17 The Functional Significance of Forest Diversity: a Synthesis

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17.1 A Lack of Functional Biodiversity Research in Forests?

Despite of the tremendous increase in knowledge about the relationship between biodiversity and ecosystem functioning during the last decade (Scherer-Lorenzen et al., Chap. 1, this Vol.), it should be noted that most of the studies were conducted with model systems, which – for very practical reasons – were small-statured, short-lived and even-aged, mainly herbaceous assemblages or microbial microcosms (e.g., Tilman et al. 1997b; Hector et al. 1999; Petchey et al. 2002; for an overview, see Schläpfer and Schmid 1999; Schmid et al. 2002). Experiments in forest ecosystems have been almost absent, with the exception of studies manipulating diversity of consumers or decomposers in the soil (e.g., Mikola and Setälä 1998; Laakso and Setälä 1999; see Scheu, Chap. 11, this Vol.). A manipulation of the producer level, i.e., trees, is obviously a difficult and long-lasting task and only recently attempts in this direction have been made (Scherer-Lorenzen et al., Chap. 16, this Vol.). The experiment by Ewel and colleagues in the tropics of Costa Rica (Berish and Ewel 1988; Ewel et al. 1991) has often been mentioned as the first manipulative diversity experiment indicating diversity effects on biogeochemistry (Vitousek and Hooper 1993). However, this experiment was designed to explore the possibilities of developing sustainable agroecosystems for the humid tropics, mimicking structural diversity of successional communities, and not to study the interaction of species richness and ecosystem functioning per se. Clear effects on soil chemistry were detectable between maize monocultures and highly-diverse (>100 species) treatments consisting of herbaceous and woody plants. Low and intermediate levels of diversity were lacking, which should be the part of the gradient where most effects are expected to occur, according to local deterministic processes involving species interactions (see below). Positive effects at such intermediate levels of tree species richness have been reported from afforestation experiments in Costa Rica, for example (Byard et al. 1996; Montagnini 2000). In contrast, mixture experiments from forestry

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sciences lack mostly intermediate and high diversity treatments, because forestry is mainly interested in one- and two-species assemblages of economically important species (Pretzsch, Chap. 3, this Vol.; Jones et al., Chap. 6, this Vol.; Kelty 1992; Malcolm and Mason 1999). Therefore, in the search for biodiversity–ecosystem functioning relations in forest ecosystems, we still have to rely mostly on observational, comparative studies rather than on experimental, manipulative experiments. This bias is also reflected in the present book, and we have to keep in mind that, albeit such approaches cannot be used to determine causality due to covarying factors (Vilà et al., Chap. 4, this Vol.), they provide many valuable insights into the correlates of ecosystem functioning (Körner, Chap. 2, this Vol.).

17.2 Mechanisms of Mixture Effects, or: Are There Differences Between Grasslands and Forests?

There are no obvious biological reasons why the mechanisms responsible for diversity effects on ecosystem processes in grassland, agricultural systems, or microcosms should not work also in slow-growing forest communities. These mechanisms have been grouped into two classes, representing (1) local deterministic processes, such as niche differentiation or resource partitioning, and/or facilitation among different species, leading to increased yield of mixtures compared to that of the corresponding monocultures (complementary effect) (Loreau et al. 2002; Tilman and Lehman 2002); (2) local and regional stochastic processes involved in community assembly of experimental systems leading to a higher probability that a certain species with strong impacts on ecosystem processes is present at higher diversity ("sampling" or "selection-effect models") (Aarssen 1997; Huston 1997; Tilman et al. 1997a). In the following, we do not consider sampling effect models here, because they are mainly relevant for experimental systems with random sampling of species out of a fixed species pool and some sort of selection for species with extreme traits.

17.2.1 Niche Partitioning and Functional Traits

Niche partitioning among tree species is well known for certain mixed forest types, as shown by Pretzsch (Chap. 3, this Vol.), Jones (Chap. 6, this Vol.), and Kelty (1992). Following Harper (1977), such complementary species are termed species with "ecological combining abilities" (Harper 1977, p. 265 and p. 762 ff.). In general, this indicates that complementarity, with a more efficient resource use in mixtures compared to monocultures, occurs if the functional traits of species cause interspecific competition to be less than intraspecific competition (called “competitive production principle” by Vandermeer 1989). Examples from forestry are stratified mixtures of sun-adapted species in the overstory and shade-adapted species in the understory, the combination of early- and late-successional species, or ontogenetically early and late-culminating species (Assmann 1970; Kelty 1992; Körner, Chap. 2, this Vol.; Pretzsch, Chap. 3, this Vol.). The many citations from old German silvicultural books presented by Pretzsch (Chap. 3, this Vol.) show that this principle was well recognized by foresters more than 175 years ago. However, for a long time, foresters were also aware of negative effects of mixing species, which are of the same magnitude as potentially positive mixing effects, due to competitive interactions where the inferior competitor can only be sustained by silvicultural interference (Pretzsch, Chap. 3, this Vol.). Additionally, comparative studies have not found strong evidence for mixture effects on productivity in temperate forests of the northern hemisphere (Schulze et al. 1996), although Caspersen and Pacala (2001) reported an asymptotic increase in wood production with increasing tree species richness in North American forests.

Similarly, there seems to be no general relation between biodiversity and nutrient cycling in boreal and temperate forests (Schulze et al. 1996; Rothe and Binkley 2001), although niche complementarity models would lead one to expect so (Tilman 1999; Loreau 2000; Chesson et al. 2002). Again, certain mixtures do show enhanced nutrient uptake in comparison to the corresponding monospecific stands, whereas others do not. The combination of shallow- and deep-rooting species, such as Norway spruce with oak, European beech, or Scots pine provides an example for belowground niche partitioning, enhancing nutrient uptake under certain circumstances (Rothe and Binkley 2001; Thelin et al. 2002), as well as for stability against windthrow (Dhôte, Chap. 14, this Vol.). However, the distribution of roots within the soil profile must not necessarily coincide with nutrient uptake, and differentiations according to site properties are to be expected (Rothe and Binkley 2001). As shown by Hättenschwiler (Chap. 8, this Vol.), diversity effects on decomposition and nutrient mineralization are known for some mixtures due to inter- and intraspecific variations in litter quality. However, the relationship between litter species richness and process rate does not yet appear to be predictable, and the identity of species within a mixture, i.e., the functional traits of the species, has been shown to be more important than the number of species.

Resource partitioning and complementarity are discussed mostly in relation to productivity of the plant community or nutrient retention, but this concept is also applicable to other interactions between species. For example, Jactel (Chap. 12, this Vol.) has documented that complementary food sources in more diverse habitats can result in enhanced fecundity and longevity of specialized parasitoids, which increases the effectiveness of parasitism on forest pests, thus reducing damage in more diverse stands.

Whether mixtures will show complementarity or not depends on the ecological differences among species within a community, i.e., on the species' functional traits; hence, it should be possible to predict diversity effects on certain ecosystem functions if the species traits are known. Such traits are well known for tree species (at least for boreal and temperate species), although they can vary enormously depending on developmental stage or site factors (Körner, Chap. 2, this Vol.). The influence of tree species on ecosystem processes based on such traits is also well documented (Wirth et al., Chap. 15, this Vol.; Zinke 1962; Binkley and Valentine 1991; Binkley and Giardina 1998; Rothe and Binkley 2001; Augusto et al. 2002; Prescott 2002). The above-mentioned examples of positive mixture effects from forestry explicitly combine species with different traits, e.g., light-demanding and shade-tolerant species. Thus, the analysis of gradients in functional diversity in contrast to variations in species richness might be more promising for detecting complementarity effects. On the other hand, because functional groups are arbitrary divisions of a continuous niche space, and if several ecosystem functions are considered simultaneously, one may end up with the notion that each species represents its own functional group (Körner 1993; Körner, Chap. 2, this Vol.; Wirth, Chap. 15, this Vol.). This underlines the usefulness of species richness as one simple measure of ecological differences between species.

At this point, we want to emphasize that agroforestry systems explicitly make use of resource complementarity and facilitation to increase and/or stabilize yields by deliberately selecting species with differing functional traits, and that many aspects of the biodiversity–ecosystem functioning relation have been discussed in that area (Ewel 1986; Huxley 1999; Ashton 2000; Kelty 2000).

17.2.2 Differences Between Grassland and Forests

The strong evidence for diversity effects on ecosystem functioning through resource partitioning or facilitation mainly derives from experiments with fast-growing model ecosystems such as grasslands, where plant diversity was directly manipulated (Schläpfer and Schmid 1999; Schmid et al. 2002). In contrast, results from comparative studies are inconsistent, partly because both diversity and some measure of ecosystem functioning (in most cases, productivity) may be limited by the same site factors, leading to spurious correlations between the two (Wardle 2001), and because such "third variables" were often not adequately measured and incorporated into the statistical analysis (Schmid et al. 2002). An obvious difference between biodiversity–ecosystem functioning relationships found in grasslands and forests may thus be grounds for different types of scientific approach: comparisons of within-habitat diversity effects (experimental grasslands) versus across-habitat diversity effects (observational studies in forests).

What kind of biological differences between fast-growing grassland systems and forests are important when considering biodiversity–ecosystem functioning relations? While herbaceous/grassland communities rebuild most of their interacting aboveground structures year by year from close to zero, trees may take a hundred or more years to fill a large three-dimensional volume, which permits very small differences among individuals to accumulate in a compound-interest fashion. In herbaceous species such interest effects also exist, but are mainly limited to reproductive output and belowground structures (which are considered to interact "symmetrically"). Individuals of herbaceous systems reach maximum height year by year, whereas trees persist at gradually increasing height. This is not just a scaling issue in space and time, but a substantial qualitative difference in how species and their individuals interact. One consequence of this difference is that far more co-dominants tend to coexist in long established and non-fertilized grassland systems, whereas mature temperate or boreal forests commonly exhibit a dominance of few, mostly one to three, species. Such mature forest ecosystems are thus much more dependent on the characteristics of a small set of species than are grassland systems. In terms of plant life "strategies," grassland systems commonly retain a large r component and forests select for a large contribution of K components.

Additionally, the woody nature of the supporting structures of trees, i.e., stems, branches, and twigs, imply a "memory effect" in the crown architecture of trees that cannot be seen in grasslands. For example, under conditions of light competition in a closed stand, the crown may develop in an asymmetrical manner foraging for light. If a gap is formed later on the opposite side of the crown's main direction, the tree is not able to make use of this additional light in the short term, and the crown remains asymmetrical for at least several years or decades. In contrast, the rapid lateral growth of grassland species (especially clonal growing ones) and the greater flexibility of the non-lignified shoot system lead to a quick recovery of the open resource space created by the loss of neighboring individuals. Additionally, many grasses and herbs show photosynthetic activity in the shoot and can immediately make use of lateral incoming light without the need to regenerate or rearrange leaves. Thus, although the additional light in a forest gap might be used by tree seedlings or the herbaceous layer, the more flexible grassland system should have relatively more constant light use at the stand level than forest communities. This will have different consequences in both systems for light complementarity, as well as for other aspects of ecosystem functioning that depend on the aboveground structure, such as susceptibility to wind damage or the habitat function of the canopy.

Finally, most late successional grasslands, including natural ones, totally depend on disturbance (fire, grazers, mowing) and would convert to forests without these disturbances (Archibold 1995). Thus, grasslands (except for wet habitats) do not reach a "steady-state" situation (and the associated ecosystem function) unless they are regularly disturbed, with the degree of disturbance determining biodiversity and functioning. Forests may, at least theoretically, arrive at a "steady state" situation if there is no disturbance, and should have corresponding ecosystem functions. Although almost all boreal and temperate forests do also have natural disturbance regimes (fire, pest outbreaks), these disturbances generally do not permanently convert the forest into a totally different ecosystem type because regrowth of tree species is fast. Interestingly, in old-growth forests growing under favorable conditions, such as the Pacific Northwest in North America, or the coast of the South Island of New Zealand, certain ecosystem functions are, however, not associated with a "steady state" (in terms of species composition): these forests presumably continue to accumulate soil carbon, for example. Although nearly all modern temperate forests are heavily disturbed (managed), the evolutionary traits of trees have not been selected to the same extent as grassland species for operation under regular disturbance. These differences have to be accounted for when biodiversity theory, derived from regularly disturbed and fast growing systems, is applied to forests.

17.3 Research Needs

What do we need in order to gain more insight into the relationship between forest diversity and ecosystem functioning? Clearly, we need more comparative, observational studies to document patterns of forest biodiversity and correlate them to ecological processes within those ecosystems. There is a large variety of mixed species stands to be explored, with its diversity being determined by biogeographical and historical conditions, abiotic and biotic site factors, and human management interventions. However, unless site conditions are extremely similar, across-habitat or across-locality comparisons can be misleading because between site differences may obscure within-habitat effects of diversity on ecosystem processes (Vilá et al., Chap. 4, this Vol.; Lawton et al. 1998; Schmid 2002). As mentioned by Körner (Chap. 2, this Vol.), careful site characterization and large site numbers are needed to come to a reasonable signal-to-noise ratio. In addition, among-site abiotic variation has to be adequately accounted for by including these "third variables" as covariates in statistical analysis (Schmid et al. 2002). The exploration of forestry inventory data in combination with thinnings emphasizing biodiversity could also yield new insights. However, management may often confound diversity effects (Vilá et al., Chap. 4, this Vol.; Mund and Schulze, Chap. 10, this Vol.), so both aspects have to be clearly separated in such observational and inventory studies.

In order to detect causal mechanisms of diversity–functioning relationships, we certainly need more experimental work specifically designed for this task, as described by Scherer-Lorenzen et al. (Chap. 16, this Vol.). However, because life cycles of trees are up to two orders of magnitude longer than normally funded research projects and because results may only be gained after several years of observation (but see work with tropical systems: Scherer-Lorenzen et al., Chap. 16, this Vol.), we may also use model systems made up of tree seedlings or saplings (e.g., Körner and Arnore 1992). Although such model systems definitively will not reflect processes in natural, highly structured forests (not even to mention old-growth forests), they may provide initial insight into mechanisms and may thus be used to formulate more specific hypotheses. At this point, we have to note that the overwhelming number of studies on the response of forest ecosystems to increasing CO_2 concentrations also arise from studies with seedling or saplings (Körner 1995), and only in two cases was the whole canopy influence of CO_2 studied in diverse mature forest tree assemblages, a mixed Mediterranean evergreen/oak forest around a natural CO_2 spring in Tuscany (Tognetti et al. 1996) and a mature temperate forest in Switzerland (Pepin and Körner 2002).

Besides comparative studies in existing stands and experimental biodiversity plantations adopting the "synthetic-community approach" (Scherer-Lorenzen et al., Chap. 16, this Vol.), a third promising way for further research is the realization of removal or addition experiments. Such experiments, where single species or entire functional groups are removed from or added to existing communities, have some drawbacks (e.g., large disturbance effects, change of density, spatial segregation of species), but can be useful in certain circumstances (Freckleton and Watkinson 2000; Díaz et al. 2003). Certainly, it would be promising to re-analyze the magnitude of thinning experiments (removals) or conversions of conifer-dominated stands into more natural, multi-species communities (additions) from a biodiversity–ecosystem functioning perspective.

Besides the adoption of such complementary approaches, we propose the following points to be considered in future work, which should not only document patterns of biodiversity–ecosystem functioning relationships, but should also be mechanistically driven:

- One aspect that should receive more attention in analyzing diversity–functioning relationships in forests is the influence of confounding factors due to changing abiotic conditions (Vilá et al., Chap. 4, this Vol.) and management interventions (Mund and Schulze, Chap. 10, this Vol.; Cannell et al. 1992; Kelty et al. 1992; Olsthoorn et al. 1999). Because silvicultural treatments tend to standardize the basal area of the stands (Kramer 1988), potential diversity effects could simply be "thinned away" by extracting biomass that normally is not accounted for in inventories. For example, the analysis of carbon stocks in aboveground biomass in beech forests of Thuringia, Germany, shows no significant differences between pure and mixed stands at all ages on similar soil conditions, which is mainly a result of thinning interventions (C. Wirth, unpubl. data). At ages between 80 and

120 years, pure stands have even slightly higher carbon stocks than mixed stands. However, it may well be that the yield by thinning is higher in mixed than in monotypic stands. Thus, the wood extraction must be known when evaluating biodiversity effects in managed forests.

- Especially the question of spatial aggregation both horizontally (neighbor analyses) and vertically (canopy stratification, and the above-mentioned "memory effect" of woody structures) may be of importance in biodiversity studies of forests because the spatial distribution of species strongly affects ecosystem processes through alteration of competitive interactions (Pacala and Deutschman 1995; Stoll and Prati 2001). A major challenge for future work will thus be the integration of different spatial scales where biodiversity may have effects.
- A further important arena will be the study of the significance of intraspecific variation among forest tree taxa (Müller-Starck et al., Chap. 5, this Vol.). From the limited evidence we have, it seems effects of such differences can even exceed consequences of interspecific differences (e.g., in the case of susceptibility to certain diseases, Pautasso et al., Chap. 13, this Vol.).
- Totally overseen has been the importance of soil microbial biodiversity at this stage. Gleixner et al. (Chap. 9, this Vol.) show that carbon storage in soils depends to a large extent on the microbial biodiversity in the soil and not on the biodiversity in the stand. Nevertheless, Schulze et al. (2004) demonstrate that ecosystem diversity and the contribution of the soil to proteins identified in the soil water are very well coupled to the composition of the vegetation. However, the whole complex of interlinkages and feedback mechanisms between above- and belowground diversity and their influence on ecosystem functioning remains a large field for research (Jactel et al., Chap. 12, this Vol., Scheu et al., Chap. 11, this Vol.). In particular, it seems to be a safe prediction that the study of interactions between trees and their mycorrhizal partners will remain among the most promising focal points of forest biodiversity research (Smith and Read 1997).
- Given the longevity of forest ecosystems, long-term continuous studies are compulsory. For instance, disturbances such as fire (Wirth, Chap. 15, this Vol.) or large temporal fluctuations in the population size of forest insects have particular relevance for ecosystem dynamics and stability (Jactel et al., Chap. 12, this Vol.), but may have different consequences depending on forest biodiversity.

17.4 Conclusions

The contributions in this volume clearly show that forest diversity can have a variety of effects on ecosystem processes and characteristics, such as productivity and timber production (Pretzsch, Chap. 3, this Vol.; Vilá et al., Chap. 4, this Vol.; Müller-Starck et al., Chap. 5, this Vol.), biogeochemistry (Baldocchi, Chap. 7, this Vol.; Jones et al., Chap. 6, this Vol.; Hättenschwiler, Chap. 8, this Vol.; Gleixner et al., Chap. 9, this Vol.; Mund and Schulze, Chap. 10, this Vol.; Wirth, Chap. 15, this Vol.), associated fauna (Scheu, Chap. 11, this Vol.; Jactel et al., Chap. 12, this Vol.), and stability against disturbances (Pautasso et al., Chap. 13, this Vol.; Dhôte, Chap. 14, this Vol.). Although most presentations have both reviewed the existing literature and analyzed data of own research projects, evidence of consistent patterns of the relationship between forest diversity and ecological processes remained scarce.

Interestingly, the strongest positive tree diversity effects were related to some aspects of stand stability, such as resistance to pest insects (Jactel et al., Chap. 12, this Vol.) or susceptibility to fungal pathogens (Pautasso et al., Chap. 13, this Vol.), supporting the often expressed notion of higher stability in mixed stands. However, Dhôte (Chap. 14, this Vol.) could not support this rule of thumb concerning resistance to strong winds.

In most cases, a variety of possible answers to the central question "Does diversity matter?" emerged. For example, under certain site conditions, effects of tree species number on soil fauna diversity (Scheu, Chap. 11, this Vol.), litter decomposition (Hättenschwiler, Chap. 8, this Vol.), and resistance to pathogens (Pautasso et al., Chap. 13, this Vol.) could be detected, but effects differed at different sites and with the involvement of different tree species. This variety of possible answers has its roots in the distinction between the effects of species numbers or species identities. The notion that the identity of species within a mixture is more important than the number of species is the thread running through all chapters. Thus, it becomes clear that there is no "magic effect of numbers of species per se," and that any effect will arise instead from functional differences between species and from species interactions (Hector et al. 2000). There cannot be any relationship between species richness and ecosystem processes without these differences between species (Lawton et al. 1998). Therefore, the characteristic traits of species and thus the diversity of functions these species perform are important determinants for ecosystem processes (e.g., Baldocchi, Chap. 7, this Vol., Wirth et al., Chap. 15, this Vol.).

However, we have to recognize that our knowledge on patterns of diversity in forests and the implications this diversity may have for ecosystem processes or services are still very limited, largely because natural temperate forests hardly exist where most researchers are based (Europe, USA), and because the nature of trees prevents conventional short-term manipulative experimentation. The former limitation opens an arena for research in the last existing natural temperate forest ecosystems (e.g., in the Far East of Asia) and the latter urges better utilization of existing silviculture management results in our landscape (as exemplified by several authors in this volume).

It also appears that a priori definitions of functional tree types may be less practical and helpful in predicting forest functioning than post hoc assessments of the consequences of presence or absence of certain tree taxa (but see Wirth et al., Chap. 15, this Vol.). Furthermore, it is obvious that the significance of forest diversity (and the presence of certain taxa) depends on the forest functions considered. Windthrow risk, nitrate retention, catchment value for water yielding, or support of high wild ungulate diversity are subjects of concern that will always foster different answers with respect to whether and how forest diversity matters. We conclude that future explorations of the functional significance of forest species diversity needs to more clearly account for those differences in forest function. From what we have learned to date, it seems that for the most basic actual ecosystem functions, such as the direct contribution to biogeochemical cycles, diversity is of less significance than might be expected, and that more subtle and indirect and longer-term effects may become crucial. This and the needed time for such effects to materialize again suggest that the study of given forest assemblages will have to remain a focal point and will continue to cause forest biodiversity research to differ from grassland biodiversity research. It remains to be seen whether theory derived from grassland research will meet the given reality in forests of contrasting diversity.

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