INVITED VIEWS IN BASIC AND APPLIED ECOLOGY

Functional role of forest diversity: Pros and cons of synthetic stands and across-site comparisons in established forests

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Abstract

In contrast to grasslands, forests have only rarely been the subject of functional biodiversity research. This paper addresses specific problems, which arise from applying the synthetic stand approach to long-lived plants, which can be taken to simulate the loss or addition of tree species or tree functional groups in forest stands. Planted synthetic stands often deviate from natural forests in several properties including trophic structure, tree age distribution, and horizontal and vertical canopy structures. Moreover, edge effects and the absence of a quasi-steady state in soil development limit the spectrum of processes which can be analysed for biodiversity effects in synthetic tree stands. We propose that these shortcomings can partly be overcome by combining the synthetic stand approach with observational studies in existing forest stands of contrasting tree diversity. The potentials and limitations of comparisons among existing stands for functional biodiversity research are briefly discussed using the example of the Hainich Tree Diversity Matrix, a species-rich temperate broad-leaved forest consisting of a small-scale mosaic of stands differing in tree diversity, which originated from a variety of historic forest-use practices.
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Zusammenfassung

Die Erforschung der ökosystemaren Funktionen der Biodiversität hat sich bisher weitgehend auf Graslandökosysteme konzentriert, während Wälder nur selten Gegenstand der Untersuchung waren. Dieser Artikel diskutiert einige Probleme, die mit Experimenten mit gepflanzten, "synthetischen" Baumbeständen unterschiedlicher Baumartenzahl oder verschiedener Anzahl von funktionalen Typen von Bäumen verbunden sind. Gehölzbestände, die für Experimente der funktionalen Biodiversitätsforschung angelegt wurden, unterscheiden sich in mehrfacher Hinsicht von naturnahen Wäldern, darunter in der trophischen Struktur ihrer Biozönosen, dem Altersaufbau der Baumpopulationen und der horizontalen und vertikalen Struktur der Krone. Darüber hinaus schränken Randeffekte und das Fehlen eines Gleichgewichts-Zustandes der Böden die Extrapolierbarkeit der gewonnenen Daten auf Wälder ein. Hier wird argumentiert, dass sich die Aussagekraft der Ergebnisse von Biodiversitäts-Experimenten mit gepflanzten Bäumen verbessern lässt, indem man sie mit vergleichenden Studien an Baumbeständen unterschiedlicher Baumartenvielfalt kombiniert. Am Beispiel der Hainich Tree Diversity Matrix-Studie in Thüringen (Deutschland) werden die Möglichkeiten und Grenzen von vergleichenden Studien in alten Wäldern diskutiert.
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For more than 10 years, research has greatly promoted our understanding of how biodiversity influences the functioning of ecosystems and affects the provision of ecosystem goods and services used by man. Convincing evidence from a number of experimental and observational studies has accumulated, which allows the safe conclusion that certain combinations of species in communities are mutually complementary in their patterns of resource use. Complementarity occurs when two or more species exhibit differences in characteristics, which cause interspecific competition to be less intense than intraspecific. Among the consequences observed were higher average rates of productivity or nutrient retention, a more stable supply of ecosystem goods and services over time, and a reduced susceptibility to invasion by exotic species in species-rich compared to species-poor communities (Balvanera et al., 2006; Hooper et al., 2005; Schmid, 2002).

For practical reasons, the bulk of studies on the functional significance of biodiversity used even-aged, short-lived test systems of simple structure such as grasslands and old-field communities, or terrestrial and aquatic micro- or mesocosm systems. In most cases, such systems contain fewer species and maintain fewer trophic interactions than their natural counterparts, but they pose certain advantages with respect to experimental manipulation and data analysis.

Such simplifying approaches are difficult to realize for forests ecosystems which exhibit a complex spatial structure and high longevity of dominant organisms. Consequently, they were mostly excluded from research on biodiversity functions despite their outstanding role in global carbon and water cycles, their importance as a source of wood and other products, and as a treasure of global biodiversity (FAO, 2001). Although foresters have conducted experiments on the effects of species mixtures, mostly two-species systems, on wood production and resistance to storms for nearly a century, well-designed research initiatives addressing the biodiversity-functioning issue in perennial woody systems have started only recently (e.g. Ewel, Mazzarino, & Berish, 1991; Scherer-Lorenzen, Körner, & Schulze, 2005a; Wright, 1996). More than 10 years of experience with synthetically assembled grassland or old-field communities has produced much progress with respect to optimal design of biodiversity experiments and the most appropriate statistical approaches for data analysis (e.g. Schmid, Joshi, & Schläpfer, 2002; Tilman & Lehman, 2002). Thus, a fertile theoretical and methodological foundation exists on which functional biodiversity research in forests can be built (see e.g. Balvanera et al., 2006; Caspersen & Pacala, 2001; Kinzig, Pacala, & Tilman, 2002; Loreau, Naeem, & Inchausti, 2002; Schläpfer & Schmid, 1999).

In this contribution we argue that the research concepts, which have been developed for experimentally created communities of short-lived plants, are only partly applicable to functional biodiversity research in permanent communities with long-lived plants because of largely different structural and functional properties of these systems. It is concluded that forests, but also permanent grasslands with long-lived forbs and grasses, require research approaches that consider the larger spatial and temporal dimensions of these systems. We cannot exclusively rely on experiments but need combined insight from both experimental and observational research.

Tree plantation experiments

Scherer-Lorenzen et al. (2005) listed seven large-scale biodiversity experiments with trees (two boreal, two temperate, three tropical locations) that have been

initiated since 1999. Another experiment has recently been initiated in China. These experiments investigate the effects of different tree species numbers (varying between 1 and 4 to 18 species) and different numbers of tree functional groups on a variety of ecosystem functions. The experimental design is suitable to answer questions such as (1) is there significant partitioning in resource use among different tree species, (2) does random species loss matter for ecosystem functioning, or (3) does a particular species affect ecosystem functioning? No doubt, there is no alternative to well-designed experiments for analysing putative causal relationships between species or functional group numbers, species identity and ecosystem functions.

However, ecological experiments are only powerful research tools as long as their methodological limitations and their relevance for the 'real world' are critically evaluated. The fascination of ecologists for manipulative experiments has its roots in the elegance of physical experiments, which, however, are poor templates for experiments at the ecosystem level. Besides statistical problems related to a number of 'hidden treatments', which are inherent to most random-selection biodiversity experiments (e.g. Huston & McBride, 2002), biodiversity experiments in synthetic forest communities face several specific caveats that are mostly caused by the long lifespan and large size of trees. Among the most notable are

(1) *Plot size* may not be large enough to address several key questions of functional biodiversity research in forests. By discussing this problem, Scherer-Lorenzen et al. (2005) recommended to use double the height of final tree height as side length of a study plot, i.e. 0.5–1.0 ha for trees reaching 30 m in height. This aim is often difficult to achieve and is likely to result in huge size of the field sites needed, typically from more than 50 ha up to 500 ha of sufficiently homogenous terrain. This is demonstrated by the present tree diversity experiments in Germany and Malaysia (Holden, 2003; Scherer-Lorenzen et al., 2005). Due to the enormous size required, the majority of tree experiments used in fact much smaller plot sizes (0.04–0.2 ha), thereby reducing the final number of mature trees in a plot to about 8–40 (assuming a final stem density of 200 ha^{-1}). This leaves only one to eight trees per species in a 5-species mixed plot after 80–100 years. In addition, in plots significantly smaller than 0.5 ha, edge effects may be substantial, introducing considerable errors in microclimate and water turnover measurements in the plots, because both variables require a homogenous fetch of at least 50–100 m in forests (Jones, 2000). Leaf area index and canopy architecture are also sensitive to edge effects in small plots as is litter input (Rothe & Binkley, 2001; Scherer-

Lorenzen et al., 2005). Moreover, small forest plots represent habitat islands in the landscape, which are partially unsaturated with respect to flora and fauna ([22]Lawrence et al. 2002). The island problem is less severe if the plots are embedded in a forest matrix. Even 1 ha plots are unlikely to harbour the complete set of characteristic mammal and bird species, which alters the trophic structure and most likely favours generalist species over specialists (Krüss & Tscharntke, 1994). Finally, it is doubtful whether forest gap dynamics and ecosystem properties such as resilience after disturbance can be adequately investigated in small synthetic forest plots.

(2) *Plot history* and the *time horizon* of the experiment determine the questions that can be addressed in forest biodiversity experiments. Processes such as carbon sequestration in soil and establishment of characteristic herb layer vegetation in temperate deciduous forests require centuries rather than decades to reach a quasi-steady state after a severe disturbance event (Jenkinson, 1990; Wulf, 2004). Therefore, ecosystem nutrient fluxes and carbon exchange with the atmosphere will differ markedly in synthetic forest communities from those in forests with a long continuity. This will particularly be true for forests with a dense herb layer vegetation, which often has a profound effect on nutrient cycling (Eggert, 1985; Gebauer & Schulze, 1997). Questions relating to diversity effects on nutrient retention and C sequestration or herb layer composition, thus, can be answered in tree biodiversity experiments only for the early phase of stand development, which represents a forest ecosystem in a state of recovery after severe disturbance. This limitation is particularly severe in experiments established on former agricultural land; these soils have lost a substantial proportion of the soil organic matter after the forest was cut (Murty, Kirschbaum, McMurtrie, & McGilvray, 2002). Certainly, many forests in temperate Europe and North America are not old-growth forests but have a long record of human use as well. However, these systems are much closer to equilibrium than the artificial grasslands or planted stands of the biodiversity experiments.

(3) Tree biodiversity experiments consist of even-aged stands, which, in most cases, do not mimic the age structure and canopy architecture of naturally established forests (Scherer-Lorenzen et al., 2005). It may well be that complementarity of resource use, if significant in mixed forests, is more pronounced in mature forests with a heterogeneous age structure than in young even-aged stands in the thinning phase of stand development. The latter will be typical for many synthetic forest plots in biodiversity experiments. For example, detailed investigation of the three-dimensional canopy structure in an old-growth

five-species broad-leaved forest in Central Germany revealed species-specific patterns of canopy space occupation with a considerable overlap of crown areas of different species, a pattern that was not observed in younger stands during the thinning phase, where height growth was the dominant strategy (Frech & Leuschner, unpubl.). Correspondingly, planted young stands typically have stem-centred fine root distribution patterns (e.g. Ford & Deans, 1977; Roberts, 1976), whereas complex patterns of root system overlap, indicating belowground niche partitioning can develop in mature mixed forests (Laurance et al., 2001; McQueen, 1968).

(4) In most tree diversity experiments, a regular spatial distribution of tree individuals and tree species and equal distances between tree individuals are established in the plots. More recently, clumped tree distribution patterns were also established in experiments. Nevertheless, on a larger scale, they represent regular tree spacing patterns as well. In any case, the spatial heterogeneity of the stand will typically be smaller in experiments with planted trees than in mature near-natural forests. There is evidence that neighbourhood effects are species-specific in mixed forests (Stoll & Newbery, 2005). It may well be that heterogeneous distribution of tree individuals and species in natural mixed stands partly reflects spatial heterogeneity of soil resources in the stand, thereby enhancing the complementarity of resource use. If so, a more homogenous stem distribution in planted stands could reduce complementarity effects.

Combining plantation experiments with cross-site comparisons in established forests

Given the shortcomings of diversity experiments with respect to the situation in mature stands, it seems straightforward to combine research in synthetic tree stands with observational studies in existing forests of contrasting tree diversity in order to understand the diversity–functioning relationship in near-natural forests with complex structure. By working with a larger number of precisely characterized study sites that were selected carefully according to pre-defined criteria concerning species richness and soil homogeneity, statistical analysis of the data is possible. In this case, site comparisons can be valuable tools for detecting correlations between different measures of tree diversity (genetic, species, structural, functional) and ecosystem properties and functions. In fact, no other approach is suitable (i) for dealing explicitly with adult trees, (ii) for addressing stands with a near-natural canopy and root system architecture, (iii) for investigating stands with an intact food web structure, and (iv) for measuring stocks

of carbon and nutrients in soil and biomass at a quasi steady-state.

However, the shortcomings of observational studies must also be kept in mind. First, plot history may be an important factor influencing stand structure, biodiversity, and biogeochemical cycles (Mund & Schulze, 2005), which can make it difficult to disentangle diversity and site history effects. Second, it is often difficult or even impossible to find certain tree species combinations in sufficient number in nature, at least, if larger plot sizes with a sufficient number of tree individuals are needed. In addition, many data sets contain a number of 'hidden treatments' with respect to soil properties that are inherent to many, if not all, observational studies in forests. This clearly limits the analytical power of comparative studies in many cases.

Hence, observational studies should serve as complementary investigations under 'real-world conditions' by defining the frame of the response variables to be tested in associated manipulative diversity experiments. Extensive screening surveys of prospective study sites for homogeneity in edaphic and climatic properties are indispensable for reducing noise in observational data sets. While the problem of covarying factors is particularly severe in such cross-site comparisons, it is also inherent to most tree diversity experiments simply because of the large size of the field sites needed (Scherer-Lorenzen et al., 2005). Multivariate statistical analyses can help to quantify the influence of confounding edaphic, climatic, and historical factors on the response variables when analysing diversity–functioning relationships.

Tree species diversity in Central European forests

Compared to the temperate regions of Eastern North America and East Asia, the woody flora of Europe's temperate region is species-poor (Ellenberg, 1996). Not more than 40 woody species participate in the canopy layer of Central Europe's forest communities, and less than 20 are common and widespread. In the majority of forest communities, less than five tree species are typically found in a relevé of $100 \, m^2$, and many beech, oak, and alder forests normally harbour only one to three different tree species (Table 1). Central Europe's forest vegetation is unique in the world due to widespread occurrence of quasi-monospecific beech forests (*Fagus sylvatica*), in which this single species occupies 80–100% of the canopy area. Before human intervention, beech forests covered about 40–50 Mio ha in Central Europe (Bohn & Neuhäusl, 2000/2003). More species-rich forests exist only in regions beyond the distribution range of *F. sylvatica* (e.g. in eastern Central

Table 1. Average number of tree species in relevés of selected lowland to montane forest communities in Southern Germany (after several hundred relevés per community type in Oberdorfer, 1992; only species with a presence > 20% in the relevés of a community were considered)

Community type	Mean number of tree species
Forests at nutrient-poor, moist to dry sites	
Acidic lowland birch–oak woods (Betulo-Quercetum)	3.2
Acidic upland oak woods (Holco-Quercetum)	4.2
Acidic beech forests (Luzulo-Fagetum)	2.0
Pine forests on sand (Leucobryo-Pinetum)	5.2
Forests at dry and/or sub-continental sites	
Thermophilous sub-continental oak forests (Potentillo-Quercetum)	6.5
Thermophilous submediterr. oak forests (Quercetum pubescenti-petraeae)	6.5
Sub-continental oak–hornbeam forests (Galio-Carpinetum)	7.5
Forests at nutrient-rich, moist to dry sites	
Beech forests at calcareous moist sites (Hordelymo-Fagetum)	3.1
Beech forests at calcareous dry sites (Carici-Fagetum)	4.5
Beech forests at mesotrophic sites (Galio-Fagetum)	2.5
Eutrophic glen and slope forests (Aceri-Tilietum)	8.5
Alluvial forests	
Alluvial oak–elm forests (Querco-Ulmetum)	7.2
Alluvial ash forests (Pruno-Fraxinetum)	4.2
Moist oak–hornbeam forests (Stellario-Carpinetum)	6.2
Alluvial lowland willow forests (Salicetum albae)	6.5
Riverine ash–alder forests (Fraxino-Alnetum)	6.0
Swamp and mire forests	
Mixed willow scrub (Salicetum pentandro-cinereae)	4.0
Oligotrophic swamp willow scrub (Salicetum cinereae)	1.2
Eutrophic alder swamp (Stellario-Alnetum)	4.5
Sub-oceanic alder swamp (Carici elongatae-Alnetum)	3.0

Europe) and at sites that are unfavourable for beech growth in terms of soil aeration or drought (Ellenberg, 1996). Particularly species rich are floodplain forests and thermophilous oak forests with six to nine tree species per relevé on average (Carbiener, 1970, see Table 1).

Forest use and forest management for more than 7000 yrs have greatly reduced Central Europe's forest cover to about 30%, but they have not resulted in a lower tree species diversity at the stand level in most regions, because the forests were species poor from the beginning (Ellenberg, 1996). A substantial reduction in tree diversity has only occurred in floodplain forests, where natural stands with six to nine tree species per relevé were widely replaced by monospecific plantations of *Populus* species and other species (Klimo & Hager, 2001). However, in large parts of Central Europe, transformation of natural forests to even-aged mono-specific production forests has resulted in a substantial decrease of forest structural diversity, and most likely, in a reduction of intraspecific genotype diversity as well. Moreover, humans have greatly altered tree species composition by replacing *F. sylvatica* forests by stands of *Picea*, *Pinus*, and other tree species.

Functional biodiversity research in a species-rich temperate broad-leaved forest – The Hainich Tree Diversity Matrix

Forest stands with contrasting tree species diversity, which are sufficiently comparable in their site conditions to fulfil the criteria of observational studies, are hard to find in nature. There is a long record of comparative studies with pure and two-species stands in many European countries (e.g. Cannell, Malcolm, & Robertson, 1992; Kelty, 1992; Oltsthoorn et al., 1999; Pretzsch, 2005), whereas comparisons with more than two tree species are the exception (e.g. Caspersen & Pacala, 2001; Vila et al., 2005). A good example of a temperate broad-leaved forest providing a large gradient of tree diversity is found in the Hainich National Park in Thuringia, Central Germany. In an area of less than $25\,km^2$ with sufficiently homogenous climate and soil conditions, a small-scale mosaic of forest ownership has generated a variety of forest use types of species-poor to species-rich forest patches close to each other. This pattern forms the basis of the Hainich Tree Diversity Matrix. It may be

viewed as the outcome of a 'biodiversity experiment' unintentionally initiated by humans many decades and centuries ago and analysed today.

The area represents a slightly sloping limestone plateau from the Triassic Upper Muschelkalk formation covered with a more or less homogenous layer of Pleistocene loess. All stands have been subject to only very extensive management since the area became part of a military training site more than 40 years ago. In this forest mosaic, two different approaches of comparative study have been pursued. First, 12 forest stands ($2500\,m^2$) with tree species numbers varying between 1 and more than 5 per plot were chosen for the study. Selection criteria for the stands were (i) comparable pedologic conditions (limestone covered by loess), (ii) similar climate conditions (precipitation $600–670\,mm\,yr^{-1}$, annual mean temperature 7.5–8.0 °C), (iii) comparable stand structure in terms of basal area and DBH, and (iv) tree diversity and abundance patterns according to pre-defined diversity classes ranging from low (0.2) to high values (1.5) of the Shannon diversity index. Four stands each of pure beech forest (diversity level DL1), beech-ash-linden forest (DL2), and beech-ash-linden-hornbeam-maple forest (DL3) were selected (Table 2). In a second approach, hundred $4\,m^2$ plots were selected in the centre of 'tree clusters' consisting of three trees each. The latter design covers all possible neighbourhood situations occurring among the five most common tree species of the forest (5 one-species, 10 two-species and 10 three-species cluster types in fourfold replication) with the tree clusters being arranged in two blocks to account for possible gradients in soil properties.

Research in the $2500\,m^2$ plots of the Hainich Tree Diversity Matrix is focussing on those structural and functional variables that are particularly sensitive to plot size, edge effects, and stand continuity (see variables marked by X or (X) in Table 3). These variables include carbon pools and fluxes in the soil, niche partitioning, and tree–tree interactions in the species-rich forest canopy, stand-level transpiration, and multitrophic interactions in the food web, variables that are difficult to address by functional biodiversity research in synthetic tree stands. In the $4\,m^2$ plots, measured variables are predominantly soil biological and chemical properties that are studied in their dependence on species diversity and species identity effects as caused by the nature of the directly neighbouring trees.

Although it is too early to draw final conclusions on the 'best practice' in functional biodiversity research in forests, we suggest that tree biodiversity experiments with synthetic forest stands bear the potential to test key hypotheses of functional biodiversity research in assemblages of long-lived woody plants and to more fully understand the causes of relationships between tree species diversity, tree functional diversity, and

Table 2. Site characteristics of the 12 stands of the Hainich Tree Diversity Matrix (plot size: $2500\,m^2$)

	Beech stands	Beech–ash–linden stands	Beech–ash–linden–hornbeam–maple stands
Diversity level	DL1	DL2	DL3
Number of replicate stands	4	4	4
Site factors			
Slope (%)	4.2 ± 1.3 a	3.9 ± 0.7 a	3.0 ± 0.4 a
Exposition (°)	315 ± 37 a	315 ± 0 a	315 ± 0 a
Loess coverage (cm)	86 ± 23 a	80 ± 28 a	66 ± 14 a
Clay content (%: 0–30 cm)	17.6 ± 5.1 a	25.8 ± 6.2 a	31.1 ± 10.0 a
Stand structural attributes			
Total basal area per plot (m^2)	10.5 ± 1.0 a	9.7 ± 1.3 a	9.0 ± 0.9 a
Stems > 7 cm DBH per plot	68.5 ± 25.7 a	150.3 ± 37.1 b	104.8 ± 17.6 ab
Mean height domin. trees (m)	35.9 ± 2.2 a	28.5 ± 1.0 b	26.6 ± 0.5 b
Percent beech in basal area	94.5 ± 4.8 a	60.6 ± 6.4 b	19.3 ± 14.4 c
Tree ssp. diversity[a]	0.19 ± 0.13 a	1.00 ± 0.10 b	1.47 ± 0.14 c

All stands grow on Luvisols with minor stagnic properties developed from Triassic limestone as bedrock with partial loess cover. Stands with similar Shannon tree diversity indices were grouped in the three diversity levels DL1, DL2, or DL3. Different letters indicate significant differences between the three diversity levels ($p < 0.05$; test for normal distribution: Shapiro–Wilk, test for homogeneity of variances: Bartlett, comparison of means: ANOVA, posthoc test: Tukey's t test). Beech – *Fagus sylvatica*, ash – *Fraxinus excelsior*, linden – *Tilia cordata* and *T. platyphyllos*, hornbeam – *Carpinus betulus*, maple-*Acer pseudoplatanus* and *A. platanoides*.

[a]Shannon Index based on the crown area of the species in the stands (due to a rather similar ecology, the species pairs *Tilia cordata/T. platyphyllos* and *Acer pseudoplatanus/A. platanoides* were counted as one species in this table).

Table 3. List of key variables measured in the Hainich Tree Diversity Matrix. Variables that are partially or highly sensitive to edge effects in small plots or plot history are marked with (X) or X

Variable	
A Abiotic site variables	
Stand microclimate	X
Soil moisture regime	
Carbon pools in biomass, humus layer and soil, soil organic compounds as biomarkers	X
Soil chemical status (CEC, base saturation, total & exchangeable nutrient pools, P fractions)	X
Nutrient content and organic compounds in biomass fractions	
B Abundance and diversity of biota	
Plants (adult trees, tree regeneration, herbs, mosses, seed bank)	(X)
Mycorrhizal fungi (diversity of morphotypes and root infection rate)	(X)
Animals (canopy arthropods, bees, wasps, saproxylic beetles, soil macro- and mesofauna)	(X)
Soil microorganisms (microbial biomass, PLFA analysis)	(X)
C Stand structure	
Aboveground phytomass characteristics (stem density, DBH, phytomass, height, crown area)	
Leaf area index and leaf mass, canopy openness	(X)
Aboveground niche partitioning	X
Herb layer mass and composition	X
Tree and herb root mass	
Belowground niche partitioning	
Stand history	
D Biogeochemical fluxes	
Canopy and soil water fluxes	
Stem sap flow and canopy transpiration	(X)
Primary productivity (stem growth, leaf production, fine root production & turnover)	
Nutrient fluxes with litter fall	(X)
Litter decomposition and soil respiration	
N transfer processes in the soil and nutrient leaching with deep seepage	
Trace gas emissions	
E Biotic interactions	
Competition processes between trees	(X)
Multitrophic interactions	(X)
Herbivory rates in canopy and herb layer	
Functional soil food web analysis	

ecosystem functions. However, the following limitations have to be kept in mind (see also Scherer-Lorenzen, Körner, & Schulze, 2005b):

(a) Tree diversity experiments will produce results relevant for tree plantations and young intensively managed forests, but the findings will mostly be of limited applicability to natural or near-natural forests and managed stands at maturity.

(b) While we can expect reliable results on variables such as tree growth, timber production, decomposition, and nutrient retention, information on attributes and processes that depend on extended spatial and temporal scales most likely will be more or less artefactual in synthetic stands. Examples are pools and fluxes of carbon at a quasi steady-state, niche partitioning in canopy and root systems, food web structure, the diversity of birds, mammals, mycor-rhizal fungi and forest herbs, and stand stability parameters. Therefore, it may well be that we miss important processes or interactions taking place in species-rich stands if we focus only on experimental stands with plots too small and stand architectures too far from nature to allow for such effects.

(c) When large study plots (> 0.5 ha) are used, environmental heterogeneity (soil and climatic conditions) across the study sites will often be substantial, thereby weakening the strength of the experimental approach. Blocking of the study plots and the use of soil or climate data as co-variables in data analysis may help to avoid hidden treatments in the experiment. However, the more an experiment deviates from the ideal conditions of ecological experimentation, the less we can be sure that the observed effect is caused by the factor assumed. Thus, manipulative experiments and observational

cross-site comparisons, which can be viewed as experiments done by nature or by the forester, become more similar.

(d) A problem of tree diversity experiments is that the initial gradient in tree species diversity may diminish in the course of the experiment due to asymmetric competition processes unless the experimentator counteracts species loss by silvicultural measures. Changing diversity patterns over time would weaken the strength of experimental data, which calls for a rather short duration of experiments. Clumping of tree species in planted mixed plots may reduce this risk, but it will also reduce the zone of physical contact between different tree species and thus the space where complementary resource use may take place.

We conclude that forest biodiversity experiments could be further improved by including plots with a more realistic stand structure than it is realised in the existing experiments. For example, different tree species could be planted at random positions and at different years to create more realistic species mixtures and age structures. In addition, the stands could be allowed to pass through a process of natural thinning, which would give the community a more natural shape. Clearly, stands of this type cannot be replicated.

We also recommend complementing experimental research programs with across-site comparative studies in established forests if suitable stands are available.

Acknowledgements

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