REVIEW AND SYNTHESIS

Biodiversity in a complex world: consolidation and progress in functional biodiversity research

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Abstract

The global decline of biodiversity caused by human domination of ecosystems worldwide is supposed to alter important process rates and state variables in these ecosystems. However, there is considerable debate on the prevalence and importance of biodiversity effects on ecosystem function (BDEF). Here, we argue that much of the debate stems from two major shortcomings. First, most studies do not directly link the traits leading to increased or decreased function to the traits needed for species coexistence and dominance. We argue that implementing a trait-based approach and broadening the perception of diversity to include trait dissimilarity or trait divergence will result in more realistic predictions on the consequences of altered biodiversity. Second, the empirical and theoretical studies do not reflect the complexity of natural ecosystems, which makes it difficult to transfer the results to natural situations of species loss. We review how different aspects of complexity (trophic structure, multifunctionality, spatial or temporal heterogeneity, and spatial population dynamics) alter our perception of BDEF. We propose future research avenues concisely testing whether acknowledging this complexity will strengthen the observed biodiversity effects. Finally, we propose that a major future task is to disentangle biodiversity effects on ecosystem function from direct changes in function due to human alterations of abiotic constraints.

Keywords

Functional diversity, functional turnover, global change, metacommunities, multifunctionality, spatial and temporal heterogeneity, species richness, species traits.

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INTRODUCTION

During the last 15 years, ecology has undergone a major paradigm shift in the scientific perception of diversity (Naeem 2002; Gamfeldt & Hillebrand 2008). Classically, diversity has been analysed as a reflection of community composition regulated by abiotic and biotic constraints on species coexistence and dominance, where the main scientific objective is to understand the regulation and maintenance of diversity (Chesson 2000; Hillebrand *et al.* 2007). This emphasis has shifted towards biodiversity effects on ecosystem functions (BDEF), where diversity is a driver of ecosystem processes and the main objective is to understand consequences of altered diversity in ecosystems. Although some elements of this concept were published much earlier (Darwin 1859; Trenbath 1974; McNaughton 1993), the new phase of research on BDEF was initiated by a book (Schulze & Mooney 1993) and a series of seminal papers at the beginning of the 90s (Naeem *et al.* 1994; Tilman & Downing 1994). BDEF research was criticized from the outset (Aarssen 1997; Huston 1997) resulting in an unusually fierce debate about the validity of the concept as well as about details of study design and interpretation (Grime 1997; Naeem *et al.* 2002). These criticisms led to more awareness of potential artifacts and the evolution of more refined studies and analysis methods.

Recent years have seen a phase of synthesis in BDEF research, marked by a series of reviews and meta-analyses (Hooper *et al.* 2005; Balvanera *et al.* 2006; Cardinale *et al.* 2006a, 2007; Worm *et al.* 2006; Stachowicz *et al.* 2007). Without reiterating the details of these reviews, the emerging picture is that (1) losing diversity in an assemblage tends to reduce ecosystem process rates mediated by this assemblage, e.g. the production of organic biomass and the

efficiency of resource use (Hooper *et al.* 2005; Balvanera *et al.* 2006; Cardinale *et al.* 2006a), (2) both effects become stronger over time (Cardinale *et al.* 2007; Stachowicz *et al.* 2008), and (3) loosing diversity also affects certain (but not all) aspects of stability (Hooper *et al.* 2005; Balvanera *et al.* 2006). These conclusions are based on a broad array of studies from marine, terrestrial and freshwater ecosystems (> 400 effect sizes were included in Balvanera *et al.* 2006).

However, we argue in this manuscript that this evidence does not enable us to resolve some of the most critical concerns about BDEF: (1) the degree to which our present models and experiments reflect the actual strength of BDEF relationships in nature, (2) the relative contribution of biodiversity to an important ecosystem function compared to direct drivers of this functions, e.g. the role of diversity in primary production compared to direct controls by resource availability and temperature (Huston & McBride 2002; Grace *et al.* 2007), and (3) the potential to scale up from individual functions to the community and ecosystem level, which implies an understanding of the mechanistic basis of the multifunctional consequences of biodiversity.

These concerns arise because the state of the art is based on experiments and models which are to a large extent stripped of environmental and biological complexity. We strongly want to emphasize that our position does not ignore the importance of these pioneering studies in establishing the idea of a functional role played by biodiversity. These studies have highlighted potential ecological consequences of a major aspect of global change and triggered an avalanche of exciting research. However, in order to transfer these results to realistic scenarios of biodiversity change, it is not sufficient to simply fill knowledge gaps over the role of certain organism groups, ecosystem types, and functions considered. Rather, we need to enter a new round of BDEF research, which has to critically examine whether the proposed links between diversity and ecosystem function are both predictable and relevant in complex natural environments. This information is mandatory to implement our understanding of BDEF in ecosystem management, conservation issues and environmental policy.

To achieve this goal, we will review some new directions in BDEF research, discuss recent conceptual advancements, and also highlight gaps of understanding. We will focus on aspects of complexity, which are hitherto poorly reflected in BDEF research ('Complexity'). A major conclusion from this part is the importance of understanding the relationship between traits mediating coexistence and functional 'effect' traits to predict consequences of altered diversity ('Coexistence'). However, we will begin with a section 'Consolidation' refining our mechanistic understanding of BDEF, as both terms 'biodiversity' and 'ecosystem function' are often rather loosely defined in this context.

CONSOLIDATION

What is the biodiversity in BDEF?

From the 446 effect sizes calculated by Balvanera *et al.* (2006) from published BDEF experiments, 393 (> 88%) were based on the manipulation of local species richness. Just 5% of the studies used number of functional groups as a diversity measure, 2.5% evenness and the remaining < 5% used another measure of diversity. Referring to BDEF research to date, the conclusion would arise that the local number of species in an assemblage is the only relevant (or at least by far the most important) aspect of biological diversity for ecosystem functioning. Below, we formulate four arguments against this conclusion.

First, the intrinsic motivation of the entire research field of BDEF is the global loss of diversity. Because biodiversity is declining in many ecosystems, we want to know if this has functional consequences for ecosystems. However, local species richness alone is not a good measure of changing biodiversity (Wilsey *et al.* 2005). Before species richness is altered by anthropogenically induced extinctions or invasions, the human domination of earth ecosystems and biogeochemical cycles often results in changes in dominance (or rarity) (Hillebrand *et al.* 2008). Human trade and travel result in the transportation of species, which leads to a regional homogenization of species composition (McKinney & Lockwood 1999). Thus, local evenness or beta-diversity may be more sensitive to global change than local richness, but neither has been intensively studied. In microbial microcosms, a strong effect of evenness on functional stability was detected (Wittebolle *et al.* 2009), whereas grassland studies have shown varied responses of productivity and stability to plant community evenness (reviewed in Hillebrand *et al.* 2008). The consequences of changing beta-diversity have to our knowledge not been systematically assessed in the BDEF framework.

Second, species richness reflects only one level of biological organization. Early studies often argued that functional group richness is more important than species richness (Hooper *et al.* 2002), whereas recent studies have also addressed intraspecific (genotypic) richness as an important driver of ecosystem processes (Gamfeldt *et al.* 2005b; Reusch *et al.* 2005; Crutsinger *et al.* 2008; Ehlers *et al.* 2008). Although the argument on the importance of functional group richness continues in the literature, the debate is superficial as it creates new points of dissent on the classification of functional groups and ignores the point that the organizational level of diversity relevant to function may differ dramatically depending on the function addressed. The sometimes assumption-prone classification of functional groups can be transcended by using functional diversity as a continuous measure of individual trait diversity (Diaz &

Cabido 2001; Petchey & Gaston 2006; Wright *et al.* 2006). Different approaches to functional diversity exist, which can be used to measure trait differentiation between individuals within population, between species within communities, or between functional or phylogenetic groups (see Box 1 for a more detailed account of functional diversity).

Box 1 A trait-based approach to BDEF

The idea that the mechanistic understanding of functional consequences of diversity has to be based on the knowledge of species traits has been put forward very early in BDEF research. Traits were considered the units defining 'functional diversity', which numerous empirical studies highlighted as driving the performance of communities (recent examples include Finke & Snyder 2008; Mokany *et al.* 2008; Cadotte *et al.* 2009; Wacker *et al.* 2009). Consequently, conceptual contributions (Diaz & Cabido 2001; Petchey & Gaston 2002, 2006) and theoretical models (Loreau 1998; Norberg *et al.* 2001; Fox & Harpole 2008) have dwelled on the role of species traits in ecosystem functioning. Trait-based approaches have been strongly advanced in the recent ecological literature (Ackerly & Cornwell 2007; De Deyn *et al.* 2008; Litchman & Klausmeier 2008; Suding *et al.* 2008) and a comprising analysis of trait-based approaches would go beyond the scope of this review. Therefore, we will focus on two aspects which seem most relevant to BDEF research: a definition of traits and a definition of functional diversity based on traits.

Traits: In the context of BDEF research, individual traits are considered to be 'functional traits', which are defined as morphological, physiological or phenological characteristics of an organism affecting its individual performance (Violle *et al.* 2007). Body size, resource uptake rates, growth rates or life history phases (e.g., resting stage production) can be considered such functional traits (Litchman & Klausmeier 2008). Thus, functional traits influence an organism's fitness by affecting survival, growth and reproduction. By upscaling from the individual to the community level, functional traits are characterized as 'components of an organisms's phenotype that influence ecosystem level processes' (Petchey & Gaston 2006). Thus, functional traits are considered to be related to 'effect traits', i.e., traits affecting ecosystem processes (Violle *et al.* 2007). The central process in this correlation, i.e. the scaling from individual functional traits to community performance, is the focus of yet unresolved debates. Community functions can be envisioned as being based on the abundance- or biomass-weighted mean of individual (functional) traits (Grime 1998; Diaz *et al.* 2007). However, traits might be context-specific and the link between functional traits and contribution to community performance might change with environmental changes or changes in biodiversity (Fox & Harpole 2008).

Functional diversity measures: Functional diversity is a measure of trait diversity, which should allow to predict the changes in ecosystem processes based on changes in community composition. Instead of defining functional groups classified according to *a priori* defined schemes, functional diversity can also be described in continuous gradients of different traits, which are directly linked to certain functions (Diaz & Cabido 2001; Petchey & Gaston 2006; Weigelt *et al.* 2008; Griffin *et al.* 2009; Wacker *et al.* 2009). Functional diversity comprises different descriptors of variation in traits (Mouillot *et al.* 2005),
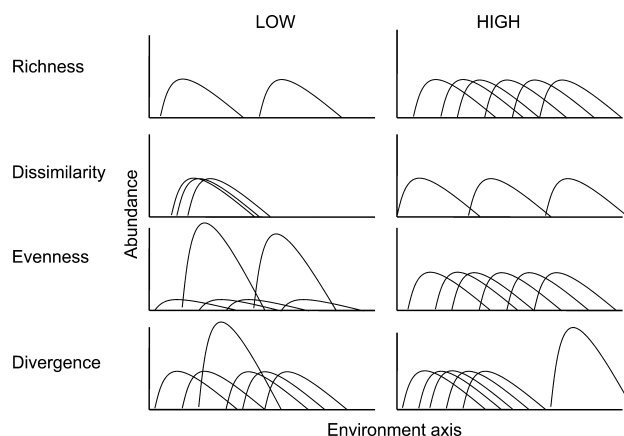

Figure 1 Abundance of traits along an environmental (niche) axis for low or high estimates of functional diversity aspects: trait richness, trait dissimilarity, trait evenness and trait divergence.

Box 1 *continued*

which together give a much more comprising picture of diversity. These descriptors are unique, but not necessarily independent of each other (Fig. 1). Trait richness corresponds to the number of distinct traits or traits attributes present (Mouillot *et al.* 2005). In the form of species richness or the number of functional groups, richness has dominated the literature on BDEF.

The more species are included in an assemblage, the more likely is an increase in the dissimilarity of the species (i.e., the coverage of the environmental axis). However, dissimilarity can also be different between two assemblages of the same richness ('trait range' according to Mouillot *et al.* 2005). The role of trait dissimilarity for BDEF has been highlighted in a number of recent studies. In an experimental study on rock pool metacommunities, sampling from a broader regional species pool (i.e., including increased trait dissimilarity) led to increased zooplankton production and cascading effects on phytoplankton (Naeslund & Norberg 2006). Likewise, a higher degree in soil macrofauna functional dissimilarity among a constant number of species led to enhanced soil respiration and leaf litter mass loss (Heemsbergen *et al.* 2004). Cadotte *et al.* (2008) showed that increasing trait dissimilarity by increasing phylogenetic diversity explained a higher proportion of plant community biomass production than any other measure of diversity.

Also the evenness or dominance structure of an assemblage (i.e., the evenness of trait abundance sensu Mouillot *et al.* 2005) can have strong consequences of ecosystem processes, either directly or by altering the functional consequences of richness (Hillebrand *et al.* 2008). If dominance becomes very high community function will reflect the traits of single species.

The higher the dominance of a single trait is, the more important it is to evaluate the divergence of this trait or the regularity of trait distribution (Mouillot *et al.* 2005). The dominant trait might reflect the average of the assemblage. Alternatively, it might represent an 'outlier' trait compared to the remainder of species. This divergence will affect the functional role of the entity (genotype, species, functional group) reflecting this trait.

Trait divergence and trait dissimilarity are two aspects of 'species identity'. Several studies partitioned the effects of diversity and identity on ecosystem functions (Bruno *et al.* 2006; Mokany *et al.* 2008), but we see 'identity' as integral parts of biological diversity related to richness and evenness. Instead, we request a more careful approach to the formulation of hypotheses for testing BDEF relationships (see main text). That is, if a function hinges on the presence of a certain trait, the hypothesis should involve trait dissimilarity and trait divergence. If a function depends on the coverage of a trait axis, richness and trait dissimilarity are to be involved. If a function depends on interactions within an assemblage (mutualistic or trophic interactions), richness and evenness are integral parts to be considered.

The implementation of trait-based approaches into BDEF research awaits further refinement. The statistical properties of functional diversity measures (Petchey & Gaston 2006) and the dependency of functional diversity measures on methodological choices (Poos *et al.* 2009) require further investigation. Our description of axes of functional diversity only considered a univariate environment axis along which traits were sorted. However, a trait-based approach becomes essential across different environmental axes and across different functions given potential trade-offs between functional traits (i.e., traits within a species) and between species (i.e., species across a functional trait axis) (see section 'Complexity: Multifunctionality' in the main text). The importance of trait-based approaches has independently been suggested in another recent review on BDEF (Reiss *et al.* 2009).

Third, richness and evenness measure the number of species and their relative abundance, but do not contain any information on the identity of the species in an assemblage. Including such information, however, may be needed to make real causal inferences on BDEF (Benedetti-Cecchi 2004). The predominant focus on richness has created much confusion about whether there is a functional consequence of diversity at all and has fueled much of the discussions about 'idiosyncratic' outcomes (Wardle *et al.* 1997; Emmerson *et al.* 2001) or identity effects (Bruno *et al.* 2006; Mokany *et al.* 2008). Integrating information on the identity of a species (or population or functional group) is necessary to successfully predict BDEF relationships.

Finally, the narrow focus on richness effects reflects a poor mechanistic understanding of BDEF relationships (Hooper *et al.* 2005). Species richness is comparably straightforward to manipulate, but richness is not a good measure of functional diversity (Diaz & Cabido 2001). The future assessment of BDEF critically relies on formulating causal linkages between particular aspects of diversity and particular functions. Relevant aspects of diversity can comprise the number of traits, the dissimilarity between traits, the dominance of traits, and the divergence of dominant traits (Mouillot *et al.* 2005; see Box 1).

What is the ecosystem functioning in BDEF?

Early BDEF research focused on primary production as the ecosystem function most often investigated. From the effects sizes in the Balvanera *et al.* (2006) database, 199

(~45%) reflect changes in primary producer abundance or biomass (or the variability of this over time) with changing diversity. However, the definition of 'function' has broadened considerably over the years and now covers a variety of important process rates (primary and secondary production, decomposition, element cycling, bioturbation, etc.) and ecosystem states (stability, nutrient retention, physical structure). A more comprehensive list published for aquatic ecosystems (Giller *et al.* 2004) also includes ecosystem goods and services, i.e. ecosystem processes and states utilized directly or indirectly by humans.

Whereas the development of BDEF research has led to a much broader array of functions considered, the mainstream study in the BDEF framework defines ecosystem function still by one ecosystem process or very few related processes. Balvanera *et al.* (2006) derived their effect sizes from > 100 studies. Almost half of these (45%) addressed only one function, whereas a minority addressed more than three functions at a time (12.8%).

A recent conceptual advancement has been the notion of biodiversity effects on ecosystem multifunctionality, which was proposed independently in two studies (Hector & Bagchi 2007; Gamfeldt *et al.* 2008). Both papers argue that studies hitherto have underestimated the functional role of biodiversity because they have focused on single ecosystem processes. If more processes are considered in combination, the effect of species loss becomes much more dramatic as species show trade-offs in their ability to perform certain functions. The number of species needed to sustain a minimum proportion of all functions considered increases with the number of functions and with the lack of functional overlap between species (Hector & Bagchi 2007; Gamfeldt *et al.* 2008). Thus, diversity effects on ecosystem multifunctionality (as the sum of states and rates in an ecosystem) are potentially much larger than diversity effects on single functions.

Why should BD affect EF?

The present discussion about neutral (Hubbell 2001) or niche-based (Chase & Leibold 2003) configurations of assemblages has strong ramifications for BDEF research. Almost all postulated mechanistic relationships between diversity and ecosystem functions require differences in traits. Therefore, BDEF holds only in a world of ecological niches. The only major exception is the so called portfolio effect, where higher richness leads to higher temporal stability of functions aggregated over the assemblage (Cottingham *et al.* 2001; Tilman *et al.* 2006). As long as the species in an assemblage show uncorrelated random fluctuations, adding more species leads to reduced variation in temporal fluctuations due to averaging effects (Doak *et al.* 1998).
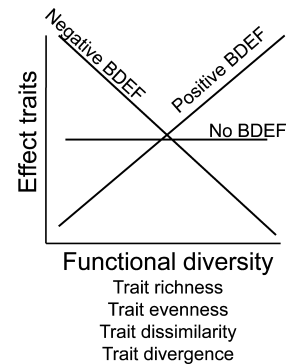

Figure 2 Potential relationships between aspects of functional diversity (see also Box 1) and effects traits, i.e., those traits defining the ecosystem effect of a species. See text for details.

For all other functions, differences in traits are necessary to explain BDEF. Trait differences in resource uptake and resource conversion into biomass production (Litchman *et al.* 2007; Thein *et al.* 2008) potentially underlie the complementarity effects (Diaz & Cabido 2001; Loreau & Hector 2001) used to explain diversity effects on productivity and resource use efficiency. Decomposition rates have been shown to depend on plant traits more strongly than on abiotic forces (Cornwell *et al.* 2008). Likewise, selection effects (Loreau & Hector 2001) must be based on species trait differences in performing certain functions. Regarding diversity effects on stability, higher resilience of assemblages relates to higher response diversity (Elmqvist *et al.* 2003), which equates with different species traits conferring ability to cope with a disturbance or stress. BDEF relationships based on positive interspecific interactions such as facilitation (Tiunov & Scheu 2005) or mutualistic interactions (Fontaine *et al.* 2006) also require trait differences resulting in strong interspecific interactions.

As functional trait diversity is necessary to explain most patterns in BDEF research, we define 'functional traits' and the different aspects of functional diversity in Box 1. Functional traits are characteristics of individual morphology, physiology and phenology (Violle *et al.* 2007). To relate these characteristics to the processes observed at the ecosystem level, there has to be an upscaling from individuals to communities (see Box 1), but also knowledge about 'effect traits', i.e., traits directly affecting ecosystem functions (Violle *et al.* 2007; Suding *et al.* 2008). As these effect traits may be context dependent, the relationship between functional diversity and ecosystem functions depends on the correlation between functional diversity and effect traits (Fig. 2). If increasing functional diversity optimizes effect traits, a positive BDEF relationship is to be expected. This would be the case if increasing functional diversity (e.g., trait richness) increases the average value of important effect traits (e.g., plant size, resource acquisition) related to the function

investigated (e.g., biomass production). If, however, average effects traits are not related to functional diversity or even decrease with functional diversity, we might see no to negative BDEF relationships. This correlation can switch when looking at another suite of functional traits or when looking at another ecosystem function.

This seemingly simple framework comprising functional diversity and effect traits allows to making a number of important predictions. First, BDEF relationships do not have to be positive. If the relative abundance or even the presence of certain traits is changed, we expect to see changes in processes and states related to these traits. Depending on the specific effect-function relationship (Fig. 2) and aspects of trait divergence and trait dissimilarity, both negative and positive changes are possible, which counteracts the one-sided view of diversity 'promoting' ecosystem function. Second, trait differences need environmental heterogeneity to play out. In a highly uniform and stable environment, functional diversity will have a small role to play. We will dwell more on this topic in the section on 'Complexity'. Third, evolutionary trade-offs between functions in species lead to trade-offs between species performance, which are a major mechanism maintaining species diversity (Chesson 2000). The same trade-offs stabilizing coexistence also define BDEF. We will get back to this topic in the section on 'Coexistence'.

COMPLEXITY

The section on 'Consolidation' provided evidence that the loss of species or their change in relative abundance should matter for ecosystem functions as soon as there is a relationship between functional traits of the organisms lost and their effect traits. So the relevant question might not be whether there is a BDEF relationship, but why the diversity effects observed in recent reviews (Balvanera et al. 2006; Cardinale et al. 2006a) are not generally much stronger. A major point of dissent on BDEF research is the structural simplicity of most empirical systems (and most models) used to test this concept. Ecologists experience ecosystems as complex systems with spatial and temporal heterogeneity within and across local habitat patches and characterized by a multitude of biotic and abiotic processes leading to very intricate states with regard to standing stocks, nutrient content and different aspects of stability. Most experiments in the BDEF framework do not reflect this complexity. Mainly one aspect of biodiversity (number of species) was manipulated for one (rarely two) trophic group(s) of organisms to assess the effect on one (rarely two or more) ecosystem process(es) or state variable(s). Most experimental systems and models lacked environmental heterogeneity in space and time, most studies ran too short to assess whether species were able to coexist and the array of

functions addressed is a very narrow subset of important ecosystem processes.

However, the addition of environmental complexity to BDEF research only makes sense if it actually changes our understanding of functional consequences of altered biodiversity. If the simple experiments and models already capture the majority of the dynamics of BDEF relationships, additional aspects should – in analogy to Occam's razor – not be added without necessity. The plea for more realistic studies is not new (Loreau et al. 2001; Hooper et al. 2005) and over the last years, BDEF studies have evolved to include more aspects of this complexity (Gamfeldt & Hillebrand 2008). We will address in this section, whether these additional aspects have changed the general conclusion that diversity affects ecosystem process rates. For each of these points, we will additionally address open questions to highlight some new directions in BDEF research.

Trophic structure

In a series of papers, Duffy (2002, 2003) highlighted the need to address consequences of consumer richness loss (in contrast to the predominant focus on plants and algae), as consumers in general were more prone to extinction and had strong effects on ecosystem function (see also Stachowicz et al. 2007). Consequently, trophic structure has been implemented in numerous studies, investigating the consequences of changes in microbivore, herbivore and predator richness or prey richness (see recent reviews in Duffy et al. 2007; Srivastava et al. 2009). At first glance, effect sizes for biodiversity on productivity and resource use efficiency did not significantly differ between trophic levels (Cardinale et al. 2006a). However, we suggest two specific aspects of trophic structure that are missing in many studies, which might limit our ability to predict effects of trophic diversity (or vertical biodiversity according to Duffy et al. 2007) on ecosystem functions:

First, very few studies have analysed both prey and consumer diversity changes simultaneously (Gamfeldt et al. 2005a; Bruno et al. 2008), although verbal arguments (Hillebrand & Shurin 2005) and theoretical insights (Thebault & Loreau 2003, 2005) propose that diversity changes across both levels result in highly interdependent consequences for consumption rates, resource use efficiency and resistance to consumption. In aquatic microcosms, e.g., a more diverse assemblage of consumers was more responsive to altered prey diversity than a single consumer species (Gamfeldt et al. 2005a). In a benthic marine system, both predator and herbivore diversity had unique effects on different ecosystem processes (Douglass et al. 2008).

Second, the details of trophic interactions are not well resolved in most studies. In their model, Thebault & Loreau

(2003, 2005) elegantly showed that the consequences of consumer diversity can strongly depend on consumer specialization and the edibility of prey. However, few studies have actually manipulated the degree of specialization in trophic links. In a very insightful study (Finke & Denno 2005), increasing predator diversity increased the strength of trophic cascades only if intraguild predation was absent. If omnivores were involved, more predator species weakened the trophic cascades. The same should be true if interference competition is the main mode of consumer interaction (Amarasekare 2003).

Spatial and temporal heterogeneity

The BDEF experiments analysed by Cardinale *et al.* (2006a) showed the general trend that mixtures were more effective in biomass production and resource use than the *average* monoculture, whereas there was no consistent transgressive overyielding compared to the *best* monoculture. In other words, the most productive single species was on average as productive as the mixture. Such transgressive overyielding was only found in long-term experiments (> 4.5 years for plant experiments, Cardinale *et al.* 2007), indicating that biodiversity plays a different role on short time scales compared to the long-term. Empirical evidence suggests an initially increasing and then stabilizing complementarity effect (Cardinale *et al.* 2007; van Ruijven & Berendse 2009). Likewise, marine seaweed diversity had higher impacts on ecosystem functions in long-term compared to short-term experiments, showing that the 'mainstream' short-term experiment published on BDEF reflect only a small subset of potential mechanisms detailing how diversity can affect ecosystem processes and properties (Stachowicz *et al.* 2008).

   In the short-term, a single species may be able to outperform a species mixture. The single most productive species can even show higher biomass yield than a corresponding mixture, when in the mixtures resources are channelled into less productive species (Norberg *et al.* 2001). However, over longer time scales, more traits are needed to allow for higher community flexibility, which enhances the importance of diversity for function (Norberg *et al.* 2001). Across a temporal gradient, the sign of the diversity – function relationship might change as different species become dominant with different traits (Weis *et al.* 2007). Otto *et al.* (2008) provided evidence that additive effects of additional predators in a trophic cascade relied on temporal niche separation. In this case, the phenology of arthropod predators played a substantial role such that increasing temporal niche complementarity (non-overlapping phenology) increased the additive effect of predator richness. Otto *et al.* (2008) also concluded that aspects of the identity of species (analogous to trait dissimilarity and divergence,

Box 1) become more important in variable than in uniform environments.

   The same argument holds for spatial heterogeneity. Most BDEF experiments have been conducted in highly uniform environments, although spatially more heterogeneous environments enhance the number of potential mechanisms linking trait diversity to ecosystem function (Stachowicz *et al.* 2008). Some aspects of heterogeneity have been addressed in recent BDEF experiments, with somewhat mixed results. When manipulating diversity and soil heterogeneity in a grassland experiment, soil heterogeneity increased the complementarity component of the net diversity effect, whereas in uniform environments selection effects prevailed (Wacker *et al.* 2008). Using structural equation models, Tylianakis *et al.* (2008) were able to show that the effect of diversity on different ecosystem functions (production, pollination, predation) increased with increasing spatial heterogeneity in resource distribution. However, an algal microcosm study showed that spatial variation in resource conditions did not *per se* lead to stronger BDEF relationship, leading to the conclusion that heterogeneity has to be coupled to differences in the relative fitness of organisms to enhance BDEF (Weis *et al.* 2008).
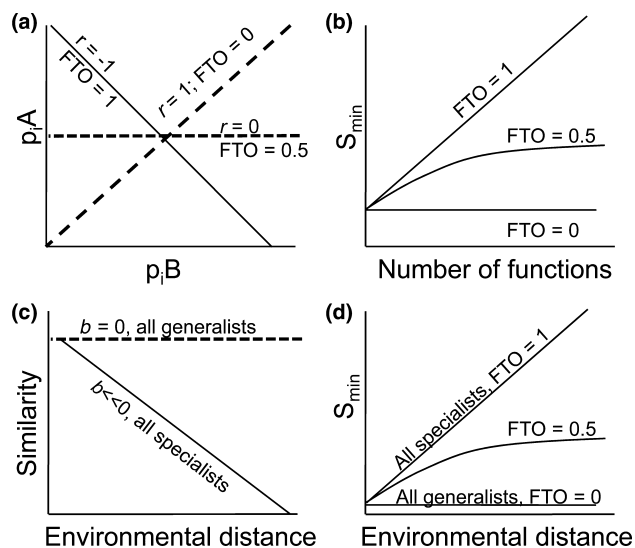

Figure 3 Conceptual diagram on functional turnover. (a) Correlation between proportional contributions p of each species i to two different functions, A and B. r = correlation coefficient, FTO = functional turnover. (b) Minimum species richness (S_{min}) needed to maintain a certain threshold level of multiple functions depending on the number of functions considered. (c) Decay of similarity of species composition with environmental distance, b = slope of the similarity vs. distance relationship. (d) Minimum species richness depending on the environmental distance.

Multifunctionality

The few studies analysing multifunctionality converge on the conclusion that consequences of diversity loss appear more dramatic if more functions are addressed (Hector & Bagchi 2007; Gamfeldt et al. 2008). However, these results were derived using calculations from monocultures and have not yet been analysed across diversity gradients. Moreover, the concept presented so far only comprised redundancy across function, which is based on the fact that a species sustaining one function in an assemblage might be less able to perform a second function due to 'functional trade-offs'. Such a functional trade-off involves different adaptations to, e.g., growth and competition, or carbon fixation and habitat structuring. As an example, the efficiency of resource use for one resource often is negatively correlated to the resource use efficiency of another resource (Tilman et al. 1982) such that more species lead to a more complete resource use (Bracken & Stachowicz 2006). Therefore the optimization of multiple functions (or more generally ecosystem multifunctionality) depends on more species than any single function (Gamfeldt et al. 2008).

Multifunctionality comprising different functions might be intensified if different species carry out a function along an environmental gradient in time or space as indicated above. A species may have limited ability to perform a certain function under different environmental conditions. In a spatially heterogeneous habitat or along temporal changes in the environments, we might see compositional turnover, i.e. the decay of similarity with increasing spatial distance (Soininen et al. 2007) or temporal distance (Korhonen et al. in press). In that case different species maintain certain functions under different conditions and the larger the environmental difference, the stronger the need for high trait dissimilarity.

In consequence, functional trade-offs and compositional turnover will lead to functional turnover (FTO), which we define as the rate of increase in the minimum number of species needed to perform a threshold level of each function in a multifunctional framework (Fig. 3). If FTO is based on functional trade-offs, the proportion p contributed by each species i for two functions A and B can be calculated (Fig. 3a). If the traits needed to perform these two functions are positively correlated (limiting case of no trade-off), a high ability to perform A includes a high ability to perform B. Then, the proportional contributions of each species to the functions A and B are positively correlated and there is no FTO (Fig. 3a). Thus, S_{min} remains constant if the number of functions considered increases (Fig. 3b). If the traits required for the different functions are uncorrelated ($r = 0$), FTO is estimated to be 0.5 (Fig. 3a), i.e., there is a 50% chance that species driving function A are also able to drive B. In this case, S_{min} increases gradually for each new function considered, resulting in a monotonically increasing, but decelerating function of S_{min} with the number of processes considered (Fig. 3b). If the functional trade-offs for function A and B are strong, a negative correlation between p_iA and p_iB appears (Fig. 3a). In this case the species needed to perform function A do not overlap with those performing function B, leading to a FTO = 1 and a linear increase of S_{min} with increasing number of functions (Fig. 3b). (Actually, linearity would require an unrestricted species pool, whereas – if the species pool is finite – the relationship between S_{min} and number of functions will decelerate and saturate).

This graphical display represents limiting cases assuming that all functions are either positively or negatively correlated. In reality, trait correlations may be nonlinear (Litchman et al. 2007) and vary for different pairs of functions as some require similar and other dissimilar adaptations (Vinebrooke et al. 2004; Litchman & Klausmeier 2008). Thus, the average correlation between proportional contributions to different functions may be close to zero. In fact, Gamfeldt et al. (2008) found very weak correlations ($-0.2 < r < 0.3$) between proportional contributions of species to different functions, suggesting uncorrelated functional traits.

In addition, FTO might also arise from temporal or spatial complementarity of species. If species are adapted to certain conditions, the similarity of species composition will decrease with increasing environmental distance, i.e., slope $b < 0$ (Fig. 3c). In a spatially or temporally heterogeneous environment, more species are therefore needed to maintain an overall threshold level of function across all environmental conditions (Fig. 3d). Only if single species show very broad environmental tolerances, similarity does not decay over environmental distance (Fig. 3c; slope $b = 0$) and S_{min} does not increase with increasing environmental distance (Fig. 3d).

The implementation of FTO into BDEF research might strongly enhance our ability to retrieve more realistic estimates for biodiversity effect sizes. Especially, it remains to be evaluated how the two sources of FTO, functional trade-offs and compositional turnover, interact. FTO from considering multiple environments or multiple functions might be additive or interactive (sub- or super-additive), potentially increasing the role biodiversity plays in ecosystem functioning.

Spatial dynamics

In addition to the spatial heterogeneity within patches, spatial dynamics between patches have been considered in BDEF experiments recently. Metacommunity dynamics have been explicitly used in models (Mouquet et al. 2002;

Loreau *et al.* 2003; Mouquet & Loreau 2003; Cardinale *et al.* 2004) and experiments (France & Duffy 2006; Matthiessen & Hillebrand 2006; Matthiessen *et al.* 2007; Venail *et al.* 2008). The inclusion of spatial dynamics is important for two reasons: on the one hand spatial dynamics allows for natural community assembly and the establishment of diversity gradients (in contrast to the artificial maintenance of gradients by the experimenter). In fact, the effects of species in a community can depend on their temporal arrival (Fukami & Morin 2003). On the other hand, spatial dynamics provide different mechanisms of coexistence, and we will show below that these different mechanisms relate to different expectations for the BDEF relationship (see 'coexistence'). Another appeal of the metacommunity framework is that the alteration of spatial dynamics directly corresponds to anthropogenic fragmentation and isolation, which are major drivers of global biodiversity decline.

We see mainly two aspects how this inclusion could be more fruitful. First, spatial dynamics have been analysed mainly within trophic groups, although space use probably increases with increasing trophic position if predators are more mobile than their prey. In a terrestrial study, the diversity effect by a mobile ladybeetle predator guild on aphid prey localized in constrained habitat patches was mainly negative due to interference competition, whereas
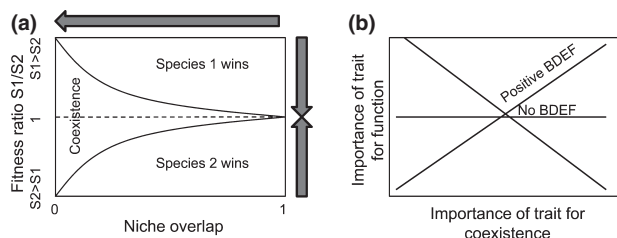
patchiness in prey availability led to aggregation of ladybeetles in habitats with high aphid density and thus to higher predator richness (Cardinale *et al.* 2006b). Second, the importance of temporal dynamics and synchronicity in metacommunities is poorly acknowledged. Temporal synchronization of within patch dynamics may lead to the regional dominance of species (Hillebrand *et al.* 2008), which will alter regional coexistence. If local patches are synchronized, the same species will dominate all patches, and only this species will profit from spatial dynamics, leading to low diversity and altered ecosystem functions. Corroborating this expectation, non-synchronizing fluctuations enhanced the stabilizing effect of diversity in experimental plankton communities (Downing *et al.* 2008).

COEXISTENCE

The mechanisms leading to coexistence will have strong impact on the shape of BDEF relationships (Mouquet *et al.* 2002). Chesson (2000) stressed that coexistence needs stabilizing mechanisms and is enhanced by equalizing mechanisms. The critical condition for stable coexistence is that intraspecific competition is stronger than interspecific competition. In his review on the maintenance of diversity, stabilizing mechanisms increase the negative feedback of intraspecific competition and can comprise a number of factors such as trade-offs in resource use [trade-off in R*, the minimal growth requirement for different elements (Tilman 1982; Tilman *et al.* 1982)], mortality [trade-off in P*, the ability to withstand and sustain predation (Holt *et al.* 1994)] as well as spatial or temporal fluctuations in environment-trait relationships (Chesson 2000). Equalizing mechanisms do not suffice to maintain coexistence, but can promote coexistence by reducing fitness differences between competing species and thus allowing for stronger intra than interspecific regulation (Fig. 4a).

Traits which minimize niche overlap or equalize fitness differences have thus a strong importance for coexistence. Whether or not biodiversity alters ecosystem functioning consequently depends on, whether this importance for coexistence is correlated to the importance for function. Thus, predicting diversity effects requires knowledge how particular coexistence traits are related to effect traits in a community (Fig. 4b). Negative, positive or neutral BDEF relationships are possible depending on this correlation. Because to date experimental tests of these correlations are lacking, we will describe a few theoretical examples showing that different coexistence mechanisms can lead to positive or negative BDEF relationships.

Coexistence by trade-offs in R* leads to niche partitioning and complementarity in resource use and hence to a positive effect of coexistence trait diversity on resource

Figure 4 Conceptual diagram on relationships between mechanisms of coexistence and effects of diversity on ecosystem functions. (a) Conditions for coexistence according to Chesson 2000 and Chesson & Kuang 2008. Species potentially coexist when their niche overlap is low or their fitness ratio tends towards one. The more similar the niche requirement of two species here, the more important is the absence of fitness differences. Grey arrows symbolize equalizing or stabilizing mechanisms (sensu Chesson 2000) that minimize niche overlap or fitness differences. To these mechanisms belong trade-offs in functional traits etc. The traits allowing species x to invade a community including species a, b, c, …, s are termed coexistence traits. (b) The BDEF relationship depends on the correlation of the value a trait has for coexistence and the value it has for the function (effect trait) in the community. A positive correlation suggests that traits favouring coexistence also favour the function under consideration, which will lead to a positive BDEF relationship. If the traits important for coexistence are not important for function, we expect a neutral BDEF relationship.

efficiency and productivity (Tilman *et al.* 1997) (Fig. 4b). Here, the number of limiting resources defines the maximum number of coexisting species (traits) and the maximum function which can be performed by the community. Similar predictions apply to coexistence via regional niche partitioning. In metacommunities with heterogeneous habitat patches (i.e. with patches representing different combinations of environmental variables (Mouquet & Loreau 2002; Loreau *et al.* 2003; Mouquet & Loreau 2003) trade-offs in R* result in regional niche partitioning as long as all species can reach all patches by sufficient dispersal (species sorting; Leibold 1998, Shurin *et al.* 2004). Regional coexistence through species sorting leads to a positive BDEF relationship through regional complementarity because local resources across a region are most efficiently used when local patches are dominated by the best adapted species and thus the match between species' traits and the environments are maximized (Mouquet *et al.* 2002).

However, coexistence of more species than limiting resources can potentially implicate a negative BDEF relationship. Metacommunity models predict that dispersal between communities leads to added diversity beyond the level possible by resource competition. Such spatial dynamics maintain locally inferior competitors with good dispersal abilities which otherwise would not sufficiently grow and reproduce under the given local conditions. These inferior species weaken local dominance by altering local species' resource use efficiency (Amarasekare & Nisbet 2001; Loreau

et al. 2003; Mouquet & Loreau 2003). Here, distraction of resources from the superior species leads to a negative relationship between diversity and community productivity (Mouquet *et al.* 2002).

Also coexistence by trade-offs between R* and P* (Chesson & Kuang 2008) might lead to lower productivity if traits leading to high P* reduce resource use efficiency. Conversely, aspects of stability (resilience or resistance) may require traits which are not correlated to R* or P*, preventing significant biodiversity – function relationships. Thus, both the mechanism stabilizing coexistence and the function under consideration can potentially lead to negative or positive BDEF relationships.

SPECIES EXTINCTION AND GLOBAL CHANGE

Changes in biodiversity are only one aspect of global change. Human domination of ecosystems has changed among others the overall availability and stoichiometry of elements, the size and connectivity of habitats, the atmospheric CO_2 concentration, and the mean and variability of temperature and precipitation. These changes alter both stabilizing and equalizing mechanisms maintaining diversity and thus indirectly affect ecosystem functioning, but they also directly change ecosystem process rates and states (Fig. 5a). To date an important question remains to be answered: how strong are relative effect sizes of diversity on ecosystem functioning compared to direct alterations of ecosystem functioning by human mediated global change? Using the increase in resource availability as an example, some have argued that diversity has little role to play (Grace *et al.* 2007), whereas others found that diversity significantly mediated the way biomass production changed with resource availability (Ptacnik *et al.* 2008; Cardinale *et al.* 2009a,b).

Suding *et al.* (2008) provided a highly valuable trait-based framework allowing for general predictions paving the way for experimental tests and modelling. The framework connects response traits (i.e. species abundance responses to environmental change), the relationship between response and effect traits (Fig. 5b), and the consequential altered sum of effect traits. The correlations between response and effect traits will strongly influence how changes in diversity caused by environmental change will transform into changed community performance (Fig. 5b). If response and effect traits are positively correlated the model predicts a strong nonlinear decline in function relative to random extinctions. That means response and effect traits are the same and the best performing species are also the ones most likely to go extinct in response to environmental change which in turn leads to abrupt loss of functioning (Fig. 5b). Compensation for the loss of effect traits in this scenario is unlikely because the remaining
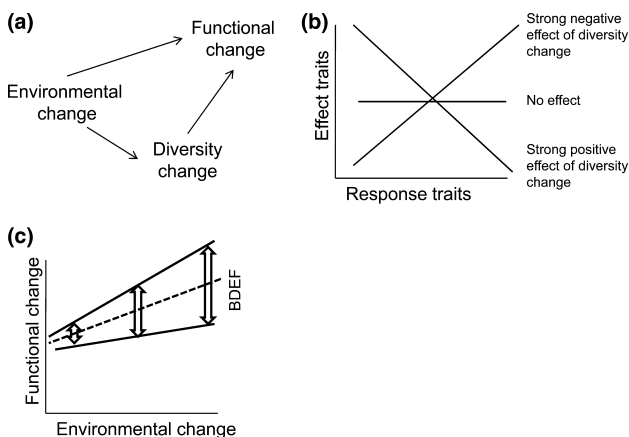

Figure 5 Graphical representation of effects of anthropogenic environmental change and biodiversity loss on ecosystem functions (a). The importance and sign of the indirect pathways depend on the correlation between response traits and effect traits (Suding *et al.* 2008). If species responding strongly to environmental change are also those driving functions, we see a strong negative effect of diversity change (b). Thus, BDEF relationships are able to modify functional changes as a consequence of environmental changes (c).

species perform worse. In contrast, if the correlation is negative, i.e. the worse performing species are prone to extinction, small loss of community functioning relative to random extinction scenarios is expected. If response and effect traits are uncorrelated the community might be able to compensate for the loss of effect traits (see related concept of response diversity, Elmqvist *et al.* 2003). Here, the different effect traits are evenly distributed across all response traits and thus remain available in the community.

Thus, different correlations between response and effect traits from positive to negative will strongly influence how changes in diversity caused by environmental change will transform into changed community performance (Suding *et al.* 2008). The relationship between effect and response traits allows presenting a conceptual framework to understand the relative role in ecosystems' responses to global change. For example, humans alter the overall availability of elements important for primary production (Vitousek *et al.* 1997). Higher availability of resources will lead to higher primary production but will also alter species richness and dominance (Hillebrand *et al.* 2007). Depending on the efficiency of conversion of nutrients into biomass production, a maximum attainable (optimal conversion) and a minimum (worst conversion) productivity can be defined (Fig. 5c). With increasing resource supply, both maximum and minimum productivity increase. The simultaneous alteration of diversity changes the probability of attaining the maximum (or minimum) function, depending on the correlation of response and effect traits. Thus, the realized productivity should depend on an interaction between direct effects of resource supply on the maximum attainable production and the presence of functional traits determining both the response to increase resource supply and the resource use efficiency.

We expect the relative contribution of changed diversity to become high when response and effect functional traits are positively correlated, i.e., when species with high resource use efficiency will be lost first due to increasing resource availability, because the remaining species do not add much to the sum of effect traits (function). In the case of a negative correlation, we expect the relative contribution of diversity to be lower because the good performing species remain in the community even though diversity declines.

The relative effect sizes of indirect (via diversity) vs. direct (via abiotic constraints) effects on ecosystem functioning in a rapidly changing world remain to be evaluated. Our conceptual diagrams only indicate that the realized response to global change involve both components. Especially at the edges of gradients (warm temperatures, extreme stoichiometry, low pH), where immigration from a differently adapted species pool is not possible, the loss of species may have strong consequences in natural systems.

CONCLUSIONS

Many of the aspects dealt with in our review have been addressed in previous original research papers and reviews (Loreau *et al.* 2001; Mouquet *et al.* 2002; Hooper *et al.* 2005; Petchey & Gaston 2006; Suding *et al.* 2008). Our review is not novel in that it views BDEF research from a different angle, but by pulling together information from different aspects of ecology, including trait-based approaches, coexistence and metacommunity theory, and global change biology. It has been our intention to answer the question, what kind of information we need to successfully predict consequences of changing biodiversity in real ecosystems (see Duffy 2009 for similar arguments). This kind of information is essential to provide ecologists with the tool to transfer BDEF knowledge into conservation biology and ecosystem management (Srivastava & Vellend 2005). We summarize our conclusions in five theses.

(1) In a world based on traits and trait-based coexistence, changes in diversity will eventually have an effect on process rates and state variables in ecosystems.
(2) Such BDEF relationships are not general; instead, the shape of the relationships depends on the match between coexistence traits and effect traits.
(3) Most BDEF relationships mechanistically rely on trait differences. In order to retrieve reliable estimates of the magnitude of BDEF, empirical studies have to comprise environments comprising the complexity to allow for these trait differences to play out.
(4) Biodiversity effects may be stronger than estimated until now if different aspects of multifunctionality are acknowledged, including that different species drive different functions (trade-off between effect traits for different process rates and state variable) and that different species drive a certain function under different environmental conditions assuming environmental heterogeneity in space or time (compositional turnover). Both aspects potentially increase functional turnover.
(5) An empirically unresolved central question is how important diversity effects are in comparison to direct effects of globally changing constraints of ecosystems.

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