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Is forest diversity driving ecosystem function and service?

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Forests unfold an exceptionally large ecosystem volume and expose a vast biotic surface, providing crucial ecosystem functions and services, including carbon sequestration and regional climate regulation. However, there is only little insight into the role of tree diversity in forest functioning. Hence, currently we cannot assess the consequences of species loss under global change for forest functioning. Here we review recent studies on tree diversity and ecosystem functioning in forests. Although several studies confirm the positive relationship between tree diversity and functions related to productivity, communities of biota, and soil parameters, many studies find stronger effects of species identity than diversity. We discuss the methodological shortcomings of the present study designs, including an isolated view on specific functions and the general negligence of confounding factors, and conclude that future studies can profit from exploiting information gained at the scale of tree individuals.

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Introduction

From the deepest tap root to the top of the canopy, forests unfold an exceptionally large ecosystem volume and expose a vast biotic surface. Trees are text book examples of ecosystem engineers [1], modifying their abiotic and biotic environment due to their sheer size. By connecting the lower atmosphere with deep ground water they regulate regional climate, speed up soil development with roots penetrating rocks and injecting organic matter into the ground, drive the carbon and nutrient cycles by locking up large amounts of elements in their woody tissues, and produce organic matter, habitat structure and microclimate thus providing food and shelter for a myriad of organisms including humans. However, faced with an accelerated loss of species, will future forests be able to maintain their functions and services? Are we at risk of approaching lower levels of forest functions and services in a world with fewer tree species [2]?

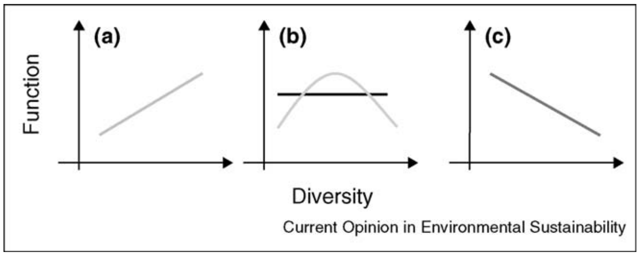
This question is at the heart of functional biodiversity research, the study of biodiversity effects on ecosystem functioning. This young discipline emerged in the early 1990s [3]. Reviews almost exclusively report the results from grassland experiments as these are easy and fast to establish [4–7]. Although the relationship between diversity and a specific ecosystem function may take any form (Figure 1), these experiments prove that diversity increases and stabilizes productivity [8,9], and increases soil carbon sequestration [10], nutrient retention [11], and stability of multiple functions [7]. Complementary resource use rather than selection of high performing species by chance (sampling effect) was identified as the main driver of these positive diversity effects [7].

In contrast to grasslands, surprisingly little is known about the role of species diversity for ecosystem functioning in forests [7,12••,13]. In their review on forest stability, Thompson *et al.* [12••] confirm that diversity generally increases productivity in tree stands. Scherer-Lorenzen *et al.* [13] summarize the knowledge on the diversity — functioning relationship in forest up to the year 2005. They conclude that forest diversity can influence productivity, biogeochemical cycles, associated fauna, and stability against disturbance. However, evidence of consistent pattern remains scarce. Here we review 31 recent articles on the diversity–functioning relationship in forests, mainly published after 2007. Additionally we outline ways to improve present study designs.

A review of current forest studies on ecosystem processes affected by biodiversity

To review the current advances in the field of forest biodiversity and ecosystem functioning we performed a literature search selecting only studies that address ecosystem functions at the stand-level. In contrast to [12••,13] we considered only studies covering a diversity gradient extending beyond two species mixtures. Given the wealth of response variables reported by the studies, we grouped them into 15 categories which were further assigned three main functional syndromes and miscellaneous functions. As functional syndromes we defined functions related to tree productivity, functions directly related to communities of biota other than trees, and functions related to soil parameters (Figure 2).

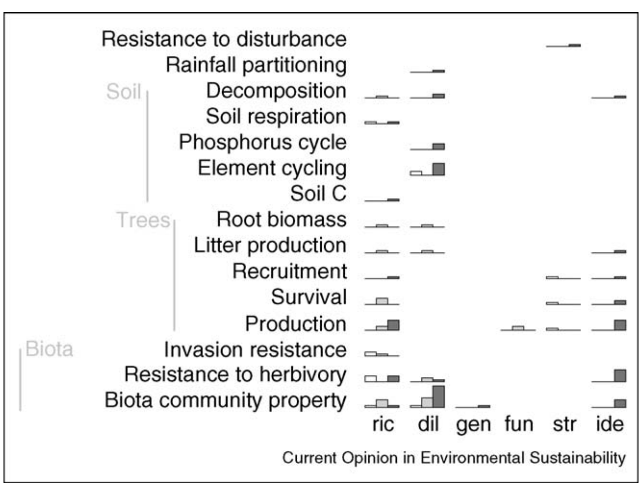
Figure 1



The relationship between tree diversity and ecosystem functioning can be described by simple functions. In our review, we coded an increase in performance with ‘1’ **(a)**, independence with ‘0’ (straight line in **b**), and a decrease with ‘−1’ **(c)**. Unimodal relationships (humped curve in b) show highest performance at intermediate diversity levels and were coded with ‘0’.

We identified five different types of richness gradients: richness (species richness gradients with different species), dilution (species richness gradients including one species in all treatments), genetic diversity, functional diversity, and structural diversity. Additionally, we recorded effects of species identity. The heterogeneity of responses and predictors forced us to rely on a simple qualitative head-count of responses as a basis of a comparison: for our figures and summaries, we coded positive relationships with ‘1’, negative with ‘−1’, and neutral or unimodal relationships with ‘0’ (Figure 1). We counted effects reported within studies, resulting in more than one effect per study in most of the cases. Effect size was not considered. In the following, we report the results along the lines of the main functional syndromes.

Figure 2



The functional significance of tree diversity treatments for ecosystem functions in forests. The studies reviewed here used five different diversity gradients (ric: richness, dil: dilution, gen: genetic, fun: functional, str: structural) as well as reporting identity (ide) effects. This figure shows the distribution of positive (dark gray), neutral or unimodal (light gray), and negative effects (white) of tree diversity on 15 ecosystem functions, which we coarsely grouped into three functional syndromes (biota: functions directly related to communities of biota other than trees, trees: functions related to trees, soil: functions related to soil parameters). The following literature was used: biota community property: [14,15•,16–23,27•,29], resistance to herbivory [25,26,27•,28,29], invasion resistance [24], production [30,32••,33,34•,35,40,43], survival [32••,34•,40] recruitment [25,40], litter production [31,44], root biomass [22,45], soil C [46], element cycling [44], phosphorus cycle [47], soil respiration [22], decomposition [31,44,48], rainfall partitioning [49], and resistance to disturbance [50].

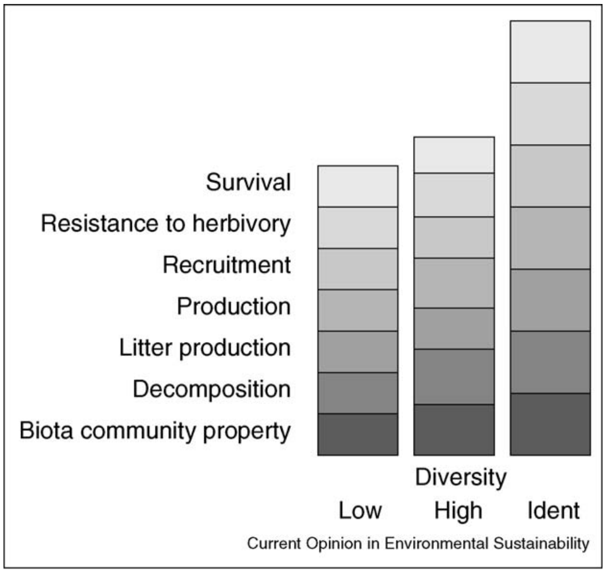
A comparatively large number of studies ($n = 16$) looked at ecosystem functions directly linked to communities of biota other than trees (Figure 2). These studies largely focused on arthropod communities [14,15•,16–20], but some also considered earth worms [21], soil microbes [22], herbs [23], and invasive plants [24]. Five studies looked at the effect of biota on trees (herbivory) [25,26,27•,28,29]. Although diversity, abundance, or stability of these communities generally responded positively or at least neutrally to gradients of tree diversity, resistance to herbivory and invasion declined with tree diversity in about half of the studies (Figure 2). Ten studies looked at aspects of productivity of the trees themselves (Figure 2), including production, survival, and recruitment. These studies also used the longest time periods of up to 70 years [30]. Although there was a consistent pattern of higher productivity in species-rich plots for above ground productivity, functions interfacing with the soil compartment (root biomass and litter production) tended to remain unaffected or showed unimodal relationships to diversity. Lastly, six studies looked at soil variables, many of which described rate parameters. The generally positive effects of tree diversity on soil variables related to decomposition and nutrient cycling (Figure 2) suggest higher turnover of organic matter in plots with higher tree species richness.

Additionally, 13 studies considered species identity in addition to diversity [16,20,25,26,27•,28–31,32••,33,34•, 35]. Although there were generally stronger effects of identity than of diversity in the particular studies (Figure 3), none of these studies looked at more than one independent ecosystem function. Thus, tree species with strong effects on specific ecosystem functions are likely to be different depending on the function considered.

Discussion and methodological considerations

Our review on current literature on tree diversity effects on ecosystem functioning confirms that species-rich forests generally show higher productivity than species poor forests [12••,36]. Given the global interest in mitigating the consequences of greenhouse gases in the atmosphere, tree species loss may thus lower the capacity of forests to sequester biomass carbon especially in growing forests. In addition, Thompson *et al.* [12••] stress the link between production and the ability to recover from disturbance in

Figure 3



Although diversity generally increases ecosystem functioning, there is an even higher chance for an increase in ecosystem functioning when looking at the effect of species identity (ident). However, different species may be needed to optimize several functional syndromes in an ecosystem simultaneously. Since current studies address only highly related ecosystem functions each, adopting a comprehensive study design by using a multifunctional perspective might dramatically change this pattern. For this plot, the head-counts for effects on ecosystem functioning variables were averaged. The height of the cells in low diversity conditions was augmented by the average found for diversity or species identity.

forest ecosystems, suggesting that diversity may also increase the residence time of the accumulated biomass carbon. However, the negative effects on resistance to herbivory reported by the studies are in contrast to earlier findings, which show that species-rich tree stands are less susceptible to herbivory and pathogens [37,38]. Finally, strong effects of particular tree species (Figure 3) on particular ecosystem function may turn into diversity effects when adopting a multifunctional perspective in diversity–ecosystem functioning research [39].

Several methodological caveats warrant a careful interpretation of the effects reported here. A large part of the studies looking at biota used dilution gradients of diversity (Figure 2). Here, monocultures and stands with low diversity are always dominated by the same species (e.g. *Fagus sylvatica* as 'matrix' species). This renders it impossible to separate true diversity effects from the effect of a particular species diluting the dominance of the matrix species. Additionally, most of the studies only looked at ecosystem functions during a short period of time, thus ignoring aspects of temporal variability in the response. Another serious shortcoming is that many studies ignore the variability induced by confounding factors, such as substrate and topographic heterogeneity (but see [22,30,32••,40]). However, due to their large size and high longevity, considering heterogeneity in space and time is especially important in tree stands [13]. Since single adult tree individuals occupy patches of up to 300 m^2 in size and can reach an age of several hundreds of years, mature tree communities have an intrinsic tendency to be subject to heterogeneous conditions. Unlike grassland experiments, studies on forest biodiversity should therefore control for a large number of covariates [32••,35].

Conclusion

Although there is a potential for tree species loss to lead to reduced functions and services linked to productivity, communities of biota, and soil parameters, at present we cannot disentangle the diversity signal from confounding factors such as environmental heterogeneity or species identity. The ideal design to study the functional significance of forest diversity would maximize three fundamental criteria, which we term orthogonality, comprehensiveness and representativity. Orthogonality refers to the ability of a design (either experimental or observational) to detect and quantify the effect of diversity against a background of various confounding variables. For example, given a dilution diversity gradient, we cannot separate the effect of diversity from that of a specific species added to the dominant species (see above). Orthogonality can be optimized by experimental design or by considering relevant covariates in the analysis. Healy *et al.* [32••] show that by chance, their species-rich plots were situated on high quality sites. By including site related covariates in their analysis, they can separate the effect of diversity from that of environmental heterogeneity. Comprehensiveness refers to the spectrum of ecosystem functions and services quantified in a study. As forest ecosystems exhibit a multitude of functions, the relevance of diversity can only be assessed by adopting a multifunctional perspective and simultaneously measuring all relevant functional syndromes (e.g. carbon sequestration, water cycling, nutrient retention, habitat provision, and timber production). Representativity refers to the relevance of the findings for the forest systems as we find them in the landscape. The better the design reflects the existing forest types, soil types and age structure, the easier it becomes to transfer results to real world conditions. All these approaches can profit from focusing on individual trees. As recently shown by Potvin and Dutilleul [41], diversity effects in forest communities can be traced down to interactions at the individual neighborhood scale. Additionally, tree individuals store their growing history in their woody tissue. This dendroecological information can provide detailed information on the individual's responses to environmental change, growing conditions, etc. The modular growth form of herbs and grasses complicates the separation of two way interactions between species from diversity effects [42]. In tree stands however, responses of tree individuals in nested neighborhoods can be used to address two way and higher order interactions between species.

Although it is evident that tree diversity can increase several ecosystem functions and services, evidence of consistent pattern remains scarce. Future studies may benefit from designs that simultaneously optimize orthogonality, comprehensiveness, and representativity, as well as exploiting performance information at the scale of tree individuals.

Conflict of interest

We are not aware of any conflicting interests.

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