Biodiversity and ecosystem functioning in dynamic landscapes

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The relationship between biodiversity and ecosystem functioning (BEF) and its consequence for ecosystem services has predominantly been studied by controlled, short-term and small-scale experiments under standardized environmental conditions and constant community compositions. However, changes in biodiversity occur in real-world ecosystems with varying environments and a dynamic community composition. In this theme issue, we present novel research on BEF in such dynamic communities. The contributions are organized in three sections on BEF relationships in (i) multi-trophic diversity, (ii) non-equilibrium biodiversity under disturbance and varying environmental conditions, and (iii) large spatial and long temporal scales. The first section shows that multi-trophic BEF relationships often appear idiosyncratic, while accounting for species traits enables a predictive understanding. Future BEF research on complex communities needs to include ecological theory that is based on first principles of species-averaged body masses, stoichiometry and effects of environmental conditions such as temperature. The second section illustrates that disturbance and varying environments have direct as well as indirect (via changes in species richness, community composition and species’ traits) effects on BEF relationships. Fluctuations in biodiversity (species richness, community composition and also trait dominance within species) can severely modify BEF relationships. The third section demonstrates that BEF at larger spatial scales is driven by different variables. While species richness per se and community biomass are most important, species identity effects and community composition are less important than at small scales. Across long temporal scales, mass extinctions represent severe changes in biodiversity with mixed effects on ecosystem functions. Together, the contributions of this theme issue identify new research frontiers and answer some open questions on BEF relationships in dynamic communities of real-world landscapes.

1. Introduction

Twenty-five years of research on the role of biodiversity in ecosystem processes and services has yielded an impressive body of literature. Generalizing over several hundred studies, there is clear evidence that the loss of biodiversity from a certain trophic group of species results in their reduced biomass production, associated with reduced efficiency of resource capture [1–3]. This relationship has been primarily observed in communities of autotrophs such as plants [4–7], but also holds in consumers of plant or animal resources [8–10] and decomposers feeding on dead organic material [11,12]. In fact, the loss of biodiversity across trophic levels has been predicted to show even stronger effects owing to the strong connection between consumer–resource energy fluxes and ecosystem processes [2,13,14]. The primary focus of BEF research has been on bivariate relationships between biodiversity and a single ecosystem process [1,4], but recent studies have provided strong evidence that the real functional importance of biodiversity lies in maintaining multiple ecosystem processes across environmental fluctuations in time or space [5,15]. The effects of biodiversity loss are rapidly seen when multiple functions are monitored...
over longer periods of time and across multiple local habitats [5], which reflects the ability of more diverse communities to stabilize processes across multiple environmental conditions [16,17]. Consequently, biodiversity effects in BEF experiments increase over time [6] with increasing resource use complementarity. This rather broad consensus on BEF experiment results is reflected by increasing awareness that changing biodiversity can affect ecosystem processes with a magnitude that is similar to other known impacts on ecosystems, such as eutrophication, disturbances or herbivory [18,19].

So what is the urgent question that warrants a special issue on BEF research? The issue stems from a discrepancy between the type of experiments done and the natural systems undergoing biodiversity change. The experiments are carried out under controlled, standardized conditions on small-scale plots over short periods of time. While these small-scale experiments have unravelled many mechanisms potentially underlying BEF relationships, they have a limited capacity to predict these relationships in multi-trophic communities at the larger spatial and longer temporal scales that are relevant for ecosystem services to human societies [20]. Hence, testing these results in real-world ecosystems with a dynamic community composition and diversity (hereafter: dynamic communities) has previously been described as a main research need in this area [21–23]. However, this requires scaling up the results of BEF experiments to (i) multi-trophic communities, (ii) non-equilibrium conditions with frequent disturbances and varying environmental conditions, and (iii) larger spatial and longer temporal scales. In the following, we will characterize these three major challenges for BEF research more concisely and introduce the articles of this special issue.

2. Issue (1): multi-trophic diversity and ecosystem functioning

Traditional BEF experiments most frequently manipulate the richness of one trophic level and keep constant the diversity of the other (prey or consumer) trophic levels, whereas in natural systems, biodiversity varies at both (or even across more than two) levels [24]. This simultaneous variation is triggered by (i) independent responses of species groups across trophic levels to environmental changes, and (ii) interdependent responses of the species groups to the biodiversity of the other level, such as predator and prey groups that covary in density and diversity. Bridging the gap between classic ecology addressing these triggers and interdependence between trophic levels and BEF studies focusing on the consequences for ecosystem functions requires a closer examination of the role of multi-trophic interactions in dynamic communities. In addition, most BEF experiments have manipulated plants or other low trophic levels [4]; whereas at global scales, species at higher trophic levels show the strongest reduction in population size and the highest risk for extinction [25–28]. Invasions, at the same time, occur predominantly at intermediate trophic levels [29], which also profit from the decline of top predators (a phenomenon called mesopredator release [30]). Thus, there is a clear mandate to analyse the functional consequences of biodiversity change in a multi-trophic food web context [28,31,32].

Superficially, this seems straightforward, because the general conclusion that biodiversity in a trophic group increases the efficiency of resource capture of this group seems to hold across trophic levels [1,3,9,12]. In real-world ecosystems, however, the clear separation between consumer and prey biodiversity effects is blurred by the complex structure of food webs [33]. While the group of autotrophs with their mineral resources are well defined, consumers of higher trophic levels often distribute their feeding interactions across resources of multiple trophic levels [24,33]. Hence, the dynamics of resource and consumer populations comprise feedback mechanisms via intraguild predation links that alter the functional consequences of biodiversity change [9,34,35]. For instance, changing predator diversity can have positive, negative or neutral effects on lower trophic levels depending on the network position of the species lost [36]. This pattern can become even more complex if non-trophic interactions across trophic levels are accounted for [37,38]. A meta-analysis of predator biodiversity manipulations showed that more-diverse predator assemblages reduce prey populations more than less-diverse ones [10]. However, another meta-analysis of studies manipulating the presence–absence of predators suggested that predator presence reduces prey abundance, but less so in more diverse predator assemblages [39]. How can two large-scale synthesis efforts come to such diametrically different conclusions? The answer very probably lies in the exact structure of the predator–prey interaction, including the degree of intraguild predation and generalism at the predator level [9,35], as well as the diversity and edibility at the prey level [39–41]. If increasing biodiversity at the consumer level increases the risk of negative intraguild interactions among consumers, the relationship between consumer biodiversity and resource capture may become nonlinear (blue line in figure 1b). In addition, if increasing species richness at the prey level increases or decreases prey edibility, then consumer biodiversity effects may be exaggerated (green line) or reduced (red line) in comparison with single prey items (figure 1b). The structure of trophic networks and the frequency of intraguild predation varies systematically with the number of species in natural communities [42]. As the exact position of these intraguild predation motifs cannot be predicted a priori, this hinders simple predictions of how ecosystem functions vary between low- and high-diversity communities. This simultaneous change in biodiversity, network structure and associated ecosystem energy fluxes may explain the frequent occurrence of idiosyncratic BEF relationships in multi-trophic experiments [43,44].

This issue provides fresh insights into how the apparent indeterminacy of effects in complex networks [45,46] can be overcome in future BEF research. For example, one article in this special issue [47] illustrates the application of trait-based approaches to characterize the functional structure of complex networks. Metrics are dovetailed to describe the functional diversity of complex food webs and the consequences for food web structure, resource use efficiency, trophic regulation, and the cycling of energy and materials in the community. This network approach opens exciting new avenues for future research on species traits and BEF in multi-trophic communities [47]. Tackling BEF in complex natural communities thus requires understanding the importance of various species traits and population characteristics, including (i) the population-averaged body mass, (ii) population abundance (or biomass density); and (iii) the stoichiometry (i.e. the content of nutrients such as nitrogen and phosphorus) of their biomass. Several empirical articles of this special issue address how these traits modify or drive BEF relationships in multi-trophic
Figure 1. Biodiversity within a trophic level is predicted to enhance ecosystem functioning (biomass production and resource capture) by this trophic group (a). However, changes in the degree of intraguild predation or interference competition with increasing consumer diversity may lead to reduced resource capture at higher diversity (b, blue line). Moreover, alterations of biodiversity at the prey level may lead to associational resistance (lower edibility, red line) or prey complementarity (higher edibility, green line).

3. Issue (2): non-equilibrium biodiversity and ecosystem functioning: disturbance and varying environmental conditions

Traditional BEF research is based on controlled manipulations of biodiversity, where treatment levels are maintained constant in biodiversity (i.e. the number of species in the plot) as well as community composition (i.e. the identities of the species remain the same) by continuous manipulations through weeding (i.e. removing individuals of species not belonging to the desired community composition) or reinoculation of the desired species. Thus, the natural dynamics of colonization and local extinction are not permitted in these assemblages. Moreover, to avoid mixing biodiversity treatments with hidden sources of variation, environmental heterogeneity among plots and disturbances are minimized even in the most complex BEF experiments. This leads to a decoupling between the processes shaping biodiversity (colonization, competition, response to consumers or disturbances) and the functional consequences of biodiversity. Interestingly, traditional biodiversity experiments are thus unable to disentangle direct effects of disturbances and environmental heterogeneity on ecosystem functions from indirect effects via induced changes in biodiversity or community composition.

Complementarity in resource use has been proposed as a main mechanism underlying BEF relationships. By definition, complementarity effects are strong if species with different resource use traits can stably coexist over extended periods of time. Frequent disturbances or fluctuating conditions might prevent strong complementarity effects, as dynamic systems are often transient between assembly and disassembly processes, which are only partly related to resource use traits. The destruction of assembled communities by disturbances precludes the dominance of equilibrium-based mechanisms of coexistence, which will strongly affect biodiversity–ecosystem functioning relationships [55], because the dominance of species will not only be based on their resource use or effect traits [56], but also by chance, e.g. through priority effects in the colonization sequence [57,58]. If successful, functional traits in non-equilibrium conditions are not related to the use of resources and growth, but to colonization and dispersal abilities, or the ability to withstand disturbances. Enhancing the number of species with such traits might not necessarily increase resource use, leading to a larger breadth of potential BEF relationships [55]. Likewise, sequence and priority effects can also restrict diversity effects as species performing certain functions or using a certain aspect of the resource spectrum are not able to enter communities [57]. The central questions are whether links between structure and function can exist in such non-equilibrium conditions, and which mechanisms constrain these links.

communities. One article of this special issue disentangles the effects of rare and common species (according to local abundances) in nine trophic groups on ecosystem multifunctionality [48]. Interestingly, they show that across these multiple trophic levels, rare species are the main drivers of ecosystem functioning, whereas common species have more variable effects [48]. Counterintuitively, these results suggest that rare species (i.e. those with low local abundance) should be prioritized in studying and maintaining natural BEF relationships. Another article of this special issue, a meta-analysis of 78 structural equation models, provides evidence that biodiversity is a strong driver of productivity [49]. Using an existing template [50] to disentangle the effects of potential productivity (resource availability and stoichiometric imbalance) on biodiversity and realized productivity (biomass production), they use standardized path coefficients as effect sizes across ecosystem types and find that, on average, the direct effect of resource availability on biomass is as strong as the effect of biodiversity change. Resource imbalance, however, plays a minor role in these datasets [49]. Recently, analyses of species’ average body masses and stoichiometry as two drivers of biodiversity, network structure, and ecosystem processes have been unified [51–53]. One article of this special issue follows this approach and combines metabolic theory and ecological stoichiometry to predict consumer growth and grazing rates as ecosystem processes in planktonic food webs [54]. Interestingly, the results of experimental microcosms mostly match the theoretical predictions, indicating that these species traits, along with environmental factors such as temperature, may provide important proxies for predicting BEF relationships in multi-trophic communities [54]. Taken together, these studies suggest that trait-based approaches may provide an important tool for overcoming the indeterminacy of effects in complex ecological networks for determining BEF relationships.
Dynamic ecosystems undergoing periodic or stochastic changes in abiotic conditions and resource availability might not easily be compared with the majority of BEF experiments. BEF experiments under controlled and mostly stable conditions have documented a saturating increase in ecosystem functions (figure 2a). In a community subject to pulse perturbations, diversity oscillates through time (figure 2b) [46]. Typically, only perturbation-resistant species (or resistant genotypes of species) will survive each pulse and the community will be re-invaded by other species (or genotypes). In our hypothetical example, community composition shifts through time towards species with higher resistance to perturbations (i.e. losing the most sensitive species and gaining tolerant species) thus dampening diversity oscillations. The combination of diversity fluctuations in time (figure 2b) with BEF relationships (figure 2a) yields a predicted oscillation of ecosystem functions in time (figure 2c, green line). In contrast to this simple prediction based on traditional BEF experiments, however, different species compositions at high and low diversity and their response to the perturbation may also cause different patterns in ecosystem functions. For instance, after perturbations, communities might be dominated by stress-resistant yet less-productive species (decreasing the minima of the oscillations in productivity), whereas after recovery communities may become dominated by more productive species (increasing the maxima of these oscillations). This would yield more strongly oscillating patterns in ecosystem functions (figure 2c, blue line). In addition, systematic shifts in community composition may favour species whose regeneration niche is favoured by disturbances. These communities may maintain higher productivity despite perturbations leading to oscillations in ecosystem functions around higher mean values (figure 2c, orange line). Measurements of ecosystem function and diversity at multiple points of these time series yield new relationships between biodiversity and ecosystem functioning (figure 2d). BEF relationships obtained under controlled conditions (green line) do not provide accurate predictions for situations with direct effects of disturbances on functions (blue points corresponding to blue line in (c)) or adaptive populations (orange points corresponding to orange line in (c)).

Figure 2. The relationship between biodiversity and ecosystem functioning is changed by disturbance or varying environmental conditions. (a) Changes in biodiversity under controlled conditions exhibit saturating effects on ecosystem functions. (b) Disturbances or varying environmental conditions cause oscillating fluctuations in species richness yielding; (c) fluctuations in ecosystem functions through time that are similar if controlled BEF relationship holds (green line, combination of lines in (a) and (b)), accelerated if functions also exhibit a direct response to disturbances (blue line) or accelerated with an increase over time if the populations adapt to maintain higher functionality despite disturbance (orange line). (d) BEF relationships obtained under controlled conditions (green line) do not provide accurate predictions for situations with direct effects of disturbances on functions (blue points corresponding to blue line in (c)) or adaptive populations (orange points corresponding to orange line in (c)).

In this species issue, several articles address the consequences of disturbances and environmental variation on BEF relationships. The flooding of one controlled experiment, the Jena experiment, provides some information on disturbance effects on BEF relationships [59]. Surprisingly, this article...
shows that the plant species richness on the plots is negatively correlated with the community resistance to flooding. This is the first detailed evidence of a negative biodiversity-stability relationship in plant communities in response to a flood disturbance. However, plant communities with higher functional trait diversity remain the most productive following the flood [59]. Multiple extreme events such as heat waves, droughts, cold snaps and floods are the focus of a article addressing multi-trophic freshwater communities [60]. Together, these studies illustrate that disturbance can substantially modify BEF relationships.

The last article [60] additionally addresses management issues: how can understanding of the consequences of extreme events at multiple organizational scale improve ecosystem management? The authors advocate for the use of models based on first principles to address ecosystem structure and functioning in a world where today’s extremes represent the new norm [60]. In a case study of this special issue, data from 360 different grassland plots are combined to address relationships between un-manipulated plant species richness and above-ground productivity [61]. Different effects of grassland management on plant species richness and productivity resulted in a wide-range ecosystem-specific BEF relationships that were either positive, neutral or negative [61]. Similarly, another article of this special issue studies the effects of land use changes and anthropogenic impacts on BEF relationships in a tropical landscape [62]. Rainforest transformation and land use intensification reduced both biodiversity and related ecosystem functions, such that economic interests and ecological properties need to be addressed jointly to inform stakeholders and decision-makers about the trade-off between crop choices and the stability of biodiversity and ecosystem functions [62]. Together, these studies highlight that anthropogenic management of ecosystems can have a tremendous effect on biodiversity–ecosystem functioning relationships strongly contrasting with those frequently observed in controlled experimental studies.

Three articles of this special issue study how varying environmental conditions affect BEF relationships. A meta-study of this special issue integrates data from 16 grassland BEF experiments to address interactions between biodiversity and one of two essential resources (soil nutrients or water) on above-ground plant productivity [63]. The results indicate that the biodiversity effects on ecosystem functioning do not interact with the resources to affect productivity [63]. Another meta-study of this special issue, an experiment replicated at 32 grassland sites on four continents, addresses how eutrophication and climate affect the invasibility of plant communities by non-native species [64]. Interestingly, this study shows that (i) invasibility is fostered by eutrophication and (ii) this effect is dampened as temperature and precipitation increases [64]. The emergent result from these two studies is that the effects of varying environmental conditions on BEF relationships are (i) non-trivial and (ii) depend on the ecosystem function that is studied. Interestingly, the ability of species to cope with varying environmental conditions can also interact with land use types. Often, variation of environmental conditions in space or time causes genetic heterogeneity within populations leading to species with variable traits. One article studies the variability of traits within populations for BEF relationships [65]. This article poses central questions which need to be addressed in order to understand whether species with greater trait variability will enhance temporal stability in their population dynamics and thus stabilize ecosystem functioning. Most central is whether species with high levels of variation for one trait regulating the response to environmental change also possess high variability in traits regulating their effect on ecosystem processes [65]. Interestingly, these three studies highlight that environmental conditions have direct as well as indirect (via changes in species richness or population traits) effects on ecosystem functions. Unlike controlled experiments, future studies of BEF relationships in natural ecosystems will disentangle these direct and indirect effects.

4. Issue (3): biodiversity and ecosystem functioning at larger spatial, landscape scales and across long time scales

A third issue is whether the focus on local (alpha-) diversity and short time scales (i.e. few generations) in BEF experiments is providing the critically important information on the consequences of extinctions in real-world ecosystems. Globally, species are going extinct at such a high rate that the current era has qualified as a period of mass extinction [50]. However, whether this global extinction also reduces biodiversity at the local level, where functional consequences occur, is an open question. In more than 450 marine data series on coastal biodiversity, the majority showed increased species richness or no significant change, only a minority showed lower richness over time—but however, these were from habitats with strong human impacts [51]. For terrestrial plant biodiversity, trends in local species richness across 168 studies were not significantly different from zero, as positive and negative trends were observed with similar frequency [52]. Global declines in species richness and homogenization of biotic composition by human transport of organisms might—rather than reducing alpha diversity—result in reduced beta diversity in real-world landscapes. Whereas extinctions and introductions lead to neutral trends in species richness at the assemblage level, the dissimilarity of composition among assemblages has been observed to change over time in a meta-analysis of 100 data series across biomes [53]. On the one hand, these results lead to the question of how biodiversity at larger spatial scales (e.g. in meta-communities) affects local and regional function. This becomes especially important if species turnover maintains functioning over time, because homogeneity of species pools across landscapes will reduce the possibility of compositional turnover. On the other hand, the role of rapid adaptation and evolution for BEF relationships comes into focus. At larger temporal and spatial scales, the evolutionary aspects of biodiversity become central, such as phylogenetic and functional relatedness or the adaptation to environmental conditions from ecological to geological time scales. There are several ways to cope with the problem of spatial and temporal scales, including (i) upscaling the results obtained by mechanistic yet small-scale experiments; and (ii) taking holistic approaches at landscape levels [20].

Scaling up results from small-scale BEF experiments to larger spatial and longer temporal scales is essential, because at these scales, the globalized human society derives ecosystem services from biodiversity. Experimental BEF studies have provided scaling relationships between ecosystem functions and biodiversity (figure 3, green line). Extrapolation of these relationships to higher diversity (figure 3, dashed green line)
systems. These results illustrate that BEF relationships at these scales, consistently across temperate and tropical ecosystems, are linked by seed dispersal by frugivorous birds are studied [66]. Genetic analyses of the plant populations allow building the spatial network. Interestingly, the spatial network is neither continuous nor random but is characterized by a modular structure of highly connected within-module trees and loose coupling of modules by long-distance dispersal [66].

5. Conclusion

The articles of this special issue demonstrate that BEF relationships in dynamic communities can differ substantially from those in controlled experiments, because ecosystem functions in real-world landscapes respond directly and indirectly (via species richness) to environmental drivers. While controlled experiments test for interactions between environmental drivers (e.g. flooding or drought) and biodiversity (usually via manipulations of community composition), only studies in real-world landscapes can also include the response of dynamic communities (composition and species richness) with knock-on effects on ecosystem functions (i.e. the indirect effects of environmental drivers). In this vein, the interaction between global-change drivers such as climate warming and eutrophication, and the multi-trophic structure of ecological communities are particularly important [71–76]. These studies demonstrate that in future research, the relative role of direct and indirect processes must be assessed from the perspective of understanding basic mechanisms [77], but also with a greater emphasis on providing ‘actionable’ knowledge to inform decision-makers [20]. Importantly, the studies in this issue demonstrate that future research also must account for human management of natural ecosystems, as these anthropogenic stressors can amplify effects of environmental drivers.

Prior research has indicated that multi-trophic BEF relationships appear to be idiosyncratic, but some of the articles of this special issue show that they can be deciphered by focusing on trait-based approaches. In this vein, traits linked to energy and matter demands, such as growth rate, feeding strength or body size [78–83], seem most promising in order to achieve a synthesis of BEF relationships in interaction networks. Ultimately, energetic and matter constraints are the primary currencies that link biodiversity to ecosystem functions in real ecosystems [14]. In this issue, we have demonstrated that large scales may be dominated by driver variables that differ from those at smaller scales [67]. Hence, the consequences of biodiversity change for ecosystem functioning may be underestimated when extrapolating results using relationships from small-scale experiments.
metabolic aspects of such energy availability and demand (body mass, temperature, abundance) and the absolute and relative availability of matter (stoichiometry) offer a promising toolbox for understanding BEF relationships in dynamic, real-world landscapes based on first principles.

Changes in biodiversity and the consequences for ecosystem functions and services to humans occur at large spatial scales and across long time scales. Research within this special issue indicates that different drivers of BEF relationships occur (i) at small plot scales (species identities, composition) and large landscape scales (biomass, species richness) as well as (ii) short and long temporal scales. These results imply that not all relationships and findings obtained by studies at small spatial and short temporal scales can necessarily be translated to the larger or longer scales that have relevance for political decisions and conservation biology. Hence, macro-ecological BEF research and novel modelling approaches are required to scale up BEF relationships across spatial and temporal scales.

While many challenges remain, the research described in this special issue demonstrates that ecologists have started the quest for BEF relationships in dynamic communities of real-world landscapes. To support effective predictions about how future changes in biodiversity will affect ecosystem functions and services, BEF relationships for multi-trophic communities at large spatial and long temporal scales in habitats under disturbance and varying environmental conditions represent the current frontier for our discipline.

Competing interests. We declare we have no competing interests.

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