

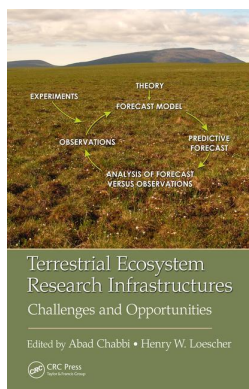
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Abad Chabbi, Henry W. Loescher

Quantifying Relationships between Biodiversity and Ecosystem Function with Experiments

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Charles A. Nock, Lander Baeten, Andy Hector, Kris Verheyen, Wolfgang W. Weisser, Michael Scherer-Lorenzen

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5

Quantifying Relationships between Biodiversity and Ecosystem Function with Experiments

Charles A. Nock, Lander Baeten, Andy Hector, Kris Verheyen, Wolfgang W. Weisser, and Michael Scherer-Lorenzen

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5.1 Why Study Biodiversity–Ecosystem Functioning Relationships?

In the early 1990s, it became increasingly recognized that despite mounting global biodiversity losses (Ehrlich and Ehrlich 1981; Wilson 1988), science was limited in its ability to predict the effects of these changes. Now widely referred to as the “biodiversity crisis,” intensive research was triggered, seeking to answer the question: *how important are diverse biotic communities for ecosystem functioning?* (Schulze and Mooney 1993). The research underpinning this question represented a paradigm shift in ecology (Hillebrand and Matthiessen 2009). Traditionally, biodiversity research emphasized the regulation and maintenance of diversity, that is, the drivers of biodiversity, whereby biodiversity was seen as the consequence of the abiotic and biotic factors regulating a community (Chesson 2000). This emphasis has shifted toward understanding the consequences of biodiversity change on ecosystem functions, whereby biodiversity itself is a driver rather than a dependent variable in ecosystems (Schulze and Mooney 1993). Ecosystem processes sustain mankind: if biodiversity is needed for the processes, and in turn the

services provided by nature to humans, then conserving biodiversity is a necessity for preserving the foundation on which our life depends (Cardinale et al. 2012; Millennium Ecosystem Assessment 2005).

In the past 20 years, the relationship between biodiversity and ecosystem functioning (BEF) has developed into a central research topic in ecology (e.g., Cardinale et al. 2012; Kinzig et al. 2002; Loreau et al. 2002; Naeem et al. 2009). Initially, individual studies generally focused on a single ecosystem function in a particular context and were of limited duration. A seminal result of the research was the demonstration of a positive effect of increasing species richness on ecosystem functioning in the short term, both in terrestrial and aquatic ecosystems (Balvanera et al. 2006; Cardinale et al. 2006, 2007; Stachowicz et al. 2007; Worm et al. 2006). As the number of studies accumulated, it became possible to bring datasets together and investigate the effects of biodiversity on multiple ecosystem functions, that is, *multifunctionality* (He et al. 2009; Hector and Bagchi 2007; Isbell et al. 2011; Maestre et al. 2012). For example, in the intensively studied grassland biodiversity experiment in Jena, Germany (Figure 5.1a), several thousand variables have been investigated in the same plots (Allan et al. 2013; Roscher et al. 2004; Scherber et al. 2010). Such analyses thus represented an achievement in broadening the scope of studies from single function studies and few explanatory variables to more comprehensive analyses. A broadening of the scope of the science in more recent studies was also made possible by a broader characterization of ecosystems by inclusion of the ecosystem consequences of a change in the diversity of taxa other than plants (insects, Cardinale et al. 2002; animals, Gagic et al. 2015). As experiments matured and evidence accumulated, it was also shown that the effects of biodiversity on diverse ecosystem functions become stronger over time (Allan et al. 2011; Cardinale et al. 2007; Reich et al. 2012).

Despite worldwide efforts to reduce rates of species loss, the biodiversity crisis is still looming (Butchart et al. 2010). This continued attrition of biodiversity is especially concerning in the context of widespread global changes. Biodiversity–ecosystem functioning experiments have now shown that when comparing the same ecosystem functions, biodiversity can have effects as large as or even greater than global change drivers such as climatic change, acidification, elevated CO₂, and nutrient pollution (Hooper et al. 2012). Because of the link of biodiversity loss to ecosystem function and in turn the provision of essential ecosystem services such as the provision of clean water and food, there is also a strong link between biodiversity conservation, ecosystem management, and poverty alleviation (Turner et al. 2012). Perhaps with greater recognition of the contribution of biodiversity to human well-being, efforts to stop the loss of species will increase. Fostering the recognition of BEF relationships is a multifaceted challenge that requires coordination from the design stage of experiments (realism and relevance) to communication of the final results of experiments to a variety of different stakeholders ranging from fellow researchers to managers and private landowners.



(a)



(b)

FIGURE 5.1

Examples from biodiversity–ecosystem functioning experiments, (a) showing a large grassland study and (b) a high-density tree plantation. In IDENT, a “synthetic assemblage experiment,” a gradient of tree species diversity was created by planting plots (~3.2 m × 3.2 m) with different numbers of species and/or functional groups. ([a]: The Jena Experiment in Germany; From Roscher, C. et al., *Basic Appl. Ecol.*, 5, 107, 2004; Photo courtesy of the Jena Experiment, Jena, Germany; [b]: IDENT experiment, Freiburg, Germany; Photo by T. Kattenborn.)

5.2 How to Study BEF Relationships in Real Ecosystems?

If one is interested in answering *how does biodiversity affect ecosystem functioning*, most often the first approach coming to one's mind would involve searching for communities that differ or contrast in one aspect of biodiversity and comparing levels of ecosystem function across the sample of communities (Scherer-Lorenzen 2005). For example, in a forest ecosystem, several forest stands with contrasting community structure could be sampled with a random or grid-based selection of plots across a specific area. Then, values for measured ecosystem functions (often biomass production) would be plotted on the y-axis against the measured biodiversity, for example, number of tree species on the x-axis. This type of study, often referred to as *monitoring or sample surveys* (Figure 5.2) reflect natural conditions with respect to age structure, canopy and root architecture, food webs, or biogeochemical cycles at quasi steady state (Leuschner et al. 2009). For example, the expansive networks of permanent forest inventory plots found in many countries are increasingly valued not only for tracking timber stocks but also as a means to study BEF relationships in forest ecosystems (Ruiz-Benito et al. 2014). While the use of such data provides large advantages in terms of realism and relevance, they also present significant challenges. These challenges arise in part because different levels of biodiversity—whether defined as species richness, functional and/or phylogenetic diversity—are rarely equally represented on the landscape. Often, the majority of plots will have biodiversity values close to the mean, and fewer plots will represent low or high biodiversity levels. Alternatively, the distribution of biodiversity levels can be highly skewed, for example, with most plots at the low end of

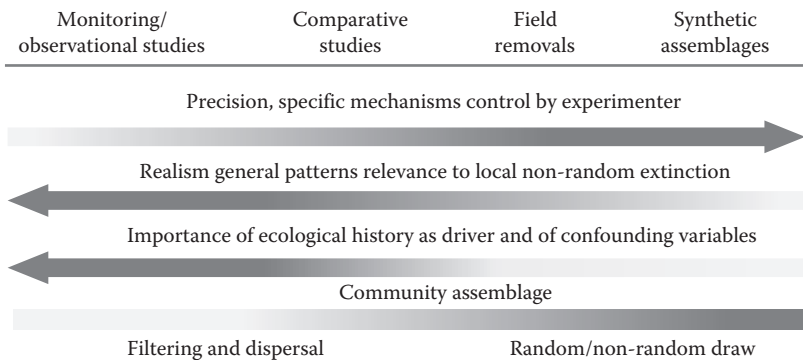


FIGURE 5.2

Comparison of scientific approaches to study the relationship between biodiversity and ecosystem functions and the different trade-offs inherent to these designs. (Modified from Díaz, S. et al., *Trends Ecol. Evol.*, 18, 140, 2003, Figure 1.)

BOX 5.1 BALANCED VERSUS UNBALANCED DESIGNS

- Balanced (orthogonal) experimental designs have the advantage that they allow the effects of two or more explanatory variables to be independently estimated.
- In contrast, with unbalanced designs, explanatory variables are partially confounded (correlated), and it is not possible to definitively separate their effects.

the diversity gradient as often found in managed ecosystems, such as plantation forests (Vilà et al. 2007).

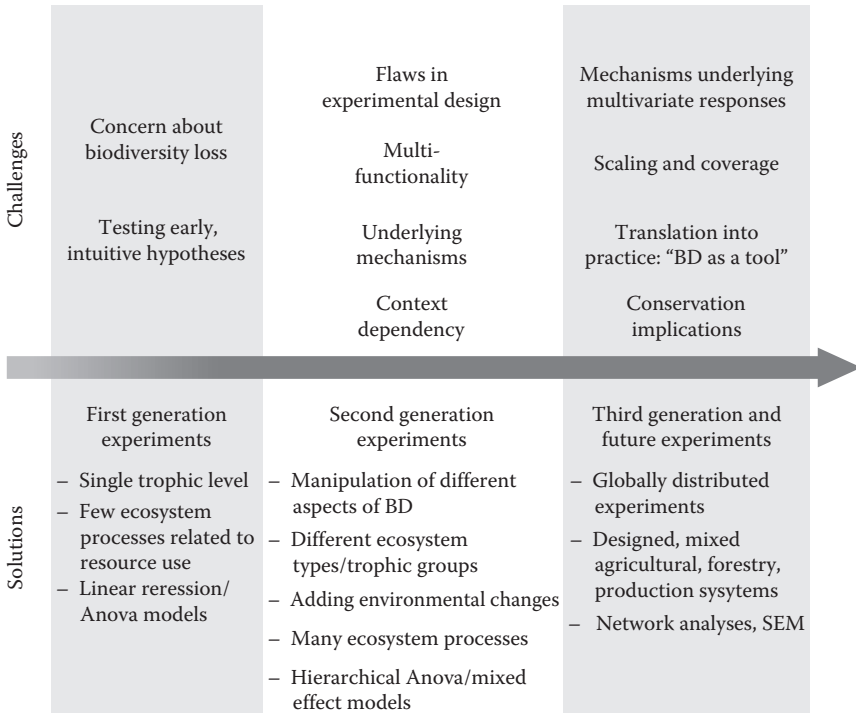
Statistically, such unbalanced designs (Box 5.1) are less powerful to detect causal relationships among variables than those experiments with a balanced design. In addition, unless site conditions are extremely similar, such across-habitat or across-locality comparisons may hide any potential effects. This can occur when differences in diversity are partly caused by environmental differences between the sampled sites, which introduce “noise” in the diversity–function relationship. Indeed, the environmental co-variables (temperature, precipitation) themselves determine the diversity of an ecosystem and the ecosystem properties and processes. For example, an asymptotical increase of biomass production with increasing plant species richness could be due to functional differences among species leading to niche differentiation and higher relative rates of resource exploitation and, hence, higher productivity rates. However, more productive stands may simply permit the coexistence of more species. Thus, such sample surveys only represent correlations between biodiversity and ecosystem processes, which are bidirectional relationships between two dependent variables (Baruffol et al. 2013), and causal relationships can only be approximated by accounting for measured environmental co-variables with suitable statistical procedures such as path analyses. To avoid some of these problems, *comparative studies* have been designed, where a similar number of plots per diversity level (e.g., species richness = 1, 2, 4, 6) are deliberately chosen along gradients of biodiversity, ideally coupled with a maximum standardization of conditions: environmental (e.g., soils, climate), stand age, or management history (e.g., Baeten et al. 2013; Bruelheide et al. 2011; Leuschner et al. 2009) (Figure 5.2). Nevertheless, there are many potentially confounding variables influencing biodiversity, and it is difficult to ascertain if they have been adequately accounted for in analyses, which is a crucial issue for the attribution of causality. In face of such “confounding variables,” experimental manipulation of plant diversity has been advocated to decouple biodiversity from environmental conditions in order to quantify causality and mechanisms of diversity effects. We will describe the basic design of such BEF experiments and their development over time in the following section.

5.3 The Basic Design of BEF Experiments and Their Development over Time

When biologists want to find out what a gene does, they develop a version of the organism without the gene of interest and grow individuals of these “knockout” organisms to see what the consequences of the loss of the gene are. Biodiversity experiments use the same basic approach to study the role of species in the functioning of ecosystems: the species to omit are chosen, experimental communities constructed from the species that are left (the species pool), and their function examined (Bell et al. 2005; Schmid et al. 2002). Such experiments fall into two main classes: “removal experiments” and “synthetic assemblage experiments” (Figure 5.2).

In the process of community assembly—the formation of a local community by a subset of a regional species pool—many potential community members are excluded or filtered by biotic or abiotic factors. For example, herbivory of palatable species by deer and the formation of a community of browsing-tolerant or unpalatable species is an example of biotic filtering. Abiotic filtering is similar but naturally involves filtering of species by abiotic factors (for plants, soil type, water availability, temperature, etc.). *Removal experiments* are conducted by manipulating, through species removals, the diversity of naturally assembled communities (species, functional groups), thus creating a gradient in species richness (or an alternative metric of diversity) ranging from natural to depauperate. These types of experiments mimic the loss of species as a result of specific pests or pathogens in the past, for instance. Removal experiments are meant to emulate natural abiotic and biotic filtering of the regional species pool, represent realistic nonrandom extinction scenarios, and usually involve a large variety of organismic and functional groups (Díaz et al. 2003; Wardle and Zackrisson 2005). However, there have been a number of limitations in studies of biodiversity effects employing removal experiments. First, appropriate experimental controls are rarely used but are important to separate the effect of local species extinction from the disturbance caused by the removal process (Guido and Pillar 2015). Second, maintaining density across the diversity gradient as the abundance of the removed species varies may not be possible. Finally, species may be clumped in space, which may lead to little or no interactions among different species in a plot even though they are defined as belonging to the same community.

Synthetic assemblage experiments establish a gradient in plant biodiversity by sowing or planting, while keeping extrinsic conditions (e.g., climate, fertility, land-use history) as constant as possible. They are conducted in microcosms and controlled environmental facilities, or in the field. For very practical reasons, these experiments mainly use fast-growing, small-sized, mainly early successional model systems such as grasslands. The first such experiments in the Ecotron facility at Imperial College, Silwood Park, U.K. (Naeem et al. 1994),

**FIGURE 5.3**

Schematic representation of the development of experimental biodiversity–ecosystem function research over the last few decades. Detailed are the key challenges that have emerged and the solutions that were presented in response. The development is coarsely divided into three periods representing the evolution from first-generation through to third-generation experiments.

in North American prairie systems at Cedar Creek, MN (USA, Tilman et al. 1996) in serpentine grasslands of California (Hooper and Vitousek 1997), and within the European BIODEPTH project (Hector et al. 1999) paved the road for even larger and more sophisticated experimental designs (Figure 5.3). These early biodiversity experiments tended to focus only on the effects of species richness and composition while holding other environmental factors constant. However, we now know that biodiversity loss has impacts of a similar magnitude as other global change drivers (Hooper et al. 2012). For example, in locations where species losses fall within intermediate projections (21%–40% of species loss), biomass production is expected to be reduced by 5%–10% below the most diverse mixtures, an effect that is comparable in size to the effects of global changes such as ultraviolet radiation and climate warming on plant production (Hooper et al. 2012). Given that species loss and global changes will act in concert in influencing ecosystem function,

next-generation experiments have started to become multifactorial: manipulating diversity and other factors related to global change such land-use intensity (e.g., agricultural intensity, mowing and fertilization, Weigelt et al. 2009) and drought (e.g., Vogel et al. 2012), eutrophication of soil resources and elevated CO₂ levels (e.g., Reich et al. 2001), and the study of multitrophic interactions (Scherber et al. 2010; Figure 5.3).

Biodiversity experiments tend to have complex designs for several reasons. First, one key aim is to assess the effect of varying species diversity (or functional groups, genotypes, etc.); however, this was challenging in initial designs because species composition (which species are present and their traits) was sometimes confounded with the number of species. In what was probably the first formal biodiversity experiment—by Naeem et al. (1994) using the British Ecotron-controlled environment facility—a single high-, medium-, and low-diversity community were compared, and consequently, the effects of species richness (number of species) could not be separated from the effects of species composition (the particular set of species used for the high-, medium-, and low-diversity communities). In turn, later first-generation designs dealt with this issue by quantifying an average effect of changing the number of species over a sample of different possible species compositions within each diversity level (e.g., Tilman et al. 1996). For example, an experiment could start with a complete community of species and ask what is the effect (on ecosystem function) of halving the number of species. The challenge then becomes that there are many different possible ways to halve the number of species and how to do so to derive an average response and to avoid bias. In one commonly applied method, bias is avoided through random selection of the composition of the depauperate communities. However, species often do not go extinct at random in nature. Rather, depending on the cause, species may go extinct at different rates depending on their vulnerability to certain extinction drivers (Box 5.2). However, often we are not sure what drives extinction. There may be several potential extinction mechanisms that may produce different patterns of species loss. Two or more extinction drivers may even be operating at the same time and potentially interacting with each other (such as climate change and invasive species, Wolkovich and Cleland 2010). Faced with these complexities and the status of randomization in experimental design, then random species loss is a sensible starting point in the absence of better information (Schmid and Hector 2004). Nonetheless, an important goal of next-generation biodiversity experiments is to examine the consequences of particular patterns of extinction loss caused by particular extinction drivers (Bruehlheide et al. 2014; Zavaleta and Hulvey 2004).

Biodiversity is more than just species richness and later generation experiments have tended to expand their focus to additional dimensions of biodiversity, such as species evenness, as well as the diversity of functional characteristics of species (a concept whose origins extend back to 300 BC and Theophrastus). In particular, many experiments focus not only on individual

BOX 5.2 RANDOM AND NONRANDOM EXTINCTION

- *Patterns of extinction*: Refers to whether extinction operates randomly or whether the probability of extinction is influenced by the traits of species.
- *Drivers of extinction*: Primarily anthropogenic-driven influences on the biosphere contributing to species extinction, such as habitat loss, harvesting, eutrophication, and climate change.
- *Random extinction*: For all members of a community, extinction is equally likely.
- *Nonrandom extinction*: Patterns of extinction in which species with similar traits are more likely to go extinct as a result of one or more extinction drivers. For example, in diverse mesic European grasslands, intensification of management has promoted species with traits favoring growth, which has led to the decline of competitively inferior species (e.g., Fuller 1986).

species but also on functional groups—species that are thought to contribute similar process rates on the overall ecosystem functions, such as biotic nutrient cycling, water usage, and productivity. These approaches are not mutually exclusive and can be combined, for example, by simultaneously manipulating the numbers of species and functional groups, albeit with practical constraints: you can have fewer groups than species but not the other way around (e.g., Roscher et al. 2004; Tilman et al. 1997). Functional diversity does not have to be approached by classifying species into groups, and, instead, various continuous measures of functional diversity (analogous to phylogenetic diversity) have been developed (Petchey and Gaston 2002; Schleuter et al. 2010). Diversity within species (i.e., genetic diversity) can also be manipulated, although this has been much less studied to date (e.g., Kotowska et al. 2010).

There has been a recent move to multisite experiments within ecology (“coordinated distributed experiments” [Fraser et al. 2013] such as Nutrient Network, Drought-Net), and this may have been partly influenced by multisite biodiversity experiments both in grasslands (Hector et al. 1999) and more recently in forests (Verheyen et al. 2015). This has implications for analysis. First-generation experiments were often analyzed with relatively simple classical least squares ANOVA and regression designs. However, later designs, particularly those with multisite experiments, require mixed-effects or multilevel models (see Box 5.3).

In summary, some of the milestones in the improvement of biodiversity experiments have been the development of designs and analyses that properly replicate both richness and composition; choice of random or directed

BOX 5.3 ANALYZING BEF EXPERIMENTS, FROM ANOVA TO MIXED-EFFECTS MODELS

The simplest of first-generation biodiversity experiments were typically analyzed using classical least squares linear regression or ANOVA models. However, as designs became more complex and also included species composition, then modern maximum likelihood mixed-effects models were a more appropriate choice (since species compositions were only a sample of the large number of possible species combinations). Mixed-effects regression models (or their Bayesian multilevel/hierarchical model counterparts) were also ideal for quantifying the variation in the intercepts and slopes of the regressions of function on diversity among the locations within multisite studies.

species loss; multifactorial designs that address biodiversity loss and other global change drivers (and their potential interactions) and multisite experiments that can look at the variability of biodiversity effects across locations. From the earlier mentioned pros and cons, it should be evident that there is no single best way to study biodiversity–ecosystem functioning relationships. The complexity of interactions among species underlying functional diversity effects, and the multitude of abiotic and biotic factors influencing ecosystem processes require a multitude of different, albeit complementary scientific approaches. Still, biodiversity experiments allow a process-based view on the underlying mechanisms of diversity effects on ecosystem functioning (Box 5.4).

5.4 The Future of BEF Platforms: Challenges for a New Generation of Experiments

While there is broad scientific consensus that changes in biodiversity cause important ecosystem responses, functional biodiversity research faces plenty of unresolved and emerging research questions that should guide future studies and the design of new platforms.

The first-generation experiments were often designed to understand fundamental mechanisms and were therefore stripped of much ecological complexity (Figure 5.3). The major advances in this field on theoretical and empirical grounds now allow making stronger linkages with real-world settings and the applied sciences, including agricultural and forestry practices. The challenge for a new generation of functional biodiversity research

BOX 5.4 RELEVANCE OF BEF EXPERIMENTS TO THE GLOBAL PROLIFERATION OF MONO-SPECIFIC TREE PLANTATIONS

Positive diversity–stability relationships can be related to the presence of species-specific responses to changing environmental conditions and functional redundancy within groups of species (“insurance hypothesis,” Yachi and Loreau 1999). Tree diversity has the potential to provide a specific type of insurance effect during replanting (or enrichment planting of selectively logged areas—we use planting as a shorthand for both practices). As with all insurance effects, it relies on ecological differences between species. In any given forestry enterprise, species are generally found to vary in their survival rates. When this is the case, there is a potential twofold cost of planting areas as monocultures (or very low diversity mixtures) that may be avoided by insurance effects of mixtures. When areas are planted as monocultures, there is the risk of recruitment and regeneration failure in the areas planted with species with low survival rates if eventual densities are insufficient to achieve the desired levels of basal area, canopy closure, and forest structure. In contrast, in the areas planted as monocultures of species with the highest survival rates, there is potential wastage of seedlings through excessive self-thinning due to intensifying intraspecific competition over time. Planting mixtures of species with different regeneration niches (conditions under which they have high and successful recruitment) may avoid this twofold cost of recruitment failure in some areas and wasteful self-thinning in others. The potential spatial insurance effect of mixtures may be particularly relevant, where forestry schemes are not able to do matching of species to sites. Most species also experience good and bad years for recruitment so that there is also a potential temporal component in which mixtures can once again bring a potential insurance effect for tree recruitment and forest regeneration.

principally involves extending both its scope and scale. In this context, we will discuss key considerations for designing future biodiversity–ecosystem functioning platforms (see also Bruelheide et al. 2014) as well as the current opportunities for doing synthesis analyses with already available data or targeted measuring campaigns in the existing infrastructures.

Novel biodiversity-oriented research platforms can extend the scope of existing infrastructures in several important ways. First, most experiments have so far created diversity gradients using random species compositions, which is a good starting point if the order of species loss in an ecosystem could follow many alternative sequences (Schmid and Hector 2004). The generality of the approach, however, is criticized for lacking relevance to

real-world scenarios of biodiversity change. Recent global syntheses found dramatic changes in plant community composition, rather than a general tendency for declines in local species diversity (Dornelas et al. 2014; Vellend et al. 2013), so future work should clearly focus on the ecosystem effects of those particular species (e.g., invasive species) and species compositions that are actually becoming widespread in nature. Species have generally been the focus and few studies attempt to link intraspecific trait variation with ecosystem processes. In large part, this is because identifying individuals in many experiments is challenging (e.g., grasses). However, in many experiments, individuals can be tracked (e.g., tree diversity experiments; Potvin and Gotelli 2008; Potvin and Dutilleul 2009), and exploring the functional effects of diversity within populations of individual species also deserves further attention (e.g., Violle et al. 2012).

While we have presented numerous arguments about the design of BEF experiments, it is important to note that in many places in the world experiments have not been conducted (Verheyen et al. 2015). The global distribution of experiments is skewed, and establishing new sites in underrepresented biomes should be a priority to further increase the scope of biodiversity experiments. Experimental tree diversity plantations, for instance, are concentrated in temperate regions, and the few located in tropical systems do not represent the largest forested areas and biodiversity hotspots (Verheyen et al. 2015). One way in which the establishment of experiments in underrepresented areas could be facilitated is through the activities of research networks that can promote the exchange knowledge across communities and provide support in the establishment and operation of experiments through shared experience and sampling protocols and methodologies (e.g., TreeDivNet: www.treedivnet.ugent.be).

The concepts and mechanistic insights gained from previous functional biodiversity research are not by any means restricted to natural or semi-natural ecosystems and have great potential for applications in economically important and intensively managed biological systems where one can virtually choose the desired number of species that grow together. Terrestrial ecosystems are predominantly managed. Management alternatives should thus be included in a greater number of biodiversity experiments in order to increase their relevance to the “real world” (Figure 5.3). Previous experiments have done so through the use of split-plot designs: for example, in Jena, a split-plot design was utilized to test the effects of agricultural management on biodiversity effects (fertilizer addition and mowing) (e.g., Weigelt et al. 2009). In BIOTREE, which has a very-long-term horizon, the influence of thinning on tree diversity effects on biomass production will be tested using a split-plot design (Scherer-Lorenzen et al. 2007). To maintain the diversity gradient that was created, experiments often require management, so careful consideration of management alternatives, developed together with stakeholders, can represent a valuable way forward. As argued by Bullock et al. (2001) based on positive biodiversity–productivity

relationships documented in British hay fields, the outreach of new experiments would dramatically increase if they were more relevant for economically important systems. In addition to production grasslands, agricultural production systems, agroforestry, and short-rotation coppices deserve more attention (Verheyen et al. 2015). Based on such studies, one could use biodiversity as a tool to achieve multifunctional and sustainable production systems. The functional biodiversity field also has clear conceptual insights and mechanisms to offer in the context of disease and pest control. For instance, plant diversity generally reduces the impact of pests and diseases through associational resistance, that is, via reduced host colonization and increased top-down regulation by natural enemies (e.g., Barbosa et al. 2006; Castagneyrol et al. 2013).

The scale of most existing BEF platforms is usually relatively small. Plots are typically only few square meters to one hectare for grasslands and forests, respectively, and are clustered in small and environmentally quite homogeneous areas. Using smaller plots generally allows for more realizations of the diversity and composition treatments in a single experiment, increasing the power to detect effects at the plot scale (Bruelheide et al. 2014), but limits opportunities to determine the context dependency of BEF relationships within these homogeneous areas, because the environmental variation covered is necessarily reduced. For instance, the relative importance of species identity effects and complementarity effects is likely to vary along environmental gradients. Indeed, the strength of diversity–functioning relationships is expected to increase with environmental stress, with stronger positive effects in stressed habitats (e.g., Jucker and Coomes 2012). Within a management context, this is important because high diversity may appear to be redundant in one context, but then increase in importance in response to a perturbation (Isbell et al. 2011). Multisite experiments (BIODEPTH, Hector et al. 1999; or FORBIO, Verheyen et al. 2013), experiments that incorporated environmental heterogeneity in their design (BEF China, Bruelheide et al. 2014) and projects that use complementary research platforms covering different scales from experiments to regional inventories (FunDivEUROPE, Baeten et al. 2013), are producing highly relevant data for understanding the relative importance of environmental drivers in directly affecting ecosystem function as well as in modifying the biodiversity effects. Plot-based approaches, even at multiple sites or along gradients, are less appropriate though to make inferences about ecosystem processes that operate at larger spatial scales such as water purification and nutrient cycles. Larger, watershed-scale platforms would be required to study those processes, which also provide opportunities to study landscape-level disturbances, including fragmentation, mammalian herbivory, and fires. Finally, biodiversity–functioning relationships appear to grow stronger with time, for instance, because complementarity effects accumulate when species are replaced by functionally dissimilar ones (Reich et al. 2012). Extending the monitoring of experiments over temporal scales that exceed typical project lives is

challenging but critically needed to fully understand diversity-dependent ecosystem responses.

Biodiversity effects on individual ecosystem processes including productivity and nutrient-use efficiency have been extensively studied (although, as argued earlier, there are numerous places on the globe where this important groundwork is still lacking). Now, the time is ripe to work on syntheses that quantify how diversity influences multiple ecological functions simultaneously (Figure 5.3; Byrnes et al. 2014). Such analyses can lead to guidelines about which species or species combinations will lead to the optimization of multiple ecosystem functions or rather create important trade-offs between functions (Gamfeldt et al. 2008). Context dependencies can be integrated in multifunctionality studies, by quantifying whether the variation in BEF relationships across environments is consistent across multiple functions. For example, increasingly strong biodiversity effects with increasing abiotic stress for both productivity (e.g., forests, Jucker et al. 2014) and drought tolerance (e.g., forests, Grossiord et al. 2014) would result in a positive covariation between the BEF relationships across environments. Comprehensive data for multifunctionality studies should come from groups of researchers from very different disciplines measuring responses on a common set of sites. Integrative research with close collaboration between researchers with various backgrounds working on different spatiotemporal scales and levels of taxonomic resolution is challenging but is now facilitated by recently developed data platforms that allow harmonizing, annotating, and sharing data in BEF research (Nadrowski et al. 2013).

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