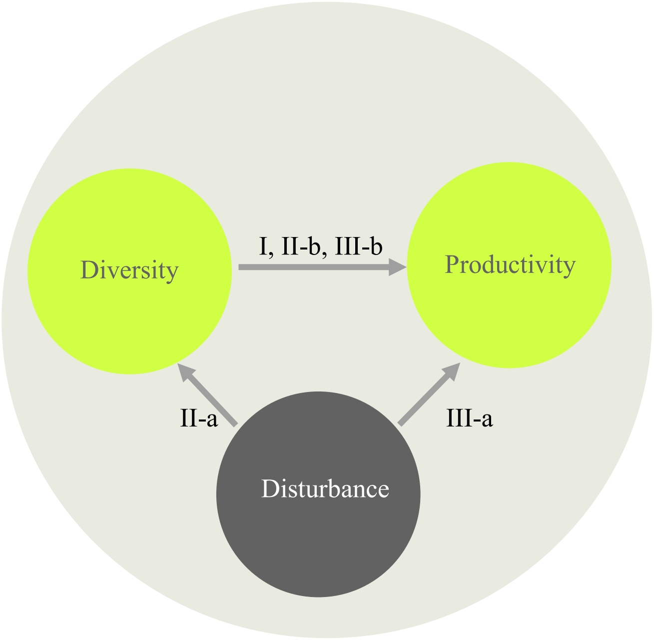
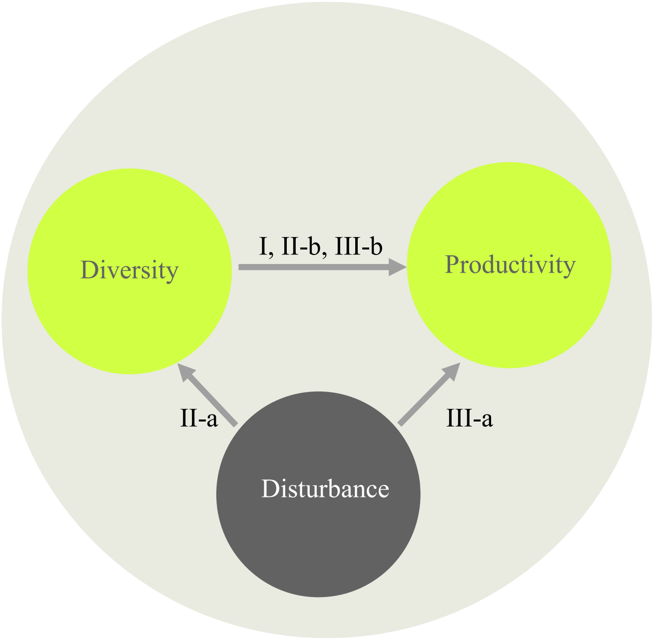


Figure 1 - Schematic representation of investigated relationships between diversity, productivity and disturbance. Roman numbers I, II and III correspond to the paths investigated in the three studies that comprise this thesis (i.e., studies I, II and III, respectively). Letters "a" and "b" indicate the order by which paths were analyzed.

An overarching objective was to investigate if and how these relationships (Fig. 1) change with forest development. Previous research suggests that biodiversity effects on ecosystem functioning and underlying mechanisms may change over the course of succession (e.g., Lasky et al. 2014), yet little is known about successional changes in DFP relationships.

I hypothesize that positive effects of both compositional (Thompson et al., 2009; Zhang et al., 2012) and structural diversity on stand productivity (Hardiman et al., 2011) persist while their relative importance differs between successional states (H1). I further hypothesize that disturbances increase tree species diversity (Thom and Seidl, 2016), and that such an increased diversity facilitates landscape productivity mainly through complementarity between tree species (Morin et al., 2011) (H2). Based on the insurance hypothesis (Naeem and Li, 1997), I expected that more diverse forests are less impacted by disturbance and that diversity enhances the resilience of forest productivity to disturbances (H3).



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2 Workflow

An overview of the tool and steps to answer the main question of this dissertation (i.e., how diversity influences forest productivity in a temperate forest ecosystem) are presented in Figure 2. The analyses conducted in the three studies comprising this thesis were based on the same ecosystem simulated with the forest landscape model iLand (Seidl et al., 2012a), but were analyzed for answering different questions (see section 1 for details).

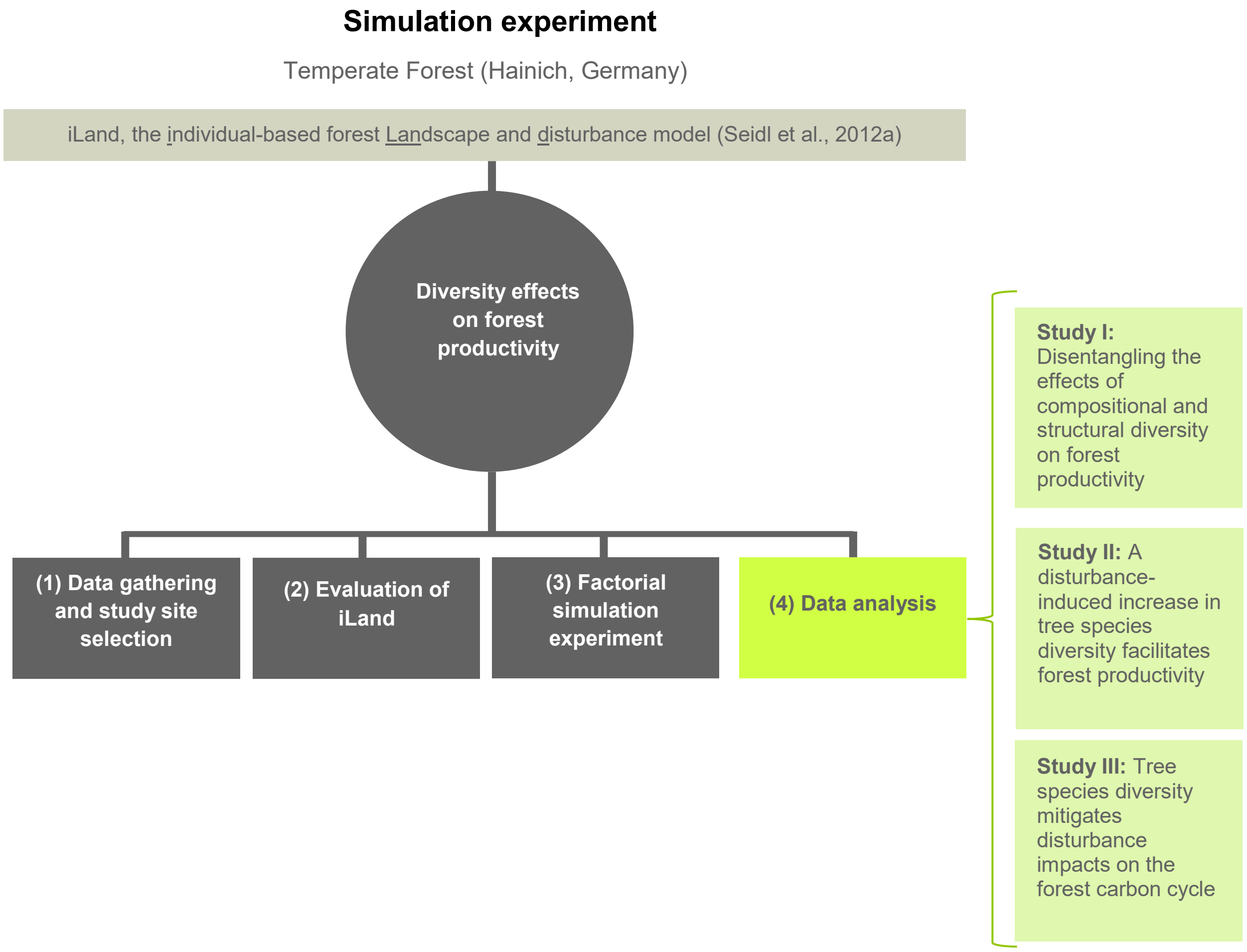

Figure 2 – Summary of the main steps conducted to investigate the relationship between diversity and productivity in a temperate forest ecosystem.

3 Material

3.1 Study site

The study focused on one of the focal regions within the FunDivEUROPE Exploratory Platform (Baeten et al., 2013), the Hainich National Park. Hainich is one of the largest unmanaged deciduous forest ecosystems in Central Europe and is located in the temperate broad-leaved forest ecoregion in Thuringia, Central Germany (N51.1°, E10.5°). The natural vegetation in the area is mainly characterized by beech forest types (Galio odorati (Asperulo)-Fagion) as well as oak-hornbeam forest types (Carpinion betuli) (Bohn et al., 2004). Hainich contains approximately 5,000 hectares of old-growth and uneven aged forests (i.e., 67% of the total park area). Management of the park was ceased completely in the 1960s, and for the past five decades natural dynamics governed the development of Hainich National Park (Mölder et al., 2008).

Quantitative data of a moderately fertile site was selected from study plots contained within the FunDivEUROPE Exploratory Platform (Baeten et al., 2013) to evaluate the simulation model iLand, and subsequently run the factorial simulation experiment. Site conditions were characterized by an effective soil depth of 100 cm, a clay-loamy soil texture (resulting in a water holding capacity of 180 mm), and 70 kg ha^{-1} $year^{-1}$ of plant-available nitrogen. Information on daily climate (i.e., temperature, precipitation, radiation, and vapor deficit) was extracted from a European gridded database (25 km horizontal resolution) representing the period 1961-1990 (Déqué et al., 2011). The climate selected to represent the study area is characterized by a mean annual precipitation sum of 627 mm and a mean annual temperature of 7.5°C.

3.2 iLand model

The present thesis uses a process-based forest landscape model to study the response of forest productivity to changes in tree diversity across different spatio-temporal scales, and to investigate how robust the DFP relationship is in the face of disturbance. In comparison to observational and experimental studies, simulation modelling offers several advantages:

1) it can control for the influence of confounding factors such as environmental heterogeneity and disturbance history;
2) it allows the analysis of a wide range of combinations of species, and
3) it can simulate forest dynamics over long time scales, enabling the study of potential changes in the DFP relationship with succession.

iLand, the individual-based forest Landscape and disturbance model (Seidl et al., 2012a), was specifically selected for this work, because:

1) it is able to simulate a variety of disturbance regimes and their interactions explicitly in space and time;
2) it can be used to simulate forest dynamics beyond the local scale (i.e., at the landscape level);
3) it has previously been successfully evaluated for diverse, multi-species forest ecosystems over extensive environmental gradients in western North America and central Europe (Seidl et al., 2012a, 2012b), and was successfully applied to investigate the relative contributions of structural and species diversity to ecosystem productivity (Seidl et al., 2012b).

iLand is a spatially explicit process-based model which simulates ecosystem dynamics as an emergent property of the interactions between environmental drivers (e.g., climate, nutrient and water availability), forest vegetation processes (e.g., growth, mortality and regeneration), and disturbances regimes (e.g., wind storms, wildfires) (Seidl et al., 2012a). Trees are simulated as adaptive agents that compete for resources (predominantly light, but also water and nutrients) and dynamically adapt to their environment (Seidl et al., 2012a). The model efficiently scales from individual trees to large forest landscapes in a hierarchical multi-scale approach.

iLand incorporates detailed process-based disturbance modules for wind disturbances (Seidl et al., 2014b), wildfire (Seidl et al., 2014c), and bark beetles (Seidl and Rammer, 2016), as well a generic interface (used in this study) that allows the implementation of different disturbance regimes based on impact type, disturbance frequency, disturbed area, and spatial spread.

A more detailed description of the model can be found in (Seidl et al., 2012a, 2012b) as well as online at http://iLand.boku.ac.at., where the model code and executable are available for download under an open source license.

4 Methods and analysis

4.1 Study design and simulations

To study the effect of tree species diversity on forest productivity, combinations of major tree species from all seral stages of natural forest development at Hainich (Bohn et al., 2004; see Table 1 for a full list of species included) were studied in a factorial design. As a prerequisite for using iLand in the analyses, the model was evaluated against expected patterns of forest ecosystem dynamics at Hainich with regard to dendrometry, productivity, mortality, as well as long-term successional trajectories, including old-growth composition and structure (see more details in Appendix 10.3). iLand was found to successfully reproduce expected values of dendrometry and growth at Hainich, and to simulate realistic species composition and trajectories of succession (Appendix 10.3).

In order to isolate the effects of tree species diversity on forest productivity, confounding factors such as topography and soil fertility were controlled for by setting up a hypothetical 5,000 × 5,000-m landscape with homogeneous environment. Simulations started from bare ground and species were introduced with a low annual probability of seed availability (see Appendix 10.3 for more details).

As the study also aimed at analyzing the interactions between diversity, forest productivity and disturbances, a factorial simulation experiment was designed in which different disturbance scenarios (including a non-disturbed scenario) were imposed over gradients of tree species richness levels (Table 1).

Using the ability of iLand to simulate a wide range of generic disturbance regimes four different disturbance scenarios were simulated, varying in their impact type and damage level:

a) “Complete”, where all trees regardless of their taxon were killed within the perimeter of a disturbance event (i.e., a disturbance severity of 100%);

b) “Species-specific”, where European beech (*Fagus sylvatica* L.) - the dominant tree species in the study area - was removed in a disturbance event. This disturbance type was only included in study II (cf. Table 1).

c) “Top-down”, where only large trees (i.e., with a diameter at breast height (dbh) ≥ 30 cm were removed within the perimeter of a disturbance, whereas saplings (≤ 10 cm dbh) survived; and

d) “Bottom-up”, where all trees ≤ 10 cm dbh within the perimeter of a disturbance were killed whereas large trees (≥ 30 cm dbh) were not affected by the disturbance;

Between the two threshold diameters in the bottom-up and top-down scenarios the mortality probability of individual trees changed linearly with dbh, i.e., decreasing from 10 to 30 cm in the bottom-up scenario and increasing in the top-down scenario. More details on the disturbance scenarios can be found in Appendix 10.3.

Each of these four disturbance scenarios was analyzed for a disturbance rotation period (DRP, i.e., the average time needed to disturb an area of the size of the study landscape) of 300 years, which approximates the current disturbance frequency in Central Europe (Thom et al., 2013). Furthermore, a more intensified DRP of 150 years for the “Complete” and “Top-down” disturbance scenarios was studied, corresponding to expectations of disturbance changes under climate change for Europe in the coming decades (Seidl et al., 2014a). In order to account for the stochasticity in the simulations 10 replicates were run for each of the fours disturbance scenarios and each of the species combinations. In addition to these four disturbance scenarios, a scenario without disturbance was also implemented (Table 1).

Simulations were run over a period of 500 years in order to compare the outcomes at different successional stages of forest development. In total, 3,904,000 simulation years of the 2,500 ha landscape (Table 1; 128 tree species combinations × (6 disturbance scenarios × 10 replicates + 1 non-disturbed scenario) × 500 years) were available for analysis. The analyses underlying the studies I, II and III (Appendix 10) were based on different subsets of the overall simulation experiment (see Table 1 for a summary).

Table 1 – Summary of the study design used across the three studies comprising this dissertation (study I, I and III).

	Study I	**Study II**	**Study III**
Tree species	*Fagus sylvatica* L. *Fraxinus excelsior* L. *Acer pseudoplatanus* L. *Quercus petraea* (Mattuschka) Liebl. *Betula pendula* Roth *Populus tremula* L.	*Fagus sylvatica* L. *Fraxinus excelsior* L. *Acer pseudoplatanus* L. *Quercus petraea* (Mattuschka) Liebl. *Betula pendula* Roth *Populus tremula* L.	*Fagus sylvatica* L. *Fraxinus excelsior* L. *Acer pseudoplatanus* L. *Quercus petraea* (Mattuschka) Liebl. *Picea abies* L. (Karst.) *Betula pendula* Roth *Populus tremula* L. *Acer platanoides* L. *Acer campestre* L. *Carpinus betulus* L. *Quercus robur* L. *Tilia cordata* Mill. *Tilia platyphyllos* Scop
Species richness gradient	1 to 6	1 to 6	1 to 7, 13
N° species combinations	63	63	128
Disturbance scenarios	Non-disturbed	Complete Top-down Bottom-up Species-specific	Complete Top-down Bottom-up
Disturbance rotation period	-	150 and 300 years	150 and 300 years
Simulation period	1-500 years	1-500 years	1-500 years
Spatial extent	2500 ha	2500 ha	2500 ha

4.2 Analysis

In the first part of this thesis (study I) total net primary production (NPP; t BM ha^{-1} yr^{-1}) calculated at 100 year intervals in each stand (i.e., cells of 100 × 100 m) was used as the response variable to study the relative influence of compositional and structural diversity on forest productivity. NPP quantifies the C uptake (converted to biomass here) in the forest and is thus an indicator of forest C cycling. Compositional diversity was quantified using indicators of species richness, entropy (Shannon and Weaver, 1949), evenness (Pielou, 1975) as well identity, whereas structural diversity was measured using horizontal (e.g., Staudhammer and LeMay, 2001) and vertical structural attributes of a stand (e.g., Seidl et al., 2012b). For a list and detailed description of the selected indicators see Table 2 and Appendix 10.1. This analysis was conducted for 250 stands randomly selected over the continuous 2500-ha forest landscape. Since structural and compositional diversity indicators revealed to be significantly correlated (Appendix 10.1), a random forest analysis (RFA) was applied to disentangle the relative contributions of these two dimensions of diversity on NPP (path I in Fig. 1).

The second component of the thesis aimed at going beyond the stand scale analyzed in study I and investigating the influence of disturbances on the DFP relationship (study II). For this purpose, two spatial scales of species diversity were considered in the analysis: alpha diversity (α) estimated as the exponential of the weighted average of the Shannon index (based on relative basal area shares) in all 100 m cells on the landscape, and beta diversity (β) obtained by employing Whittaker's multiplicative law (Jost, 2007). A more detailed description of how α and β diversity were calculated is described in the analysis section of Study II (see Appendix 10.2). As a first step of the analysis, the impact of the different disturbance scenarios on tree species diversity (path II-a in Fig. 1) was determined as the ratio between a disturbed simulation and the respective undisturbed simulation with the same species combination for both alpha and beta diversity (α_r and β_r). Subsequently, the relationship of α and β with landscape productivity (path II-b in Fig. 1) was assessed over all richness levels and disturbance scenarios (Table 2). An ecosystem service indicator for timber provisioning, i.e. mean annual stemwood volumne increment (MAI, m^3 ha^{-1} $year^{-1}$), was here used as a surrogate of forest productivity. MAI is a good indicator to investigate how tree species diversity can modulate the sustainable provisioning of timber under intensified disturbances. MAI was estimated from the total growth of each species computed at the stand level (i.e., cells of 100×100 m), and aggregated over the landscape for each simulation and for each 100 year period. To quantify the effects of tree species diversity on MAI, net diversity effects (DE, m^3 ha^{-1} $year^{-1}$) were calculated according to Loreau and Hector (2001). DE was derived as the difference between the simulated MAI of a multi-species forest and that of corresponding monospecific landscapes under the null hypothesis that there is no complementarity or selection effect (Loreau and Hector, 2001). To further distinguish the mechanisms underlying the diversity effects, DE was partitioned into complementary (CE; m^3 ha^{-1} $year^{-1}$) and selection (SE; m^3 ha^{-1} $year^{-1}$) effects (Table 2; Loreau and Hector, 2001). In order to investigate a potential role of functional diversity on results, species were classified into three different groups according to their life-history strategy (pioneer, intermediate and old-growth species), and the response variables DE, SE and CE were compared between different combinations of species life-history strategies.

In the last study (study III), the question of how diversity modulates the impact of disturbances was investigated (path III in Fig.1). Similar to study I, NPP (kg C ha^{-1} $year^{-1}$) was used as an indicator of forest productivity. In the context of predicted intensified disturbance regimes for Europe in the coming decades (Seidl et al., 2014a), this indicator allows to estimate how robust the productivity of central European forests could be in the future. NPP was spatially aggregated to landscape-scale averages, and mean values over 100-year simulation period were used in the analysis. Disturbance impact was quantified as the percentage difference of a disturbed simulation to the respective undisturbed simulation of the same species pool (NPP_{impact}). The variation between the replicated simulations for any given diversity and disturbance scenario, quantified by the coefficient of variance (CV) of annual NPP (NPP_{cv}), was calculated in order to study the effect of tree species diversity (here described by tree species richness and entropy) on the disturbance-induced variability of NPP. Statistical analysis, namely ordinary least squares regression and analysis of variance, were performed to analyze the effect of tree diversity on both response variables NPP_{impact} and NPP_{cv} (Table 2).

All analyses were conducted using the R language and environment for statistical computing (R Core Team 2013). In this synthesis, results are separately shown for the two 100-year periods at the beginning and end of our 500-year simulation period (henceforward referred to as early and late seral stage, respectively). Detailed analysis and results can be found in the three respective papers (see Appendix 10).

Table 2 – Summary of predictors and response variables as well type of analyses used in three studies comprising this dissertation (study I, I and III).

	Study I	**Study II**	**Study III**
Predictors			
Compositional diversity	n_{sp}; H'_{sp}; J'_{sp}; P_{Fs}	α and β diversity (H'_{sp})	n_{sp}; Shannon-index (H')
Structural diversity	dbh_{cv}; J'_{dbh};H'_{dbh}; RI	-	-
Functional diversity	-	Variation in species life-history strategies	-
Response variables	NPP [t BM ha^{-1} yr^{-1}]	MAI [m^3 ha^{-1} yr^{-1}] DE [m^3 ha^{-1} yr^{-1}] CE [m^3 ha^{-1} yr^{-1}] SE [m^3 ha^{-1} yr^{-1}]	NPP [kg C ha^{-1} yr^{-1}] NPP_{impact} NPP_{cv}
Grain of analysis	Stand (1 ha)	Landscape (2500 ha) Stand (1 ha)	Landscape (2500 ha)
Type of analyses	Spearman-correlation analysis Random forest analysis	Ordinary least squares regression Analysis of variance	Ordinary least squares regression Analysis of variance

Abbreviations: NPP, net primary production; NPP_{impact}, disturbance impact on NPP; NPP_{cv}, disturbance induced-variability in NPP ; MAI, mean annual increment; DE, net diversity effect on productivity; SE, selection effect; CE, complementarity effect; n_{sp} = realized tree species richness; H'= tree species Shannon index; H'_{sp} = exponent of tree species Shannon index; J'_{sp} = tree species evenness; P_{Fs} = relative abundance of *Fagus sylvatica*; dbh_{cv} = coefficient of variation of the diameter at breast height; J'_{dbh} = evenness of basal area over dbh classes; H'_{dbh} = exponent of the Shannon index applied to dbh classes; RI= rumple index.

5 Results

5.1 Compositional and structural diversity effects on stand productivity

Using the RFA to elucidate the relative importance of diversity in species and structures while addressing the multicollinearity found between predictors (Appendix 10.1), an overall positive effect of compositional and structural diversity on stand productivity was found. However, their influence varied distinctly with the stage of forest development. While compositional diversity was most influential in early stages of forest development, in later stages structural diversity indicators were the most important drivers of productivity (Fig. 3a). In earlier seral stages, the abundance of beech was identified as the most influential factor on forest productivity (species identity effect). In later seral stages, however, the influence of beech sharply decreased and this indicator was found to be the least influential factor, while indicators of structural diversity (e.g., the coefficient of variation of the diameter distribution, dbh_{cv}) were found to have the strongest influence on NPP (Appendix 10.1).

5.2 DFP relationship in landscapes under disturbance

In general, disturbances increased tree species diversity within and between stands (α and β diversity, respectively). The positive effect of disturbance on diversity was higher for landscapes with a larger species pool and increased with disturbance severity, i.e. being highest in the complete and species-specific disturbance scenarios (Appendix 10.2). The disturbance-induced increase in species diversity strongly increased the net diversity effect on forest productivity (here measured in terms of MAI) for both early and late seral stages of forest development. In other words, the more diverse forests resulting from disturbances generally showed higher MAI than their monoculture counterparts. While both α and β diversity had significant positive effects on productivity, the magnitude of their effect changed with forest development, with α diversity showing a higher positive effect in early seral stages, and β in later stages of forest development (Fig. 3b).

Complementarity effects emerged as the primary mechanism leading to the observed positive net diversity effects on forest productivity, with CE being stronger than SE by on average 85.5%. Increasing diversity at both within and between scales increased mostly CE (Appendix 10.2), i.e., the positive diversity-productivity relationships are mainly driven by complementarity resource use between species, and occur not only within stands but also between stands. Landscapes holding species with different life-history traits (i.e., pioneer and intermediate or old-growth tree species) showed the strongest positive diversity effect on MAI, in particular in early-seral systems, thus suggesting a positive effect of functional diversity (Fig. 3b; Appendix 10.2). In contrast to early-seral systems, the influence of species with different life-history traits was less prevalent in old-growth systems (Fig. 3b; Appendix 10.2).

5.3 Tree species diversity effects on disturbance impacts on forest productivity

Tree species diversity significantly mitigated the negative impacts of disturbances on NPP for both early and late seral landscapes (Fig. 3b; Appendix 10.3). The positive effect of diversify on NPP_{impact} was strongest in the disturbance scenario with the highest severity (i.e., complete disturbance scenario; Appendix 10.3). Results also suggested a decreasing benefit of increasing species richness, i.e., adding more species to an already diverse system did not result in the same reduction in disturbance impact as for a species-poor system. Furthermore, the mitigation effect of tree diversity on disturbance impacts was strongest under the higher disturbance frequencies (Appendix 10.3). In addition to mitigating NPP loss, tree species diversity significantly dampened the disturbance-induced variability in NPP (Fig. 3b). For example, under a complete disturbance scenario, adding an additional species to the landscape reduced NPP_{cv} by 13% in the early stage of forest succession. Similar to NPP_{impact}, results indicated that the positive effect of diversity on NPP_{cv} is amplified under higher disturbance frequencies (Appendix 10.3), demonstrating that diversity can buffer ecosystem functioning from the effects of expected future increases in disturbance frequency.

5.4 Summary

Overall, the analyzed ecological dimensions of tree diversity (i.e., compositional, structural and functional diversity) showed positive effects on forest productivity and resilience for the system studied here. However, these effects changed in their magnitude with the spatial scale and successional development (Fig. 3). Without considering disturbances, an increased benefit of compositional diversity on stand productivity compared to structural diversity was found in early seral forests (Fig. 3a). Contrastingly, structural diversity was found to have a higher influence on NPP in late seral forests (Fig. 3a). Under disturbances, landscapes with higher species entropy at both within and between stands (i.e., α and β diversity) showed higher positive diversity effects on productivity (Fig. 3b). While α diversity had its stronger effect on productivity in early stages of forest development, β diversity showed a more pronouncing effect in later stages. A higher variation in species life-history traits (functional diversity) in particular at early stages of forest development further contributed to productivity. Finally, more diverse forests showed also a higher resilience (i.e., a reduced impact on productivity and a decreased variability in productivity) (Fig. 3b).

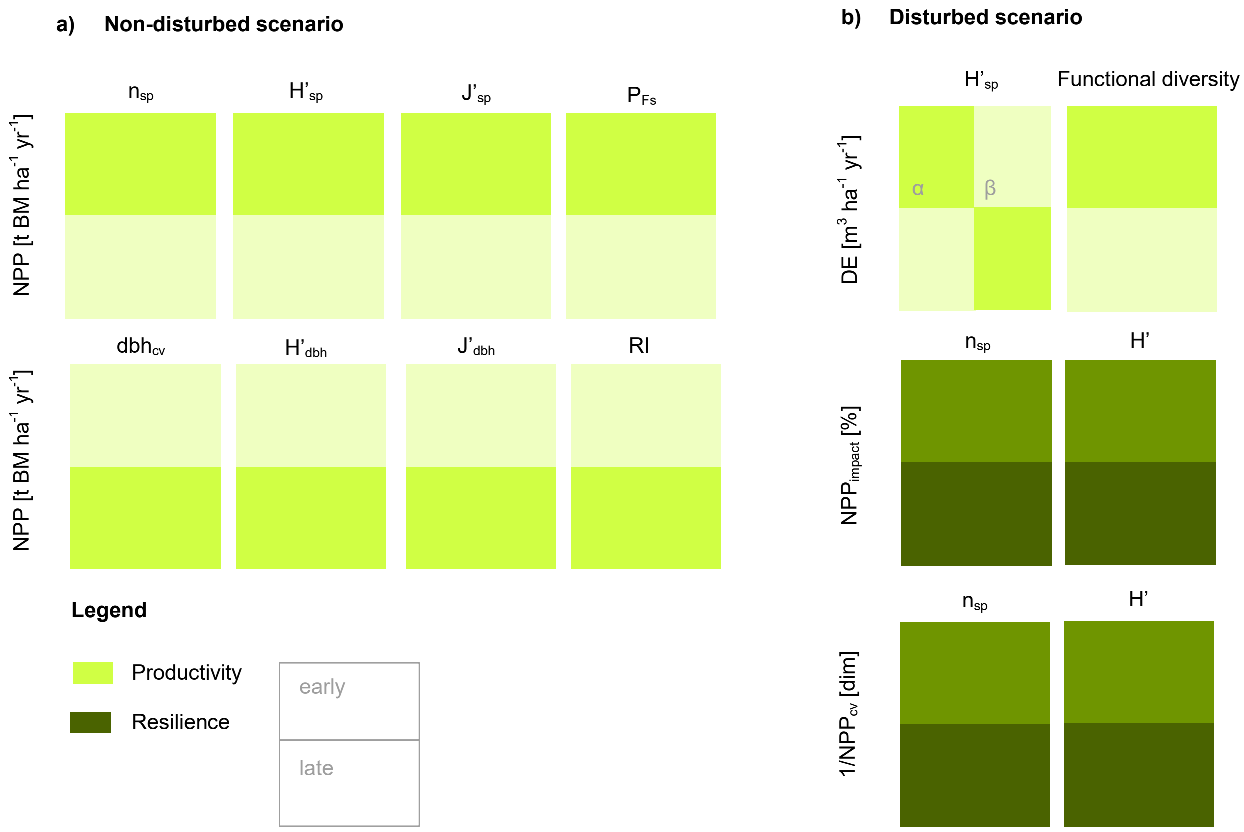

Figure 3 – Qualitative summary of the main results. Results show the changing influence of different diversity dimensions as predictors on indicators of productivity (light green) and resilience (dark green) as response variables over succession. Panel a) shows the results associated to the non-disturbed scenario whereas panel b) shows the results obtained under disturbances. A detailed description of each variable is given in Table 2 (see also Appendix 10 for details). The top part of each box relates to the early stages of forest development, while the bottom part relates to the late seral stage. The relative influence strength between early and late seral stages is indicated via the level of shading, i.e., lighter and darker colors indicate weaker and stronger relationships, respectively. Note that all influences here shown are positive and that a comparison of influence strength between the analyzed indicators of diversity or spatial scales is not shown. H'_{sp} effect on DE is analyzed at two spatial scales: within stands (left side; α diversity) and between stands (right side; β diversity).

6 Discussion

The present thesis aimed at investigating the long-term relationship between tree diversity and forest productivity in temperate forest ecosystems using a simulation approach. Overall, results show that tree diversity can significantly enhance forest productivity. Other studies, using several approaches from analyses of forest inventories (Paquette and Messier, 2011) and stand-level experiments (Pretzsch et al., 2013) to simulations with forest dynamics models (Morin et al. 2011) have also found positive diversity effects on productivity in temperate forests. However, the DFP relationship and the underlying mechanisms differed considerably between (i) the disturbance scenarios, (ii) indicators of diversity considered, (iii) spatial scales and (iv) stages of forest development analyzed

For the undisturbed scenario, both compositional and structural dimensions of diversity positively affected stand forest productivity, yet their influence on forest productivity varied with the stage of forest development (H1). In early-seral stages, diversity effects on NPP were dominated by aspects of tree species composition, and displayed a strong positive selection effect for European beech. Beech is the most productive species within the set analyzed here, and is able to develop multi layered canopies (Valladares et al., 2002) that have high leaf area and are highly efficient in utilizing canopy space (Jacob et al., 2010; Seidel et al., 2013). In later stages of forest development, diversity effects on NPP were dominated by structural diversity, with productivity increasing with increased variation in tree diameter and canopy complexity. This is in line with recent studies reporting high importance of processes related to structural diversity for forest productivity, such as vertical stratification (i.e., resource partitioning in space and time through contrasting architecture; Hardiman et al. 2011; Morin et al. 2011) and canopy plasticity (i.e., adjustment of crown shapes in response to local environmental conditions; Pretzsch, 2014; Jucker et al. 2015).

A further objective of the present study was to investigate the influence of disturbances and spatial scale on the DFP relationship. Overall, disturbances increased tree species diversity at both within- and between-stand scales (H2). This observed positive disturbance effect on diversity, however, was contingent on the available species pool in the landscape as well as on disturbance type. In particular, a stronger disturbance-induced increase in diversity was found for species-rich landscapes and for high severity disturbances. For a relatively productive site as the one studied here, disturbances disrupt competitive exclusion (a process found to predominate undisturbed systems – see Appendix 10.1), freeing up resources and regeneration niches and increasing tree species diversity (Franklin et al., 2002; Shea et al., 2004). The disturbance induced-variation of species diversity at both α and β spatial scales, in turn, facilitated landscape productivity (H2). Interestingly, between-stand diversity was found to have a larger effect on landscape productivity than within-stand diversity. Other studies indicated a decreasing positive influence of diversity on productivity with increasing scale (e.g., Chisholm et al., 2013). However, these analyses did not include the effect of disturbances, and thus were likely to underestimate the role of β diversity. In contrast to undisturbed forest stands where a selection effect of beech was found to be a predominating process, in disturbed landscapes the observed positive diversity effect on productivity was found to be mainly a result of niche complementarity (driven by the coexistence of species with different life-history traits). In particular, mixed forests containing species that are able to quickly respond to disturbances, i.e., where pioneer-species co-occur with intermediate or old-growth species, showed the highest mean positive diversity effects.

Lastly, I found that diverse systems not only promote ecosystem functioning but are also able to reduce the negative disturbance impact on NPP and dampen the disturbance-induced variability in NPP (i.e., show a higher resilience) (H3). This finding supports the insurance hypothesis (Naeem and Li, 1997; Yachi and Loreau, 1999) and, in the light of the findings in study II, can be explained by the increased diversity in species with different life-history strategies (i.e., with higher response diversity). More diverse forests are better in utilizing the increased resource availability, facilitating productivity and counteracting the negative impacts of disturbances on NPP. Nevertheless, a decreasing benefit of species richness on disturbance impact and, to a lesser degree, on resilience was observed, specifically for late seral stages. This finding is in accordance with the saturation effect of species richness on forest productivity found in other studies (e.g., Morin et al., 2011), and suggests that species-poor landscapes benefit more strongly from an increase in diversity levels than landscapes which are already rich in species. Furthermore, the dampening effects of diversity on disturbance impacts increased with increasing disturbance severity and frequency (here represented by a reduced disturbance rotation period), being most pronounced in the complete disturbance scenario and for a DRP of 150 year, respectively.

7 Conclusion

One of the greatest challenges in forest management today is to sustain the provisioning of ecosystem services and functions, while simultaneously maintain biodiversity in an uncertain world. In European forests, where a century-long management practice has favored a small number of tree species (Spiecker et al., 2004) and where disturbances are predicted to increase in the future as a result of climate change (Seidl et al., 2014a), finding a timely solution to this challenge is particularly important.

From a methodological point of view, this study underlined that simulation modelling is a powerful tool for exploring the different effects of tree species diversity on forest productivity, highlighting its value as a complementary approach to empirical studies. The applied simulation experiment successfully allowed, for instance, to consider extended spatio-temporal scales and explore "what if" questions (particularly, regarding the role of tree diversity under intensified disturbances), which are relevant in the context of decision making. Nevertheless, it has to be noted that many important aspects which occur in natural ecosystems such as mutualism among coexisting species (e.g., species facilitation through nutrient transfers), crown plasticity processes, or the differential disturbance sensitivity of species were not considered in this study. Consequently, the species diversity effect on productivity reported here is likely a conservative estimate.

The findings of my study strongly support the overarching hypothesis that tree diversity promotes forest productivity. In particular, fostering both structural and compositional diversity could be important means to increase the robustness of temperate forest functioning. This is an important insight for ecosystem management particularly in areas like Central Europe where a large proportion of the forest area is currently relatively simple in structure and composition (Spiecker et al., 2004), and where further challenges of species loss may lie ahead. A reduction in productivity associated with the loss of a canopy tree species (e.g., due to the invasion of an alien pest species) can, for example, to some degree be compensated through increased structural diversity.

I further conclude that it is important to consider disturbances in future DFP studies (which until today have been rarely addressed in this context) in order to address the significance of tree diversity in a fluctuating and uncertain future. According to my findings, intensifying disturbance regimes under climate change have negative impacts on forest ecosystems and their productivity, but will strongly foster tree diversity. This increased diversity, however, facilitates productivity and prevents even greater disturbance-related losses, and increases ecosystem resilience. An important applied aspect of my work is that forest managers could incorporate the diversity created by disturbances into stand development by retaining early seral species while keeping intermediate or old-growth species in order to mitigate disturbance-related productivity losses. Here it is important to note that modifying diversity in species and structures via management will not only benefit ecosystem resilience and productivity but will also affect other ecosystem attributes such as the habitat quality or the aesthetics and recreational value of forests. Nevertheless, in the context of forest management, where management objectives are diverse, the trade-offs between increased diversity and the sustainable provisioning of ecosystem services should be thoroughly evaluated.

8 Acknowledgments

The last four years that culminated in this dissertation were fulfilled with challenges, lonely over-hours work, ups and downs and doubts whether these lines would ever be written. Luckily, I have found the right people on my way which have motivated me and offered me support along this path.

I thank most my supervisor Assoc. Prof. Dr. Rupert Seidl for his support, expert guidance, and encouragement throughout these years. He revealed to have not only a high intellectual quotient but also a high emotional one. With his constant motivation, he helped me to overcome many of my "Imposter Syndrome" moments and to progress my research. He played an important role from my first steps in a new country and institute to the person I am now, and for that, I will be always grateful.

I further would like to express my deepest gratitude to Dr. Werner Rammer, without his technical support this PhD would have certainly taken much more years! He is not only a great professional but also a very cool, relaxed and empathic person with whom you can talk and learn about a variety of topics.

I am grateful to Dominik Thom for his friendship, insights into my work and honest personality. He is a great listener and I take with me our many interesting talks at lunch breaks and Friday's evenings.

Thanks also to Prof. Dr. Manfred Lexer and former colleagues Michael Maroschek and Stefan Schörghuber for their support and introduction to modelling and forestry/ecology topics. Their initial help was crucial for the subsequent steps in my PhD.

I am very grateful to many friends and colleagues at BOKU which I had the honor to have met; we have shared many parties and happy moments which I will miss (or better, feel "Saudade"). These are Susana Pérez, Christopher Thurner, Adam Moreno, Mathias Neumann, Dominik Thom, Florian Irauschek, Dave Chakraborty and Gabriele Wolfslehner.

And last but not least, I thank my parents who put all their efforts to offer me the opportunity to study at the University and taught me to be persistent in the hardest times.

To my boyfriend Florian for his never-ending love and patient along this path.

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10 Appendix

10.1 Study I: Silva Pedro, M., Rammer, W., Seidl, R. Disentangling the effects of compositional and structural diversity on forest productivity. J. Veg. Sci. in revision

Disentangling the effects of compositional and structural diversity on forest productivity

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Abstract

Questions: Tree species diversity is widely reported to positively influence forest productivity. Yet, a consistent attribution of productivity effects is complicated by the fact that compositional and structural diversity are often related in forest ecosystems. Here, our objective was to disentangle the effects of diversity in species and structures on forest productivity. We furthermore assessed whether the influence of structure and composition on productivity changes over the course of forest development.

Location: Hainich National Park, a temperate forest landscape in central Germany

Methods: We conducted a factorial simulation experiment in which 63 unique combinations of six different tree species were studied over 500 years of forest development. The model used was iLand, a process-based simulator operating at individual-tree resolution. The indicators of compositional diversity considered included species richness, entropy, evenness and identity, while structural diversity was characterized by indicators describing vertical and horizontal stand structure. Net primary production (NPP) was studied as response variable, and random forest analysis was used to synthesize simulation output.

Results: We found positive effects of both compositional and structural diversity on productivity, but their influence changed distinctly over the course of forest development. In early-seral stages, diversity effects on NPP were dominated by aspects of tree species composition, and displayed a strong positive selection effect for European beech (*Fagus sylvatica* L.). In later stages of forest development, diversity effects on NPP were dominated by structural diversity, with productivity increasing with increased variation in tree diameter and canopy complexity.

Conclusion: To better understand the effects of diversity on ecosystem functioning, both the compositional and structural dimensions of diversity in forest ecosystems (and their changes over time) need to be considered. In the context of ecosystem management our results suggest that the reduction in productivity associated with the loss of a canopy tree species (e.g., due to the invasion of an alien pest species) can to some degree be compensated through increased structural diversity. Fostering both compositional and structural diversity are important means to increase the robustness of forest ecosystem functioning.

Key words: Tree species diversity; Structural diversity; Forest productivity; Forest successional development; iLand model, Net primary production; Ecosystem functioning

1. Introduction

Forests are among the richest biological systems on earth, providing habitat for the large majority of the world's known terrestrial species (Shvidenko et al. 2005; Aerts & Honnay 2011). However, forest biodiversity has been subject to increasing pressures from changes in both anthropogenic (e.g., habitat fragmentation, soil degradation, introduction of non-native species) (Brockerhoff et al. 2008) and natural (e.g., more frequent and severe disturbances) (Seidl et al. 2014) processes. The ongoing loss of biodiversity has prompted concerns about the ability of forests to sustainably deliver goods and services (e.g., carbon (C) and nutrient cycling , provisioning of clean water and timber, climate regulation) to society (Klenner et al. 2009; Thom & Seidl 2016), and has stimulated research to better understand the relationships between biodiversity and ecosystem functioning (see Zhang et al. 2012; Scherer-Lorenzen 2014 for reviews).

With regard to forest productivity, the most commonly analyzed ecosystem function, an increase in tree diversity is frequently reported to be associated with an increase in biomass production (Scherer-Lorenzen 2014). The reported higher growth performance of species-rich forests compared to monocultures can be explained by three hypotheses: niche complementarity (i.e., more diverse ecosystems are better able to exploit limited resources due to different and complementary traits of species) (Tilman 1994; Morin et al. 2011), a selection effect (i.e., resulting from an increased likelihood of including a highly productive species as the species pool increases) (Tilman et al. 1997; Tobner et al. 2016), and ecological insurance (i.e., species-rich ecosystems are more likely to contain species that are better able to cope with and recover from perturbations) (Morin et al. 2014; Naeem & Li 1997;Silva Pedro et al. 2015). However, also negative or non-significant relationships between biodiversity and forest productivity have been reported (e.g., Nguyen et al. 2012; Potter & Woodall 2014), with differences in soil fertility and climate (Pretzsch et al. 2013) but also in successional stages and spatiotemporal scales (Lasky et al. 2014) contributing to the wide variation in biodiversity-productivity relationships.

In addition to the diversity in tree species, structural diversity – characterized as the heterogeneity in vertical and horizontal structures (Pach & Podlaski 2014) – is another important dimension of diversity in forest ecosystems (Moser & Hansen 2006). Also structural diversity has been reported to promote forest productivity (e.g., Hardiman et al. 2011; Fahey et al. 2015).

For example, late successional forests feature complex three-dimensional structures, and their high level of structural diversity has been suggested to enhance the carbon (C) uptake in such systems (Hardiman et al. 2011). These forests are characterized by the simultaneous presence of trees of variable sizes and developmental stages (i.e., from saplings to mature trees and from understory and sub-canopy trees to individuals that dominate the upper canopy), which allows the stand to utilize resources such as light more efficiently, thus enhancing productivity and C uptake. Insights on the benefits of structural diversity are increasingly applied in forest management, with strategies managing for uneven-aged forests and continuous forest cover (i.e., maintaining high structural diversity through selectively cutting individual trees or small groups of trees) (Laiho et al. 2011; Brang et al. 2014). Due to their optimization of vertical growing space, uneven-aged forests are also associated with higher levels of productivity compared to even-aged forests (Kuuluvainen et al. 2012).

However, as a high diversity in species is frequently also linked to high structural diversity and vice versa (Neumann & Starlinger 2001; Ishii et al. 2004), the mechanisms underlying the effects of diversity on productivity remain uncertain. Are species-rich systems found to be more productive because they are also more structurally diverse, or is increased productivity a true effect of compositional diversity? Likewise, are structurally diverse forests found to be more productive because they are frequently also more species-rich than their structurally homogeneous counterparts? Answers to these questions are important for forest management, as forest structure and composition are the two main characteristics of forest ecosystems that can be influenced by management. This is particularly important in Central Europe, where a large proportion of the forest area is currently relatively simple in structure and composition, as a result of a century-long management practice favoring a small number of selected species managed in an even-aged silvicultural regime (Spiecker et al. 2004; Ayanz et al. 2015). With the aim to foster and stabilize forest productivity managers could, for instance, either aim to convert monocultures to mixed forests, or even-aged forests to uneven-aged forests (Seidl et al. 2007; Kuuluvainen et al. 2012).

Most previous studies have focused on either compositional or structural diversity, and are thus not well suited to disentangling the effects of compositional and structural diversity on forest productivity. One reason for such a reductionist approach is that empirical observations along systematic gradients of structural and compositional diversity are rarely found in forest ecosystems. However, simulation modeling can be used as a diagnostic tool to address this question, as it allows the analysis of a wide range of combinations of species, realistically simulate emerging structures, and track their interactions of forest development, while simultaneously controlling for confounding factors such as the variation in site conditions or disturbance history.

Here, our objective was to disentangle the contributions of compositional and structural diversity on the productivity of a temperate forest ecosystem in Central Europe using simulation modelling. Specifically, we aimed to answer three main questions: (1) How are structural and compositional diversity associated with each other, and how are they related to forest productivity, (2) how much of the overall diversity effect on productivity can be attributed to structural and compositional diversity, respectively, and (3) does the influence of structure and composition on productivity change with successional development? Based on previous studies we expected that both structural and compositional diversity are positively related to productivity (H1), but also that diversity in species and structures are positively correlated (H2). We furthermore hypothesized that positive effects of compositional and structural diversity on productivity persist over the course of forest development, while their relative importance changes with succession (H3).Previous research suggests that we could expect an important influence of compositional diversity in early-seral forests where competitive exclusion is still moderate and canopy structure still relatively simple (Silva Pedro et al. 2016). In later stages of stand development, on the other hand, the role of structural diversity is expected to increase due to increasing three-dimensional complexity in the canopy, which facilitates complementary resource use (Hardiman et al. 2011).

2. Methods

2.1.iLand

We used the “individual-based forest Landscape and disturbance model iLand (Seidl, Rammer, et al. 2012) to disentangle the effects of compositional diversity and structural diversity on forest productivity. iLand is a spatially explicit process-based model which simulates the interactions between environmental drivers (nutrient, water availability and climate regime), vegetation processes (i.e., regeneration, growth and mortality), and disturbance regimes (e.g., windstorms, wildfires). Net primary production (NPP) is derived at stand level (i.e., regular cells of 100 × 100 m horizontal resolution in this study) based on a light-use efficiency approach (Landsberg & Waring 1997), in which scalar modifiers are used to account for the effects of environmental limitations on utilizable radiation at daily time steps. Tree mortality is calculated from a species' maximum longevity as well as from an individual's carbon balance (reflecting its competitive status and level of environmental stress). Tree regeneration is spatially explicit and depends on the availability and distribution of seeds as well as favorable light and climatic conditions (Seidl, Spies, et al. 2012). A more detailed description of the model is provided in Appendix S1, as well as online at http://iLand.boku.ac.at, where also the model code and executable are available for download under an open source license.

2.2.Study site and simulations

Hainich National Park (henceforward referred to as Hainich) is located at N51.1°, E10.5° in the western part of Thuringia, Germany. It is dominated by old-growth and uneven-aged beech (*Fagus sylvatica* L.) forest types (Galio odorati (Asperulo)-Fagion) as well as oak-hornbeam forest types (Carpinion betuli) (Bohn et al. 2004). iLand was found to successfully reproduce expected values of dendrometry and growth at Hainich, and simulated realistic species composition and trajectories of succession (Silva Pedro et al. 2015). More details on site-specific model evaluation can be found in Appendix S2. In order to isolate the effects of compositional and structural diversity in our analysis we controlled for confounding factors such as topography and soil fertility, and set up a 2500 ha simulation landscape of homogeneous site conditions. Based on data from inventory plots implemented in the area (Baeten et al. 2013) we selected moderately fertile site conditions for our analyses. Soil conditions were characterized by an effective soil depth of 100 cm and a clay-loamy soil texture (representing a water holding capacity of 180 mm), as well as 70 kg ha^{-1} yr^{-1} of plant-available nitrogen (Baeten et al. 2013). The climate regime - extracted from a gridded European database at 25 km horizontal resolution (Déqué et al., 2011) and representing the period 1961-1990 - was characterized by a mean annual precipiation sum of 627 mm and a mean annual temperature of 7.5°C.

We selected six major species from all seral stages of natural forest development at Hainich (Bohn et al. 2004) for our analysis, i.e., two early-seral species (*Betula pendula* Roth and *Populus tremula* L.), and four mid- to late seral species (*Acer pseudoplatanus* L., *Fraxinus excelsior* L., *Fagus sylvatica* L., and *Quercus petraea* (Mattuschka) Liebl). The selected tree species were combined to create a species diversity gradient with mixtures of up to six species (n=1 to 6), resulting in a total of 63 unique combinations of species. Each species combination formed the species pool for a separate landscape-scale simulation with iLand. As we were particularly interested to study the roles of compositional and structural diversity over long-term forest development, simulations were started from bare ground (i.e., a common starting point of succession) and were run over 500 years, with species being introduced with a low annual probability of seed availability on each 2 x 2 m cell (P_{seed}=0.01). Both natural and anthropogenic disturbances were omitted in the simulations.

3. Study design

3.1. Indicators

We randomly selected 250 stands (i.e., cells with 100 m × 100 m horizontal resolution) from the simulated continuous forest landscapes in order to minimize effects of spatial autocorrelation between stands, and to not influence statistical analyses by overly large sample sizes (cf. White et al. 2014). Total net primary production (NPP, t BM ha^{-1} yr^{-1}) was used as the response variable for the analysis, calculated at 100 year intervals in each stand. Compositional diversity was quantified for each stand using indicators of species richness, entropy, evenness, and identity. We estimated species richness as the number of tree species with at least one individual >4 m in height (n_{sp}). We additionally included species entropy and evenness in the set of compositional diversity indicators studied. Species entropy was derived as the exponential of the Shannon index (H'_{sp}; Shannon & Weaver 1949; Jost 2007), representing the realized tree species richness in a stand if species shares are equal (Jost 2007). H'_{sp} was calculated using the proportion of basal area of each species at stand level. Species evenness (J'_{sp}) was derived from the ratio between the Shannon index and its corresponding maximum attainable value (i.e. the natural logarithm of n_{sp}) (Pielou 1975). Values of J'_{sp} range from zero to one, with values close to zero representing a stand where the relative abundance of the different species is highly unevenly distributed. Since previous research revealed the presence of beech to be an important factor determining productivity at Hainich (Seidel et al. 2013), we additionally included the presence of beech via its basal area proportion in the stand (P_{Fs}) among the set of indicators used to characterize compositional diversity.

Structural diversity was quantified based on horizontal (e.g., Staudhammer and LeMay 2001) and vertical (e.g., Seidl et al. 2012b) attributes of a stand. To quantify structural diversity along the horizontal plane (i.e., in x-y dimensions), the coefficient of variation of the dbh (dbh_{cv}) as well as the entropy and evenness of the tree diameter distribution (H'_{dbh} and J'_{dbh}, respectively) within a stand were calculated. For the latter we also applied the exponent of the Shannon index to the proportion of tree basal area distributed over 10 cm dbh classes (H'_{dbh}) (Staudhammer & LeMay 2001; Jost 2007). H'_{dbh} thus represents the equivalent number of dbh classes with evenly distributed trees. J'_{dbh} was determined by dividing the Shannon index of dbh classes by its potential maximum value. Structural diversity along the vertical axis (i.e., the z dimension) was quantified using the rumple index (RI) (Parker et al. 2004; Seidl et al. 2012b). RI is defined as the ratio between the canopy surface area and the projected ground area at each stand (i.e., 100 × 100 m cells) (Parker et al. 2004; Seidl et al. 2012b). Canopy surface area was calculated based on canopy top heights at 10 m horizontal resolution following the method of Jenness (2004), and RI was derived by dividing the canopy surface area by the ground area for each 100 × 100 m stand. A RI of 1 (= minimum value) indicates that the canopy surface area is equal to the projected ground surface area, and higher values of RI correspond to greater vertical structural diversity within a stand.

3.2.Analyses

As a first step of our analysis, we individually investigated the links between compositional and structural diversity and NPP (H1), using non-parametric Spearman correlation analysis. Subsequently, we tested for interdependencies between the two dimensions of diversity (H2) also using correlation analysis. Finally, we used Random Forest analysis (RFA) (Breiman 2001; Liaw and Wiener 2002) to disentangle the confounding effects of compositional diversity and structural diversity on NPP. RFA is a well suited method to address the complex interacting predictors of the current analysis since (1) it is a nonparametric method suited for the analysis of high-dimensional and hierarchical ecological data (e.g., Silva Pedro et al. 2015; Zald et al. 2016), (2) is robust to non-linear relationships among predictor variables and between predictor and response variables (Sandri & Zuccolotto 2006; Cutler et al. 2007) and (3) has been shown to be less sensitive to collinearity among predictors than regression approaches (Dormann et al. 2013).

We fitted Random Forests by growing 1000 trees and used the increase in mean square error (MSE) as a measure of variable importance. This importance indicator quantifies the increase in MSE when observed values of the respective predictor are randomly permuted while all others are left constant, with higher MSE indicating more important variables. A ranking of predictors in terms of their importance was used to determine relevant factors influencing the response variable NPP. Since we were interested in whether the relative influence of compositional diversity and structural diversity changes with forest development (H3), all analysis were conducted separately for all 100 year periods of the 500-year simulation. We furthermore used RFA to analyze the expected changes in NPP over a range of combinations of compositional and structural diversity indicators. This analysis was conducted to highlight interactions between these two dimensions of diversity (and their changes over time), but also to better illustrate the effect of structural and compositional diversity on NPP for management decision makers. Statistical analyses were conducted using the R language and environment for statistical computing (R Core Team 2013).

4. Results

4.1 Correlative relationships between compositional diversity, structural diversity, and NPP

Forest productivity was weakly but significantly correlated with the species richness in a stand across all stages of successional development (r = 0.05 to 0.23; see Table 1). Overall, NPP was positively related to n_{sp}, however it stabilized in stands containing more than 3 species in early stages of forest development (Fig. 1). Conversely, a moderate negative relationship was found between NPP and the entropy and evenness of tree species, particularly in later stages of forest development (Table 1). However, the share of European beech was strongly positively related to NPP.

All analyzed attributes of structural diversity showed moderate to high positive correlations with NPP (Table 1). Furthermore, the overall positive effect of stand structure on NPP was more pronounced in old-growth systems than in early stages of forest development. Over the 500 year study period, the variation in tree diameters (dbh_{cv}) had the strongest relationship with NPP (average r of 0.65), followed by RI, H'_{dbh} and J'_{dbh} (Table 1). Similar to n_{sp}, a saturating relationship was also found between dbh_{cv} and NPP, with only small NPP gains for coefficients of variation in dbh greater than one (Fig. 1). However, correlation analyses also indicated strong associations between individual attributes of diversity (see Appendix S3). Consequently, multicollinearity is strongly limiting the interpretation of relationships between individual dimensions of stand diversity and productivity.

4.2 Disentangling the effects of compositional and structural diversity on NPP

To further elucidate the relative importance of diversity in species and structures while addressing the complex interrelationships between predictors we used RFA. Overall, RFA with indicators of compositional and structural diversity as predictors was very well able to explain the simulated variation in NPP (average explanatory power of 98.2% over the 500 year study period). The RFA-derived variable importance measure revealed that the most influential drivers of NPP varied strongly with forest development. While compositional diversity was most influential on NPP in early stages of forest development, structural diversity was the most important driver of productivity in later stages of succession (Fig. 2). In earlier seral stages, P_{Fs} was identified as the most influential factor on forest productivity. In later seral stages, however, the influence of P_{Fs} sharply decreased, while indicators of structural diversity – specifically dbh_{cv} and RI – had the strongest influence on NPP.

To further illustrate the interacting effects of structural and compositional diversity we used RFA to predict NPP response surfaces over the studied ranges of $n_{sp,}$ and dbh_{cv}, while keeping all other indicators constant. This analysis indicated an overall higher NPP benefit of structural diversity compared to compositional diversity. On average, across all species richness levels, an increase in dbh_{cv} from 0.6 to 1.4 increased NPP by +15.2% and +27.9% for early and late seral stages, respectively (Fig. 3). Furthermore, a compensation effect between compositional and structural diversity was evident from this analysis: while in monospecific early seral stands an increase in the coefficient of variation of tree dbh from 0.6 to 1.4 resulted in a NPP increase of +25.5, the effect was negligible (-0.02%) in compositionally diverse stands (n_{sp}=6). Also, increasing compositional diversity had contrasting results in different stages of forest development. In early seral systems, a distinct positive effect of species richness on NPP was evident, albeit lower than the effect of structural diversity (NPP increase of between +0.4% and +12.3% for an increase in n_{sp} from 1 to 6). In later stages of forest development (i.e., year 500), on the other hand, the positive effect of species richness on NPP diminished or was even slightly negative (Fig. 3). The general responses of NPP to compositional and structural diversity over time remained consistent also when other indicators of compositional diversity were used (see Appendix S4).

5. Discussion

We here investigated the long-term interactions between compositional diversity, structural diversity, and forest productivity using a simulation approach. Our findings of strong interactions and a shifting influence of drivers over forest development underline that an integrated approach towards the different dimensions of ecological diversity is important when aiming to understand how biodiversity influences ecosystem functioning. We generally found a positive effect of structural diversity on productivity, while the effects of compositional diversity were weaker and varied with indicator and developmental stage (H1). For the system studied here our results suggest that the positive effect of structural diversity is greater than that of compositional diversity. This is in line with other recent findings, suggesting a high importance of vertical stratification (i.e., resource partitioning in space and time through contrasting architecture; Hardiman et al. 2011; Morin et al. 2011) and canopy plasticity (i.e., adjustment of crown shapes in response to local environmental conditions; Pretzsch 2014; Jucker et al. 2015) for forest ecosystem functioning.

With regard to the effects of compositional diversity it is interesting to note that entropy and evenness were negatively correlated to NPP when analyzed individually (Table 1). An in depth analysis of the underlying processes showed that competitive exclusion was increasingly dominant as forest development progressed (Appendix S5), and that there was a strong positive relationship between the relative abundance of beech (i.e., the most productive and dominant species of natural forest dynamics at Hainich) and NPP (r = 0.64 to 0.85; Table 1). Consequently, when interpreted at the level of individual relationships, the negative correlations of entropy and evenness with NPP are in fact the result of their negative relationship with beech abundance, which in turn is positively associated with productivity (H2). When the multicollinearity between compositional variables was accounted for, however, the effects of evenness and entropy on NPP were overall moderately positive (Appendix S4). This underlines that simple correlative relationships between biodiversity indicators and productivity (e.g.,Nguyen et al. 2012) are prone to errors in the attribution of diversity effects due to multicollinearity.

We found a positive effect of tree species richness on NPP, yet the effects of compositional diversity were weaker overall compared to structural diversity. Here it is important to put our findings in the context of the site conditions and species mixtures investigated, i.e., a set of broadleaved species growing on productive site. Other studies have suggested that mixed forests comprised of both conifer and broadleaved tree species might result in higher productivity gains than mixtures consisting solely of broadleaves (Aiba et al. 2007; Ishii & Asano 2010). Furthermore, while on poor sites positive effects of compositional diversity are pronounced (Pretzsch et al. 2013), they may be lower or even reverse at productive sites due to a more prominent role of competitive exclusion (Paquette & Messier 2011).

Natural disturbances, which are predicted to intensify in the future (Seidl et al. 2014), are also modifying the diversity effect on productivity, but were not considered here. Disturbances disrupt competition exclusion and increase compositional diversity, which can in turn facilitate forest productivity (Silva Pedro et al. 2016). Other aspects not considered in our simulations and thus contributing to a potential underestimation of the compositional diversity effect on NPP are mutualism among coexisting species (e.g., species facilitation through nutrient transfers) and crown plasticity processes, which may further enhance productivity in mixed stands compared to mono-specific stands (Pretzsch & Schütze 2009; Pretzsch et al. 2013; Pretzsch 2014). In addition, we here did not analyzed the relative importance of functional diversity (e.g., diversity in architectural and physiological traits), which is expected to play an important role in enhancing forest productivity (Morin et al. 2011).

Our results corroborated the hypothesis that the effects of compositional diversity and structural diversity on NPP differ with successional stage (H3). In early stages of forest development, we found that the share of beech was the most influential factor driving NPP, i.e., a species selection effect was prominent in these developmental stages in our simulations. Beech is the most shade tolerant species within the set studied here, and is able to develop multi layered canopies (Valladares et al. 2002) that have high leaf areas and are highly efficient in utilizing canopy space (Jacob et al. 2010; Seidel et al. 2013). Furthermore, beech is the most productive species in our area, and strongly dominates natural forest development in later stages of succession (Appendix S5). Consequently, our findings suggest that introducing late-seral dominants (such as beech) already early in forest development has a positive effect on forest productivity. In later stages of forest succession NPP was most strongly driven by attributes of vertical and horizontal stand structure, in particular the variability of diameter at breast height and the rumple index. This is in line with previous findings that late successional forests maintain significant rates of C uptake as a result of the spatial and temporal differentiation in their three-dimensional structure (Hardiman et al. 2011). In the context of management our study thus highlights a clear benefit of structurally diverse forests on productivity.

Our findings also suggest that a reduction in tree species richness (e.g., as a result of losing a tree species to an invasive alien pest species, or focusing on a reduced set of economically important species in management) can to some degree be compensated by increased structural diversity. Here it is important to note, however, that modifying diversity in species and structures via management will also affect other ecosystem attributes besides productivity, e.g. the habitat quality of a landscape or the aesthetics and recreational value of forests (Millennium Ecosystem Assessment 2005). In this regard recent efforts to understand the role of biodiversity in forest ecosystems have made great progress towards understanding the potential impacts of the currently ongoing decline in biological diversity (e.g., Jucker et al. 2014). Inspired by work done in structurally simpler systems such as grasslands, a large majority of these studies have, however, focused primarily on the short-term effects of compositional diversity (Scherer-Lorenzen 2014). Forest ecosystem modelling is an essential tool in the study of the complex interactions of forest dynamics; it enables to not only controlling for confounding factors such as the variation in site conditions but also to consider the spatial and temporal differentiation that occurs during forest development. Our study emphasizes the importance of considering not only compositional diversity but also the diversity in horizontal and vertical structures to obtain a deeper and more mechanistic understanding of biodiversity-productivity relationships in forest ecosystems. We conclude that structural diversity in forest stands is not only important for habitat quality (Spies et al. 2007) and in the context of forest disturbance (Mason & Valinger 2013), but also relevant for fostering forest productivity.

Acknowledgements

This study was conducted under the European Commission collaborative research project FunDivEUROPE (project no. 265171). R. Seidl acknowledges further support from a European Commission's Marie Curie Career Integration Grant (PCIG12-GA-2012-334104). The simulation results presented here have been derived using the Vienna Scientific Cluster (VSC). We thank two reviewers for helpful comments on an earlier version of the manuscript.

Table 1 – Spearman correlations between indicators of structural and compositional diversity with forest productivity (NPP, t BM ha^{-1} yr^{-1}) for different stages of forest development.

	Year				
Variables	**100**	**200**	**300**	**400**	**500**
Compositional diversity					
n_{sp}	0.23 (<0.0001)	0.07 (0.0322)	0.05 (<0.0001)	0.14 (<0.0001)	0.19 (<0.0001)
P_{Fs}	0.85 (<0.0001)	0.64 (<0.0001)	0.68 (<0.0001)	0.82 (<0.0001)	0.84 (<0.0001)
H'_{sp}	-0.03 (0.0001)	-0.27 (<0.0001)	-0.31 (<0.0001)	-0.41 (<0.0001)	-0.46 (<0.0001)
J'_{sp}	-0.21 (<0.0001)	-0.27 (<0.0001)	-0.30 (<0.0001)	-0.43 (<0.0001)	-0.49 (<0.0001)
Structural diversity					
RI	0.55 (<0.0001)	0.51 (<0.0001)	0.63 (<0.0001)	0.68 (<0.0001)	0.63 (<0.0001)
dbh_{cv}	0.64 (<0.0001)	0.61 (<0.0001)	0.61 (<0.0001)	0.69 (<0.0001)	0.72 (<0.0001)
H'_{dbh}	0.66 (<0.0001)	0.52 (<0.0001)	0.51 (<0.0001)	0.59 (<0.0001)	0.53 (<0.0001)
J'_{dbh}	0.02 (0.0125)	0.42 (<0.0001)	0.51 (<0.0001)	0.67 (<0.0001)	0.68 (<0.0001)

P-values (in parenthesis) were calculated using Holm's method (Holm 1979). Abbreviations: n_{sp} = realized tree species richness; H'_{sp} = exponent of tree species Shannon index; J'_{sp} = tree species evenness; P_{Fs} = relative abundance of Fagus sylvatica; RI= rumple index; dbh_{cv} = coefficient of variation of the diameter at breast height; H'_{dbh} = exponent of the Shannon index applied to dbh classes; J'_{dbh} = evenness of basal area over dbh classes.

Figures

Fig. 1

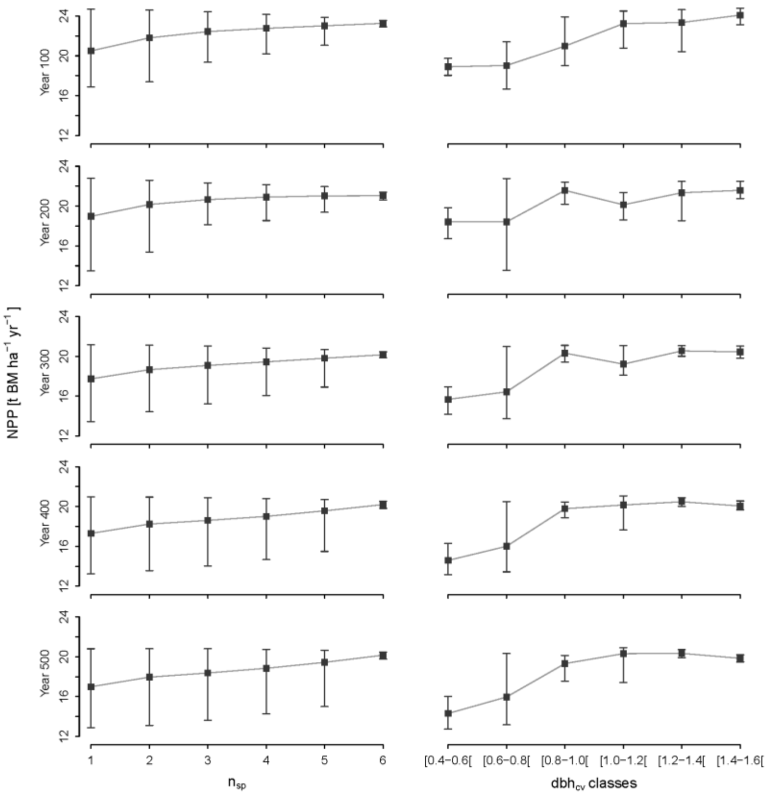

Fig. 1 – The effects of realized species richness (n_{sp}) and the coefficient of variation of diameters at breast height (dbh_{cv}) on stand productivity (NPP, t BM ha^{-1} yr^{-1}) displayed in 100 year time steps (panel rows). *Points* indicate the mean NPP of all stands per number of realized species and dbh_{cv} class, *whiskers* the 5th to 95th percentile interval of NPP values.

Fig. 2

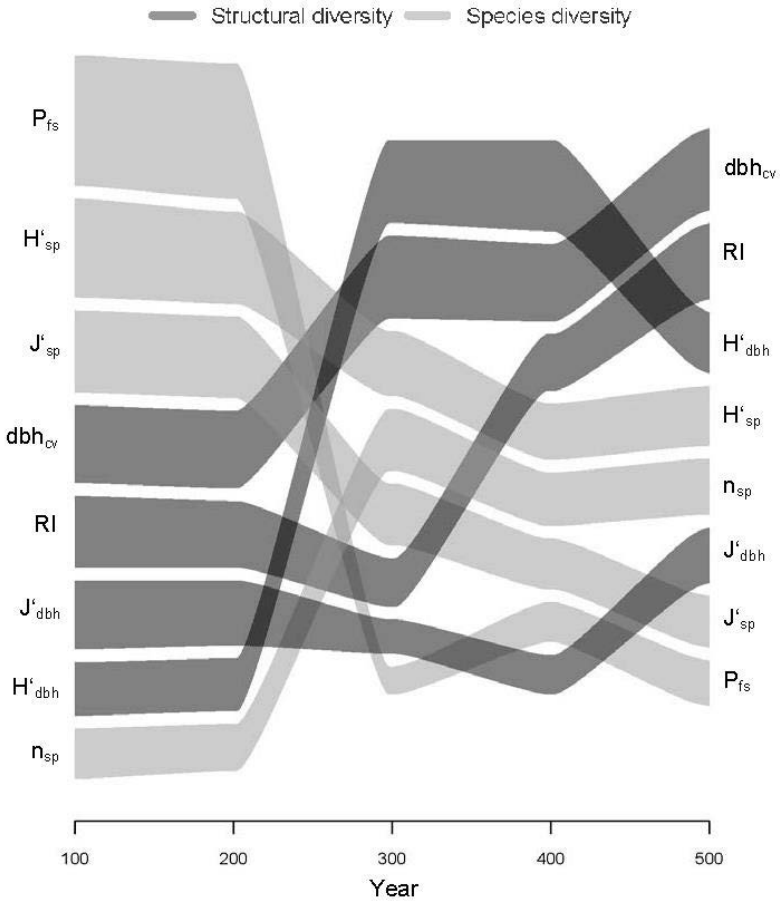

Fig. 2 – Relative importance of indicators of compositional diversity (*light grey*) and structural diversity (*dark grey*) on NPP in different stages of forest development. Variables are ranked for each time step in decreasing order of their relative importance on NPP, derived from the Random Forest analysis. Variable importance describes the percent increase in the mean square error (MSE) when values of the respective variable are randomly permuted, and is indicated in the width of the individual bands. See Table 1 for a description of the abbreviations used.

Fig. 3

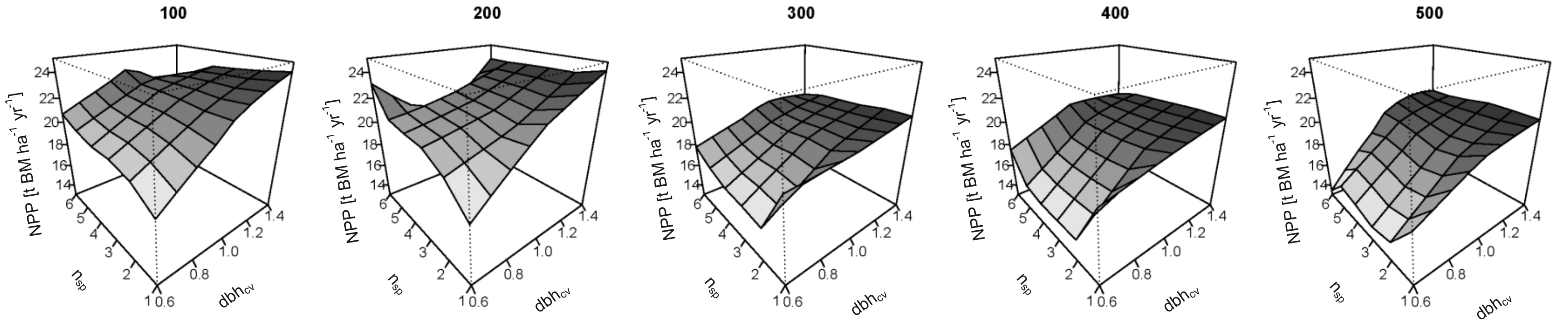

Fig. 3 – Response surface of NPP as a function of tree species richness (n_{sp}) and the coefficient of variation of diameters at breast height (dbh_{cv}) . The response surfaces were derived using random forest predictions over the range of n_{sp} and dbh_{cv} values, while keeping all other variables at their mean values.

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Supporting Information

Appendix S1. iLand process details.

Forest structure, composition, and succession are properties emergent dynamically in simulations with iLand. The emergent species composition reflects the relative competitive strengths of the respective species in the species pool (here experimentally permutated to the 63 species combinations of the 6 studied tree species). At the stand level, individual tree competition for resources (light, water, nutrients) is simulated based on ecological field theory (EFT) (at a horizontal resolution of 2 × 2 m), in which a tree's local competitive strength is characterized by a size- and species-specific kernel of competitive influence (Seidl et al. 2012). Following the EFT approach, the influence of each individual tree is defined by its influence domain and field intensity. Light influence patterns (LIPs) are derived for discreet tree states – defined by a tree's height, crown shape, and leaf area – by means of detailed ray-tracing (see Fig. S1 for examples). These LIPs are subsequently used in the dynamic simulations and combined to derive a spatially explicit estimate of competitive influence and resource availability across the simulated landscape. Resource use is subsequently determined by species traits such as light demand and responses to suboptimal environmental conditions, ultimately leading to differences in tree growth. A more detailed description of the processes simulated in iLand can be found in Seidl et al. (2012) and an online documentation of the model is available at http://iLand.boku.ac.at.

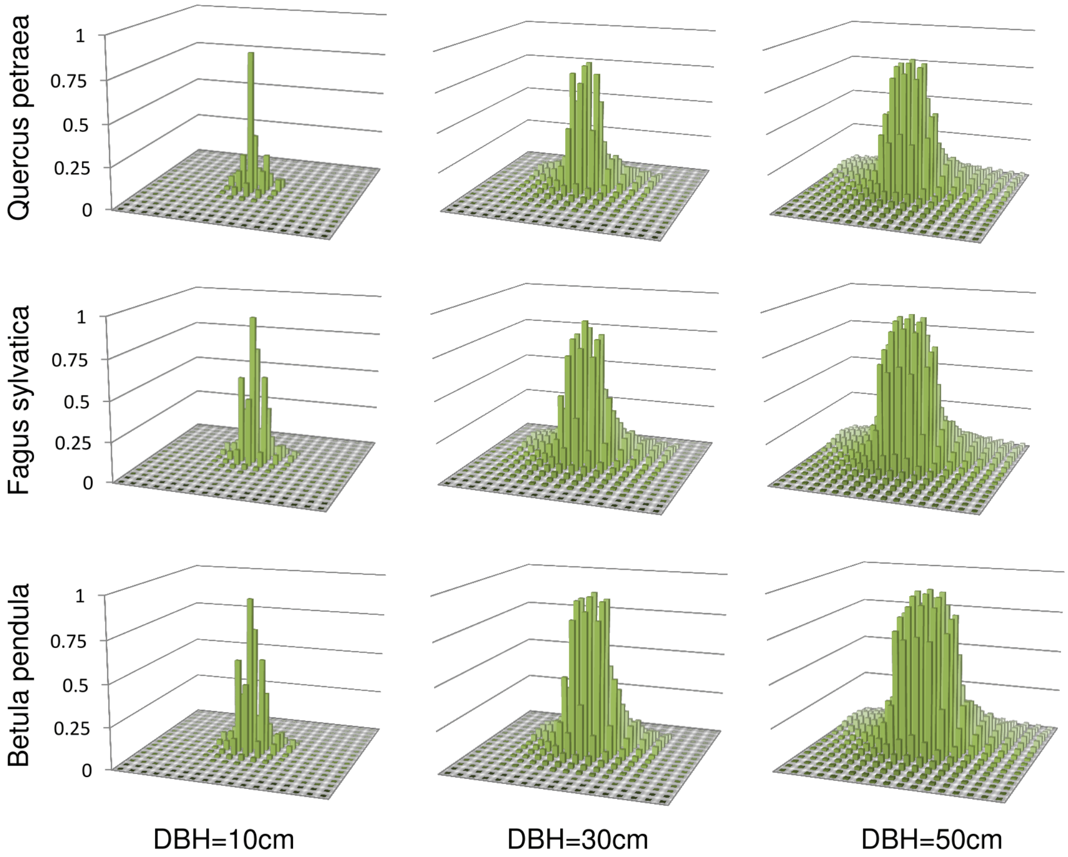

Fig. S1 - The light influence patterns (LIPs) of individual trees for three species (*Quercus petraea*, *Fagus sylvatica* and *Betula pedula*) and tree dimensions (dbh=10, 30 and 50 cm). The spatial resolution of each cell is 2 × 2 m. DBH: diameter at breast height (cm)

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Appendix S2. iLand evaluation.

iLand was evaluated in two exercises, aiming to test the model with regard to (1) tree dendrometry, growth and mortality, and (2) species composition and long-term successional trajectories at Hainich (see also Silva Pedro et al. 2015). In the first evaluation exercise, tree height, diameter growth, and productivity of four major mid- to late-seral species at Hainich were evaluated against yield table data. For this purpose, simulations in monospecific 100 ha simulation units were run over 100 years under a regime of random thinnings (i.e., a non-selective, no-size-specific removal of trees) at regular intervals, implemented to replicate the treatments and stand densities reported in yield tables (Wimmenauer 1919; Jüttner 1955; Marschall 1975). Subsequently, the target variables mean diameter at breast height (d_{mean}, cm), dominant height (h_{dom}, m) and mean annual increment (MAI, m^3 ha^{-1} $year^{-1}$) were compared to yield table data at age 100. Results show that the model is well able to reproduce the expected tree dimensions of the major tree species (Table S2). Furthermore, the relative differences between species were captured satisfactorily, which is important for faithfully reproducing the dynamics in mixed-species forests. Simulated productivity levels corresponded well with expectations, which is relevant in the context of the focal variable of interest for this study. In addition, we also assessed simulated tree mortality by testing stand density trajectories against the empirical self-thinning rule established by Reineke (1933) (data not shown - see Silva Pedro et al. 2015 for more details).

Table S2 - Comparison of simulated dominant height (h_{dom}), mean diameter (d_{mean}), and mean annual increment (MAI) at age 100 to yield table data for four major tree species. YT: yield table (Wimmenauer 1919; Jüttner 1955; Marschall 1975).

Tree species	h_{dom} [m]		d_{mean} [cm]		MAI [m^3 ha^{-1} $year^{-1}$]	
	YT	iLand	YT	iLand	YT	iLand
Acer pseudoplatanus L	22.2	21.6	23.8	23.9	5.3	4.9
Fagus sylvatica L.	27	24.9	29.2	26.1	6.0	6.3
Fraxinus excelsior L.	32.4	30.9	35.5	40.7	5.8	8.1
Quercus petraea (Mattuschka) Liebl.	24.5	24.7	32.1	34.2	5.4	6.3

In the second evaluation exercise we tested iLand's ability to reproduce observed species composition as well as long-term trajectories of forest dynamics at Hainich. Simulations were initialized from bare ground and a 2500 ha landscape simulated over 500 years. Analyses were conducted for 250 stands of 100 ×100 m, randomly selected from the simulated landscape. Six major species from all seral stages of natural forest development at Hainich (Bohn et al. 2004) were allowed in the simulation with a constant and uniformly distributed background probability of seed availability of P_{seed}=0.01. Sensitivity tests for P_{seed} indicated that results were robust to different levels of background probabilities of seed availability (data not shown).

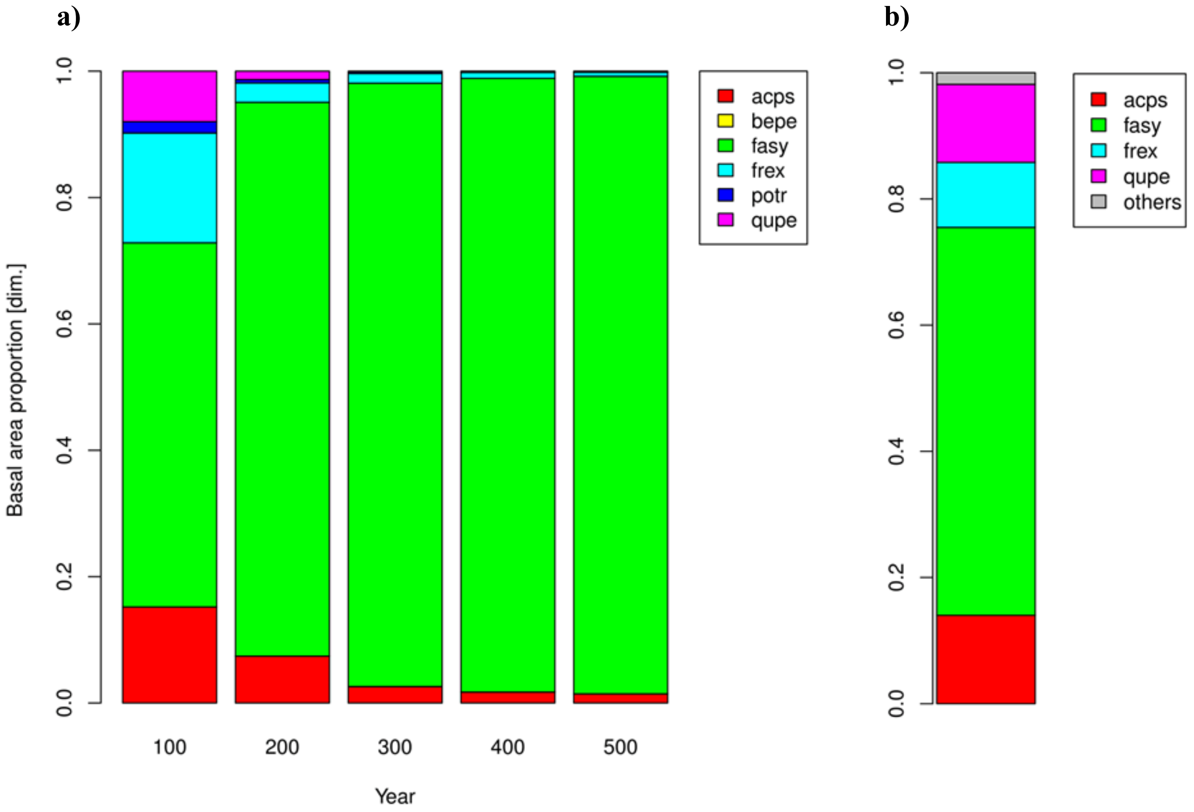

Fig. S2 - Comparison between (a) simulated species composition over 500 years for a fertilie site at Hainich and (b) observed species composition of an approximately 100-150 year old stand (exact tree ages were unvailable, (Baeten et al. 2013)) for a similar site. Shown is the sucessional development with a species pool containing the six species studied in this analysis. Abbreviations: acps – *Acer pseudoplatanus* L.; bepe: *Betula pendula* Roth. ; fasy – *Fagus sylvatica* L.; frex – *Fraxinus excelsior* L.; potr – *Populus tremula* L.; qupe – *Quercus petraea* (Mattuschka) Liebl. others: tree species not investigated here.

Results show a succession from a state characterized by the coexistence of early- (*Populus tremula*), mid- (*Acer pseudoplatanus* and *Fraxinus excelsior*) and late-seral species (*Fagus sylvatica*) to a state dominated mainly by beech (Figure S2a). The simulated early-stage species composition corresponds well to that observed at a similar site at Hainich (Fig. S2b). The simulated endpoint of succession – a strongly beech-dominated forest, is well in line with the potential natural vegetation composition expected for the area (Bohn et al. 2004). It has to be noted, however, that we here deliberately omitted spatial heterogeneity in soil and climate on the landscape, and that the simulated dominance of beech pertains specifically for the fertile site conditions and moderate climate conditions investigated here. Overall, these two evaluation experiments indicate that iLand is able to reproduce expected values of dendrometry and growth, as well as trajectories of long-term forest dynamics at Hainich National Park.

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Appendix S3. Indicators of diversity and their relationship.

Due to the omission of disturbances, stochasticity had only a minor effect on the simulations and allowed us to forego the analysis of multiple replicates per simulated landscape. Even in the most diverse simulations (with a species pool of n=6) the coefficient of variation between the sampled stands on the landscape remained moderate (Table S3-a).

Table S3-a – Mean and coefficient of variation (CV, %) of tree species entropy (H'_{sp}) and structural diversity (dbh_{cv}) over the sampled 250 stands in the forest landscape. Results are from forest stands containing all six study species in the species pool and are shown at 100 year intervals over the 500-year simulation period. Abbreviations: SD=Standard deviation; CV=Coefficient of variation.

	H'_{sp}		**dbh_{cv}**	
Year	Mean	CV[%]	Mean	CV[%]
100	3.26	5.57	1.08	3.35
200	1.64	7.59	1.44	2.75
300	1.25	4.60	1.33	3.70
400	1.17	3.59	1.29	3.77
500	1.14	2.88	1.26	3.76

As expected, both compositional and structural diversity varied over time (Tables S3-b and S3-c), and indicators were strongly correlated. We found positive correlations between indicators of structural and compositional diversity. Our results indicate that an increase in the realized number of tree species enhances structural diversity across the entire range of indicators investigated here (Fig. S3-a). The relative abundance of beech was even more strongly related to stand structure than tree species richness, with higher beech shares being associated with elevated horizontal and vertical structural diversity (Table S3-d). However, other components of compositional diversity, namely H'_{sp} and J'_{sp}, were found to be moderately negatively associated with structural diversity (average r= -0.22 and -0.26, respectively). H'_{sp} and J'_{sp} further differed in their relationship with species richness, and over the course of forest development. While in earlier stages a clear positive relationship between species richness and entropy was found, in later stages this relationship was less pronounced (Fig. S3-b). Species evenness was only weakly correlated with species richness over the course of forest development. However, particularly in the intermediate stages of forest development a moderate increase in evenness with an increase in richness was observed (Fig. S3-b).

Table S3-b – Variation in compositional and structural diversity over a gradient of tree species richness (n=1- 6) after 100 years of forest development. (mean ± standard deviation over all species combinations and the 250 stands sampled from the landscape). Abbreviations: H'_{sp} = exponent of tree species Shannon index; J'_{sp} = tree species evenness; P_{Fs} = relative abundance of beech; RI= rumple index; dbh_{cv} = coefficient of variation of the diameter at breast height; H'_{dbh} = exponent of the Shannon index applied to dbh classes; J'_{dbh} = evenness of basal area over dbh classes.

	Realized richness level (n)					
Indicators	1	2	3	4	5	6
Compositional diversity						
H'_{sp}	-	1.57±0.35	2.08±0.47	2.52±0.52	2.90±0.48	3.26±0.18
J'_{sp}	-	0.61±0.34	0.64±0.21	0.65±0.15	0.65±0.10	0.66±0.03
P_{Fs}	-	0.30±0.42	0.41±0.40	0.48±0.34	0.53±0.25	0.57±0.04
Structural diversity						
RI	1.04±0.03	1.05±0.04	1.06±0.03	1.07±0.03	1.07±0.03	1.08±0.02
dbh_{cv}	0.93±0.06	1.02±0.06	1.05±0.06	1.07±0.06	1.08±0.06	1.08±0.05
H'_{dbh}	5.19±1.56	5.78±0.95	5.89±0.62	5.84±0.48	5.74±0.39	5.63±0.35
J'_{dbh}	0.83±0.07	0.87±0.04	0.88±0.03	0.87±0.03	0.86±0.03	0.86±0.03

Table S3-c – Variation in compositional and structural diversity over a gradient of tree species richness (n=1- 6) after 500 years of forest development. (mean ± standard deviation over all species combinations and the 250 stands sampled from the landscape). Abbreviations: see Table S3-b.

	Realized richness level (n)					
Indicators	1	2	3	4	5	6
Compositional diversity						
H'_{sp}	-	1.27±0.34	1.37±0.42	1.39±0.49	1.30±0.44	1.14±0.03
J'_{sp}	-	0.30±0.35	0.25±0.26	0.20±0.23	0.13±0.17	0.07±0.02
P_{Fs}	-	0.34±0.47	0.50±0.50	0.66±0.47	0.82±0.37	0.57±0.04
Structural diversity						
RI	1.07±0.06	1.1±0.06	1.12±0.06	1.14±0.06	1.16±0.06	1.19±0.05
dbh_{cv}	0.72±0.31	0.87±0.2	0.97±0.14	1.04±0.11	1.14±0.08	1.26±0.04
H'_{dbh}	4.98±1.62	6.1±1.23	6.53±0.84	6.68±0.71	6.8±0.63	7.08±0.5
J'_{dbh}	0.81±0.07	0.86±0.05	0.87±0.05	0.88±0.04	0.89±0.04	0.91±0.02

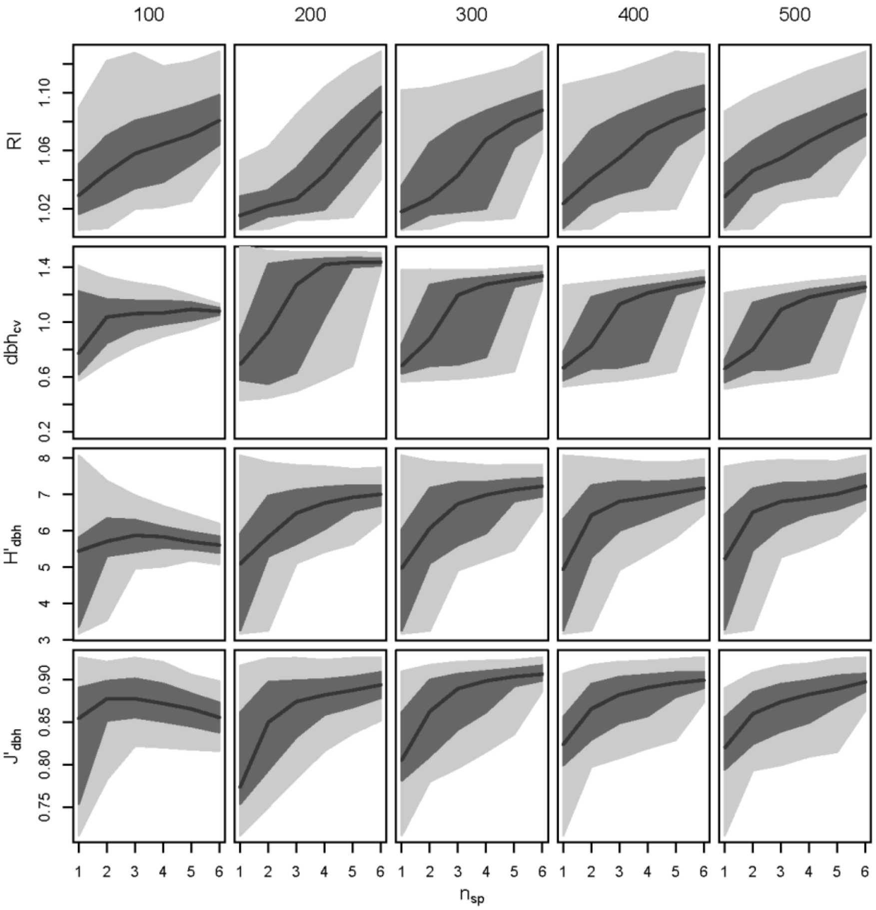

Fig. S3-a – The relationship between species richness and different indicators of structural complexity. Results are grouped in 100 year intervals over the 500-year simulation period (panel columns). See Table S3-b for description of variables and abbreviations. The solid lines indicate mean values, while filled areas denote the range between the 25th and 75th percentile (dark grey), and between the 5th and 95th percentile (light grey).

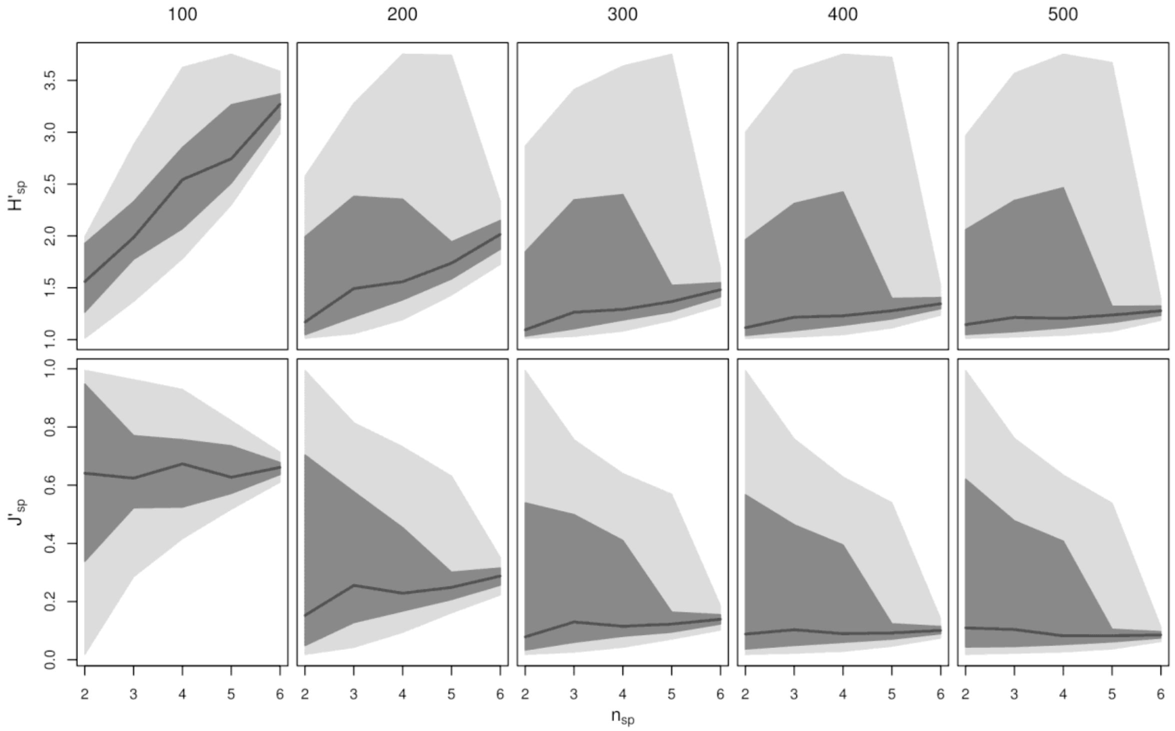

Fig. S3-b - The relationship of entropy and evenness to tree species richness. Results are shown over different richness levels (n = 2–6) and grouped in 100 year intervals over the 500-year simulation period (panel columns). Abbreviations: n_{sp} = realized tree species richness; H'_{sp} = exponent of tree species Shannon index; J'_{sp} = tree species evenness. Solid lines indicate mean values, while filled areas denote the range between the 25th and 75th percentile (dark grey), and between the 5th and 95th percentile (light grey).

Table S3-d - Spearman correlations between attributes of tree compositional diversity and structural complexity over 500 years of forest development.

	$\mathbf{n_{sp}}$	$\mathbf{H'_{sp}}$	$\mathbf{J'_{sp}}$	$\mathbf{P_{Fs}}$
RI	0.35	-0.29	-0.34	0.78
dbh_{cv}	0.35	-0.19	-0.23	0.79
H'_{dbh}	0.29	-0.25	-0.28	0.73
J'_{dbh}	0.31	-0.15	-0.17	0.64

All coefficients are significant at $P<0.001$. Levels of significance were obtained using Holm's method (Holm 1979) Abbreviations: nsp = realized tree species richness; see Table S3-b.

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Appendix S4. Interactions between compositional and structural diversity.

We used random forest analysis (RFA) to disentangle the roles of structural and compositional diversity on forest productivity. As the importance of variables changed over forest development particularly for indicators of forest composition (Fig. 2) we also replicated our response surface analysis (cf. Fig. 3) for other prominent indicators of compositional diversity. This analysis showed that the general pattern of NPP response was consistent between all three indicators of compositional diversity (Fig. S4-a and S4-b). Both evenness and entropy were found to positively influence NPP when the effect of multicollinearity (particularly with P_{Fs} - see Table 1 and Table S3 in Appendix S3) was controlled for by means of RFA.

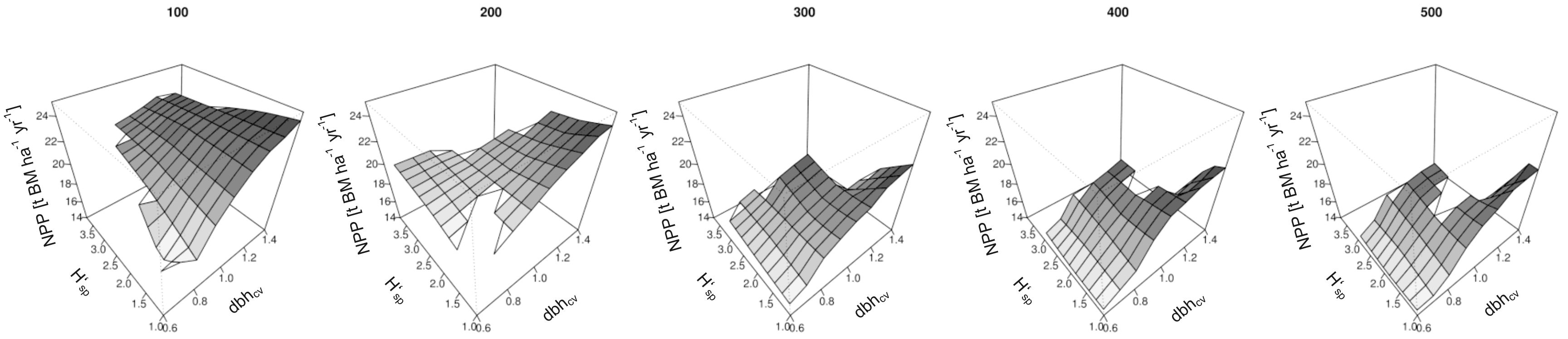

Fig. S4-a – Response surface of NPP as a function of species entropy (H'$_{sp}$) and structural diversity (dbh$_{cv}$). The response surfaces were derived using random forest predictions over the simulated range of H'$_{sp}$ and dbh$_{cv}$ values, while keeping all other variables at their mean values. Open areas in the surface indicate parameter combinations that were not found in the simulated data set.

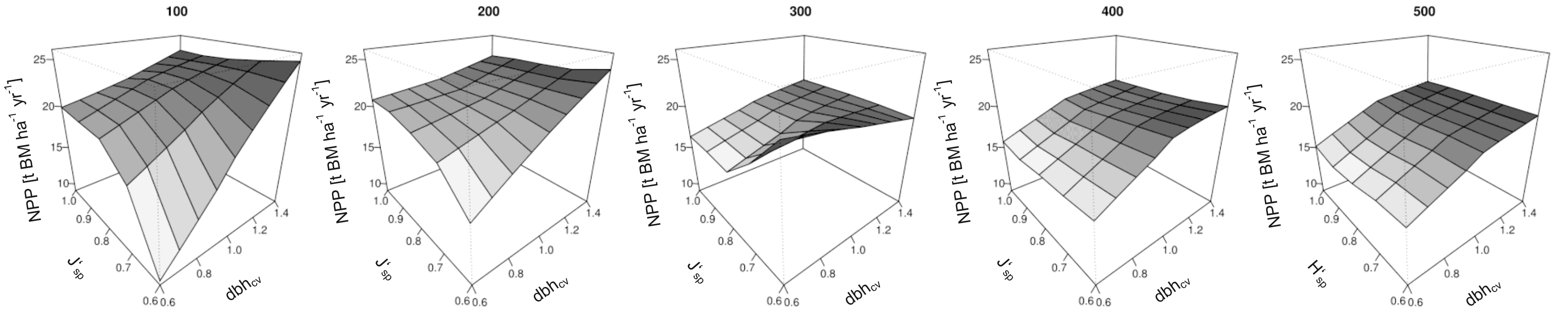

Fig. S4-b – Response surface of NPP as a function of species evenness (J'$_{sp}$) and structural diversity (dbh$_{cv}$). The response surfaces were derived using random forest predictions over the simulated range of J'$_{sp}$ and dbh$_{cv}$ values, while keeping all other variables at their mean values.

Appendix S5. Simulated productivity and abundance of beech.

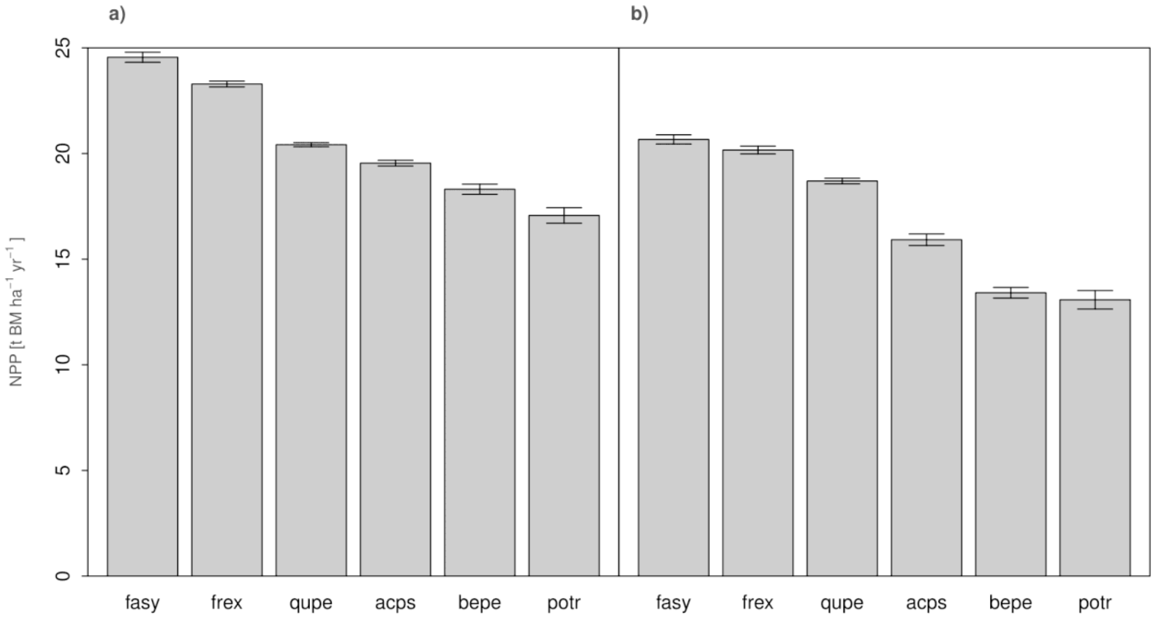

Fig. S5-a – Simulated productivity (NPP, t BM ha^{-1} yr^{-1}) of monospecific forest stands after (a) 100 and (b) 500 years for the study area (mean ± standard deviation over the 250 stands sampled from the landscape). Abbreviations: acps – *Acer pseudoplatanus* L.; bepe: *Betula pendula* Roth. ; fasy – *Fagus sylvatica* L.; frex – *Fraxinus excelsior* L.; potr – *Populus tremula* L.; qupe – *Quercus petraea* (Mattuschka) Liebl.

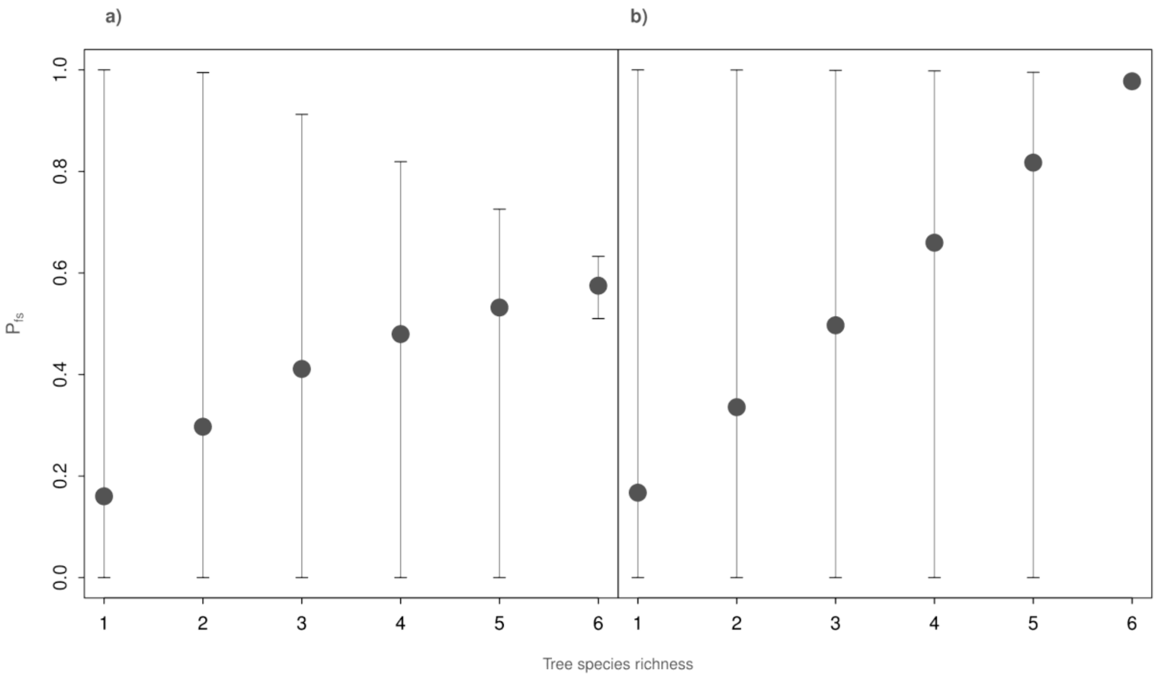

Fig. S5-b – Simulated basal area proportion of beech (P_{Fs}) over a gradient of tree species richness (n=1- 6) for (a) 100 and (b) 500 years of forest development at Hainich. Points represent the mean basal area proportion of beech per each richness level (whiskers represent the 5th – 95th percentile interval).

10.2 Study II: Silva Pedro, M., Rammer, W., Seidl, R., 2016. A disturbance-induced increase in tree species diversity facilitates forest productivity. Landsc. Ecol. 31, 989–1004. doi:10.1007/s10980-015-0317-y

A disturbance-induced increase in tree species diversity facilitates forest productivity

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Date of the manuscript draft: November 12th, 2015

Manuscript word count: 9684

Abstract

Context. Natural disturbances can have a considerable negative impact on the productivity of forest landscapes. Yet, disturbances are also important drivers of diversity, with diversity generally contributing positively to forest productivity. While the direct effects of disturbance have been investigated extensively it remains unclear how disturbance-mediated changes in diversity influence landscape productivity. Considering that disturbances are increasing in many ecosystems a better understanding of disturbance impacts is of growing importance for ecosystem management.

Objectives. Here, our objectives were to study the effect of disturbance on tree species diversity at different spatial scales (α and β diversity), and to analyze how a disturbance-mediated variation in tree species diversity affects forest productivity.

Methods. To account for long-term interactions between disturbance, diversity, and productivity and test a range of disturbance scenarios we used simulation modeling, focusing on a temperate forest landscape in Central Europe.

Results. We found an overall positive effect of disturbance on tree species diversity both with regard to α and β diversity, persisting under elevated disturbance frequencies. Productivity was enhanced by within- and between-stand diversity, with the effect of α diversity decreasing and that of β diversity increasing through the successional development. Positive diversity effects were found to be strongly contingent on the available species pool, with landscapes containing species with different life-history strategies responding most strongly to disturbance-mediated diversity.

Conclusions. We conclude that, rather than homogenizing disturbed areas, forest managers should incorporate the diversity created by disturbances into stand development to capitalize on a positive diversity effect on productivity.

Key words: Alpha diversity – Beta diversity – Forest productivity – Natural disturbances – Forest landscape dynamics – iLand model – Tree species diversity

1. Introduction

Natural disturbances are discrete events in time that disrupt the structure of an ecosystem, community, or population, and change resource availability or the physical environment (White and Pickett 1985; Turner 2010). In forest ecosystems, major agents of disturbance are wildfire, wind, and insects, among others. Disturbance processes are of growing importance for forest landscape dynamics, as disturbance damage is increasing in many ecosystems as a result of climatic and anthropogenic changes (Seidl et al. 2011). In addition, disturbances are expected to further increase in the future in forest ecosystems (Williams et al. 2001; Westerling et al. 2006; Seidl et al. 2009; Seidl et al. 2014; Tian et al. 2014) , which makes understanding the causes and consequences of disturbances an increasingly central issue for ecosystem management (Dale et al. 2001; Mori 2011).

Disturbances influence a wide range of ecosystem functions and services in forest ecosystems (Thom and Seidl 2015). And while our understanding of short-term disturbance impacts on individual parameters of ecosystems is increasing, the long-term effects of disturbances and their complex interactions at the ecosystem level are still incompletely understood. This can be illustrated in the context of ecosystem productivity, where both direct effects of disturbance as well as indirect effects (e.g., disturbance-mediated changes in diversity, which in turn affect productivity) exist. With regard to direct effects previous studies showed that disturbances initially affect forest landscapes negatively. A disturbance-induced loss in leaf area results in reduced carbon uptake and ecosystem productivity (Lindroth et al. 2009; Peters et al. 2013). Furthermore, the structural damage caused by disturbances, e.g., through the breakage of branches and roots in a storm event, can lead to a reduction in tree growth (Busby et al. 2008; Seidl and Blennow 2012). Soil losses often associated with disturbances result in additional negative effects on forest productivity (Nave et al. 2011; Mayer et al. 2014). Yet, most forest ecosystems are remarkably resilient to the impacts of natural disturbances, and productivity usually recovers within a relatively short time frame (of typically years to a few decades) after disturbance (Gough et al. 2013; Peters et al. 2013; Taylor et al. 2014).

However, disturbance is also a strong driver of diversity in forest ecosystems, which can exert an indirect influence on landscape productivity. The most prominent hypothesis of how disturbances shape diversity is the intermediate disturbance hypothesis (IDH; Connell 1978). The IDH predicts that species richness is maximized at intermediate levels of disturbance, because competitively dominant species exclude other species at low levels of disturbance, whereas at high disturbance levels only the most resistant species subsist. However, studies testing the prediction of the IDH have reported inconclusive results on the relationship between disturbance and diversity (Mackey and Currie 2001; Shea et al. 2004; Hughes et al. 2007). Consequently, a debate on the validity of the IDH is currently ongoing in the literature (Fox 2013; Huston 2014), yet the general influence of disturbance on diversity is widely acknowledged.

Diversity, in turn, is assumed to contribute positively to ecosystem functioning and productivity (Tilman et al. 1996; Kondoh 2001;Thompson et al. 2009; Zhang et al. 2012; Scherer-Lorenzen 2014). Three main mechanisms have been suggested to explain the observed higher growth performance of species-rich forests compared to monocultures: niche complementarity, selection effect and ecological insurance (Scherer-Lorenzen 2014). Niche complementarity occurs when more diverse forests are better able to exploit limited resources due to different and complementary traits of species (Morin et al. 2011; Lasky et al. 2014). The selection effect results from an increased likelihood of including a highly productive species in the species pool, which is optimally able to utilize site resources in forests of higher diversity (Morin et al. 2011). And finally, ecological insurance recognizes that species-rich forests are more likely to contain species that can cope with perturbations (Lebourgeois et al. 2013; Perot et al. 2013; Morin et al. 2014; Silva Pedro et al. 2015).

Disturbances can thus influence productivity not only directly but also indirectly via their effect on diversity. We here focus on the latter effect, and hypothesize that disturbances increase tree species diversity, and that such an increased diversity facilitates landscape productivity. Testing this hypothesis is challenging because of the intricacies in the relationships between disturbance, diversity, and productivity. For instance, the contradictory findings from studies analyzing the disturbance – diversity relationship may be a result of the variety of mechanisms that are subsumed under the “umbrella” of disturbance (Shea et al. 2004; Dornelas 2010; Turner et al. 2012). In order to obtain a clear process-based understanding of the effect of disturbances on diversity it is essential to disentangle the roles of different disturbance regime attributes such as duration (Roxburgh et al. 2004), timing (Miller et al. 2012b), spatial and temporal autocorrelation (Elkin and Possingham 2008; Garrison et al. 2012), disturbance type, spatial extent, frequency, and severity (Shea et al. 2004; Miller et al. 2012a). Furthermore, while the majority of previous studies demonstrated a positive effect of diversity on forest productivity (see Zhang et al. 2012 for a recent review), some have also found negative (e.g., Moser and Hansen 2006; Nguyen et al. 2012; Potter and Woodall 2013) or non-significant relationships (Vilà et al. 2005). These inconsistent findings may arise from differences in soil fertility and climate (Scherer-Lorenzen 2014), but also from studying different successional stages and spatiotemporal scales (e.g., Thompson et al. 2009; Paquette and Messier 2011; Zhang et al. 2012; Lasky et al. 2014). The majority of existing studies consider relatively short temporal and spatial scales (where direct effects might dominate) (see Scherer-Lorenzen 2014; Thom and Seidl 2015 for reviews), and often disregard later stages of successional development and the contribution of diversity beyond the local scale.

Here, our objectives were to investigate how different disturbances regimes (i.e., differing in disturbance type, damage and frequency) influence tree species diversity, and how this diversity effect relates to productivity in a temperate forest landscape in Central Europe. As disturbances are key processes shaping ecological systems across several scales (Turner 2010), and as the importance of diversity beyond the local scale is increasingly recognized (Pasari et al. 2013), we explicitly considered within- and between-stand diversity in our analysis. Using simulation modeling allowed us to take a long-term perspective on disturbance – diversity – productivity relationships, and to consider how successional development in forest landscapes is modulating these relationships. Within this framework our specific objectives were (i) to study the effect of disturbance on tree species diversity at different spatial scales (α and β diversity), and (ii) to analyze how a disturbance-mediated variation in tree species diversity affects forest productivity.

2. Methods

2.1. iLand

We used the individual-based forest Landscape and disturbance model iLand (Seidl et al. 2012a) to analyze the relationship between disturbance, diversity, and productivity at different spatial scales. iLand was developed to dynamically simulate the interactions between forest vegetation processes (i.e., growth, mortality, and regeneration), environmental drivers (e.g., climate, nutrient and water availability), and disturbance regimes (e.g., large-scale mortality agents such as wind storms and wildfires) at the landscape scale (Seidl et al. 2012a). Individual trees are dynamically competing for resources (i.e., light, water, nutrients) and adapting to their environment in the model (Seidl et al. 2012a). Tree regeneration is spatially explicit on the landscape, and is determined by the availability and distribution of seeds, light, and a favorable climatic environment (Seidl et al. 2012b). Primary production is derived at the stand-level (i.e., for regular cells of 100 × 100 m horizontal resolution in this study) using a light-use efficiency approach (Landsberg and Waring 1997), where scalar modifiers are used to account for the effects of environmental limitations on utilizable radiation at daily time steps. Within stands, individual tree competition for resources is accounted for by an approach based on ecological field theory (at a horizontal resolution of 2 × 2 m), in which a trees local competitive effect is characterized by a size- and species-specific influence pattern (Seidl et al. 2012a). Allocation of carbohydrates to tree compartments is based on empirical allometric ratios (Duursma et al. 2007) and accounts for dynamic adaptation of trees to their biotic and abiotic environment. Tree mortality depends on a species' maximum longevity as well as on an individual's carbon balance. Furthermore, mortality can result from disturbance events or management. A more detailed description of the model can be found in Seidl et al. (2012a, b) and online at http://iLand.boku.ac.at, where also the model code and executable are available under an open source license.

iLand has been successfully evaluated for simulations in diverse, multi-species forest ecosystems over extensive environmental gradients in western North America and central Europe (Seidl et al. 2012a). It was also successfully applied to investigate the relative contributions of structural and species diversity to ecosystem productivity and C storage previously (Seidl et al. 2012b). Recently, Silva Pedro et al. (2015) used the model to investigate how tree species richness modulates the effect of disturbances on the forest C cycle.

2.2.Study landscape and simulations

Our study was conducted at Hainich National Park, one of the largest unmanaged deciduous forest ecosystems in Central Europe. Hainich is located in the German federal state of Thuringia (N51.1°, E10.5°) and consists of approximately 5,000 hectares of old-growth and uneven-aged forests (i.e., 67% of the total park area). The natural vegetation is mainly characterized by beech forest types (Galio odorati (Asperulo)-Fagion) as well as oak-hornbeam forest types (Carpinion betuli) (Bohn et al. 2004). In a previous study, iLand was successfully tested against independent data from the Hainich ecosystem, documenting its ability to reproduce expected values of dendrometry and growth, as well as trajectories of long-term forest dynamics and composition (see Silva Pedro et al. 2015 for details)

Here, we were particularly interested in how disturbance-mediated variation in tree species diversity influences forest productivity. In order to isolate the disturbance effect we controlled for environmental heterogeneity in simulating a generic 2,500 hectare landscape in which all factors other than the study variables (disturbance regime and available species pool – see below) were fixed. All simulations were started from bare ground and spatially homogeneous site conditions were assumed. We selected a moderately fertile site from study plots implemented at Hainich National Park (Baeten et al. 2013). Site conditions are characterized by an effective soil depth of 100 cm, a clay-loamy soil texture (resulting in a water holding capacity of 180 mm), and 70 kg ha^{-1} year^{-1} of plant-available nitrogen. Information on daily climate (i.e., temperature, precipitation, radiation, and vapor deficit) was extracted from a gridded European database (25 km horizontal resolution) representing the period 1961-1990 (Déqué et al. 2011). The selected climate is characterized by a mean annual precipitation sum of 627 mm and a mean annual temperature of 7.5°C.

To address a wide variety of disturbance impacts we studied four disturbance types which varied in their type of impact and damage level. In two disturbance scenarios severity (i.e., the tree mortality occurring within a disturbance perimeter) varied with tree size: Under the bottom-up scenario (“botttom-up”), saplings (≤10 cm diameter at breast height (dbh)) were completely eliminated within a disturbance perimeter, whereas large trees (≥30 cm dbh) survived the disturbance event. An inverse pattern was assumed in the top-down disturbance scenario (“top-down”), where large trees (≥30 cm dbh) were removed within the disturbance perimeter while saplings (≤10 cm dbh) were assumed to survive. Between these two threshold diameters the mortality probability of individual trees changed linearly with dbh, i.e., decreasing from 10 cm to 30 cm in the bottom-up scenario and increasing in the top-down scenario. The two threshold diameters were chosen to approximately represent the onset of the stem exclusion and mature stages of stand development, respectively. The top–down disturbance scenario thus loosely resembles disturbance agents such as wind, which predominately affect mature trees while leaving younger cohorts widely unaffected, while the bottom-up scenario corresponds to the impact of a low severity fire regime, only killing individuals with thin bark and their live crown close to the ground.

In addition to these two size-related disturbance scenarios we simulated two high-severity disturbance scenarios which removed all trees within the perimeter of a disturbance event. The complete disturbance scenario ("complete") eliminated all trees regardless of their taxon, whereas the species-specific scenario ("species-specific") removed all European beech (*Fagus sylvatica* L.) trees in a disturbance event. While the former scenario represents the highest possible severity for a given disturbance size and frequency, the latter scenario is related to disturbance agents such as pathogens or insects which can cause major damage but usually are host-specific (e.g., many phytophthora and bark beetle species) (Tomiczek et al. 2006; Boyd et al. 2013). Beech was targeted in this scenario as it is the dominant tree species in our study area. For each of these four disturbance scenarios, an identical disturbance rotation period (DRP) of 300 years (i.e., the average time needed to disturb an area of the size of the study landscape) was assumed, corresponding approximately to historic disturbance frequencies in central Europe (Thom et al. 2013). In order to also investigate increased disturbance on the landscape, we simulated an intensified disturbance regime with a DRP of 150 years for the top-down and complete disturbance types. This intensified DRP corresponds to expectations of disturbance changes under climate change for Europe in the coming decades (e.g., Seidl et al. 2014).

The same disturbance size distribution was assumed for all combinations of disturbance type and rotation period. We used a negative exponential distribution to model disturbance size (see, for example, Wimberly et al. 2000), parameterized for a mean disturbed area of 25 ha (i.e., 1/100th of the simulated landscape extent). For every disturbance event, its size was drawn randomly from this distribution, and its position randomly determined in the landscape. A circular disturbance footprint was assumed, and the 5,000 × 5,000 m hypothetical landscape was implemented as a toroid to control for edge effects with regard to disturbance impact.

We hypothesized that disturbance effects on diversity are contingent on the available species pool on the landscape, as species-rich systems also have higher response diversity to disturbance (Mori et al. 2013). To further explore how the available species pool of a system modulates the disturbance-diversity relationship, we set up a factorial design studying all disturbance scenarios over a gradient of richness levels. In order to include a variety of life-history traits and responses towards disturbance we selected major tree species from all seral stages of natural forest development at Hainich (Bohn et al. 2004), i.e., *Betula pendula* Roth, *Populus tremula* L. (both pioneer species), *Acer pseudoplatanus* L., *Fraxinus excelsior* L. (both intermediate species), *Fagus sylvatica* L., and *Quercus petraea* (Mattuschka) Liebl. (both old-growth species), resulting in 63 unique combinations of species (N) in six richness levels (*n*=1 to 6) (i.e., $N=2^6-1$).

Simulations were started from bare ground and species were introduced in the simulation with a low constant background probability for seeds ($P_{seed}=0.01$) uniformly distributed over the simulation area. Sensitivity tests for different P_{seed} values showed no significant differences in the results (data not shown). Simulations were run for 500 years in order to compare the outcomes at different successional stages of forest development. For each of the six disturbance scenarios (i.e., four disturbance types and two DRP) and each of the 63 species combinations, we ran 10 replicates in order to account for the stochasticity in the simulations. As a reference run we furthermore included an undisturbed scenario for all species combinations. In total, 1,921,500 simulation years of the 2,500 ha landscape were available for analysis.

2.3.Analysis

First, we aimed at understanding how disturbances affect tree species diversity within and between stands (here defined as 100 m × 100 m cells of a grid overlaying the continuous forest landscape), i.e., at the level of alpha (α) and beta (β) diversity, respectively. To quantify and compare disturbance impact across scenarios we for every run calculated the annual disturbance percentage as the relative standing timber volume damaged by disturbance on average every year. We chose Shannon index (H') (Shannon and Weaver 1949; Jost 2007) as the indicator of species diversity, since it not only accounts for species richness but considers the relative abundances of species (i.e., species evenness). Species richness alone can be a relatively insensitive metric as it doesn't account for shifts in evenness that can strongly affect ecosystem functioning (Gaston and Fuller 2008). For a more intuitive interpretation of our results, we report the exponential of the Shannon index [exp (H')] in our analysis, which equals tree species richness if all species shares are equal (Jost 2007). Within each simulation and 100-year time step we used the proportion of basal area of each species to calculate the Shannon index of the landscape, obtaining gamma diversity (γ). α diversity was derived as the exponential of the weighted average of the Shannon index in all 100 m cells on the landscape (i.e., using the contribution of each cell to landscape-level basal area as weights). Subsequently, β diversity was estimated from α and γ diversity using Whittaker's multiplicative law ($\gamma = \alpha \times \beta$) (Jost 2007), thus representing the effective number of distinct communities on the landscape. The diversity levels of α and β were calculated as averages for 100-year periods over the 500-year simulation period.

To quantify the impact of disturbance on diversity we calculated the ratio between a disturbed simulation and the respective undisturbed simulation with the same species combination for both alpha and beta diversity components (α_r and β_r). Values lower than one indicate a disturbance-induced reduction of diversity, while values higher than one correspond to simulations where disturbance increases diversity. We used ordinary least squares regression to statistically analyze the effect of disturbance damage on the response variables α_r and β_r. This analysis was conducted separately for each disturbance type and DRP as well as richness level, in order to compare the effects of the different simulated disturbance scenarios on α_r and β_r. Finally, analysis of variance was used to determine the relative contributions of richness level, disturbance damage, and disturbance type on α_r and β_r. Since exploratory analyses suggested functionally different behavior over time all statistical analyses were conducted separately for 100-year time periods. In the discussion of the results we focus predominately on the first and last period of our 500-year study period, which we henceforward referred to as early and late seral stages, respectively. The assumptions of normality and homoscedasticity required for regression analysis were found to be satisfactorily met, and standard transformations of independent variables did not improved regression diagnostics.

Subsequently, we explored how α and β diversity over all richness levels and disturbance scenarios contribute to the productivity of the simulated forest landscapes. We selected mean annual increment (MAI, m^3 ha^{-1} $year^{-1}$) as proxy of forest productivity, as it is closely related to the ecosystem service of timber production and thus of high managerial importance. MAI was estimated from the total growth of each species computed at the stand level (i.e., for each 100 m × 100 m cell) for each 100 year period. For each simulation and time step, the total growth of each species was aggregated over the landscape and averaged to derive the response variable for the analysis. To quantify the effect of tree species diversity on MAI, the net diversity effects (DE, m^3 ha^{-1} $year^{-1}$) was calculated according to Loreau and Hector (2001). DE was derived as the difference between the simulated MAI of a multi-species forest (MAI_O) and that of corresponding monospecific landscapes (MAI_E) under the null hypothesis that there is no complementarity effect or selection effect (Loreau and Hector 2001):

$$DE = MAI_O - MAI_E \tag{1}$$

MAI_E was derived as a weighted average from simulations of monospecific landscapes of the respective species, using the species' basal area shares of the corresponding multi-species forest as weights. DE values higher than zero correspond to simulations where mixed forests show a higher productivity than the one expected from their monospecific counterparts, while DE values below zero represent a negative effect of species diversity on productivity. We subsequently partitioned a positive DE (also referred to as overyielding) into transgressive overyielding and non-transgressive overyielding (Kirwan et al. 2009). Transgressive overyielding occurs when mixtures show higher productivity than the single most productive monoculture, while non-transgressive overyielding refers to mixtures with higher productivity than the average of the monoculture productivities, but lower than the most productive single-species landscape (Kirwan et al. 2009). Furthermore, in order to understand the mechanisms behind the observed net diversity effects on forest productivity, we partitioned DE into complementary (CE; m^3 ha^{-1} $year^{-1}$) and selection (SE; m^3 ha^{-1} $year^{-1}$) effects following the approach suggested by Loreau and Hector (2001). CE was calculated as:

$$CE = n \times \overline{\Delta \mathrm{RMAI}_i} \times \overline{M_i} \tag{2}$$

where n is the number of tree species in the mixture and M_i is the productivity of species i in the monospecific landscape. $\Delta RMAI_i$ is the deviation from expected relative productivity of species i in the mixture:

$$\Delta RMAI_i = RMAI_{Oi} - RMAI_{Ei} \qquad (3)$$

where $RMAI_{Oi}$ is the observed relative productivity of species i in the mixture derived from the ratio of the observed productivity of species i in the mixture to its productivity in the monospecific landscape:

$$RMAI_{Oi} = MAI_{Oi} / M_i \qquad (4)$$

$RMAI_{Ei}$ is the expected relative yield of species i in the multi-species forest, here defined as the averaged species basal area shares in each 100-year analysis periods in the simulated mixtures.

SE was derived from the covariance between the productivity of species in the monospecific landscape and their change in relative productivity in the mixture:

$$SE = n \times \mathrm{cov}(\Delta RMAI_i, M_i) \qquad (5)$$

We conducted ordinary least square regression and analysis of variance for each 100-year analysis period to determine how the independent variables α and β influenced the dependent variables DE, CE, and SE through successional development. To further elucidate the relative contribution of α and β diversity we not only used their respective absolute levels directly in the analysis but also standardized them by subtracting the mean and dividing by the standard deviation, in order to adjust for possible design-related disparity in the ranges of α and β.

Acknowledging the wide variety of β diversity metrics in the literature (Legendre and De Cáceres 2013; Barwell et al. 2015), we furthermore investigated the sensitivity of our findings to a distinctly different approach to estimating β diversity. To that end we selected the total variance of community data approach of Legendre and De Cáceres (2013), which estimates β diversity independently from α and γ. This alternative β diversity (hence referred to $\beta_{L\text{-}D}$) was determined by considering the species proportions of basal area in all 100 m cells of the landscape as community data, and applying Chord transformation to the raw abundance data [see

Legendre and De Cáceres (2013) for details]. We averaged $\beta_{L\text{-}D}$ over each 100-year analysis period and compared results obtained by both β diversity indices in order to further corroborate the robustness of our findings. All statistical analyses were performed in the R language and environment for statistical computing (R Core Team 2013).

3. Results

3.1 Disturbance effect on diversity

We found an overall positive effect of disturbance on diversity, both with regard to α and β diversity, and regardless of the seral stage of the landscape. Our simulations showed that increasing disturbance damage generally boosts α diversity, especially for species-rich landscapes (Fig. 1). Over all disturbance scenarios, the positive effect of disturbance damage on α diversity was on average 5.5-fold greater for landscapes containing all six species compared to landscapes consisting of only two species, illustrating a strong positive interaction between the size of the species pool and disturbance level.

The effect of disturbance damage on diversity was found to be strongly contingent also on the type of the disturbance (Fig. 1). In other words, at the same damage percentage, diversity effects varied distinctly between disturbance scenarios. Over all richness levels, the positive effect of disturbances on α diversity was strongest in the complete disturbance scenario (i.e., the most severe disturbance type), followed by the species-specific, top-down and bottom-up disturbance types [Fig. 1, Tables A1 and A2 in the Electronic Supplementary Material (ESM)]. For the late-seral landscape, the mean α diversity over all richness levels of the complete disturbance regime (effective severity: 100%) increased by 30.2% compared to undisturbed simulations, whereas α diversity of the bottom-up disturbance regime (average effective severity of 12.8%) increased by only 2.7%. For the late-seral landscape (i.e., in the last 100 years of the 500 year simulation period), the disturbance-induced variation in α was mostly explained by disturbance type, followed by damage level, richness level, and their respective interaction (Table 1). Furthermore, our results indicate a weakening of the positive relationship between disturbance damage and α diversity with a doubling of disturbance frequency (see Table A2 in the ESM). For the complete disturbance scenario, for instance, the positive effect of disturbance damage on α diversity under a DRP of 300 years decreased by between 16.8% and 90.1% in a DRP scenario of 150 years.

We found similar positive patterns for the effect of disturbance on β diversity, although the effect strength was generally weaker for between-stand diversity compared to within-stand diversity (Table A2). Disturbances always increased β diversity in the landscape (Fig. 1) and – similar to α diversity – the positive effect of disturbance damage was higher for landscapes with a larger species pool and higher disturbance severity (Table A2). For an increase in disturbance damage by +0.1% year^{-1}, α diversity increased by between +1.6 % and +6.0%, while β diversity responded with a change of between +0.1% and +1.6% (richness level n=6, last 100 years of the simulation) (Fig. 1; Table A2). Disturbance type had the highest relative contribution to the increase in β diversity, while also damage level, richness level, and their respective interaction had a significant effect (Table 1).

For the early-seral landscape (i.e., the first century of the study period), the effects of disturbance on diversity were less pronounced compared to the late-seral systems (Table A1 in the ESM). Over all richness levels and disturbance scenarios, disturbance increased α diversity by between 0.3% and 6.8%, while for β diversity this increase was between 0.5% and 8.3%. Similar to the late-seral stage, positive disturbance effects were stronger for species-rich landscapes and high severity disturbance types. However, in the early stage of forest succession, species richness level had the highest relative contribution to the increase of α diversity, indicating that diversity in early-seral systems is more strongly contingent on the available species pool on the landscape than on disturbance effects. Overall, between 4.4% and 65.3% of the variation in diversity was explained by disturbance (Table 1).

3.2 Diversity-productivity relationships

Both main design variables of our study – disturbance impact and richness of the landscape species pool – influenced productivity positively. Yet their influence changed over time, with the disturbance effect increasing with successional development (Fig. 2). Furthermore, both factors interacted, with the highest productivity levels observed for species-rich and highly disturbed landscapes. Subsequently, we thus analyzed how diversity drives landscape productivity. We observed a strong positive net diversity effect on forest productivity over the 500-year simulation period in our simulations, i.e., diverse forests generally showed higher MAI than their monoculture counterparts. For the early stage of succession, 90.5% of our simulations showed a higher productivity in multi-species forests compared to the respective monospecific forests (Table 2). However, from these simulations, only 11.9% achieved a higher productivity than the most productive monoculture (i.e., transgressive overyielding; Table 2). A similar albeit slightly weaker pattern was found for the late-seral landscape, with the majority of mixtures (70.1%) showing positive net diversity effects but only 6.3% resulting in transgressive overyielding (Table 2).

We found that both α and β diversity had significant positive effects on DE (Fig. 3; Table 3). An increase in diversity by a Shannon exponent of one increased net diversity effects on productivity by +0.32 m^3 ha^{-1} $year^{-1}$ (α diversity) and +1.62 m^3 ha^{-1} $year^{-1}$ (β diversity) in the early-seral system. In the late-seral stage of forest development, a diversity increase by the same amount resulted in a productivity response of +0.17 m^3 ha^{-1} $year^{-1}$ (α diversity) and +1.66 m^3 ha^{-1} $year^{-1}$ (β diversity), respectively. The relationship between productivity and diversity was generally stronger for α diversity (i.e., with a higher portion of the variance explained by within-stand than between-stand diversity). However, β diversity showed higher effects (i.e., slopes of the regression) compared to α diversity (Table 3). Similar results on the importance of β diversity were also obtained using a different indicator of between-stand diversity (Table A4 and Fig. S1). Yet, if accounting for the range disparity in α and β diversity by standardizing them, this relationship reversed for the early-seral system (Table A3 in the ESM).

3.3 Mechanisms driving the net diversity effect on productivity

Both CE and SE ranged from negative to positive values. In the early-seral stage, CE were positive in 90.5% of the simulations, while SE were positive in 55.8% of the simulations (Table 2). Furthermore, we found that CE were stronger than SE in 87.0% of the simulations, i.e., CE was the primary mechanism behind diversity effects and generally stronger than SE. Positive SE were found to be generally less prevalent after several hundred years of forest dynamics (Table 2). Subsequently, we also investigated how α and β diversity components relate to the CE and SE as the underlying mechanisms of diversity effects. Increasing diversity at both spatial scales in general increased CE and decreased SE in our simulations (Table 3). This illustrates that positive diversity – productivity effects are mainly driven by complementarity resource use between tree species in our study, and are not only related to within- but also to between-stand diversity.

Analyzed at the level of species groups we found that particularly a mixture of species that are well able to quickly respond to disturbances (i.e., pioneer species) and those that are able to dominate the community in the long term (i.e., intermediate to old-growth species) resulted in positive productivity responses (Fig. 4). This effect is particularly evident in the early-seral stage, in which landscapes holding species from all three different species groups (i.e., pioneer, intermediate and old-growth tree species) showed the highest mean DE. Interestingly, there is a significant increase in DE also in all runs where pioneer species co-occur with intermediate or old-growth species. However, the positive influence of species with different life-history traits was less distinct in old-growth systems compared to the early-seral systems (Fig. 4).

4. Discussion

Here we have investigated how disturbances affect diversity at different spatial scales in a temperate forest landscape, finding that disturbances generally boost both α and β diversity. In particular, we observed a positive relationship between disturbance damage and tree species diversity. However, we also found a decreasing diversity benefit of increasing disturbance frequency, which may suggest a unimodal relationship between disturbance and diversity beyond the range of studied disturbance levels. This is supported by the fact that for productive sites as the one studied here the diversity optimum is expected to be found at higher disturbance levels compared to less productive sites (Huston 1994; Kondoh 2001).

We found that besides the commonly studied disturbance attributes such as disturbance frequency or severity (Shea et al. 2004), also the type of disturbance strongly influences the relationship between disturbance and diversity. In addition, and in line with the findings of Miller et al. (2012a), we could show that species life-history traits and the species pool available at the landscape highly modulate the disturbance-diversity relationship. However, it has to be noted that our study did not investigate other important disturbance aspects such as the interactive effects of disturbance frequency and spatial extent, which can influence competitive outcomes and thus species diversity (Miller et al. 2012a). In searching for generality in disturbance – diversity relationships it is thus not only important to consider diversity responses at different spatial scales (Svensson et al. 2012), but also to aim for a more comprehensive and process-oriented characterization of the disturbance regime (Miller et al. 2011).

Furthermore, our detailed analysis of the disturbance – diversity relationships over time scales of forest succession revealed important insights with regard to the differences between early- and late-seral systems. While in early-seral systems the increase of α diversity was less pronounced and mainly driven by the species pool available on the landscape, in late-seral systems positive effects were more strongly dependent on disturbance type. Generally, in later stages of successional development, superior competitive species dominate the ecosystem and strongly limit the relative abundance of other species, i.e., competitive exclusion occurs (e.g., Paquette and Messier 2011; Lasky et al. 2014). Disturbances here act as a disruption of the exclusion processes, freeing up resources for other species and, consequently, increasing structural and species diversity (e.g., Franklin et al. 2002; Shea et al. 2004). The stronger response of late-seral systems compared to early-seral systems also illustrates that disturbances have a long-lasting legacy on the compositional dynamics of forest landscapes, and that the spatiotemporally heterogeneous impact of disturbances on diversity accumulates over time. Furthermore, we found that not only α but also β diversity – a diversity dimension much less studied to date – responded positively to disturbance. It has to be noted, however, that we did not include extreme disturbance scenarios in our analysis here, but rather restricted disturbance frequencies to current observations and predictions for the coming decades. Here our analysis suggests that at least for productive sites in temperate forests the tree species diversity impact of the disturbance changes expected for the future (e.g., Seidl et al. 2014) might overall be positive.

We subsequently investigated the link between diversity and forest productivity at different spatial scales. Our results document that disturbances are responsible for between 4.4% and 65.3% of diversity on the landscape (Table 1), and that both α and β diversity contribute to enhanced productivity in forest landscapes. We found that species-rich landscapes were generally more productive than the weighted average of their respective monoculture counterparts, but that only a small number of diverse landscapes achieved greater productivity than their single most productive species. These findings are in congruence with an earlier study on diversity – productivity relationships in temperate forest ecosystems (Pretzsch and Schütze 2009). Moreover, diversity effects on forest productivity remained positive over time, indicating a persistent pattern of diversity-related productivity gains over successional development (Morin et al. 2011).However, our analysis indicates that the processes contributing to this persistence over time might change with succession, with the role of disturbance gaining in importance over that of the species pool on the landscape (cf. Fig. 2). We furthermore found the positive productivity response to be mainly a result of a complementarity effect prevailing through the forest successional development. However, in contrast to previous studies we did not observe a saturating effect of increasing diversity on productivity (e.g., Paquette and Messier 2011; Morin et al. 2011), possibly due to the relative low number of species included in our simulations, and their orthogonal selection aiming for complementarity in their life-history strategies. Also the relatively weak selection effect found in our analysis can be partly explained by the restricted species pool considered in the simulations.

In extension to many previous studies we here not only focused on α diversity but also included β diversity in our analysis. While we here found between-stand diversity to have an even larger effect on productivity than within-stand diversity, a recent study focusing on perennial grasslands reported a greater importance of α compared to β diversity (Pasari et al. 2013). The same was recently reported for tropical forests, where the positive influence of diversity on productivity was found to decrease with increasing level of scale (Chisholm et al. 2013). However, both of these studies did not explicitly consider disturbances in their analyses, and might thus underestimate the role of β diversity in the context of responding to and recovering from disturbances (Mori et al. 2013, Silva Pedro et al. 2015). Also the choice of β diversity metric might influence results and limit comparability between studies. Yet we here found that β diversity based on Whittaker's multiplicative approach (Jost 2007) and β diversity measured as the total variance of the community (Legendre and De Cáceres 2013) showed similar results, demonstrating the robustness of our findings. Nevertheless, when controlling for the diverging ranges of α and β diversity in our analysis the relative advantage of β diversity compared to α diversity was diminished, indicating that methodological considerations might indeed complicate a comparison across studies. Future analyses should thus lay an increased focus on landscape-level diversity and its influence on ecosystem functioning. Other factors contributing to β diversity, such as spatial heterogeneity in topography and biophysical conditions (e.g., climate, soil) across the landscape should also be considered for a comprehensive assessment of the effect of landscape-level heterogeneity on ecosystem functions and services (Turner et al. 2012; Seidl et al. 2012b).

5. Conclusion

Our study highlights that not only local (α) but also landscape-level diversity (β) affect forest productivity positively, and that successional dynamics strongly modulate these relationships in temperate forest landscapes. Disturbances enhanced diversity in our study system (even under elevated disturbance frequencies), a mechanism that counters losses in productivity e.g., through a disturbance-induced reduction in leaf area. This underlines the importance of considering disturbance, succession and scale more explicitly to deeper understand the links between diversity and forest productivity.

Our results are also of considerable relevance for ecosystem management as they document that disturbance effects are not limited to negative impacts on ecosystems and their productivity (Lindroth et al. 2009; Peters et al. 2013; Silva Pedro et al. 2015), but that a disturbance-induced increase in diversity can also foster productivity. An important take-home message for management in this regard is that we found positive disturbance responses to be strongly contingent on the species pool available on the landscape. In particular, adding a pioneer species to a species pool of intermediate or old-growth species strongly facilitated a diversity-related increase in productivity. This effect was found to be especially pronounced in early stages of forest succession, i.e., here simulated as structurally simple systems that are in many regards not unlike managed forests. These are important insights in particular for temperate forest ecosystems in Central Europe, where century-long management practice has favored a limited number of highly productive coniferous species (Spiecker et al. 2004). We conclude that, rather than homogenizing disturbed areas in striving for a swift recovery to a narrow set of target species, forest managers should incorporate the diversity created by disturbances into stand development and retain early-seral species on the landscape. Fostering response diversity and harnessing the positive effects of disturbance might be a way forward to dealing with a climate-mediated increase in future disturbance damage in ecosystem management.

Acknowledgements

This study was conducted under the European Commission collaborative research project FunDivEUROPE (project no. 265171). R. Seidl acknowledges further support from a European Commission's Marie Curie Career Integration Grant (PCIG12-GA-2012-334104). The simulation results presented here have been derived using the Vienna Scientific Cluster (VSC). We are grateful to two anonymous reviewers for helpful comments on a previous version of the manuscript.

Tables

Table 1 – Amount of variance in alpha and beta diversity (α_r and β_r) explained by disturbance damage, disturbance type and richness level (disturbance rotation period of 300 years).

	Early-seral stage (years 1-100)		**Late-seral stage (years 401-500)**	
Explanatory variables	α_r	β_r	α_r	β_r
Disturbance damage [% vol. year^{-1}] [a]	2.41	9.55	21.57	17.25
Disturbance type [b]	1.43	43.85	22.32	46.28
Richness level [c]	8.35	5.05	18.36	10.67
Disturbance damage × richness level interaction	0.52	1.62	6.34	1.8

Shown is the percentage of variance explained by the respective factor in an analysis of variance. All results were statistical significant at $P<0.05$.

[a] Disturbance damage was estimated as the mean annual disturbance percentage relative to the total standing volume.

[b] Disturbance type refers to the four different disturbance severity scenarios investigated (see text for details).

[c] Richness level corresponds to the number of species present on the landscape.

Table 2

Effect and attribution of tree species diversity on landscape productivity.

Period [years]	Effect			Attribution		
	Positive net diversity effect [a] DE>0 [%]	**Non-transgressive overyielding [b] [%]**	**Transgressive overyielding [c] [%]**	**Complementarity effect [d] CE>0 [%]**	**Selection effect [e] SE>0 [%]**	**Complementarity stronger than selection CE>SE [%]**
1-100	90.5	78.6	11.9	90.5	55.8	87.0
101-200	79.4	75.4	4.0	90.2	4.8	89.9
201-300	76.8	71.2	5.6	85.2	8.2	86.8
301-400	69.3	64.0	5.3	80.7	8.5	85.7
401-500	70.1	63.8	6.3	75.4	9.5	78.3
Mean	**77.2**	**70.6**	**6.6**	**84.4**	**17.4**	**85.5**

Shown are the percentages of simulation runs that showed a positive net diversity effect, non-transgressive overyielding and transgressive overyielding, respectively. For purposes of attribution of diversity effects the share of runs for which complementarity (CE>0) and selection (SE>0) effects are positive are also reported.

[a] A positive net diversity effect expresses that mixtures are more productive than the species share-weighted average of their respective monoculture counterparts (see also Equation 1).

[b] Non-transgressive overyielding occurs if mixtures are more productive than the average of their monoculture counterparts, but less so than the most productive single-species landscape.

[c] Transgressive overyielding occurs if mixtures are more productive than the most productive monoculture.

[d] See Equation 2 for details

[e] see Equation 5 for details

Table 3

Influence of alpha (α) and beta (β) diversity on the net diversity effect on productivity (DE), as well as on the selection (SE) and complementarity (CE) effects contributing to DE.

Period [years]	Diversity level	DE		CE		SE	
		Coefficient [$m^3\ ha^{-1}\ yr^{-1}$]	Variance explained [%]	Coefficient [$m^3\ ha^{-1}\ yr^{-1}$]	Variance explained [%]	Coefficient [$m^3\ ha^{-1}\ yr^{-1}$]	Variance explained [%]
1-100	α	0.32	54.2	0.26	47.3	0.09	4.0
	β	1.62	1.0	3.89	6.4	-3.62	12.9
101-200	α	0.09	8.5	0.30	17.2	-0.10	0.95^{ns}
	β	0.41	2.0	0.56	0.86	0.46^{ns}	0.44^{ns}
201-300	α	0.11	18.4	0.25	29.2	-0.11	7.2
	β	1.00	17.4	1.49	16.8	-0.40	2.23
301-400	α	0.11	17.2	0.19	26.7	-0.07	11.5
	β	1.50	23.7	2.37	32.1	-0.99	22.1
401-500	α	0.17	22.4	0.25	30.5	-0.07	16.2
	β	1.66	20.8	2.68	30.4	-1.13	30.4

Shown are the coefficients of multiple linear regression models using α and β diversity as independent variables, with the proportion of the variance explained derived from an analysis of variance.

The dependent variables (DE, SE and CE) were calculated following the method by Loreau and Hector (2001) – see Equations 1 through 5.

All coefficients are significant at $P<0.05$, except where indicated with ns. Abbreviations: ns = not significant

Figure legends

Fig. 1– The effect of disturbance damage on the variation of alpha (α_r; top panels) and beta (β_r; bottom panels) diversity relative to undisturbed simulations. Results are for the late-seral system (simulation years 401-500) and different tree species pools on the landscape (n= 2 to 6). Both investigated disturbance rotation periods of 300 and 150 years are shown, with disturbance damage expressed as the mean annual disturbance percentage relative to the total standing volume (% vol year^{-1}). α diversity was estimated as the exponential of the weighted average of the Shannon index [exp(H')] in all 100 m cells on the landscape, while β diversity was obtained by employing Whittaker's multiplicative law (Jost 2007). Lines indicate linear regressions for each disturbance type and richness level using disturbance damage as independent variable.

Fig. 2 – Net diversity effect on productivity (DE, m^3 ha^{-1} year^{-1}) as a function of disturbance damage and species richness on the landscape for both (a) early and (b) late successional stages (i.e., the first and last centuries of the 500 year simulation period) over all disturbance scenarios. DE is the difference between the productivity of a multi-species forest and the species share-weighted average of the corresponding monospecific forests (Loreau and Hector 2001). Species richness corresponds to the available tree species pool on the landscape. Ribbons were derived by fitting local polynomial regressions.

Fig. 3 – Net diversity effect on productivity as a function of alpha (α) and beta (β) diversity for both early (green) and late (gray) successional stages over all disturbance scenarios. Marginal boxplots display the distribution of the data over DE, α and β diversity.

Fig. 4 – Net diversity effect on productivity in simulations containing combinations of species with different life-history strategies in (a) early- and (b) late-seral stages of forest succession. Abbreviations: P – Pioneer species (here: *Betula pendula* Roth and/ or *Populus tremula* L.); I – Intermediate species (here: *Acer pseudoplatanus* L. and/ or *Fraxinus excelsior* L.); O – Old-growth species (here: *Fagus sylvatica* L. and/ or *Quercus petraea* (Mattuschka) Liebl.).

Figures

Fig. 1

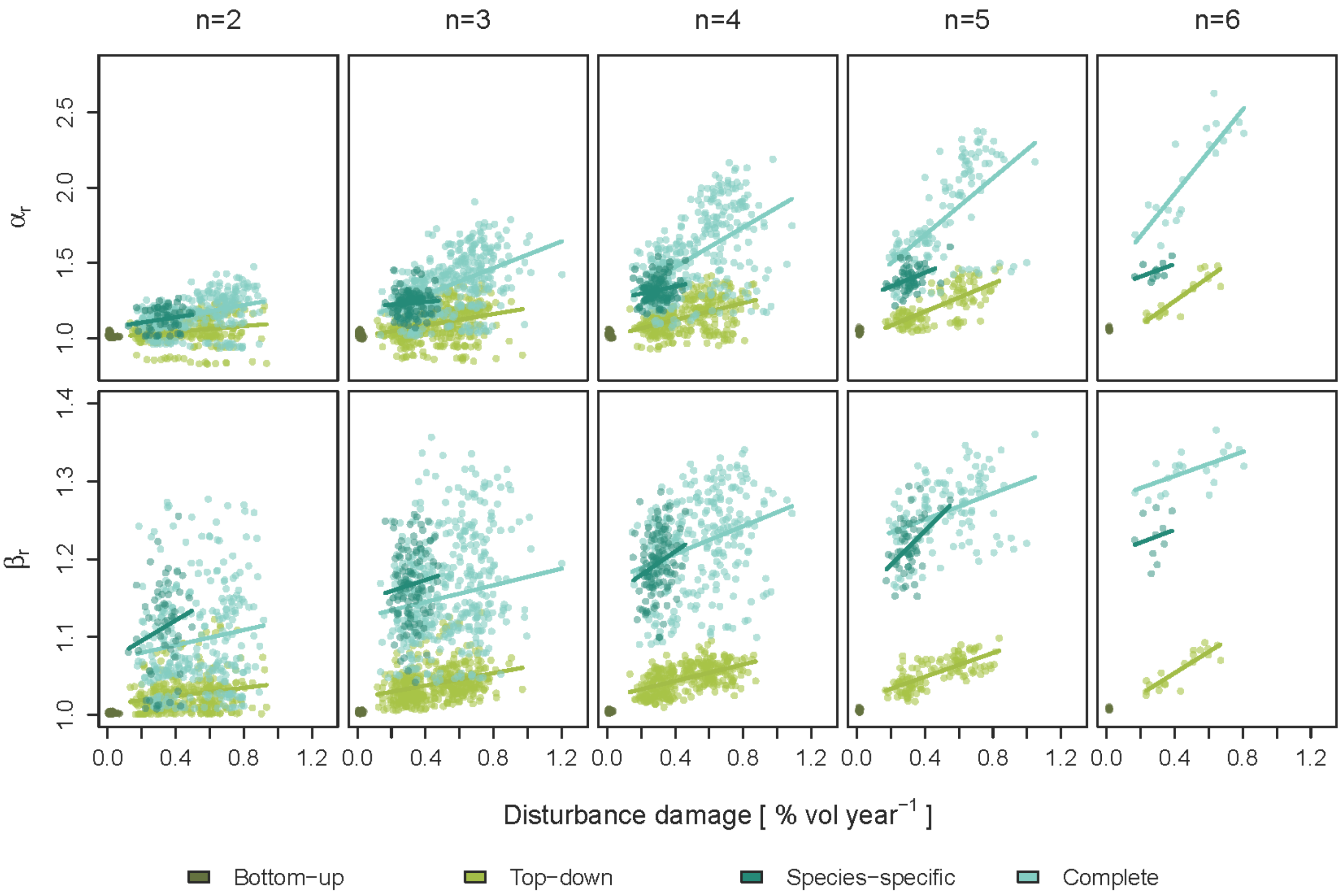


Fig. 2

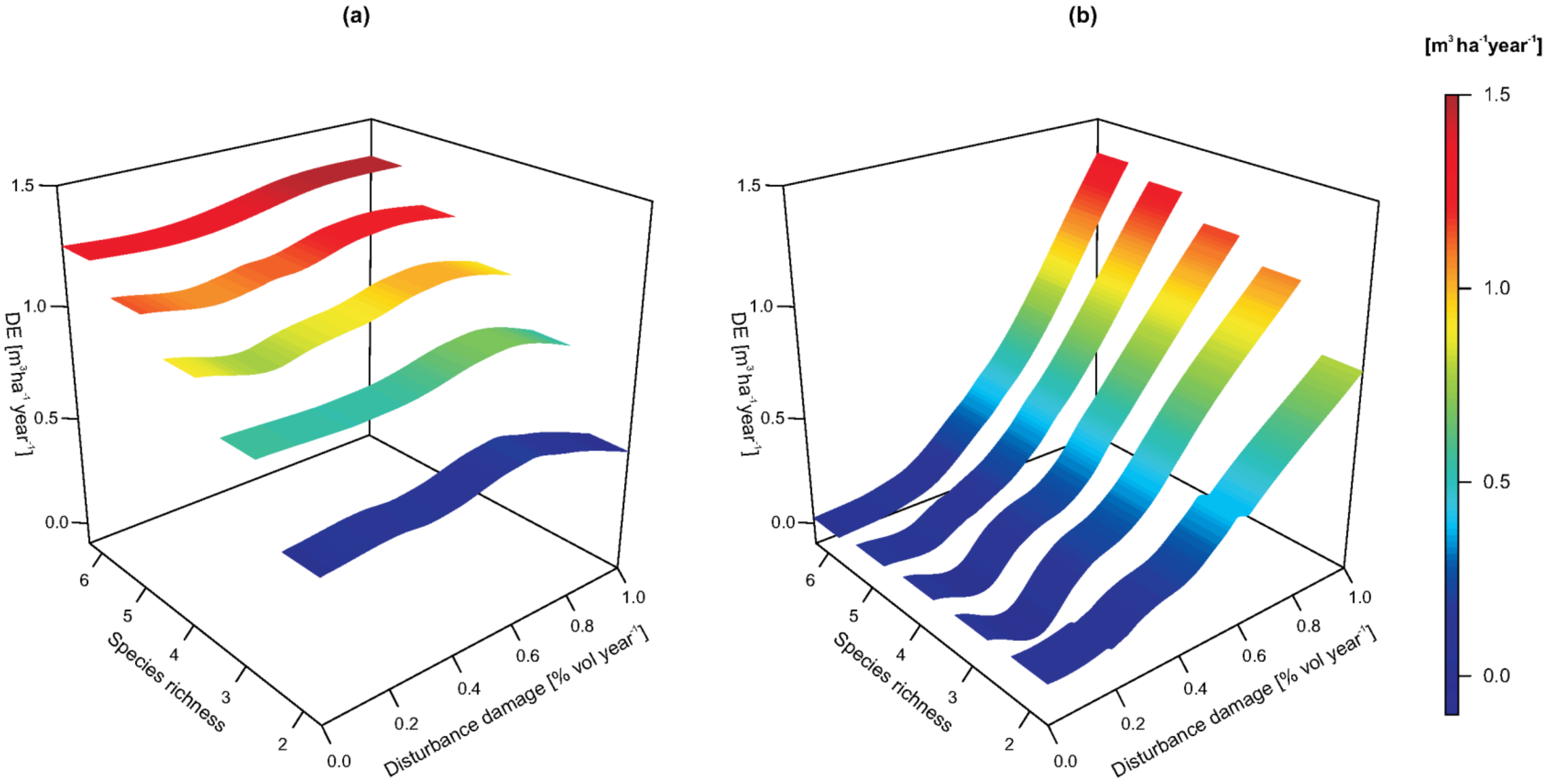
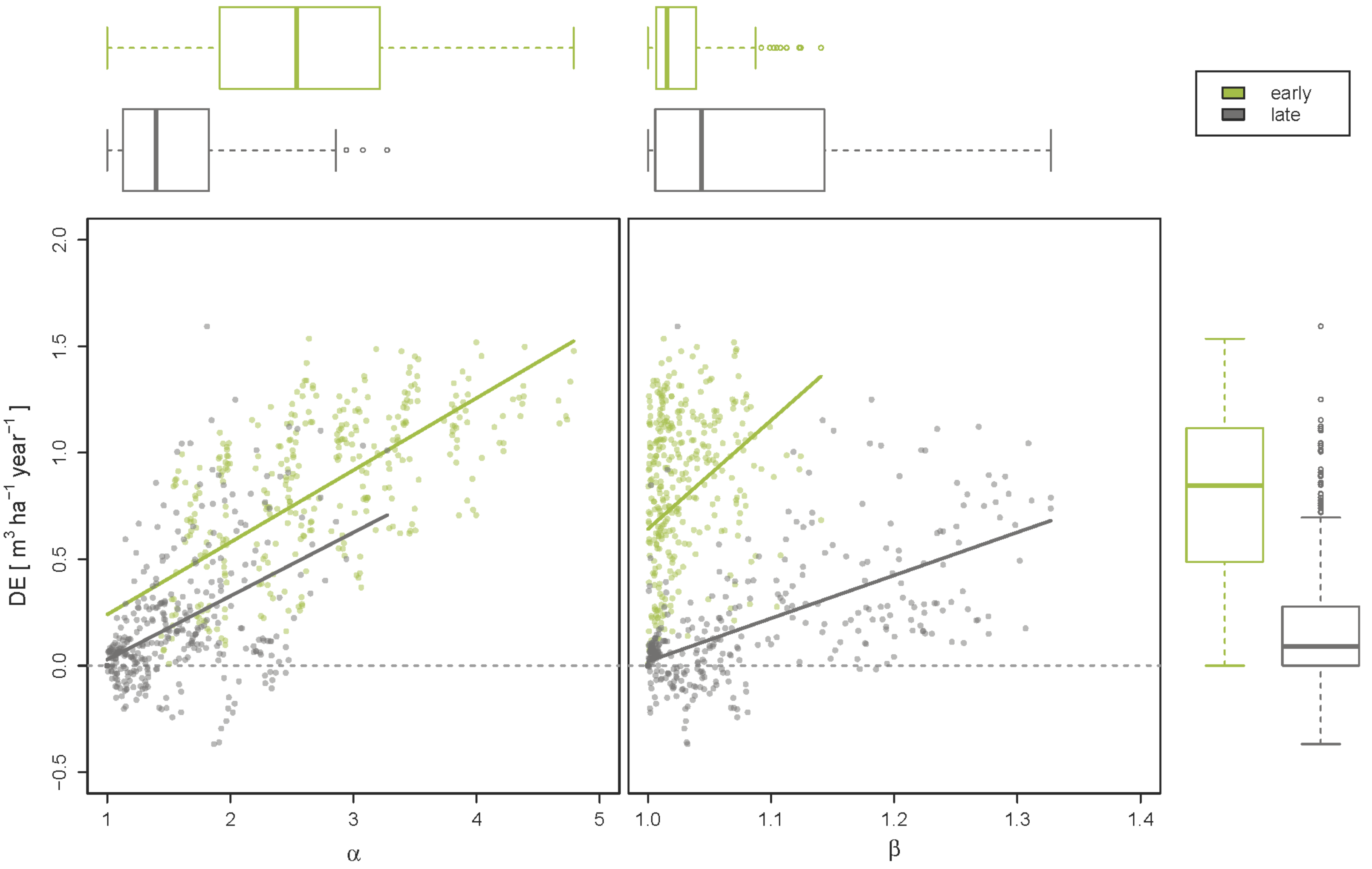
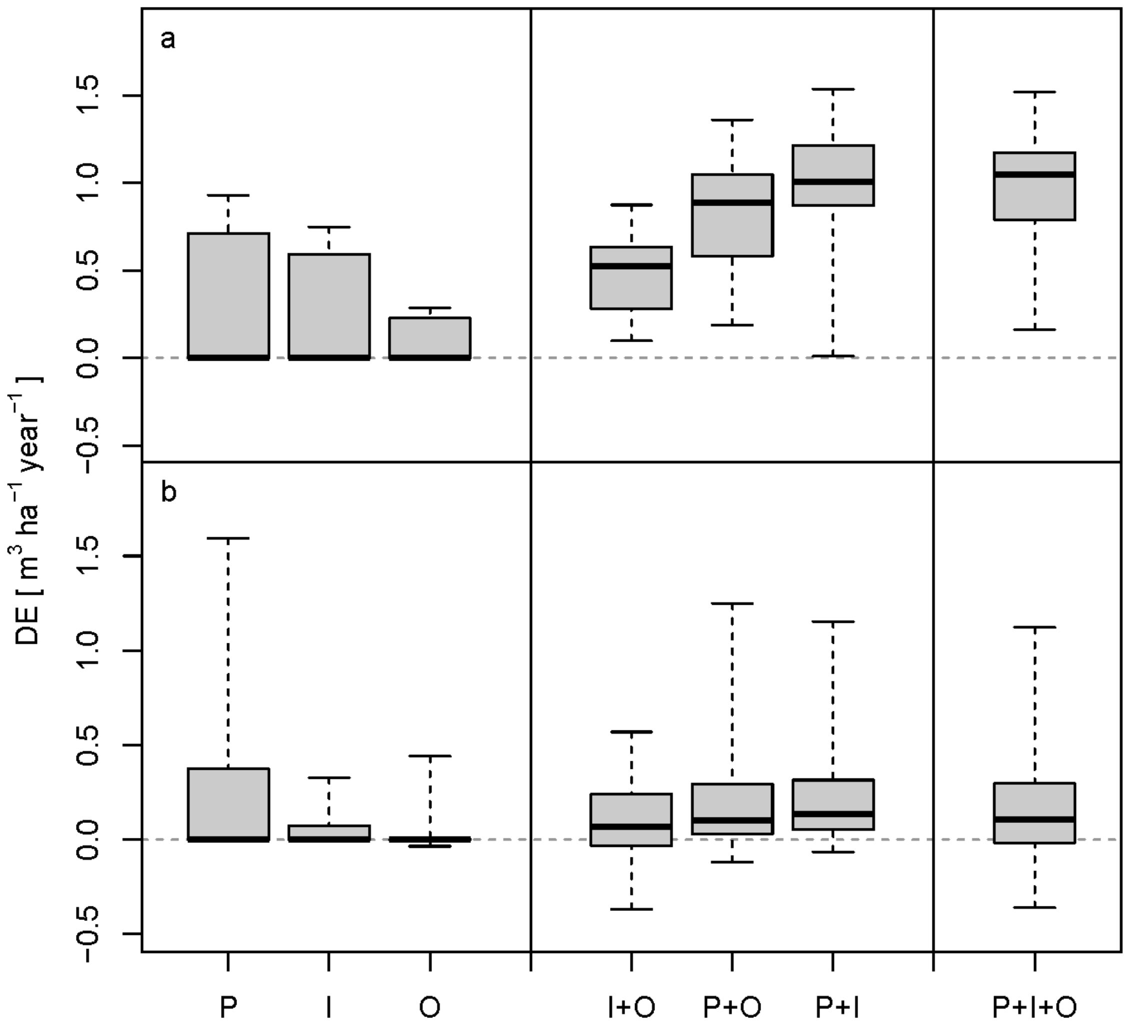

(a)
(b)
DE [m^{3}ha^{-1} year^{-1}]
0.0
0.5
1.0
1.5
Species richness
2
3
4
5
6
Disturbance damage [% vol year^{-1}]
0.0
0.2
0.4
0.6
0.8
1.0
[m^3 ha^{-1}year^{-1}]
1.5
1.0
0.5
0.0

Fig. 3



early
late
DE [m^3 ha^{-1} year^{-1}]
−0.5
0.0
0.5
1.0
1.5
2.0
1
2
3
4
5
α
1.0
1.1
1.2
1.3
1.4
β

Fig. 4



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ELECTRONIC SUPPLEMENTAL MATERIAL (ESM)

A disturbance-induced increase in tree species diversity facilitates forest productivity

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Table A1 - The effect of disturbance damage on the variation of alpha and beta diversity (α_r and β_r) in the early stage of forest development (i.e., first 100 years of the simulation).

			Richness level (*n*)				
Diversity level	**Disturbance type**	**DRP**	**2**	**3**	**4**	**5**	**6**
α_r	Complete	300	0.0014 ± 0.042	0.040 ± 0.022	0.086 ± 0.048	0.070 ± 0.083	0.090 ± 0.027*
		150	0.036 ± 0.026	0.0077 ± 0.027	0.030 ± 0.045	0.12 ± 0.062	0.099 ± 0.11
	Top-down	300	0.060 ± 0.032	-0.019 ± 0.038	0.025 ± 0.048	-0.031 ± 0.085	0.043 ± 0.031
		150	-0.029 ± 0.027	0.0096 ± 0.031	0.042 ± 0.037	0.080 ± 0.056	0.0094 ± 0.016
	Species-specific	300	0.047 ± 0.032	0.15 ± 0.034*	0.10 ± 0.036*	0.033 ± 0.12	0.054 ± 0.011*
	Bottom-up	300	0.30 ± 0.059*	-0.19 ± 0.25	-1.50 ± 0.60*	2.83 ± 1.77	0.37 ± 0.21
β_r	Complete	300	0.041 ± 0.015*	0.067 ± 0.014*	0.10 ± 0.019*	0.076 ±0.020	0.095 ±0.045
		150	0.027 ± 0.014	0.052 ± 0.014*	0.014 ± 0.015	0.053 ± 0.019	0.029 ± 0.025
	Top-down	300	0.056 ± 0.015*	0.033 ± 0.013*	0.10 ± 0.017*	0.086 ± 0.020	0.072 ± 0.029
		150	-0.0012 ± 0.015	0.038 ± 0.016*	0.048 ± 0.017*	0.019 ± 0.019	0.049 ± 0.019
	Species-specific	300	0.24 ± 0.058*	0.24 ± 0.028*	0.17 ± 0.021*	0.17 ± 0.022	0.13 ± 0.030
	Bottom-up	300	0.17 ± 0.030*	0.091 ± 0.054	0.32 ± 0.091*	0.54 ± 0.18	0.093 ± 0.22

Shown are the coefficients and respective standard deviations of linear regression models for different disturbance scenarios and richness levels using disturbance damage (i.e., mean annual disturbance percentage relative to the total standing volume) as the independent variable. See Fig. 1 for a graphical representation of the data.

Asterisks indicate statistical significance of the linear regression models at $p<0.05$.

[a] α diversity was estimated as the weighted mean of the Shannon index in all 100 m cells on the landscape, while β diversity was obtained by employing the Whittaker's multiplicative law (Jost 2007). The diversity levels of α and β were calculated as averages over the 100-year analysis periods (i.e., the early- and late-seral stages).

[b] Disturbance type refers to the four different disturbance severity scenarios investigated.

[c] DPR indicates disturbance rotation periods of 300 and 150 years.

Table A2 - The effect of disturbance damage on α_r and β_r in the late stage of forest development (i.e., the last 100 years of the 500 year simulation period).

			Richness level (*n*)				
Diversity level [a]	**Disturbance type** [b]	**DRP** [c]	**2**	**3**	**4**	**5**	**6**
α_r	Complete	300	0.089 ± 0.074	0.42 ± 0.088*	0.44 ± 0.15*	0.60 ± 0.20*	0.60 ± 0.40
		150	0.074 ± 0.10	0.19 ± 0.11	0.040 ± 0.17	-0.20 ± 0.30	0.21 ± 0.34
	Top-down	300	0.076 ± 0.062	0.13 ± 0.064*	0.19 ± 0.071*	-0.059 ± 0.094	0.15 ± 0.15
		150	0.0094 ± 0.071	0.0040 ± 0.085	-0.024 ± 0.097	0.27 ± 0.14	0.53 ± 0.29
	Species-specific	300	0.17 ± 0.13	0.092 ± 0.12	0.24 ± 0.12	0.46 ± 0.14*	0.41 ± 0.27
	Bottom-up	300	-0.30 ± 0.077*	-0.90 ± 0.14*	-1.01 ± 0.18*	-0.12 ± 0.42	-1.95 ± 1.55
β_r	Complete	300	0.095 ± 0.064	0.12 ± 0.047	0.20 ± 0.049*	0.17 ± 0.050	0.16 ± 0.059*
		150	0.080 ± 0.054	0.091 ± 0.039*	0.058 ± 0.037	0.0078 ± 0.042*	0.064 ± 0.072
	Top-down	300	0.027 ± 0.019	0.028 ± 0.016	0.056 ± 0.016	0.072 ± 0.032*	0.010 ± 0.045
		150	0.0070 ± 0.020	-0.00090 ± 0.016	-0.0038 ± 0.011	0.029 ± 0.016	0.050 ± 0.044
	Species-specific	300	0.13 ± 0.10	0.071 ± 0.070	0.15 ± 0.061*	0.22 ± 0.063**	0.082 ± 0.16
	Bottom-up	300	-0.0067 ± 0.0071	0.0070 ± 0.013	-0.0075 ± 0.018	-0.0088 ± 0.057	-0.072 ± 0.24

Shown are the coefficients and respective standard deviations of linear regression models for different disturbance scenarios and richness levels using disturbance damage (i.e., mean annual disturbance percentage relative to the total standing volume) as the independent variable. Asterisks indicate statistical significance of the linear regression models at $p<0.05$.

Table A3 - Influence of standardized values of α and β diversity on the net diversity effect on productivity (DE), as well as on the selection (SE) and complementarity (CE) effects contributing to DE.

Period [years]	**Diversity level**	**DE**		**CE**		**SE**	
		Coefficient [m^3 ha^{-1} $year^{-1}$]	**Variance explained [%]**	**Coefficient [m^3 ha^{-1} $year^{-1}$]**	**Variance explained [%]**	**Coefficient [m^3 ha^{-1} $year^{-1}$]**	**Variance explained [%]**
1-100	α	0.29	54.2	0.24	47.3	0.08	4.0
	β	0.04	1.0	0.11	6.4	-0.10	12.9
101-200	α	0.05	8.5	0.17	17.2	-0.06	0.95^{ns}
	β	0.03	2.0	0.04	0.86	0.04^{ns}	0.44^{ns}
201-300	α	0.05	18.4	0.12	29.2	-0.06	7.2
	β	0.09	17.4	0.14	16.8	-0.04	2.2
301-400	α	0.05	17.2	0.09	26.7	-0.03	11.5
	β	0.14	23.7	0.22	32.1	-0.09	22.1
401-500	α	0.08	22.4	0.12	30.5	-0.03	16.2
	β	0.15	20.8	0.24	30.4	-0.10	30.4

Shown are the coefficients of multiple linear regression models using standardized values of α and β diversity as independent variables, with the proportion of the variance explained derived from an analysis of variance.
The dependent variables (DE, SE and CE) were calculated following the method by Loreau and Hector (2001).

α diversity was estimated as the weighted mean of the Shannon index in all 100 m cells on the landscape, while β diversity was obtained by employing the Whittaker's multiplicative law (Jost 2007). Both α and β diversity values were standardized by subtracting the mean and dividing by the standard deviation.

All coefficients are significant at *P*<0.05, except where indicated with ns. Abbreviations: ns = not significant

Table A4 - Influence of α and $\beta_{L\text{-}D}$ on DE as well as on SE and CE effects contributing to DE.

Period [years]	Diversity level	DE		CE		SE	
		Coefficient [$m^3\ ha^{-1}\ year^{-1}$]	Variance explained [%]	Coefficient [$m^3\ ha^{-1}\ year^{-1}$]	Variance explained [%]	Coefficient [$m^3\ ha^{-1}\ year^{-1}$]	Variance explained [%]
1-100	α	0.32	54.2	0.26	47.3	0.10	4.0
	β	1.03	0.8	2.45	5.1	-2.26	10.1
101-200	α	0.07	8.5	0.28	17.2	-0.12	1.0^{ns}
	β	0.77	7.8	0.85	2.2	0.59^{ns}	0.8^{ns}
201-300	α	0.07	18.4	0.19	29.2	-0.11	7.2
	β	1.39	29.7	1.98	25.8	-0.46	2.6
301-400	α	0.02	17.2	0.09	26.7	-0.03^{ns}	11.5
	β	2.12	41.0	3.12	47.8	-1.08	23.4
401-500	α	0.07	22.4	0.13	30.5	-0.04	16.2
	β	2.36	37.5	3.50	46.1	-1.21	31.6

Shown are the coefficients of multiple linear regression models using α and $\beta_{L\text{-}D}$ diversity as independent variables, with the proportion of the variance explained derived from an analysis of variance.

$\beta_{L\text{-}D}$ was measured as the total variance of community abundance data following the approach described in (Legendre and De Cáceres 2013).

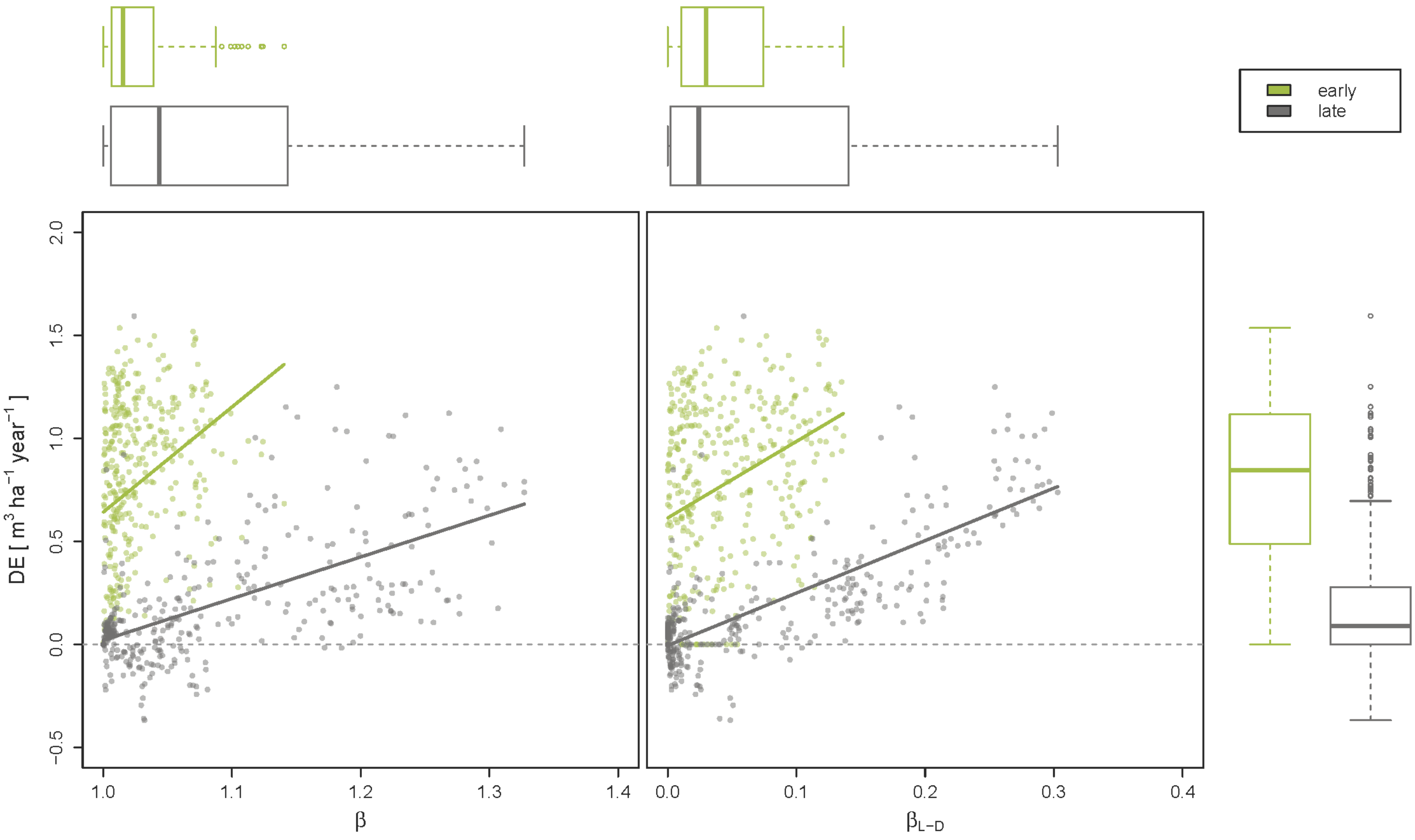

Figure A1 – Comparison between the net diversity effects on productivity (DE, m^3 ha^{-1} year^{-1}) as a function of β diversity calculated using the Whittaker's multiplicative law (β; Jost 2007) (left) and β diversity estimated as the total variance of the community (β_{L-D};

Legendre and De Cáceres 2013) (right). Shown are values for both early (green) and late (gray) successional stages over all disturbance scenarios (i.e., for the first and last century of the 500-year simulation period, respectively). DE is the difference between the productivity of a multi-species forest and the weighted average of the correspondent monospecific forests productivities (Loreau and Hector 2001). Marginal boxplots display the distribution of the data over DE, β and $\beta_{L\text{-}D}$.

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10.3 Study III: Silva Pedro, M., Rammer, W., Seidl, R., 2015. Tree species diversity mitigates disturbance impacts on the forest carbon cycle. Oecologia 177, 619–630. doi:10.1007/s00442-014-3150-0

Tree species diversity mitigates disturbance impacts on the forest carbon cycle

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Abstract

Biodiversity fosters forest ecosystem functioning and stability, and consequently the provisioning of crucial services for human life-support and well-being. In particular, it has been suggested that tree species diversity buffers ecosystems against the impacts of disturbances, a relationship known as the insurance hypothesis. Considering that natural disturbances have increased across Europe in recent decades, and that climate change is expected to amplify the frequency and severity of disturbance events, mitigating disturbance impacts and increasing resilience is of growing importance Here we tested how tree species diversity modulates the impact of disturbance on net primary production and the total carbon stored in living biomass for a temperate forest landscape in Central Europe. Using the simulation model iLand to study the effect of different disturbance regimes on landscapes with varying levels of tree species richness, we found that increasing diversity generally reduces the disturbance impact on carbon storage and uptake, but that this effect weakens or even reverses with successional development. Furthermore, our simulations indicate a clear positive relationship between diversity and resilience, with more diverse systems experiencing lower disturbance-induced variability in their trajectories of ecosystem functioning. We found that positive effects of tree species diversity are mainly driven by an increase in functional diversity, and a modulation of traits related to recolonization and resource usage. Our study suggests that increasing tree species diversity could mitigate the effects of intensifying disturbance regimes on ecosystem functioning, and improve the robustness of forest carbon storage and the role of forests in climate change mitigation.

Key words: carbon cycle; natural disturbances; forest landscape dynamics; tree diversity; iLand model

1. Introduction

Historical and recent anthropogenic influence has resulted in strong alterations of European landscapes and dramatic losses of biodiversity (FAO, 2007). This decline of biodiversity may impair forest ecosystem functioning and the provisioning of ecosystem services (Bengtsson et al. 2000; Klenner et al. 2009) which are crucial for human life-support and well-being (e.g., carbon (C) and nutrient cycling, climate regulation, water retention, and provision of timber, fiber, food, and freshwater). Over the past two decades, a major focus of research was thus to quantify how changes in diversity may affect the provisioning of ecosystem services, and to increase the understanding of the causal relationships between diversity and ecosystem functioning (see Thompson et al. 2009; Zhang et al. 2012; Scherer-Lorenzen 2014 for reviews). Most studies have found a positive effect of plant species diversity on ecosystem functioning, and complementarity (i.e., with diversity resulting in improved utilization of limited resources) and positive selection (i.e., an increased likelihood of including a high productive species which will dominate the community's response) effects were identified as the main underlying mechanisms (Loreau and Hector 2001; Morin et al. 2011).

However, many of these insights relate to relatively short temporal scales. And while the majority of studies demonstrated a positive effect of diversity on forest productivity (Zhang et al. 2012), some also revealed non-significant (Vilà et al. 2005) or negative (e.g., Moser and Hansen 2006; Nguyen et al. 2012; Potter and Woodall 2013) relationships between species diversity and forest ecosystem functioning. These divergent findings may arise from differences in study design (manipulative experiments vs. natural communities), but could also relate to differences in the successional stages investigated (e.g., Paquette and Messier 2011; Zhang et al. 2012; Lasky et al. 2014). A number of empirical studies have suggested that the positive diversity effect on productivity found in short-term experiments might only be a transient effect, as niche complementarity may be overwhelmed by competitive exclusion and the saturation of niche space in later seral stages of successional development (e.g., Paquette and Messier 2011; Zhang et al. 2012; Lasky et al. 2014). This underlines that a consideration of long-term successional dynamics is essential to understand diversity – ecosystem functioning relationships in forests.

In addition to negatively affecting the level of ecosystem functioning and service provisioning biodiversity loss may also reduce ecological stability, for instance, through a lowered resistance to perturbations and resilience to disturbances of less diverse ecosystems (e.g., Bengtsson et al. 2000; Hooper et al. 2005; Thompson et al. 2009). In the context of the recently observed increases in disturbance frequency and severity in Europe's forests (Schelhaas et al. 2003; Seidl et al. 2011), the contribution of biodiversity to resistance and resilience of ecosystems is of growing importance. However, most studies on biodiversity effects have focused on the central tendency in ecosystem functioning or provision of services to date, while the diversity effect on stability to perturbations and disturbances of these variables remains less well understood (Thompson et al. 2009; Cardinale et al. 2013).

Based on theoretical considerations, Yachi and Loreau (1999) showed that diversity buffers ecosystems from the effects of perturbation, and decreases temporal variability in ecosystem functioning (i.e., insurance hypothesis). This dampening effect can be explained by the capacity of diverse ecosystem constituents to respond in different ways to disturbance and perturbation, conferring stability at the ecosystem level (Thompson et al. 2009).The insurance hypothesis has been confirmed for grasslands (see Tilman 1996; Cardinale et al. 2013b; Gross et al. 2014b for reviews), but an in-depth quantitative analysis for forest ecosystems has to our knowledge not yet been conducted. Here, we test the insurance hypothesis for a temperate forest landscape in Central Europe, and investigate how tree species diversity modulates the effect of disturbance on forest C cycling. The question of diversity effects is of particular importance in temperate forest ecosystems of Central Europe, as a century-long management history has widely reduced tree species richness by favoring only a small number of commercially viable and fast growing species. The C cycle is not only a powerful indicator of ecosystem functioning (Waring and Running 2007), but constitutes also an increasingly important and highly policy-relevant ecosystem service in the context of mitigating anthropogenic climate change (Canadell and Raupach 2008). We here investigated effects on both fluxes and stocks of C, using net primary production (i.e., carbon uptake in the forest landscape) and total carbon in living biomass (i.e., live C stored in the system) as response variables. As a main source of perturbation in forest ecosystems we studied natural disturbances (White and Jentsch 2001) and their impact on the forest C cycle. Our overall objective was to investigate how tree species diversity modulates the effect of disturbance on the forest C cycle. In particular, we addressed (i) whether tree diversity can mitigate disturbance impacts on C uptake and storage, and (ii) whether tree diversity dampens the disturbance-induced variability in C uptake and storage. Based on the insurance hypothesis we expect that more diverse forests are less impacted by disturbance, and that diversity enhances the resilience of forest C cycling to disturbances.

2. Materials and methods

2.1. iLand

To study how tree diversity modulates the impact of natural disturbances on ecosystem functioning over extended spatio-temporal scales we used iLand, the individual-based forest Landscape and disturbance model (Seidl et al., 2012). iLand is a spatially explicit, process-based model which has been specifically developed to simulate the complex interactions of ecosystem processes dynamically at the landscape scale. iLand simulates ecosystem dynamics as an emergent property of the interactions between environmental drivers (e.g., climate, nutrient and water availability), forest vegetation processes (e.g., growth, mortality and regeneration), and disturbances regimes (e.g., wind storms, wildfires) (Seidl et al., 2012). The model efficiently scales from individual trees to large forest landscapes in a hierarchical multi-scale approach. Trees are simulated as adaptive agents that compete for resources (predominantly light, but also water and nutrients) and dynamically adapt to their environment (Seidl et al., 2012).

iLand uses a light-use efficiency approach to model primary production (see Landsberg and Waring 1997). Scalar modifiers are applied to account for the effects of temperature, soil water availability, vapor pressure deficit, as well as the effects of nutrient availability and atmospheric CO_2 concentration on primary productivity. Allocation to tree compartments is modeled based on empirical allometric ratios (Duursma et al. 2007). The probability of stress-related mortality is calculated from an individual's carbon balance (Güneralp and Gertner 2007). Regeneration is modeled spatially explicit in the landscape, considering the availability and distribution of seeds (via a two-part exponential dispersal kernel, Lischke and Löffler 2006) as well as the spatial distribution of resources such as light, water and nutrients. Species-specific thermal limitations to tree establishment (e.g., chilling requirements, frost damage) are modeled based on a phenology approach (Nitschke and Innes 2008).

iLand was developed to simulate a variety of disturbance agents and their interactions explicitly in space and time. The model incorporates detailed process-based disturbance modules for wind disturbances (Seidl et al. 2014a) and wildfire (Seidl et al. 2014b). In addition, iLand contains a generic interface that allows the implementation of different disturbance regimes based on impact type, disturbance frequency, disturbed area, and spatial spread. iLand has been successfully evaluated for simulations in diverse, multi-species forest ecosystems over extensive environmental gradients in western North America and central Europe (Seidl et al. 2012a; Seidl et al. 2012b). It was also successfully applied to investigate the relative contributions of structural and species diversity to ecosystem productivity and C storage, while controlling for the influence of environmental heterogeneity at the landscape scale (Seidl et al. 2012b).

2.2.Study area

Hainich National Park is a forest-dominated national park located in the temperate broad-leaved forest ecoregion of Europe in Thuringia, Central Germany (N51.1°, E10.5°). The natural vegetation in the area is mainly characterized by beech forest types (Galio odorati (Asperulo)-Fagion) as well as oak-hornbeam forest types (Carpinion betuli) (Bohn et al. 2004). Hainich contains approximately 5,000 hectares of old-growth and uneven aged forests (i.e., 67% of the total park area). The forest management practice from the middle of the 19th century until the early 20th century was coppice with standards (i.e., an overstorey of sparsely distributed and mostly generatively regenerated trees managed over long rotation cycles combined with an understorey of frequently cut trees regenerated via sprouting), later followed by high forest and continuous cover systems (Schmidt et al. 2009). Management of the park area was ceased completely in the 1960s, and for the past five decades natural dynamics governed the development of Hainich National Park (Mölder et al. 2008).

Quantitative information on the Hainich ecosystem was available from 38 study plots contained within the FunDivEUROPE Exploratory Platform (Baeten et al. 2013). These data were used to evaluate the simulation model iLand (see Electronic Supplemental Material) and subsequently served as drivers of the simulation (see below). For a subset of the available plots detailed soil data on effective soil depth, soil physical properties (e.g., depth, texture, and stone fraction), and soil fertility (nitrogen content) were available (Baeten et al., 2013). Daily climate data for the parameters temperature, precipitation, radiation, and vapor pressure deficit were extracted from a database of gridded climate for Europe (25 km horizontal resolution), representing the period 1961-1990 (Déqué et al., 2011). As a prerequisite for using iLand in our analyses we evaluated the model against expected patterns of forest ecosystem dynamics at Hainich (see the Electronic Supplemental Material for details). In particular, we tested the model's ability to reproduce observed tree dimensions, productivity, and mortality (Figure S1, Table S1), as well as the expected successional trajectories and equilibrium landscape composition and structure (Figures S2 and S3).

2.3.Study design

Beyond tree species composition and diversity a variety of other factors potentially modulate the effect of disturbances on ecosystem functioning (e.g., landscape-level heterogeneity in soil types, topography). Since we here were interested in determining the first-order effects of diversity, and since the insurance hypothesis was formulated for homogeneous environments (Yachi and Loreau 1999), we controlled environmental heterogeneity in our study by setting up a hypothetical 2,500 ha landscape with homogeneous environment. We selected the site characteristics of a moderately productive site at Hainich as reference conditions, with an effective soil depth of 100 cm, a clay-loamy soil texture (water holding capacity of 180 mm), and 70 kg ha^{-1} year^{-1} of plant-available nitrogen. The average climatic conditions are characterized by a mean annual precipitation sum of 627 mm and a mean annual temperature of 7.5°C.

For this idealized landscape we studied how different levels of tree species diversity modulate the effects of different disturbance scenarios. Tree species diversity was studied in a factorial design, simulating all possible combinations of seven different species. We included species from all seral stages of natural forest development at Hainich in our analysis (Bohn et al. 2004), in order to represent a wide gradient of responses towards disturbance impacts in our simulations. We selected five mid- to late seral species (i.e., *Fagus sylvatica* L., *Fraxinus excelsior* L., *Acer pseudoplatanus* L., *Quercus petraea* (Mattuschka) Liebl. , *Picea abies* (L.) Karst.) as well as two early-seral species (*Betula pendula* Roth and *Populus tremula* L.), resulting in 127 unique combinations of species in seven richness levels. The selected mid- to late seral species not only relate to the dominant species currently observed in the area, but also correspond to the empirically studied species mixtures at Hainich within the frame of a large-scale European diversity study (Baeten et al. 2013). In addition to these 127 unique combinations of tree species we also conducted model runs where we allowed all major species of the potential natural vegetation to occur in the simulation (n=13), adding *Acer platanoides* L., *Acer campestre* L., *Carpinus betulus* L., *Quercus robur* L., *Tilia cordata* Mill., and *Tilia platyphyllos* Scop. to the above mentioned seven focal species (Bohn et al. 2004).

Simulations for all 128 combinations of species were started from bare ground and were run for 500 years. Only the species of the respective combination were allowed in each simulation, with seeds provided uniformly distributed over the simulated landscape at a background probability of $P_{seed}= 0.01$ (Seidl et al. 2012b) . Sensitivity tests for this parameter indicated that our results were robust to different levels of background probabilities of seed availability (data not shown). It has to be noted that while the boundary conditions (available species pool, background seed availability) for each run was experimentally restricted by the factorial simulation design, forest dynamics and succession are emergent properties of the iLand simulations and the simulated species composition reflects the relative competitive strengths of the respective species (see also Figure S2).

For each of 128 unique species combinations we analyzed the effect of three different types of disturbance. Under the complete disturbance scenario (“Complete”), we assumed that all trees within the perimeter of a disturbance event are killed. This disturbance scenario thus assumes a generic disturbance severity of 100%, and represents the maximum level of disturbance for a given disturbance frequency. Such complete disturbances are, however, rare under real-world conditions (and most closely resemble management-related disturbance). We thus also studied two additional disturbance scenarios in which severity varied with tree size. Under the top-down scenario (“Top-down”) only large trees (≥30 cm diameter at breast height (dbh)) were completely eliminated within the disturbance perimeter, whereas saplings (≤10 cm dbh) were assumed to survive the disturbance event. Between these two threshold diameters the mortality probability was assumed to increase linearly with dbh (see also Figure S4). The top-down disturbance scenario thus represents disturbance agents such as wind or many important bark beetle species, which predominately affect large trees while leaving younger cohorts widely unaffected (Schmidt et al. 2010; Pasztor et al. 2014). The third disturbance type investigated was the inverse of the top-down scenario, i.e., a scenario where all trees ≤10 cm dbh within the disturbance perimeter are killed and the mortality probability decreases linearly with dbh to zero for trees ≥30 cm ("Bottom-up" disturbance scenario). This latter scenario corresponds loosely to the pattern frequently caused by wildfire disturbance, as fire predominately kills individuals with canopies close to the ground and fire resistance generally increases with tree size (as e.g., bark thickness is closely related to tree diameter) (Fernandes et al. 2008).

Each of these three disturbance types was studied for a disturbance rotation period (DRP) of 300 years (i.e., the average time needed to disturb an area of the size of the study landscape), which roughly corresponds to historic disturbance frequencies in central Europe (Thom et al. 2013). In order to test if the effect of tree species diversity on disturbance impacts is conditional on disturbance frequency we also simulated an intensified disturbance regime with a DRP of 150 years for the complete disturbance type. The thus assumed doubling of disturbance frequency corresponds to expectations of disturbance changes under climate change for Europe in the coming decades (e.g., Seidl et al. 2014c).

For all scenarios of disturbance type and interval the same disturbance size distribution was assumed. We used a negative exponential function to model disturbance size (see e.g., Wimberly et al. 2000), parameterized for a mean disturbed area of 25 ha (i.e., 1/100th of the simulated landscape extent). For every disturbance event, its size was drawn randomly from this distribution, and its position randomly determined in the landscape. A circular disturbance footprint was assumed, and the 5,000 m × 5,000 m hypothetical landscape was implemented as a toroid to control for edge effects with regard to disturbance impact. As a reference for assessing the disturbance effect on forest ecosystem functioning we also ran our simulations for the 128 species combinations without any disturbance event (undisturbed scenario).

All simulations were run for 500 years, enabling us to assess the diversity effect in different successional stages. The focus on extended spatio-temporal scales also limited the effect of single, stochastic disturbance events on landscape-scale C stocks and fluxes. Furthermore, to account for the stochasticity in the simulations and investigate the divergence within scenarios, 10 replicates were run for each species combination and disturbance scenario. In total we conducted 5120 simulations (Table S2; 128 tree species combinations × 6 disturbance scenarios including the undisturbed scenarios × 10 replicates) for 500 years and 2,500 hectares, resulting in a data pool for analysis of $6.4 \cdot 10^9$ hectare-years.

2.4. Analysis

We chose the forest C cycle as the response variable for our analysis of how tree species diversity (richness and Shannon index) mediate the impact of disturbance regimes. In particular, we focused on two crucial indicators of forest C cycling, total net primary production (NPP, kg C ha^{-1} $year^{-1}$) which quantifies the C uptake in the forest, and total carbon in living biomass (aboveground compartments and roots) (TLC, kg C ha^{-1}) as a measure of important carbon pools in the forest. Our analysis thus investigated effects on both C uptake and storage in forest landscapes. NPP and TLC were spatially aggregated to landscape-scale averages, and mean values over 100 simulation years were used in the analysis. To test whether the effect of diversity on disturbance impact differs between successional stages of forest development we separately analyzed the two 100-year periods at the beginning and end of our 500 year simulation period (henceforward referred to as early and late seral stage, respectively).

In order to test the two predictions made by the insurance hypothesis, i.e., that diversity reduces the impact of perturbations, and increases the stability of ecosystem functioning, we studied separate indicators for impact and stability. To quantify disturbance impact, we calculated the percentage difference of a disturbed simulation to the respective undisturbed simulation with the same species combination for both TLC and NPP (TLC_{impact} and NPP_{impact}). Negative values represent a disturbance-induced reduction of TLC or NPP, while positive values correspond to simulations where disturbance increases C cycle indicators. To test the second prediction of the insurance hypothesis we focused on the resilience of the landscape in the face of disturbance. As an indicator for resilience we selected the variation between the replicated simulations for any given diversity and disturbance scenario, quantified by the mean annual coefficient of variance (cv) of TLC and NPP (TLC_{cv} and NPP_{cv}). A higher value implies a higher variation in ecosystem functioning between the otherwise identical realizations of a scenario (see also Seidl et al. 2014b). Since the main element inducing variation between realizations within any given scenario is the stochastic timing and realization of disturbance events TLC_{cv} and NPP_{cv} describe to what degree the simulations re-converge after disturbance. Furthermore, since we here report centennial averages, and since swift recovery from disturbance will decrease the variation between individual realizations, a second component indirectly assessed by this indicator is recovery speed. TLC_{cv} and NPP_{cv} are thus combined indicators for engineering and ecological resilience (i.e., recovery rate and convergence of trajectories) *sensu* Holling (1996), describing the strength of the attractor of the system for different levels of species richness (see also Figure S5). It has to be noted that TLC_{cv} and NPP_{cv} are inversely related to resilience, with low values indicating high resilience of the system and vice versa.

The main variable used to describe tree species diversity was tree species richness, i.e., the number of tree species present on the landscape. However, species richness alone is an insufficient measure of diversity, as it does not account for the abundances of species in a system (Zhang et al. 2012). As an additional indicator of diversity we therefore used the Shannon index (Shannon and Weaver 1949), which incorporates both richness and relative species abundance. Shannon index was calculated using the mean proportion of basal area of the species present in the landscape. While we here report results relative to the maximum richness level that was prescribed for the respective scenario (i.e., the main design variable of our simulation experiment), the realized diversity (richness and Shannon index) on the landscape at any given point in time is also influenced by processes of competition and succession. However, since we here simulated a large landscape (rather than a small number of patches or stands, cf. Morin et al. 2011), the diversity of the initial design was relatively well preserved in the simulation over time, i.e., initially species-rich landscapes were always more diverse also after several centuries of forest dynamics (cf. Figures S6 and S7).

To statistically analyze the effect of diversity (i.e., tree species richness and Shannon index) on the response variables of disturbance-mediated ecosystem functioning (i.e., TLC_{impact}, NPP_{impact}, TLC_{cv} and NPP_{cv}) we used ordinary least squares regression and analysis of variance, conducted with the R language and environment for statistical computing (R Core Team 2013). We conducted our analyses separately for tree species richness and Shannon index, as these two diversity indicators were highly correlated. Species richness was log-transformed to meet the assumptions of normality and homoscedasticity required for regression analysis. Since exploratory analyses suggested functionally different behavior between successional stages, all analyses were also conducted separately for early and late seral stages.

To further elucidate the functional drivers of diversity effects we subsequently analyzed how species identity and traits contributed to emergent patterns of our simulations, using the unsupervised machine learning algorithm Random Forest (Breiman 2001; Liaw and Wiener

2002). Random Forest is a powerful nonparametric method for identifying key variables influencing complex ecological processes such as disturbance (e.g., Thompson and Spies 2010) It is applicable to high dimensional and hierarchically structured datasets and is robust to non-linear relationships among predictors as well as predictors and response variables (Sandri and Zuccolotto 2006; Cutler et al. 2007). In particular, we were interested to attribute diversity effects to three mechanisms: (i) an influence on the mean traits at the system level (e.g., an additional early-seral species on the landscape will increase the overall ability to disperse and recolonize disturbed areas), (ii) an effect on system level variation in traits (e.g., a high variation in shade tolerance traits on the landscape will allow the system to optimally utilize light resources, as both open conditions as well as sub-canopy light will be used efficiently), and (iii) a species identity effect (testing whether it is not so much the increased number of species but the particular ecological role of the added species that improves ecosystem functioning under disturbance). We selected nine species traits of relevance for disturbance response and recovery and directly used the parameter values for these traits as applied in the simulation for the analysis (see Table S4 for details). Mean trait values were calculated using basal-area weighted averages for each simulation run and time step, while trait variation was described by the trait range of the present species. For testing an identity effect the seven main species of our analysis were included as individual factorial explanatory variables in the analysis. TLC_{impact} and TLC_{cv} were used as response variables, and the analysis was again conducted separately for early and late seral stages. After conducting a sensitivity analysis on crucial parameter settings we settled on growing 1000 trees for every random forest with a minimum terminal node size of five. The increase in mean square error (MSE) when observed values of the respective variable are randomly permuted while all others are left unchanged was used as a measure of variable importance.

3. Results

3.1 Tree diversity effects on disturbance impacts

On average over all disturbance types and species levels, a disturbance regime with 300 year rotation period reduced the live C stored in the landscape by -3.8% and -8.7% for early and late seral stages, respectively. For both C stocks and fluxes the disturbance impact was greatest for the complete disturbance scenario, followed by the top-down and bottom-up disturbance types (see Figure S9). Furthermore, the C uptake was lowered by -2.2% and -1.0% in early and late seral stages, respectively (Figure S9). For the early seral landscape, tree diversity significantly mitigated the disturbance impact on both NPP and TLC. This effect was evident over all disturbance types, and was strongest in the complete disturbance scenario (Figure S13). TLC_{impact} was more strongly buffered by increasing levels of diversity than NPP_{impact}, with the effect differing only moderately between the two investigated indicators of diversity, i.e., species richness (log-transformed) (Table 1) and Shannon index (Table S3). For the complete disturbance scenario, the disturbance impact on TLC and NPP was on average reduced by 0.4 and 0.3 percentage points for every additional species on the landscape (Figure 1). While TLC_{impact} in a monospecific landscape was on average –11.3%, the same disturbance regime reduced live C stocks by only -6.7% in a landscape with all seven main study species present. However, our results also suggest a decreasing benefit of increasing species richness, i.e., adding more species to an already diverse system does not result in the same reduction in disturbance impact as it would for a species-poor system (cf. the asymptotic relationship in Figure 1).

The late successional landscape showed a more complex pattern of diversity effects on disturbance impacts. While NPP_{impact} was reduced by increasing species richness, particularly in systems with low richness levels, higher richness was found to increase TLC_{impact} for all three disturbance types in the last 100 years of the 500 year simulation period (Table 1; Figure 1). In other words, the TLC of species-rich late-seral landscapes responded more negatively to disturbance than their species-poor counterparts.

3.2 Tree diversity effects on the resilience of ecosystem functioning

Similarly to results for disturbance impact, the effects of diversity on resilience varied between different disturbances types, with the strongest diversity effects in the complete disturbance scenario (Figure S14). Generally, C uptake was less variable and more resilient to disturbances than C stocks, with the coefficient of variance on average 40% higher for TLC_{cv} compared to NPP_{cv} under a DRP of 300 years (Figure S10). Overall, tree species diversity significantly dampened the disturbance-induced variability in NPP and TLC. Under the latter scenario adding an additional species to the landscape on average reduces TLC_{cv} and NPP_{cv} by 12% and 13% in the first 100 years of the simulation (Figure 2). Furthermore, the average TLC_{cv} for a monospecific system was almost twice as high as for a seven-species landscape in the early successional stages (Figure S5). As with disturbance impact, the diversity signal did not differ substantially between the indicators tree species richness and Shannon index (Figure S14). Conversely to disturbance impact though, the different successional trajectories between species-rich and species-poor systems did not lead to a general reversal of the diversity effect on resilience for the late seral system (Figure 2).

3.3 The effect of increasing disturbance frequency

In order to investigate if and how an increase in disturbance frequency changes the role of diversity we also conducted all simulations of the complete disturbance scenario with a DRP of 150 years. This doubling of the disturbance frequency also doubled the average disturbance percentage on the landscape (0.67% yr^{-1} for the complete disturbance scenario), as well as the TLC_{impact} and NPP_{impact} (Figure S11). Our results indicate that the positive effect of diversity is amplified under higher disturbance frequency (Tables 1 and S3). Over all scenarios, the changes in disturbance effect with species richness (i.e., the slopes of the regression analysis) are between 1.7 and 2.9-fold greater under a DRP of 150 years. Diversity thus buffers from an increasing disturbance frequency. For early-seral systems, for instance, the increased TLC_{impact} caused by the elevated disturbance frequency (from -11.3% under a DRP of 300 years to -20.8% under a DRP of 150 years in a monospecific system) is almost fully buffered by increasing the richness on the landscape from one to seven tree species (to a TLC_{impact} of -12.9% under a DRP of 150 years).

3.4 Underlying mechanisms of diversity effects

For all analyzed aspects (disturbance impact and resilience) and seral stages (early and late) the diversity-related changes in system-level mean trait values had a stronger influence on TLC than trait variation or species identity effects (Figure 3). The patterns and individual traits identified as most influential, however, differed strongly with seral stage: a lower maturity age (i.e., minimum tree age for reproduction) was found to dampen disturbance impacts in the early seral system, as it increases the recolonization speed after disturbance events (see also Figure S15). With regard to resilience, shade tolerance was the most influential trait in the early seral system, indicating that increasing shade tolerance first stabilizes the system, but that systems comprised of only shade-tolerant species again experience increased variation (see Figure S18). Trait variation within the system affected both TLC_{impact} and TLC_{cv} positively in the early seral system, decreasing disturbance impact and increasing disturbance resilience, and thus underlining the contribution of functional diversity to our findings (Hooper et al. 2005; Thompson et al. 2009). Species identity effects were overall least influential, underlining that the diversity effects reported here are more strongly linked to diversity-related changes in individual traits rather than the presence or absence of particular species (and their specific trait combinations). For the early seral system the strongest identity effect was found for species that fill a mid-successional niche in our system, i.e., *Fraxinus excelsior*, *Picea abies*, and *Acer pseudoplatanus* (cf. Figure S2).

The diversity – disturbance relationship in late seral system, on the other hand, was more strongly driven by resource- and size-related traits, indicating that the late-seral systems are more strongly connected and driven by competitive exclusion. Traits related to competitive abilities with regard to light and water resources (i.e., maximum attainable tree height, minimum soil water potential for which water can be extracted from the soil) were found among the most influential indicators (Figure 3). Generally, however, influence patterns of mean traits and trait variation were less pronounced in old-growth systems compared to the early seral stage. Interestingly though, the strongest species identity effects were found for early- and mid-successional species, indicating that their presence on the landscape – despite having low abundance (cf. Figure S2)– can help to buffer the system from disturbances.

4. Discussion

Here we have quantitatively assessed how different levels of tree species diversity modulate the impact of disturbances on forest ecosystem functioning. We found that increasing diversity generally reduces the disturbance impact on carbon uptake and storage. Furthermore, our simulations indicate a clear positive relationship between diversity and resilience, with more diverse systems showing lower disturbance-induced variability in their trajectories and a faster recovery from disturbance events. Our results are thus in congruence with those observed in herbaceous communities (Tilman 1996; Cardinale et al. 2013b; Gross et al. 2014b) and overall support the two predictions made by the insurance hypothesis (Yachi and Loreau 1999). However, an in depth analysis of the diversity – disturbance relationship also revealed that the complexities of forest dynamics can strongly modulate and even reverse the patterns predicted from theories developed for simpler systems such as grasslands. We found that successional dynamics of forest landscapes – which are contingent on the available species pool and thus species diversity – can reverse the positive effect of diversity on moderating disturbance impacts. While species-poor systems (by definition) do not show strong successional changes in species composition over time, species-rich systems feature a pronounced change in dominant species in the 500-year simulation period (Figure S2).

Generally, the species that dominate forest composition at the end of this successional trajectory are also those that store the most C, as they exceed others in height and diameter, and are generally long-lived in nature (i.e., long C residence times). In species-rich systems, disturbance sets back this successional trajectory in the disturbed parts of the landscape, which means that the development towards a (C-rich) late-seral state is delayed in these systems. In species-poor systems, on the other hand, the species recolonizing disturbed areas are – due to the lack of competitors – in many instances already those that will ultimately dominate the system (Figure S8). Under the influence of disturbance, species-poor landscapes thus short-cut the successional development compared to species-rich landscapes, which leads to a higher TLC_{impact} in the latter systems.

This reverse pattern was also indicated in previous studies focusing on the diversity effect on forest ecosystem functioning, (e.g., Jiang et al. 2009; Potter and Woodall 2013). This highlights the importance of taking into account the full complexity of forest dynamics over the extended time scales of forest succession in order to comprehensively understand the links between disturbance, diversity, and ecosystem functioning (Thompson et al. 2009). The fact that we didn’t find a reversal of the diversity effect with successional development also for resilience points towards multiple pathways of how diversity influences disturbed ecosystems, and calls for further research on the dynamic interplay between diversity and disturbance (Franklin et al. 2002).

Our results also suggest a decreasing benefit of increasing species richness on disturbance impact and – to a lesser degree –resilience. This finding is in congruence with previous studies reporting a saturation effect of diversity on ecosystem functioning also in the absence of disturbance (e.g., Hooper et al. 2005; Morin et al. 2011). Our study thus predicts that species-poor forest landscapes will benefit more strongly from increased diversity levels than landscapes that are already rich in species. This is an important insight for ecosystem management, particularly in areas like central Europe, where century-long management practice has favored a small number of species at the expense of tree species richness (Spiecker et al. 2004). Even a small increase in species richness in such systems has the potential to considerably mitigate disturbance impacts and increase their stability.

A further interesting finding in the context of forest management is that the effects reported here are 'true' diversity effects rather than responses related to particular species (identity effect). For early seral systems, the traits crucially influencing our findings point towards recolonization and niche complementarity as the main processes driving the diversity effect (Morin et al. 2011; Lasky et al. 2014). Late-seral systems, on the other hand, are more strongly driven by competitive exclusion (Zhang et al. 2012; Lasky et al. 2014). Yet, the presence of mid-successional species was found to have a positive influence in both early and late seral systems, a finding that could be further explored in the context of forest ecosystem management.

However, it has to be noted that several important pathways of how diversity influences disturbance impact and resilience were not considered in our analysis. We, for instance, did not consider the effects of differential disturbance sensitivity of species, and only accounted for size-related differences in sensitivity to disturbance in our top-down and bottom-up scenarios. Yet, it is well documented that individual tree species differ in their ability to withstand disturbances such as wind and fire (Fernandes et al. 2008; Mitchell 2013). Furthermore, many important disturbance agents such as insects are host-specific, and thus only affect selected species within a landscape (Pasztor et al. 2014). These mechanisms decrease the disturbance severity in diverse landscapes, and further contribute to the mitigating effect of diversity on disturbance impacts. Moreover, spatial heterogeneity in biophysical conditions (e.g., climate, soil) across the landscape not only influence disturbance processes but also induce variation in local ecosystem functioning (Turner et al. 2012; Seidl et al. 2012b), and contribute to the resilience of forest ecosystems. Our analysis only considers first-order effects of tree species diversity (related to the response diversity to disturbance), and is likely a conservative estimate of the overall diversity effect.

We also found that diversity effects varied in magnitude with disturbance severity and frequency. Our simulations indicate that with increasing disturbance severity (i.e., an increasing level of mortality within the disturbed patches on the landscape) also the positive effects of diversity increases, being most pronounced in the complete disturbance scenario of our analysis. Furthermore, our results suggest that the positive effect of tree species diversity on ecosystem functioning increases with an increasing frequency of disturbance (represented here by a reduced disturbance rotation period). In other words, the more disturbed a system was in our simulations, the stronger it benefited from higher levels of species richness. This finding could be of high relevance for future ecosystem management, considering that disturbance levels are predicted to increase in the future as a result of climate change (Seidl et al. 2014c).

We here show that the negative impact of intensifying disturbance regimes could be buffered by increasing the diversity of forest landscapes. Such an increase in tree species diversity would thus not only have positive effects for habitat quality and plant species diversity (Vockenhuber et al. 2011) it would also make the climate change mitigation function of forest ecosystems (i.e., their ability to sequester carbon from the atmosphere and sustain high C densities over time) more robust to potential future changes in the disturbance regime.

Acknowledgements

This study was conducted under the European Commission collaborative research project FunDivEUROPE (project no. 265171). R. Seidl acknowledges further support from a European Commission’s Marie Curie Career Integration Grant (PCIG12-GA-2012-334104). We are thankful to S. Kolb for kindly providing soil data, T. Wutzler for sharing yield table data and to M. Liebergesell for giving important insights on the potential natural vegetation in Hainich National Park. We also acknowledge M.J. Lexer for fruitful discussion and administrative support, as well as one anonymous Reviewer and the Editor for helpful comments on an earlier version of the manuscript. The computational results presented here have been achieved in part using the Vienna Scientific Cluster (VSC).

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Tables

Table 1 – Tree species richness effects on disturbance impact and disturbance induced-variability (cv) of net primary productivity (NPP) and total live carbon (TLC) in two seral stages of forest succession. Shown are the coefficients of separate linear regression model using tree species richness (log-transformed) as the independent variable. Disturbance type refers to different disturbance severity levels and size-specific vulnerabilities (see Figure S4), while DPR indicates different disturbance frequencies (disturbance rotation periods (DRP) of 300 and 150 years, respectively). All coefficients are significant at α=0.05, except when indicated with ns Abbreviations: ns = not significant; dim = dimensionless.

Seral stage	**Disturbance type**	**DRP**	**TLC_{impact}**		**NPP_{impact}**		**TLC_{cv}**		**NPP_{cv}**	
			Intercept [%]	Slope [%]	Intercept [%]	Slope [%]	Intercept [dim.]	Slope [dim.]	Intercept [dim.]	Slope [dim.]
Early	Complete	300	-11.30	2.37	-7.37	1.94	0.030	-0.0060	0.020	-0.0052
	Complete	150	-20.79	4.04	-14.06	3.57	0.046	-0.010	0.030	-0.0089
	Top-down	300	-5.32	1.09	-0.79	0.21	0.015	-0.0039	0.0029	-0.00095
	Bottom-up	300	-2.45	1.56	-2.38	1.08	0.008	-0.0020	0.0072	-0.0023
Late	Complete	300	-10.62	-4.24	-5.33	2.09	0.035	-0.0043	0.024	-0.0090
	Complete	150	-23.50	-2.84	-14.16	6.02	0.046	-0.0072	0.031	-0.011
	Top-down	300	-6.24	-2.37	4.70	-0.62	0.016	0.0020	0.0077	-0.0017
	Bottom-up	300	1.01	-2.04	-4.4	1.87	0.0049	-3.2E-05^{ns}	0.0083	-0.0034

Figure legends

Figure 1 –Disturbance impact on net primary productivity (NPP) and total live carbon stocks (TLC) as a function of tree species richness for early and late successional stages (disturbance rotation period (DRP) of 300 years, complete disturbance scenario). Points represent the mean impact per each richness level, bold lines denote the interquartile range, and whiskers the 5th - 95th percentile interval.

Figure 2 – Disturbance-induced variation in NPP and TLC variation (coefficient of variance, cv) as a function of tree species richness for early and late successional stages (DRP=300 years, complete disturbance scenario). A decreasing indicator value signifies increasing resilience. Points represent the mean value for each richness level, bold lines denote the interquartile range, and whiskers the 5th - 95th percentile interval.

Figure 3 – Relative importance of factors influencing diversity – disturbance relationships for TLC impact (top row) and resilience (bottom row) in early (a, c) and late (b, d) seral stages. The two most important variables for the effects of (i) mean traits, (ii) trait variation, and (iii) species identity are displayed over all disturbance types, rotation periods, and replicates (mean ± standard deviation). The relative importance of predictors was determined by means of Random Forests, and is expressed as the percentage increase in mean square error (MSE) when values of the respective variable are randomly permuted. High values indicate a high relevance of the variable for the simulation results.

Figures

Figure 1

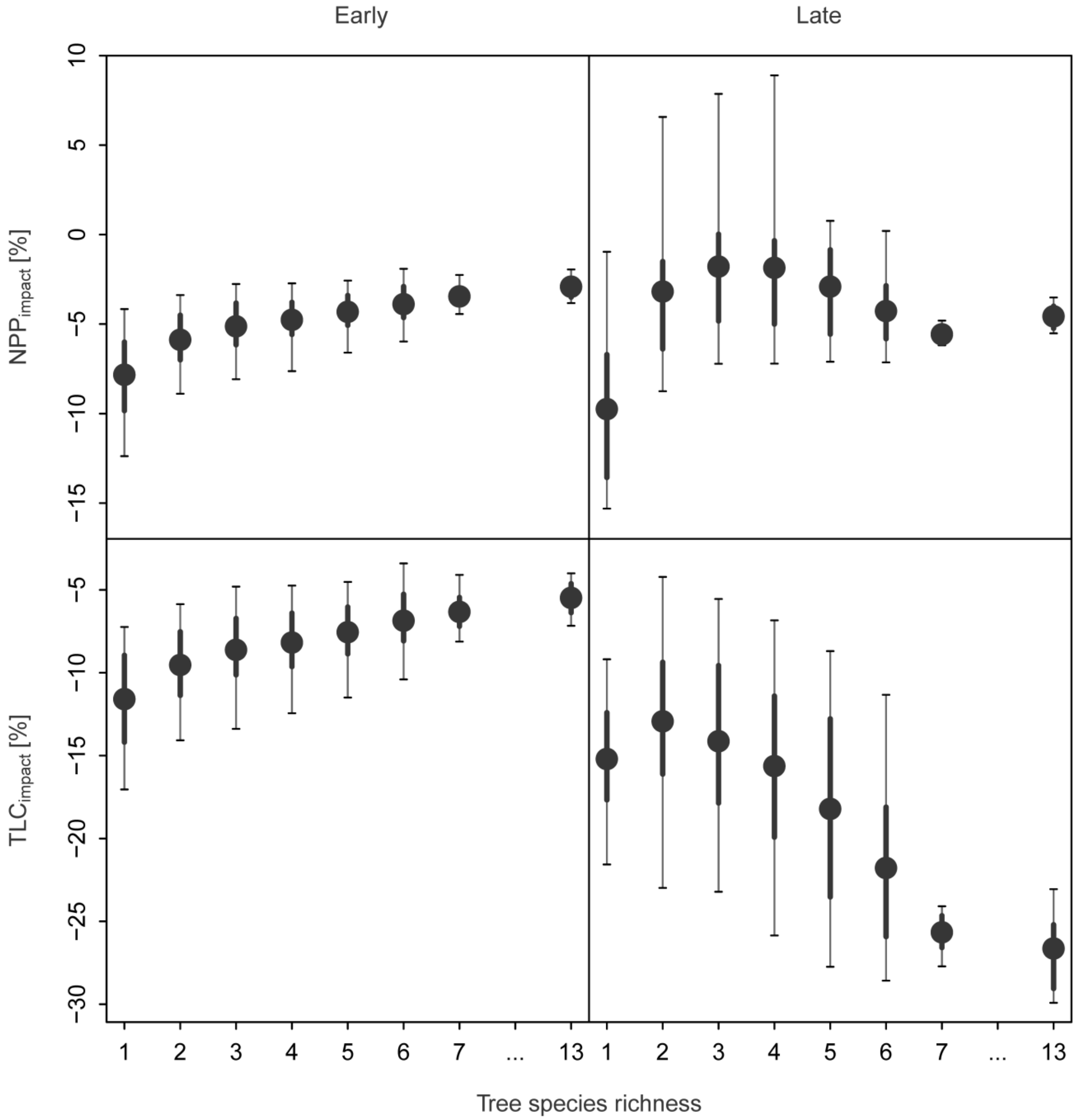


Figure 2

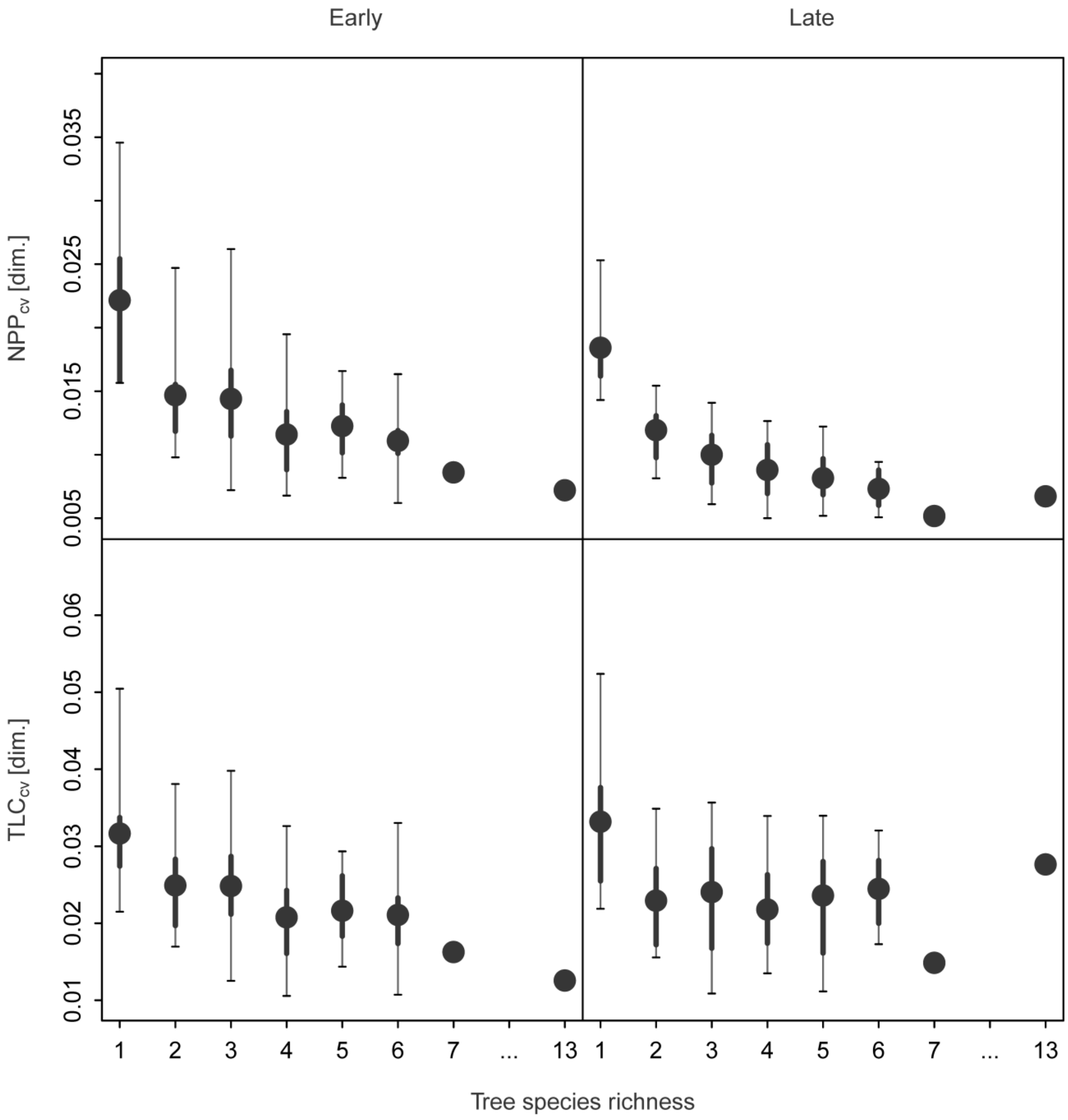
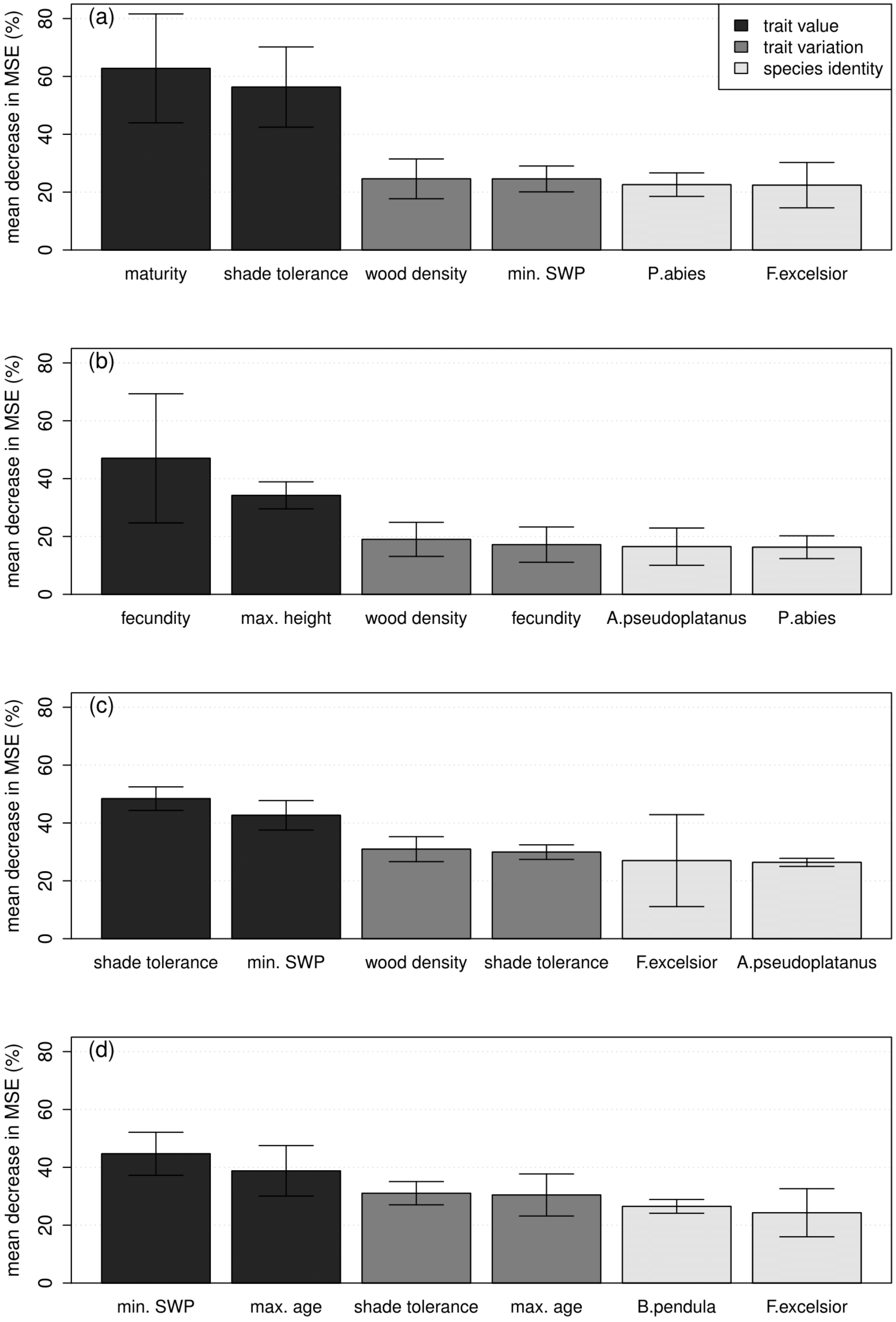

Early
Late
NPP$_{cv}$ [dim.]
0.005
0.015
0.025
0.035
TLC$_{cv}$ [dim.]
0.01
0.02
0.03
0.04
0.05
0.06
1
2
3
4
5
6
7
...
13
1
2
3
4
5
6
7
...
13
Tree species richness

Figure 3



(a)
mean decrease in MSE (%)
0
20
40
60
80
trait value
trait variation
species identity
maturity
shade tolerance
wood density
min. SWP
P.abies
F.excelsior
(b)
mean decrease in MSE (%)
0
20
40
60
80
fecundity
max. height
wood density
fecundity
A.pseudoplatanus
P.abies
(c)
mean decrease in MSE (%)
0
20
40
60
80
shade tolerance
min. SWP
wood density
shade tolerance
F.excelsior
A.pseudoplatanus
(d)
mean decrease in MSE (%)
0
20
40
60
80
min. SWP
max. age
shade tolerance
max. age
B.pendula
F.excelsior

ELECTRONIC SUPPLEMENTAL MATERIAL (ESM)

Tree species diversity mitigates disturbance impacts on the forest carbon cycle

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Evaluation of iLand at Hainich

The capacity of iLand to simulate forest ecosystem dynamics at Hainich National Park was evaluated in two phases, aiming to test (a) simulated tree species mortality, dendrometry and productivity, and (b) long-term successional trajectories as well as old-growth composition and structure.

In the first evaluation phase, we analyzed mortality, tree height, diameter growth, and productivity for the five major mid- to late-seral species at Hainich (Baeten et al. 2013) in monospecific 100 ha simulations over 100 years. To evaluate growth and productivity against yield table data (i.e., the expected stand development trajectories over age for a given site index) we simulated random thinnings (i.e., a non-selective, not size- or cohort-specific removal of trees) at regular intervals in order to replicate the stand densities reported in yield tables (Wimmenauer 1919; Jüttner 1955; Marschall 1975) in the simulation. Subsequently, the target variables diameter at breast height (d_{mean}, cm), dominant height (h_{dom}, m) and mean annual increment (MAI, m^3 ha^{-1} $year^{-1}$) were compared to yield table data at age 100 years (Table S1). To test simulated tree mortality, iLand was initialized with the same young, even-aged, pure stands of randomly distributed individuals as for the yield table runs, but simulations were run for 100 years without management interventions. Stand density trajectories were tested against the empirical self-thinning rule established by Reineke (1933) (Figure S1).

Table S1 - Comparison of simulated dominant height (h_{dom}), mean diameter (d_{mean}), and mean annual increment (MAI) at age 100 to yield table data for the five main tree species at Hainich National Park. YT: yield table (Wimmenauer 1919; Jüttner 1955; Marschall 1975).

Tree species	h_{dom} [m]		d_{mean} [cm]		MAI [m^3 ha^{-1} $year^{-1}$]	
	YT	iLand	YT	iLand	YT	iLand
Acer pseudoplatanus L	22.2	21.6	23.8	23.9	5.3	4.9
Fagus sylvatica L.	27	24.9	29.2	26.1	6.0	6.3
Fraxinus excelsior L.	32.4	30.9	35.5	40.7	5.8	8.1
Picea abies (L.) Karst.	29.3	25.0	31.2	34.0	9.0	8.1
Quercus petraea (Mattuschka) Liebl.	24.5	24.7	32.1	34.2	5.4	6.3

In the second evaluation phase we tested iLand's ability to reproduce the expected equilibrium composition and structure at Hainich. Simulations were initialized from bare ground for a landscape of 2500 ha and were run for 500 years. 13 species were allowed in the simulation with a constant background probability of seed availability of P_{seed}=0.01, uniformly distributed over the simulation landscape area. The results show a sensible succession from early-seral species such as *Betula pendula* to an intermediate phase where *Fraxinus excelsior* and *Picea abies* dominate, and to a late-seral stage dominated by *Fagus sylvatica* (Figure S2). This corresponds well with the potential natural vegetation composition expected for the area (Bohn et al. 2004). Furthermore, also the stand structure at the end of the 500 year simulation period conformed to expectations, with stem number decreasing exponentially with diameter (Figure S3).

These two evaluation experiments indicate that iLand is able to reproduce expected values of dendrometry and growth, as well as trajectories of long-term forest dynamics at Hainich National Park.

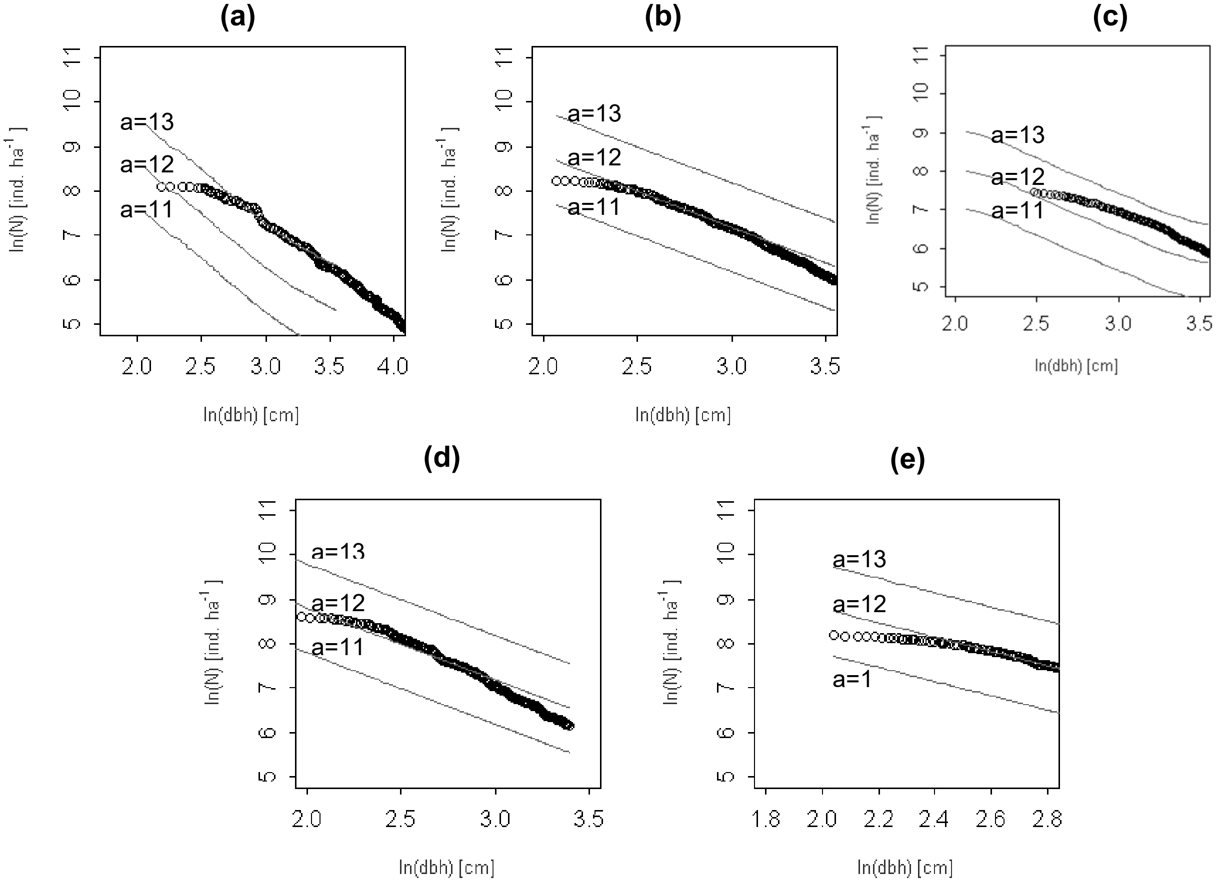

Figure S1 - Simulated stand density (N) reduction over dbh for pure stands of (a) *Picea abies*, (b) *Acer pseudoplatanus*, (c) *Fraxinus excelsior*, (d) *Fagus sylvatica*, and (e) *Quercus petraea* in comparision to Reinekes rule (Reineke, 1933). Lines in gray correspond to theoretical trajectories of N and dbh based on Reinekes rule, with a=11 referring to stands with low site index (i.e., an indicator of site quality and productivity based on the height of the dominant trees at a specific age,) and a=13 to those with high site index (Pretzsch and Biber 2005). Dots are individual years in the simulation with iLand. Please note that the axes are logarithmically scaled.

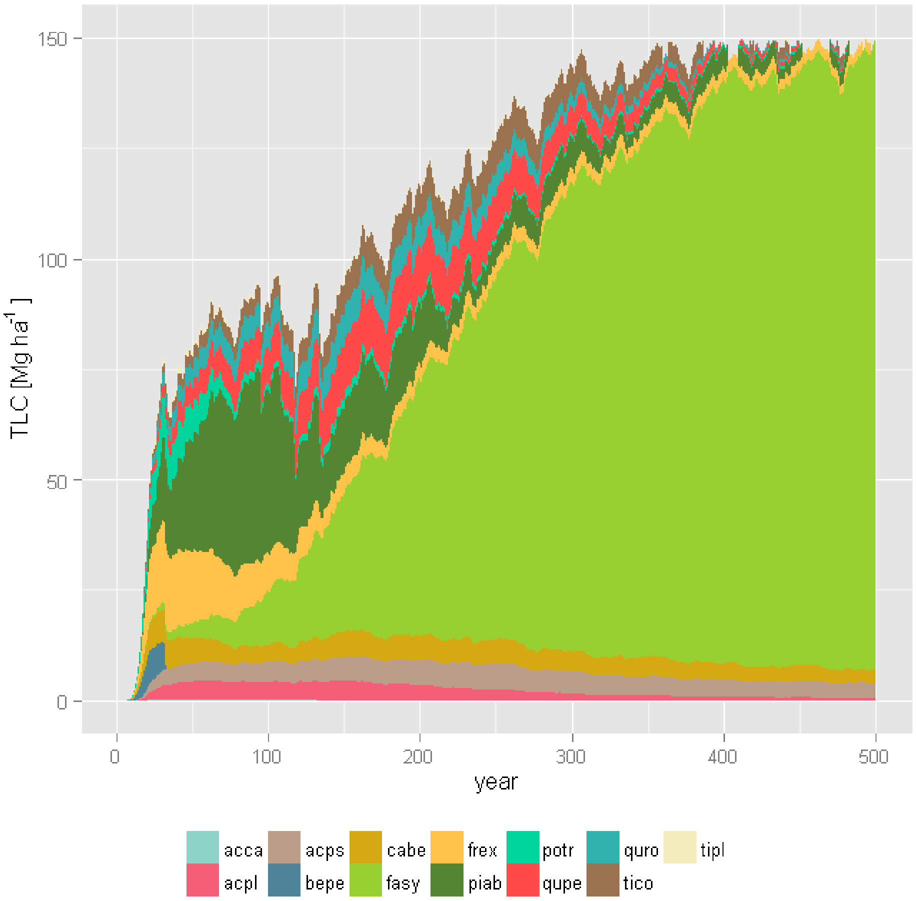

Figure S2 – Simulated species composition and total live carbon stocks (TLC, Mg ha $^{-1}$) over 500 years at Hainich National Park. Shown is the forest sucession of an undisturbed simulation with all 13 species of the potential natural vegetation composition (Bohn et al. 2004) potentially present at the landscape. Abbreviations: acca – *Acer campestre* L.; acpl – *Acer platanóides* L.; acps – *Acer pseudoplatanus* L.; bepe: *Betula pendula* Roth. ; cabe – *Carpinus betulus* L.; fasy – *Fagus sylvatica* L.; frex – *Fraxinus excelsior* L.; piab – *Picea abies* (L.) Karst.; potr – *Populus tremula* L.; qupe – *Quercus petraea* (Mattuschka) Liebl.; quro – *Quercus robur* L.; tico – *Tilia cordata* Mill.; tipl – *Tilia platyphyllos* Scop.

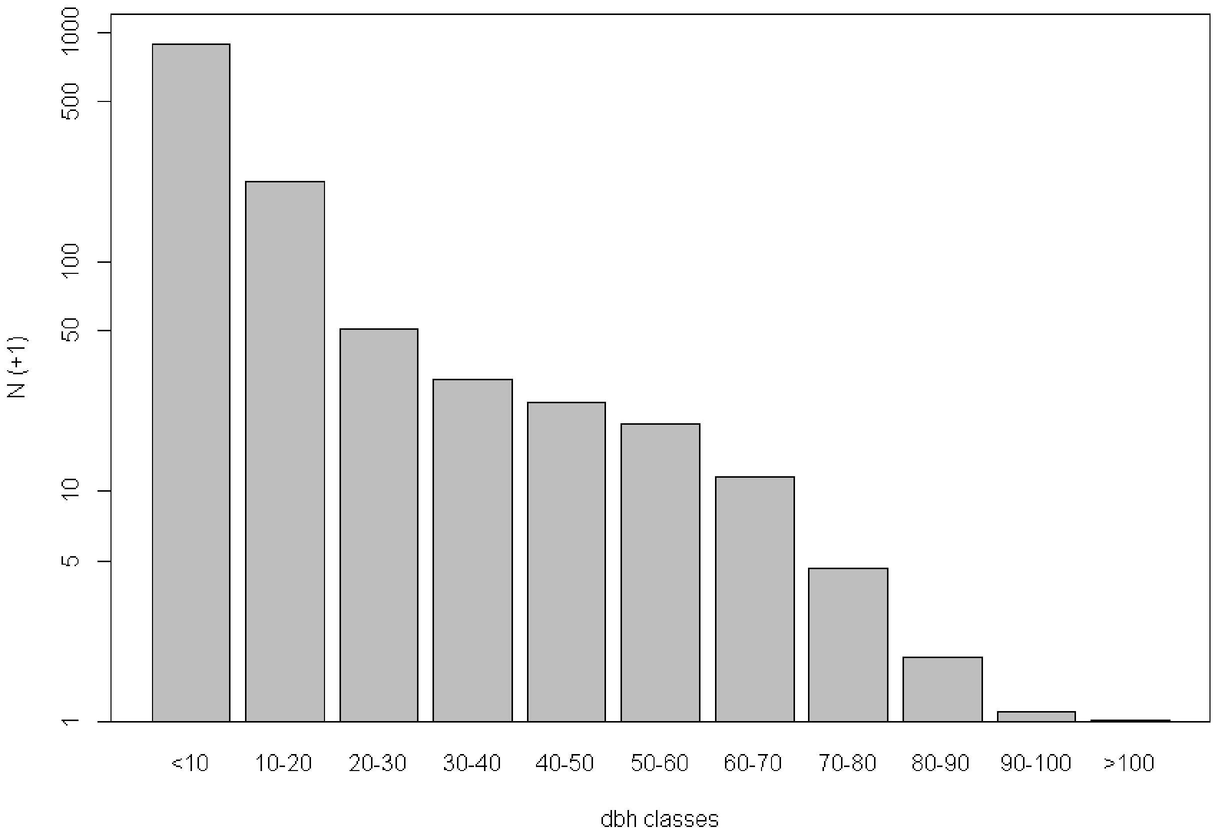

Figure S3 – Simulated stem number (N) distribution over diameter at breast height (dbh) after 500 years for the study area.

Study design

Table S2 – The total number of simulations performed for each richness level (n=1 to 13), disturbance rotation period (DRP 150 and 300 years), and disturbance type (complete, top-down and bottom-up).

Richness level	DRP=300			DRP=150	Σ
	Complete	Top-down	Bottom-up	Complete	
1	70	70	70	70	280
2	210	210	210	210	840
3	350	350	350	350	1400
4	350	350	350	350	1400
5	210	210	210	210	840
6	70	70	70	70	280
7	10	10	10	10	40
13	10	10	10	10	40
Σ	**1280**	**1280**	**1280**	**1280**	**5120**

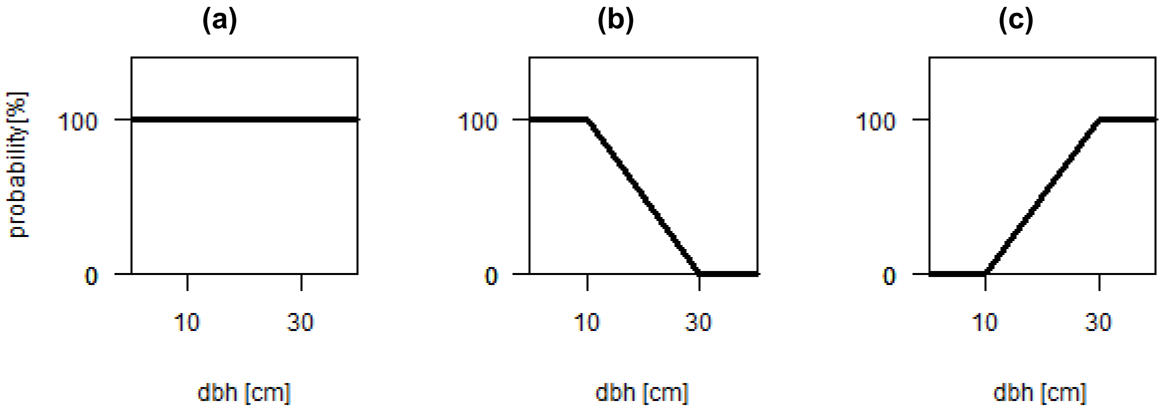

Figure S4 – Schematic representation of the simulated disturbances types (a) complete, (b) bottom-up , and (c) top-down disturbance with regard to their size-specific (dbh= diameter at breast height) mortality probability within the disturbed patches.

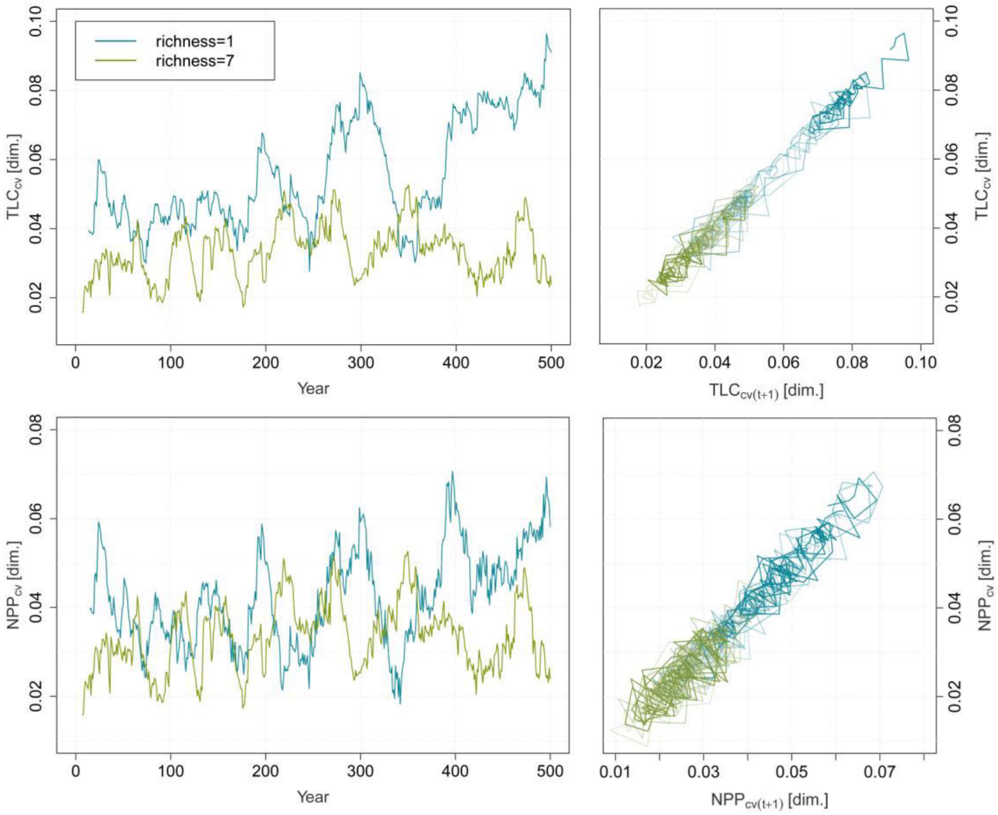

Figure S5 – Examples for the temporal development of the coefficients of variation (cv) between replicated simulations for NPP and TLC (left panels), and the corresponding attractor plots (right panels). The figure illustrates the increased resilience (convergence towards an attractor of significantly lower variability) of both TLC and NPP in the scenario of higher species richness (complete disturbance type and disturbance rotation period of 300 years). Blue corresponds to a single species scenario (*Quercus petraea* (Mattuschka) Liebl.), while green indicates a richness level of seven species (*Acer pseudoplatanus* L.; *Betula pendula* Roth; *Fagus sylvatica* L.; *Fraxinus excelsior* L.; *Picea abies* (L.) Karst; *Populus tremula* L.; *Quercus petraea* (Mattuschka) Liebl. In the attractor plots (right panels) elapsed time is displayed by increasing line opacity.

Tree species richness and diversity over time

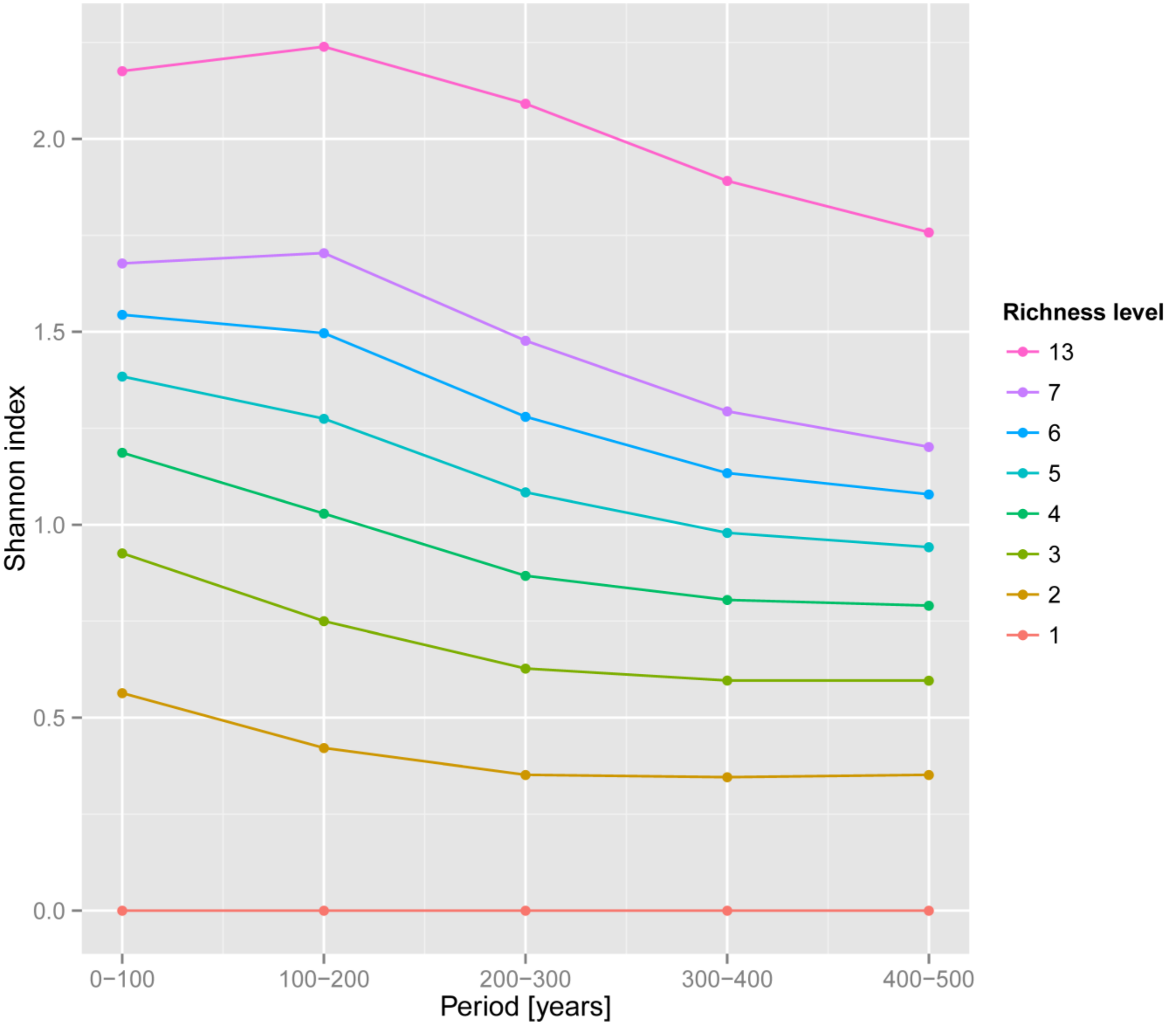

Figure S6 – Variation in Shannon index over the 500 year simulation period for the studied richness levels (1-7 and 13). Points indicate the mean Shannon index in the corresponding 100 year period. All disturbances types and disturbance rotation periods were included in the figure.

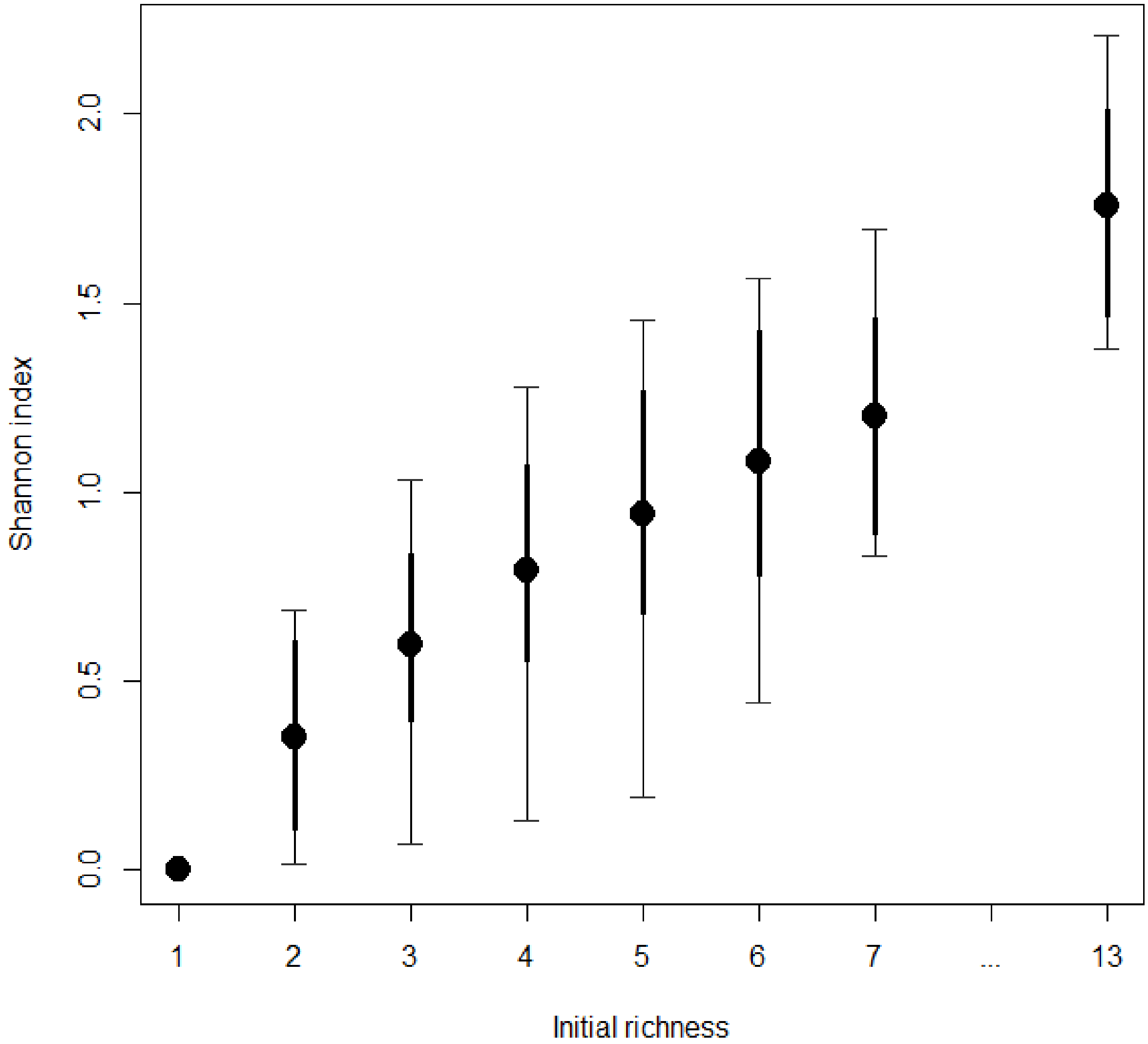

Figure S7 – Relationship between the initial richness level of the study design and the mean Shannon index over last 100 years of the simulation. All disturbances types and disturbance rotation periods were included in the figure. Points represent the mean Shannon index over last 100 years of the simulation per each richness level, bold lines denote the interquartile range, and whiskers the 5th – 95th percentile interval.

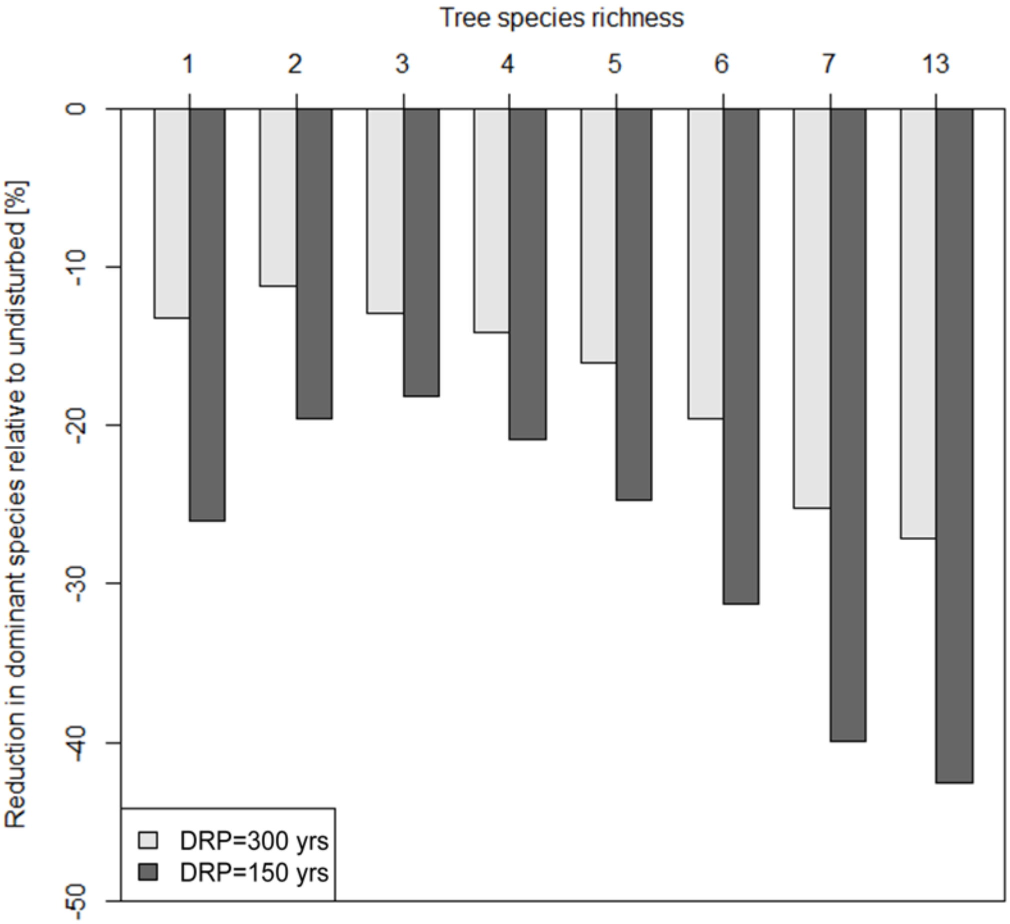

Figure S8 – Successional setback resulting from disturbance at two disturbance rotation periods (DRP), and its variation with tree species richness level. Disturbed landscapes are compared to undisturbed simulations for the respective species set, and the y-axis indicates the deviation of the species share of the dominant species at the end of the simulation (i.e., the dominating late-seral species, e.g., *Fagus sylvatica* in Figure S2). For instance, compared to the undisturbed run in Figure S2 (tree species richness: 13), the share of *Fagus sylvatica* is reduced by -30.2% in the last 100 years of the study period under a DRP of 300 years (complete disturbance scenario).

Disturbance impact on forest ecosystem C cycling

Disturbance impacts on C stocks and fluxes varied considerably with the disturbance type (i.e., complete, top-down, and bottom-up). This is mostly the effect of variable disturbance severities in the different disturbance scenarios, which translate to considerable differences in disturbance percentages (i.e., TLC removed per year on average, relative to pre-disturbance TLC) despite an equal disturbance frequency. Disturbance percentage was highest for the complete disturbance scenario (0.33% yr^{-1}), while top-down (0.28% yr^{-1}) and bottom-up (0.04% yr^{-1}) disturbances differed strongly in their disturbance percentage due to size-specific severities (DRP 300 years, early-seral system).

Under a DRP of 300 years, complete disturbance on average reduced NPP by -5.1% and TLC by -8.5% in the early stages of forest development (Figure S9). Bottom-up disturbance of the same frequency and rotation period reduced TLC by only -0.6%, and had the lowest impact on C storage among the three studied disturbance types. In general, disturbances reduced TLC more strongly in late-seral stages than in early-successional landscapes. While overall also negative, the disturbance impact on NPP was more complex. Top-down disturbance, for instance, increased NPP particularly in late successional landscapes (average NPP_{impact}= +3.9% over all species combinations; Figure S9) as a result of a thinning effect (i.e., reduced density resulting in improved resource use and growth of remaining trees) and rejuvenation of the landscape (i.e., younger, more productive trees). In the complete disturbance scenario these positive effects of disturbance on NPP were, however, offset by reduced leaf area levels and thus reduced overall resource utilization on the landscape (average NPP_{impact}= -4.9%).

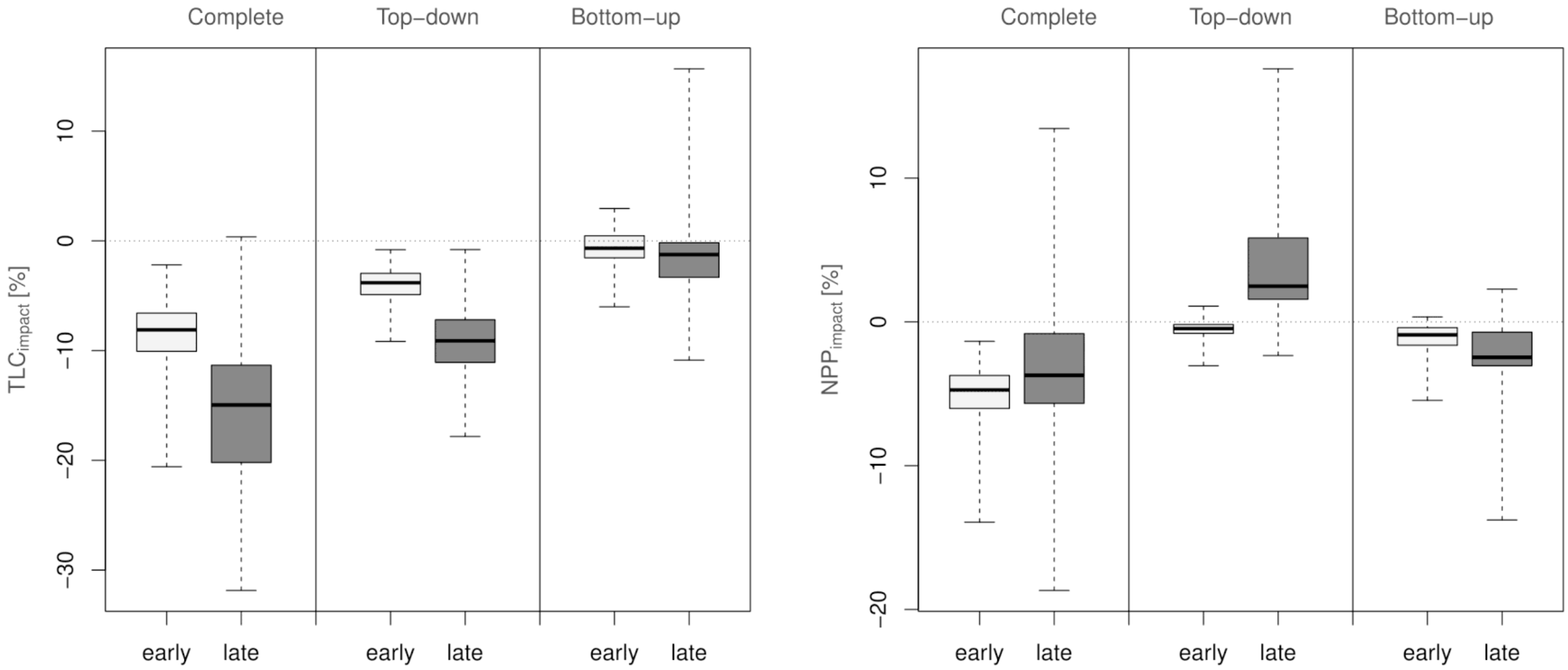

Figure S9 – Disturbances impact on total live carbon stocks (TLC) and net primary productivity (NPP) at Hainich forest for early and late seral stages (first and last 100 years of the 500 year study period). Shown is the impact of complete, top-down and bottom-up disturbances on TLC (left panel) and NPP (right panel) under a disturbance rotation period (DRP) of 300 years.

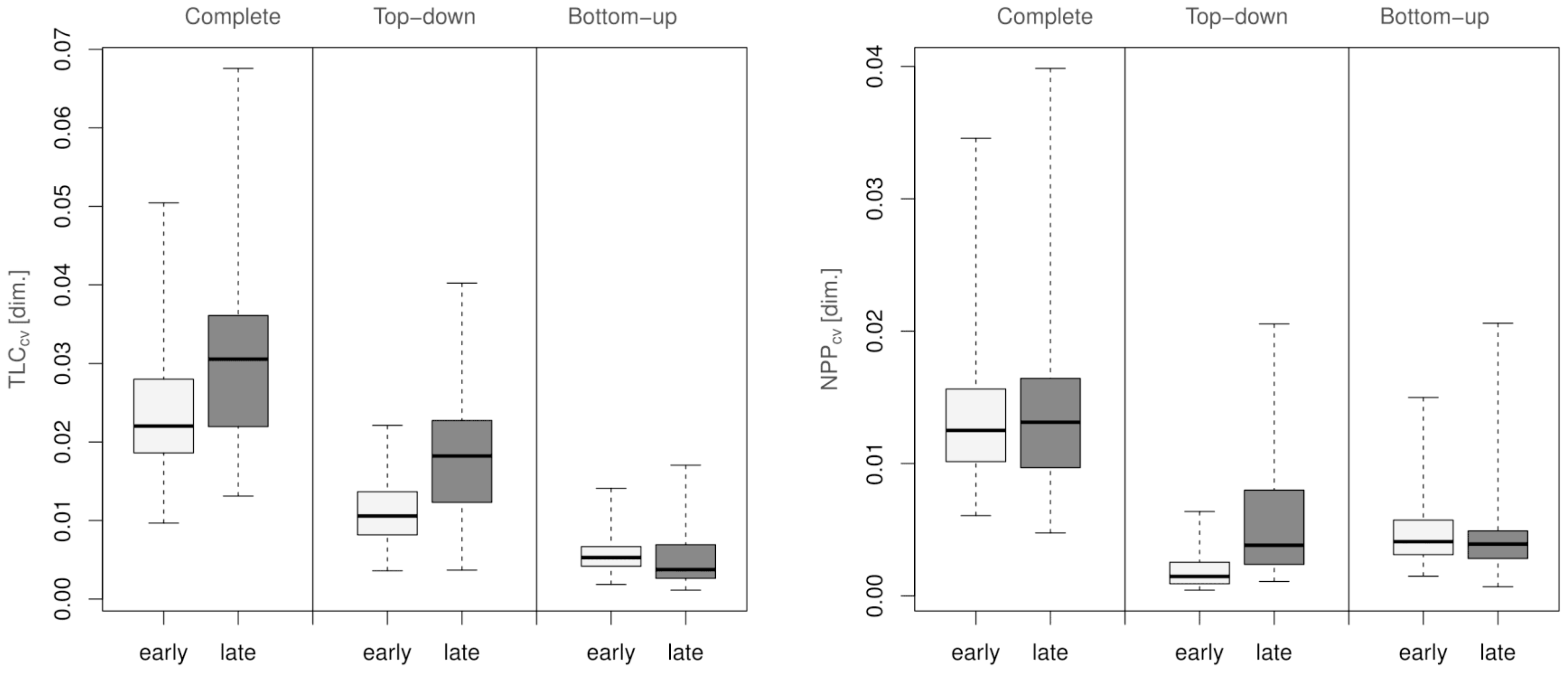

Figure S10- Disturbances-induced variability of TLC and NPP at Hainich forest for early and late seral stages. Shown is the coefficient of variance of TLC (left panel) and NPP (right panel) under complete, top-down and bottom-up disturbances for a DRP of 300 years.

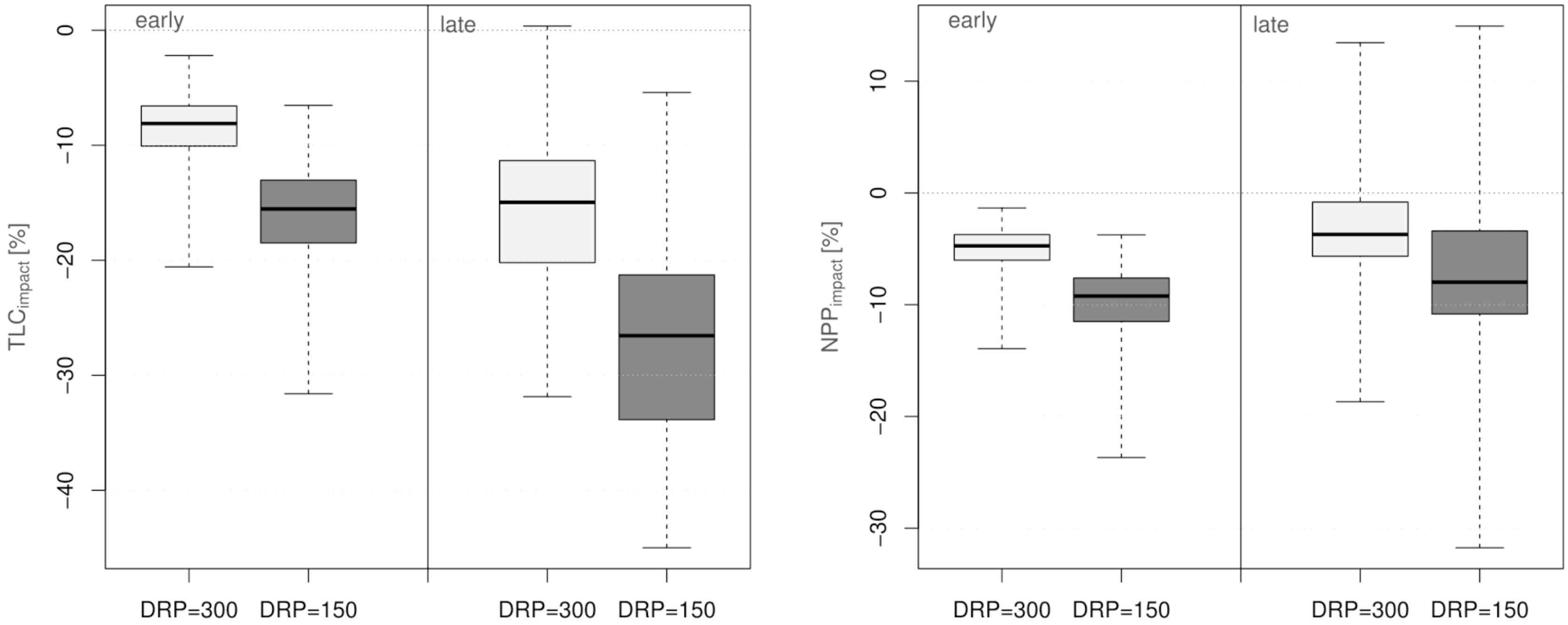

Figure S11 –Disturbance impact on TLC (left panel) and NPP (right panel) under two different disturbance rotation period (DRP=150 and 300 years) in early and late seral stages (complete disturbance scenario).

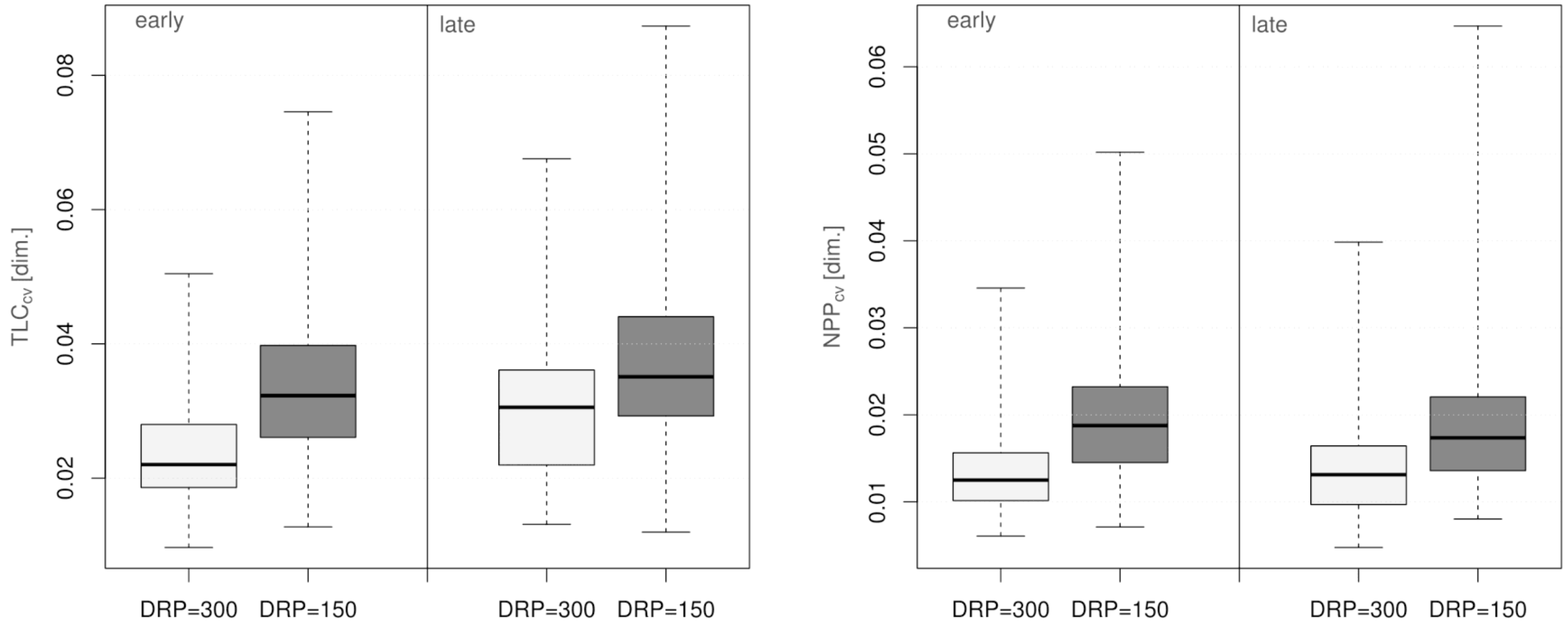

Figure S12 – Disturbance-induced variability of TLC (left panel) and NPP (right panel) under two disturbance rotation period (DRP=150 and 300 years) in early and late seral stages (complete disturbance scenario).

Tree diversity effects on disturbance impact

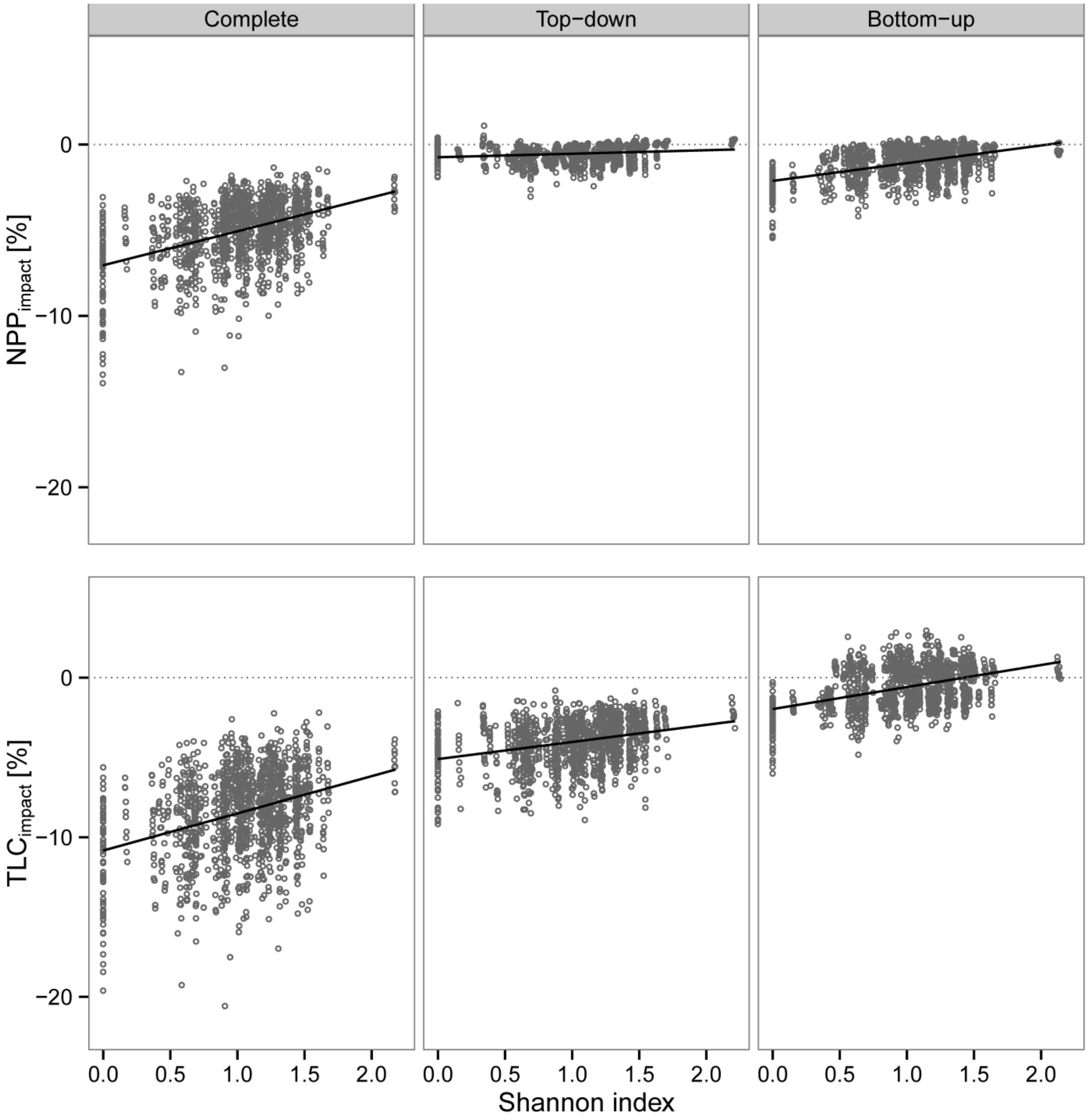

Figure S13 –Disturbance impact on NPP and TLC as a function of Shannon index (early seral stage, DRP=300 years). Panel columns refer to different disturbance types – see text and Figure S4 for details. Disturbance impact was calculated as the percent difference between a disturbed simulation to the respective undisturbed simulation with the same species combination. Black lines indicate a linear regression over the data.

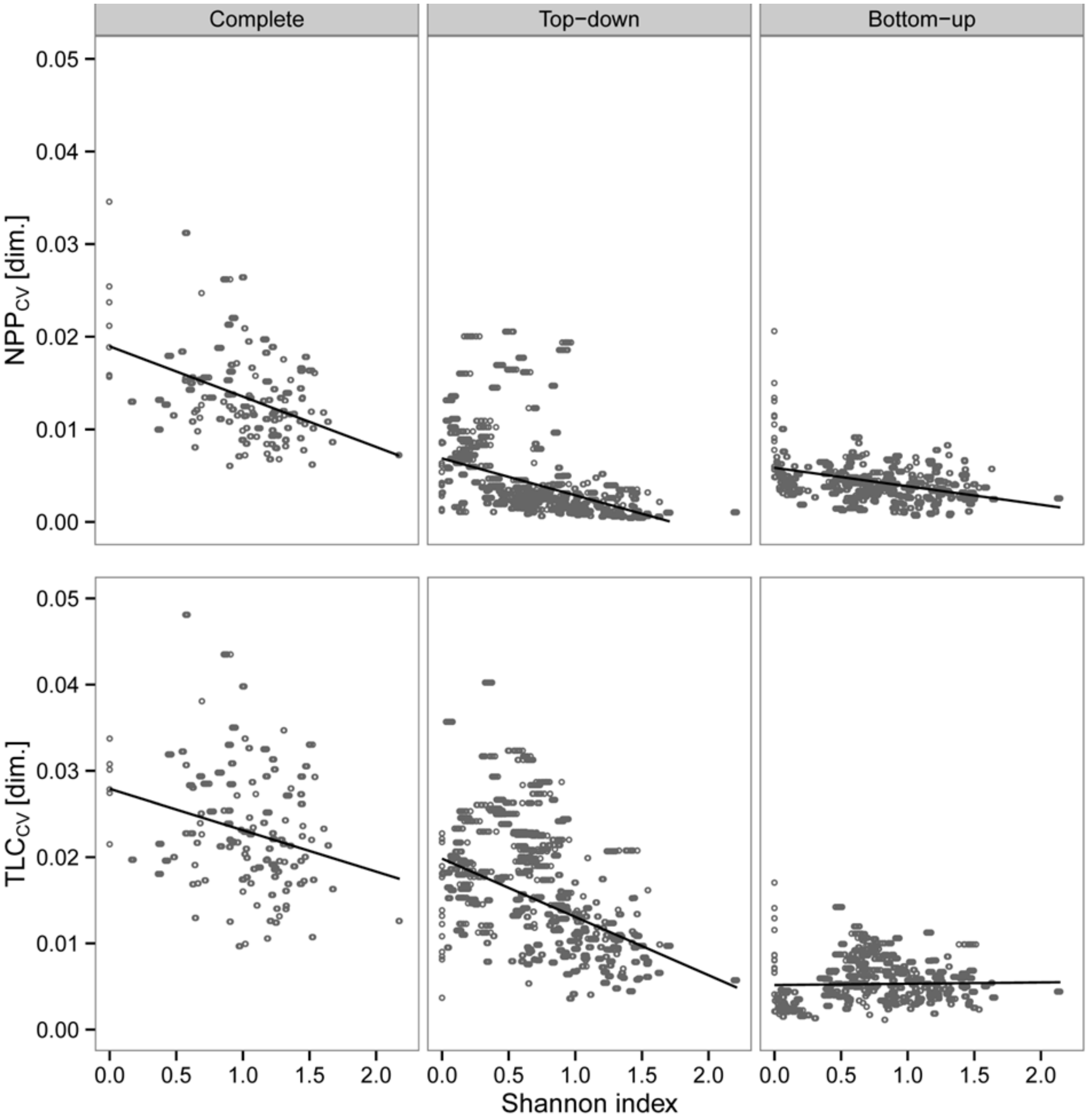

Figure S14 – Disturbance- induced variation in NPP and TLC (coefficient of variance, cv) as a function of Shannon index (early seral stage, DRP 300 years). Panel columns refer to different disturbance types – see text and Figure S4 for details. The cv was here used to measure the variability between otherwise identical scenario realizations, and is thus inversely related to system resilience. Black lines are from the linear regression models.

Table S3 – Diversity effects on disturbance impact and disturbance induced-variability (cv) of net primary productivity (NPP) and total live carbon (TLC) in two seral stages of forest succession. Shown are the coefficients of separate linear regression model using Shannon index as the independent variable. Disturbance type refers to different disturbance severity levels and size-specific vulnerability (see Figure S4), while disturbance rotation period (DRP) indicates different disturbance frequencies (DRP of 300 years and 150 years, respectively). All coefficients are significant at α=0.05.

Seral	**Disturbance**		**TLC_{impact}**		**NPP_{impact}**		**TLC_{cv}**		**NPP_{cv}**	
stage	**type**	**DRP**	Intercept [%]	Slope [%]	Intercept [%]	Slope [%]	Intercept [dim.]	Slope [dim.]	Intercept [dim.]	Slope [dim.]
Early	Complete	300	-10.82	2.32	-7.05	1.98	0.029	-0.0059	0.018	-0.0054
	Complete	150	-19.97	3.94	-13.48	3.61	0.045	-0.011	0.029	-0.0096
	Top-down	300	-5.10	1.07	-0.74	0.20	0.015	-0.0041	0.0028	-0.001
	Bottom-up	300	-1.97	1.38	-2.12	1.03	0.0078	-0.0022	0.0068	-0.0023
Late	Complete	300	-12.23	-4.28	-5.32	3.11	0.036	-0.0073	0.021	-0.0100
	Complete	150	-23.14	-4.03	-12.87	6.33	0.045	-0.0085	0.029	-0.011
	Top-down	300	-8.65	-0.80	5.44	-2.74	0.0079	-0.0040	0.0079	-0.004
	Bottom-up	300	-1.55	0.25	-3.82	3.30	0.0041	0.0014	0.0061	-0.0039

Underlying mechanisms

Table S4 – Traits of the seven main tree species studied. The trait values given are the species-specific parameters used in the iLand simulation model (Seidl et al. 2012). dim. = dimensionless

Species code	Wood Density [kg/m3]	Maximum Age [years]	Maximum Height [m]	Shade Tolerance [dim.]	Maturity Years [years]	Fecundity [n/m^2]	Sapling Height Growth Potential [m]	Seed Dispersal [m]	Minimum Soil Water Potential [MPa]
acps	570	500	37	3.73	27	16.5	2.6	190	-1.2
bepe	610	160	29	1.5	30	500	3.0	250	-0.725
fasy	680	600	48	4.4	55	15	2.4	90	-1.08
frex	650	300	42	2.66	32	24.2	2.9	190	-1.15
piab	430	600	56	3.5	40	171	2.5	190	-0.675
potr	420	140	30	2.22	15	2013	3.1	250	-1.395
qupe	650	1000	45	2.7	35	25	2.5	90	-1.53

Species abbreviations:

acca – *Acer campestre* L.; acpl – *Acer platanoides* L.; acps – *Acer pseudoplatanus* L.; bepe: *Betula pendula* Roth. ;cabe – *Carpinus betulus* L.; fasy – *Fagus sylvatica* L.; frex – *Fraxinus excelsior* L.; piab – *Picea abies* (L.) Karst.; potr – *Populus tremula* L.; qupe – *Quercus petraea* (Mattuschka) Liebl.; quro – *Quercus robur* L.; tico – *Tilia cordata* Mill.; tipl – *Tilia platyphyllos* Scop.

Species parameters description:

Wood Density - density of the stem wood (kg/m^3)

Maximum Age - maximum attainable age for a species (years)

Maximum Height - maximum attainable height for a species (m)

Shade tolerance - classification where 1 equals very shade intolerant, and 5 is very shade tolerant (dimensionless)

Maturity Years - minimum age for trees of a species to produce seeds (years)

Fecundity – viable seedlings per m^2 canopy surface area (n/m^2)

Sapling Height Growth Potential - maximum height growth of a sapling of 2 m height under optimal environmental conditions (m)

Seed Dispersal – seed dispersal distance that is exceeded by only one percent of all seeds produced by an individual

Minimum soil water potential (SWP) - the minimum pressure level up to which a species is still able to extract water from the soil

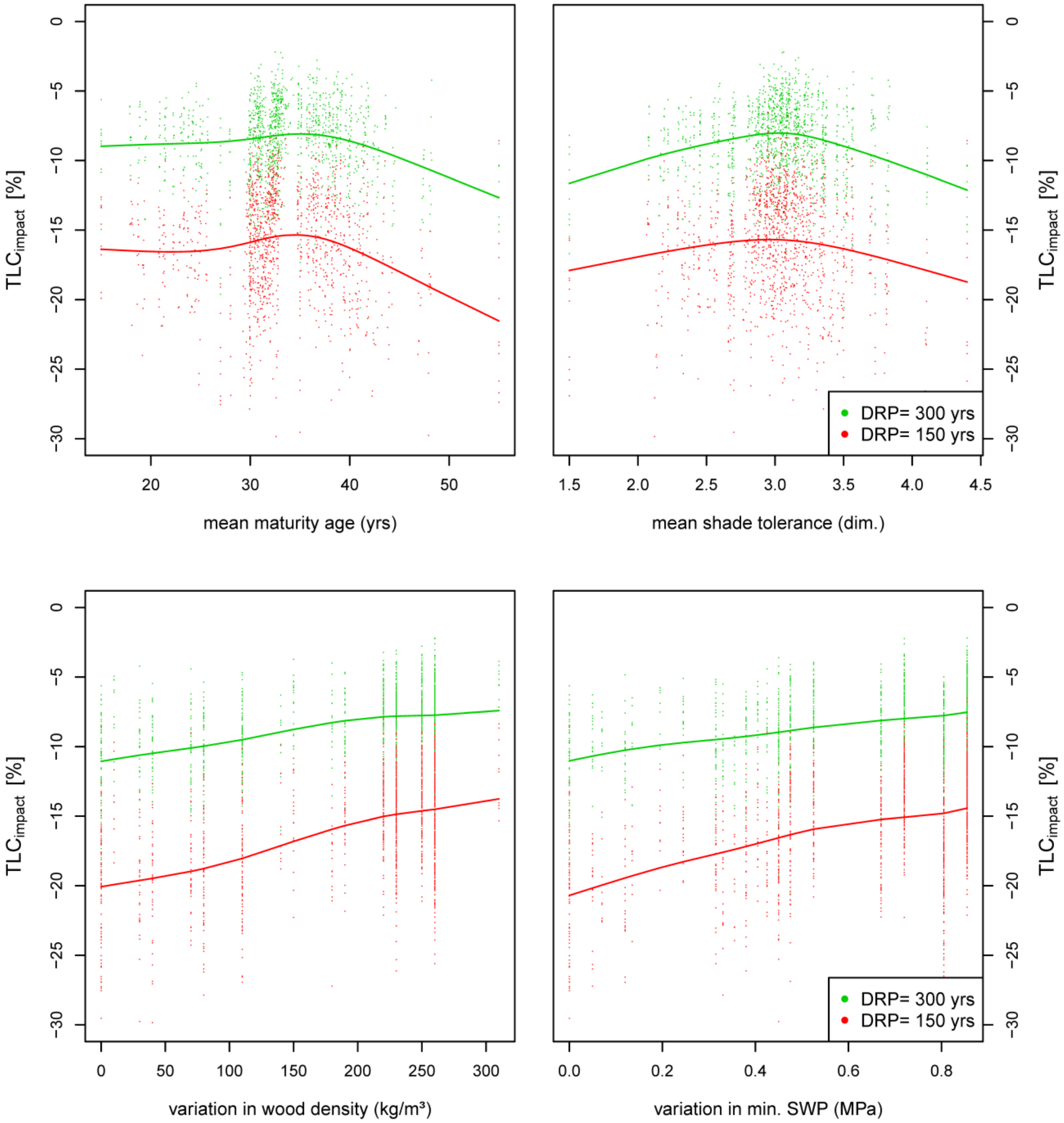

Figure S15– Partial dependence plots of the two most important variables (Figure 3) of mean traits (top row) and the variation in traits (bottom row) on TLC$_{impact}$ for the early seral system. All three disturbance types (Bottom-up, Top-down, and Complete) were included, and the two disturbance return period (DRP) levels were distinguished by means of colors. Lines were created using a smooth spline function.

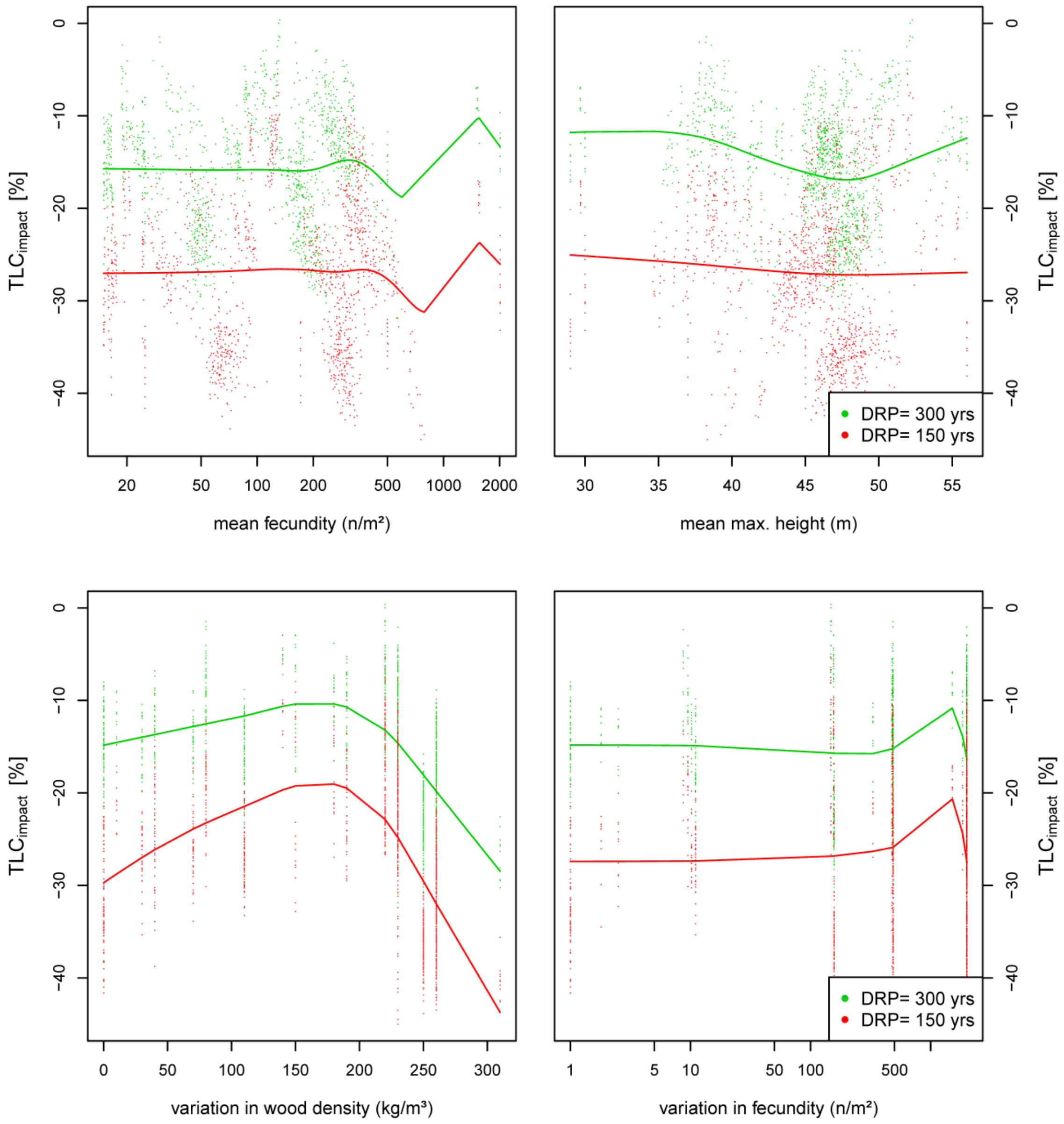

Figure S16 – Partial dependence plots of the two most important variables (Figure 3) of mean traits (top row) and the variation in traits (bottom row) on TLC$_{impact}$ for the late seral stage. All three disturbance types (Bottom-up, Top-down, and Complete) were included, and the two disturbance return period (DRP) levels were distinguished by means of colors. Lines were created using a smooth spline function.

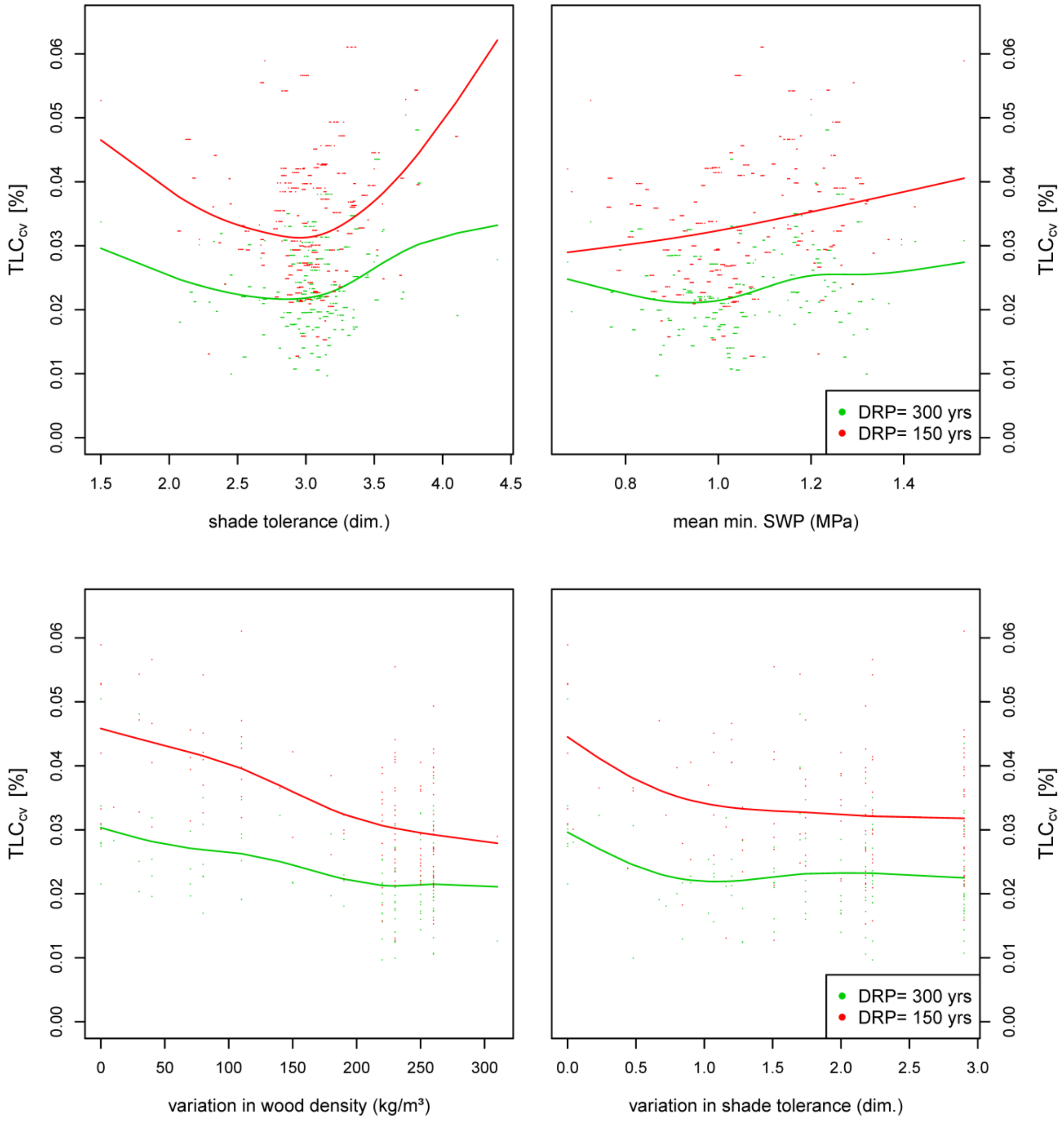

Figure S17 – Partial dependence plots of the two most important variables (Figure 3) of mean traits (top row) and the variation in traits (bottom row) on TLC_{cv} for the early seral stage. All three disturbance types (Bottom-up, Top-down, and Complete) were included, and the two disturbance return period (DRP) levels were distinguished by means of colors. Lines were created using a smooth spline function.

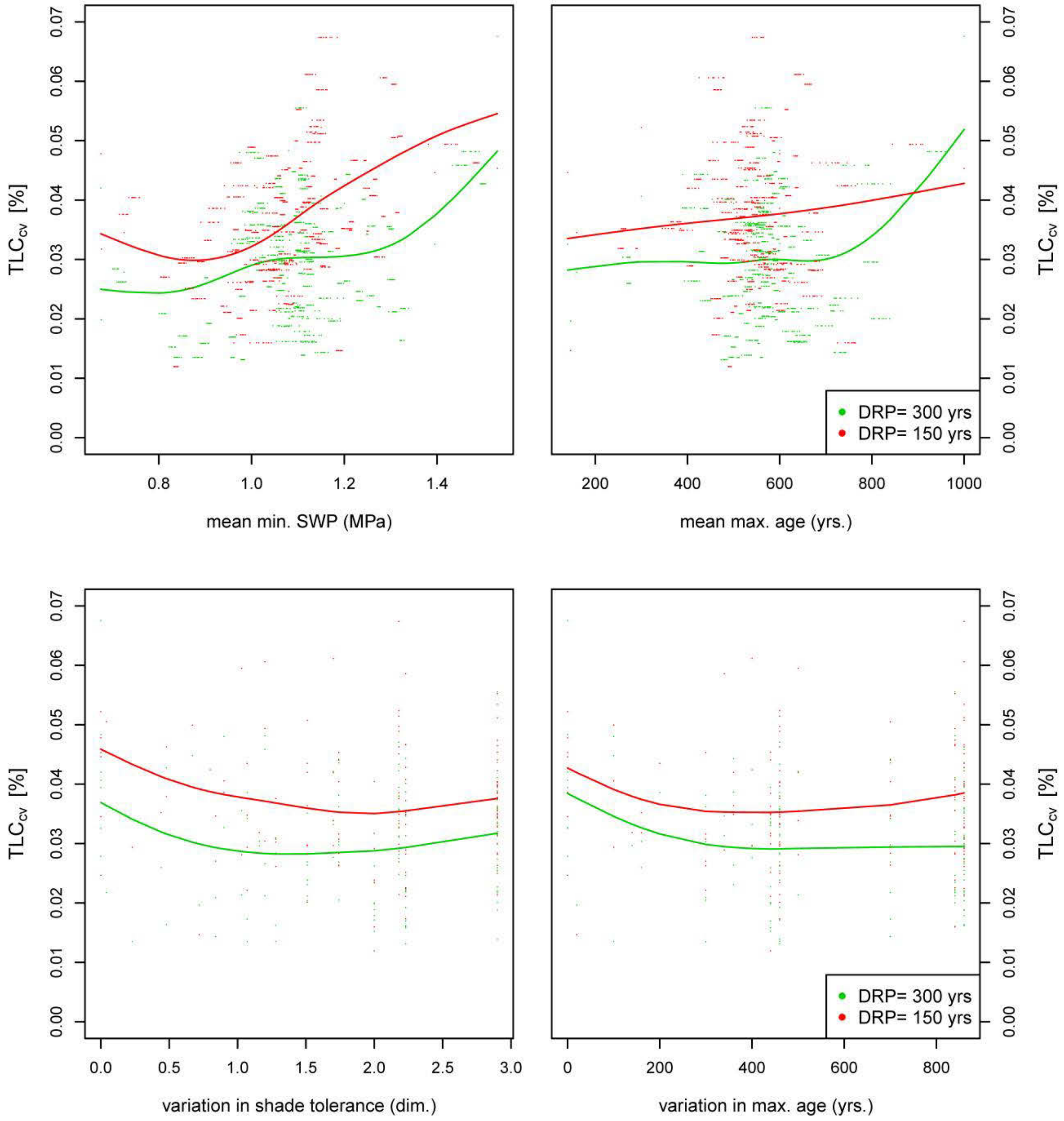

Figure S18– Partial dependence plots of the two most important variables (Figure 3) of mean traits (top row) and the variation in traits (bottom row) on TLC$_{cv}$ for the late seral stage. All three disturbance types (Bottom-up, Top-down, and Complete) were included, and the two disturbance return period (DRP) levels were distinguished by means of colors. Lines were created using a smooth spline function.

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2 Workflow

An overview of the tool and steps to answer the main question of this dissertation (i.e., how diversity influences forest productivity in a temperate forest ecosystem) are presented in Figure 2. The analyses conducted in the three studies comprising this thesis were based on the same ecosystem simulated with the forest landscape model iLand (Seidl et al., 2012a), but were analyzed for answering different questions (see section 1 for details).

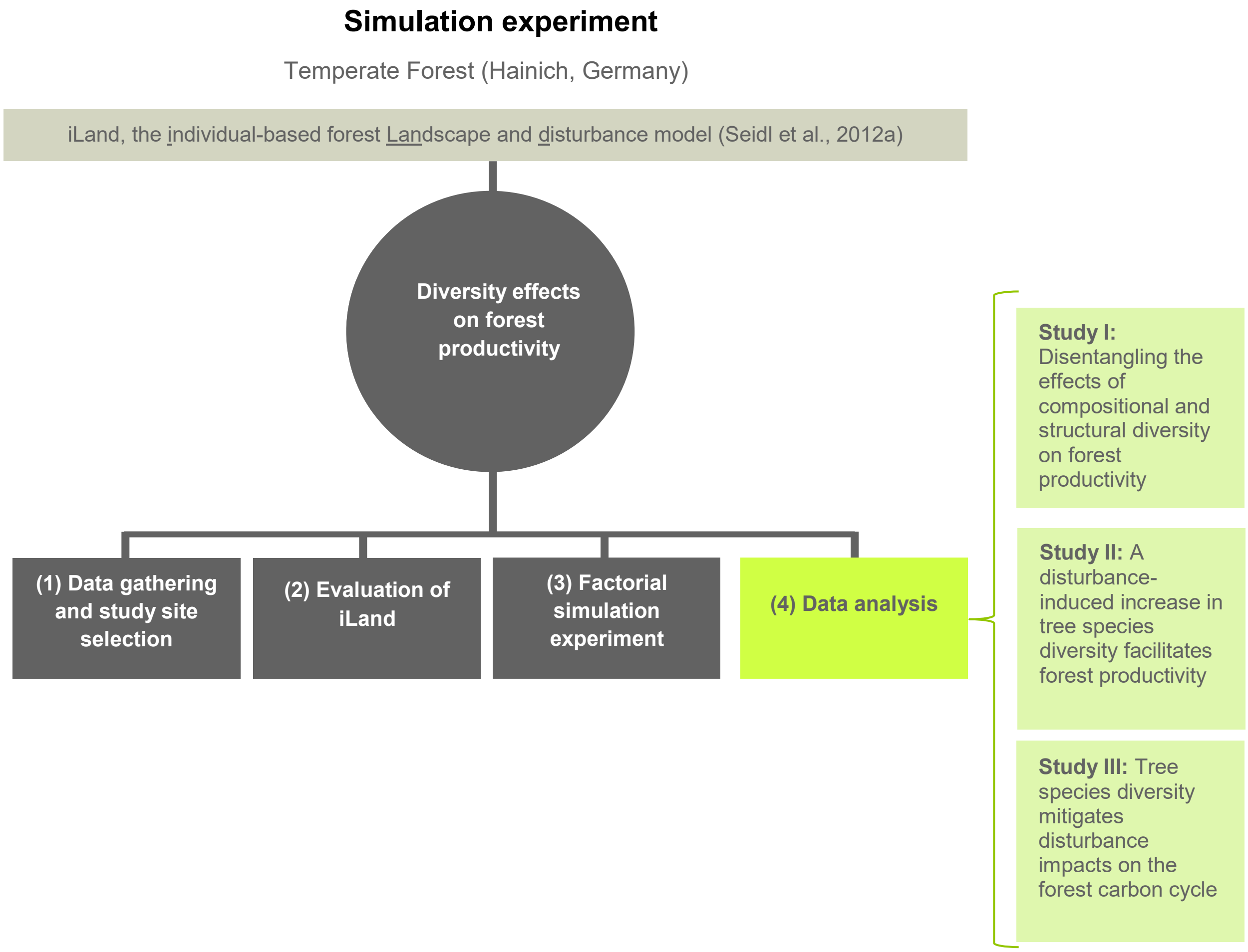

Figure 2 – Summary of the main steps conducted to investigate the relationship between diversity and productivity in a temperate forest ecosystem.

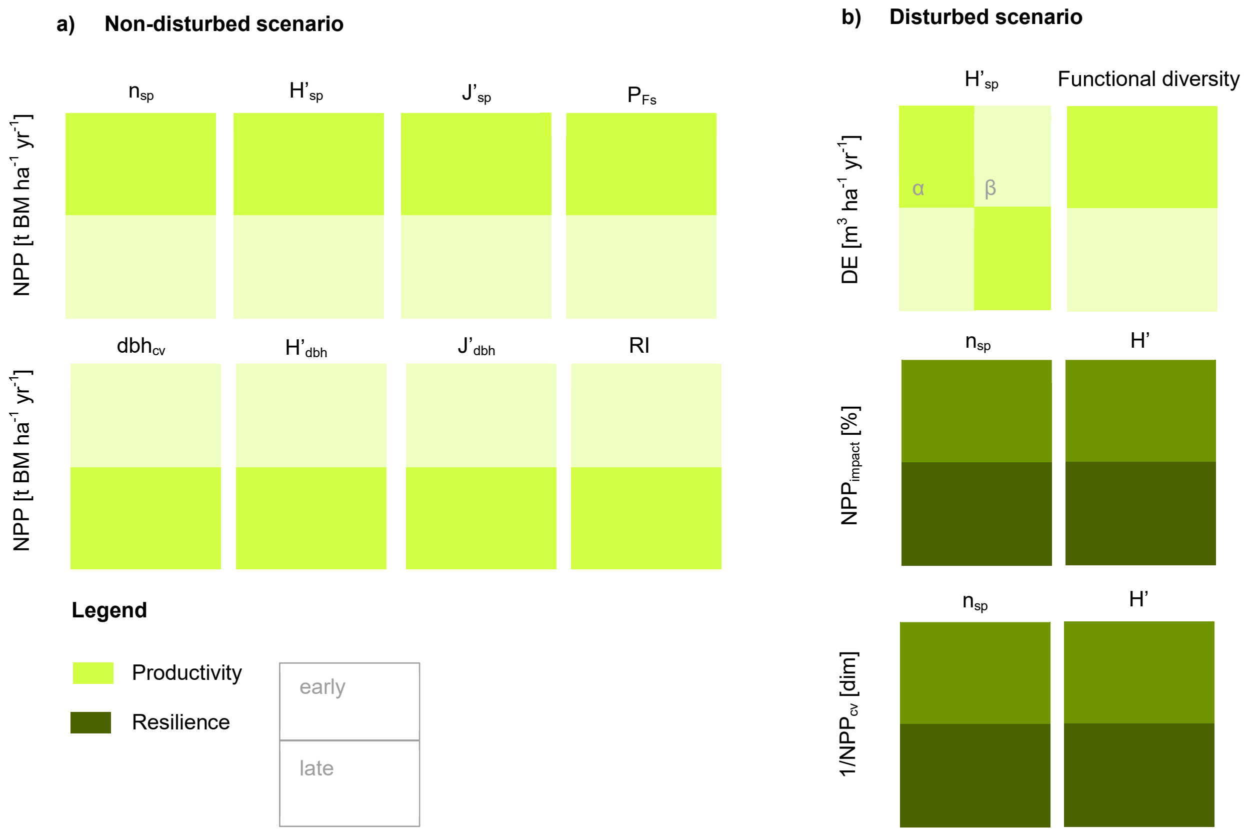

Figure 3 – Qualitative summary of the main results. Results show the changing influence of different diversity dimensions as predictors on indicators of productivity (light green) and resilience (dark green) as response variables over succession. Panel a) shows the results associated to the non-disturbed scenario whereas panel b) shows the results obtained under disturbances. A detailed description of each variable is given in Table 2 (see also Appendix 10 for details). The top part of each box relates to the early stages of forest development, while the bottom part relates to the late seral stage. The relative influence strength between early and late seral stages is indicated via the level of shading, i.e., lighter and darker colors indicate weaker and stronger relationships, respectively. Note that all influences here shown are positive and that a comparison of influence strength between the analyzed indicators of diversity or spatial scales is not shown. H'_{sp} effect on DE is analyzed at two spatial scales: within stands (left side; α diversity) and between stands (right side; β diversity).

Fig. 3

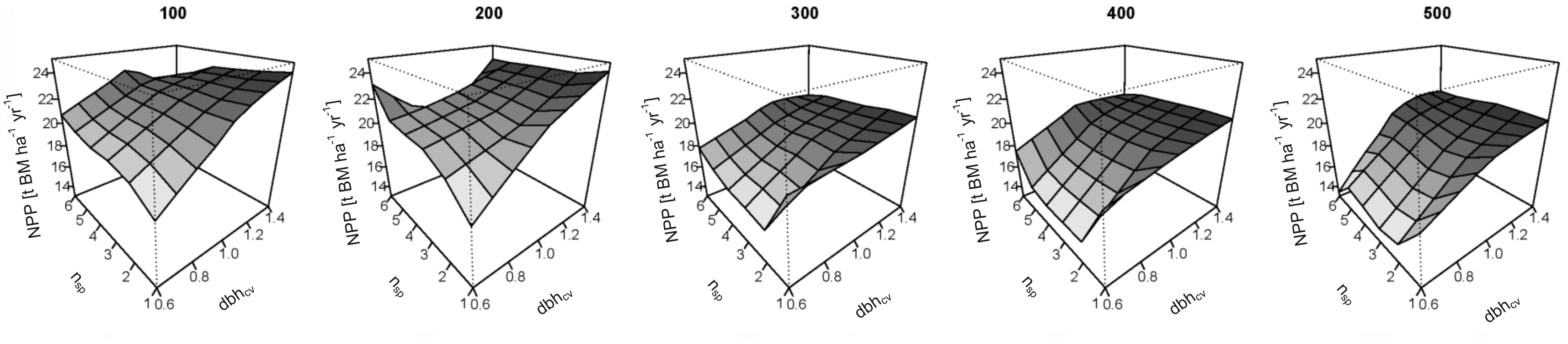

Fig. 3 – Response surface of NPP as a function of tree species richness (n_{sp}) and the coefficient of variation of diameters at breast height (dbh_{cv}) . The response surfaces were derived using random forest predictions over the range of n_{sp} and dbh_{cv} values, while keeping all other variables at their mean values.

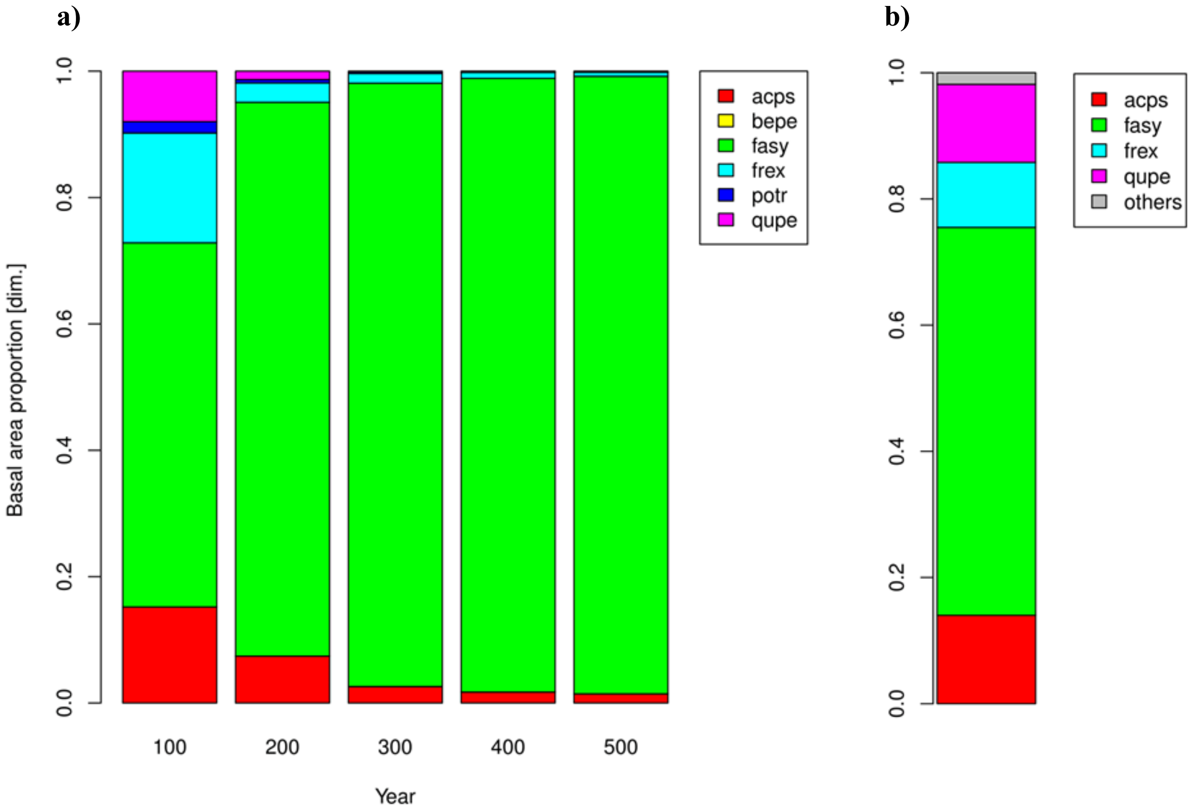

Fig. S2 - Comparison between (a) simulated species composition over 500 years for a fertilie site at Hainich and (b) observed species composition of an approximately 100-150 year old stand (exact tree ages were unvailable, (Baeten et al. 2013)) for a similar site. Shown is the sucessional development with a species pool containing the six species studied in this analysis. Abbreviations: acps – *Acer pseudoplatanus* L.; bepe: *Betula pendula* Roth. ; fasy – *Fagus sylvatica* L.; frex – *Fraxinus excelsior* L.; potr – *Populus tremula* L.; qupe – *Quercus petraea* (Mattuschka) Liebl. others: tree species not investigated here.

Results show a succession from a state characterized by the coexistence of early- (*Populus tremula*), mid- (*Acer pseudoplatanus* and *Fraxinus excelsior*) and late-seral species (*Fagus sylvatica*) to a state dominated mainly by beech (Figure S2a). The simulated early-stage species composition corresponds well to that observed at a similar site at Hainich (Fig. S2b). The simulated endpoint of succession – a strongly beech-dominated forest, is well in line with the

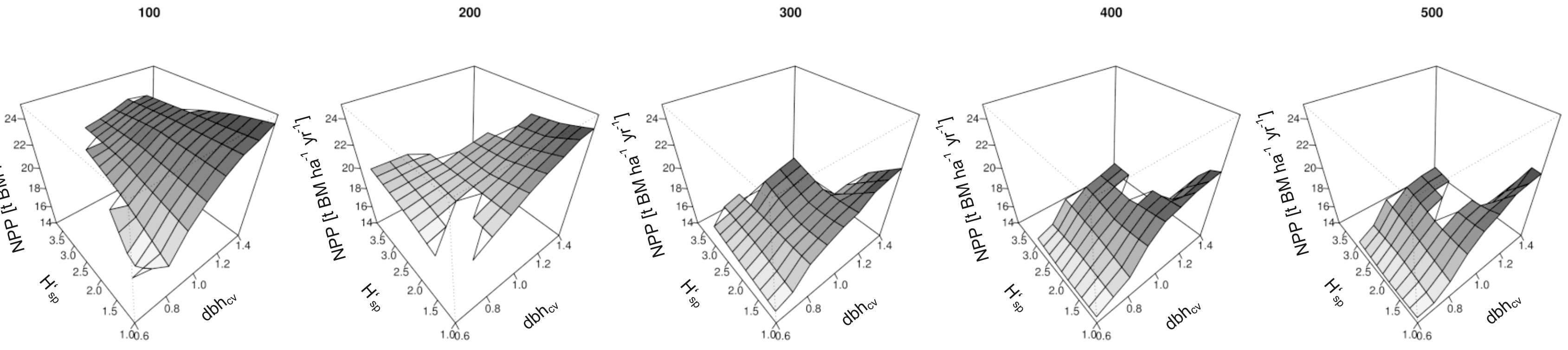

Fig. S4-a – Response surface of NPP as a function of species entropy (H'$_{sp}$) and structural diversity (dbh$_{cv}$). The response surfaces were derived using random forest predictions over the simulated range of H'$_{sp}$ and dbh$_{cv}$ values, while keeping all other variables at their mean values. Open areas in the surface indicate parameter combinations that were not found in the simulated data set.

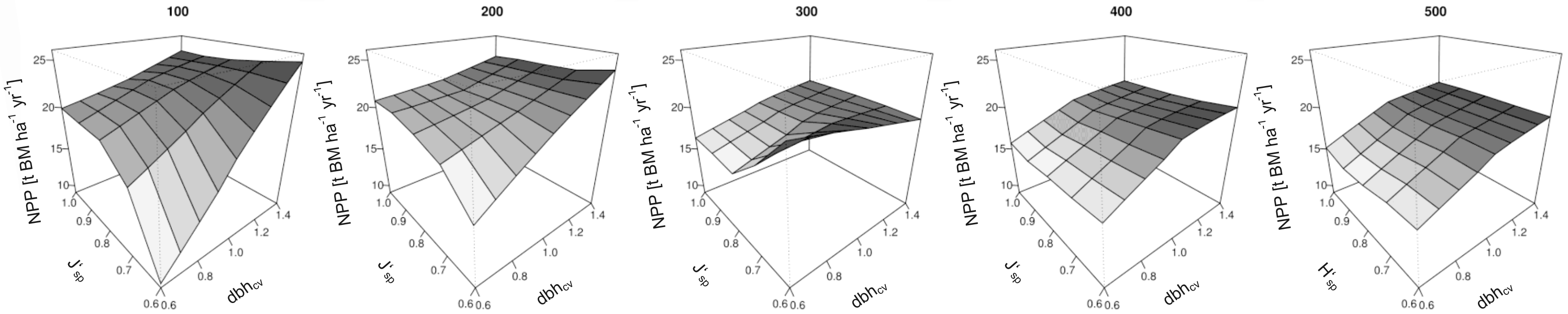

Fig. S4-b – Response surface of NPP as a function of species evenness (J'$_{sp}$) and structural diversity (dbh$_{cv}$). The response surfaces were derived using random forest predictions over the simulated range of J'$_{sp}$ and dbh$_{cv}$ values, while keeping all other variables at their mean values.

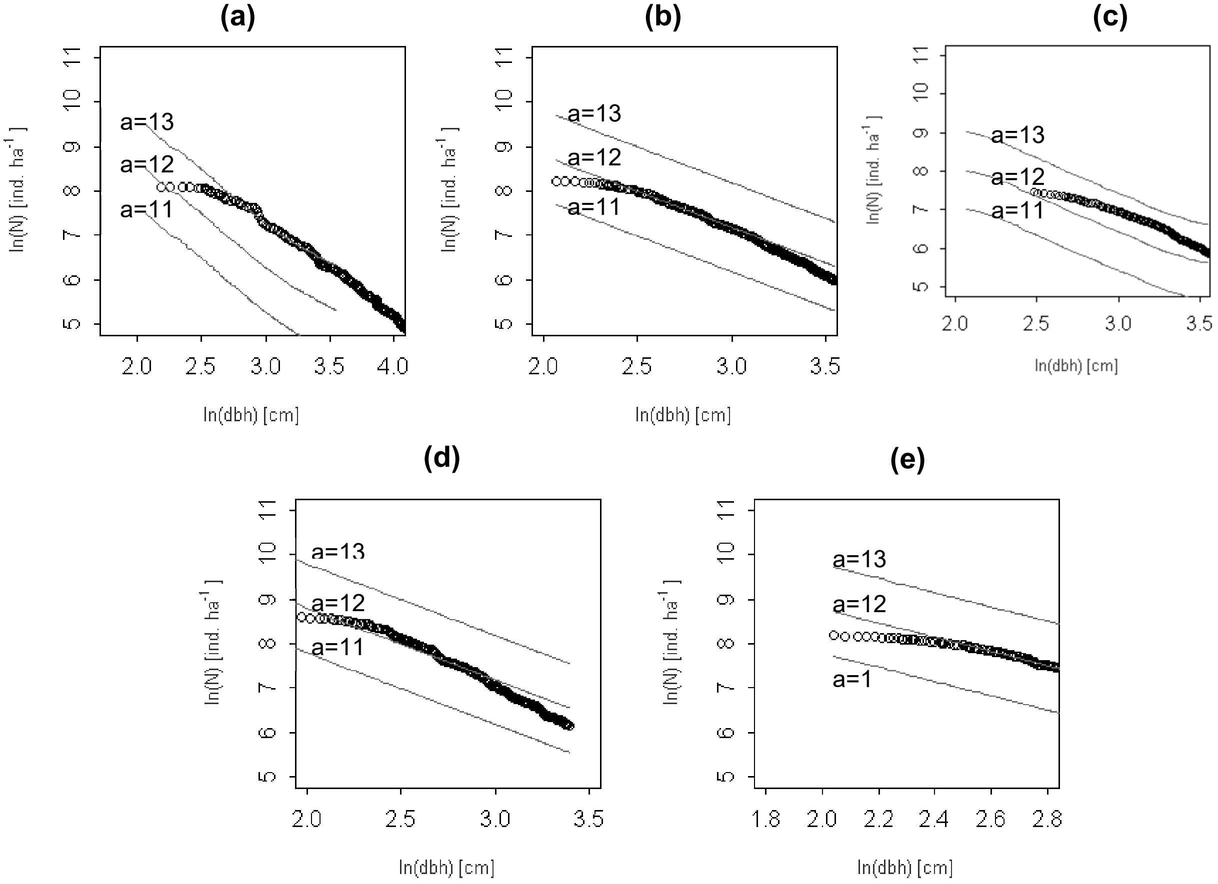

Figure S1 - Simulated stand density (N) reduction over dbh for pure stands of (a) *Picea abies*, (b) *Acer pseudoplatanus*, (c) *Fraxinus excelsior*, (d) *Fagus sylvatica*, and (e) *Quercus petraea* in comparision to Reinekes rule (Reineke, 1933). Lines in gray correspond to theoretical trajectories of N and dbh based on Reinekes rule, with a=11 referring to stands with low site index (i.e., an indicator of site quality and productivity based on the height of the dominant trees at a specific age,) and a=13 to those with high site index (Pretzsch and Biber 2005). Dots are individual years in the simulation with iLand. Please note that the axes are logarithmically scaled.