

Emerging horizons in biodiversity and ecosystem functioning research

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Two decades of intensive research have provided compelling evidence for a link between biodiversity and ecosystem functioning (B-EF). Whereas early B-EF research concentrated on species richness and single processes, recent studies have investigated different measures of both biodiversity and ecosystem functioning, such as functional diversity and joint metrics of multiple processes. There is also a shift from viewing assemblages in terms of their contribution to particular processes toward placing them within a wider food web context. We review how the responses and predictors in B-EF experiments are quantified and how biodiversity effects are shaped by multitrophic interactions. Further, we discuss how B-EF metrics and food web relations could be addressed simultaneously. We conclude that addressing traits, multiple processes and food web interactions is needed to capture the mechanisms that underlie B-EF relations in natural assemblages.

Why and how we measure biodiversity effects on ecosystem functioning

Earth's biota regulates numerous fluxes of energy and matter, including carbon uptake, nutrient cycling and oxygen production. When measured at local scales, these rates are referred to as 'ecosystem processes.' Attributes of the biological assemblage, in terms of the number and types of organisms and their interactions, not only determine ecosystem processes but also ecosystem properties (such as resistance to invasion of exotics [1]) and how both processes and properties are sustained over time and space [1]. In combination, these three characteristics – processes, properties and their maintenance represent ecosystem functioning [2].

Although it might seem intuitive that a suite of functionally diverse organisms is needed to sustain ecosystem functioning, it is only in the last two decades that the relationship between biodiversity and ecosystem functioning (B-EF) has received detailed scientific interest (e.g. [3–5]). Besides its theoretical and intellectual appeal, much of B-EF research has been motivated by the alarming rates of species loss seen across the globe [6,7] and the demand to maintain the goods and services these species supply to humans [8]. The principal goals of B-EF research have been to investigate how biodiversity and ecosystem functioning are linked and to understand the mechanisms that underpin the relationship.

Early B-EF studies tested whether ecosystem functioning was enhanced in species-rich versus depauperate assemblages [9]. Since the 1990 s, a large body of work has demonstrated that biodiversity generally enhances many process rates, such as resource use or biomass production, across a wide spectrum of organisms and systems [10–12]. Biodiversity has also been shown to determine ecosystem properties, such as the ability to stay close to equilibrium in the face of environmental perturbation [1] or resistance of an assemblage to top-down control by consumers [13]. However, the evidence for positive effects of biodiversity on ecosystem functioning is neither ubiquitous nor unequivocal [8,14]. This has stimulated considerable scientific debate [1], but the central B-EF question has now moved on from the discussion of whether diversity matters to a consideration of how it matters [2]. Some recent studies have shown that the strength of biodiversity effects can increase over time (e.g. [15]). In a wider context, this finding suggests that the interpretation of B-EF relationships might be dependent on the level of observation. This includes temporal–spatial scales [16], but also evaluations of biotic

Glossary

Biodiversity:: refers to the extent of genetic, taxonomic and ecological diversity over all spatial and temporal scales [71].

Ecosystem function:: a synonym for 'ecosystem process.'

Ecosystem functioning:: the joint effects of all processes that sustain an ecosystem. Some authors also use the term for ecosystem properties such as resistance to invasion [1].

Ecosystem goods and services:: are products of ecosystem functioning that are of (usually socioeconomic) value to humans.

Ecosystem process:: the changes in energy and matter over time and space through biological activity, which are measured as response variables to biodiversity in B-EF experiments. These rates are also governed by the interplay of abiotic factors (physical and chemical), but the focus of B-EF research is mediation of processes (abiotic or biotic) by organisms. Examples include production of carbon, resource consumption, respiration, denitrification and nutrient uptake.

Functional trait:: component of an organism's phenotype that determines its effect on processes [19] and its response to environmental factors [2]. The term 'trait' should be used for the individual level only [72]. For example, body mass is a trait, biomass is not.

Horizontal diversity:: the taxonomic or functional richness and evenness of entities (traits, individuals, species, genes, functional groups, etc.) within a subset of similar entities (e.g. trophic level) (after Ref. [54]).

Trait:: any morphological, physiological or phenological feature measurable at the individual level [72].

Trait attribute:: a particular value or modality taken by the trait which varies both along environmental gradients and through time [72].

Vertical diversity:: a general term summarising the functional complexity of a system in the vertical (i.e. consumer–resource) dimension. Examples include food chains within the wider food web.

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Table 1. Overview of past and present B-EF research with a focus on traits, multiple processes and integrating food web theory

| | Pioneers | | Early excursions | | Emerging horizons | | Future directions |
|---------------------------|---|---|--|--|--|--|---|
| | Topic [e.g.] | Conclusions | Topic [e.g.] | Conclusions | Topic [e.g.] | Conclusions | Topic |
| Experiments | | | | | | | |
| Biodiversity measure | Species richness [22] ^b | Evidence of positive B-EF relationship, but also of redundancy and/or idiosyncratic effects | Trait-based measure [89] ^a , [2] ^b | Functional diversity, rather than species diversity <i>per se</i> , enhances ecosystem processes | Continuous trait-based measures [48] ^a , [19,49] ^b | Categorical measures (such as functional group richness) are not a good descriptor for functional richness; a continuous measure is more appropriate | Continuous trait measure based on traits of the individual, not species |
| Ecosystem process measure | Single process [22] ^b | Evidence of positive B-EF relationship, but also of redundancy and/or idiosyncratic effects | Multiple processes [51] ^a | The B-EF relationship (positive and negative, etc.) can vary depending on the process measured | Joint measure for multiple processes [17,52] ^a | When overall functioning is defined as the joint effect of many ecosystem processes, redundancy declines | Continuous measure where processes can overlap in a multivariate fashion |
| Interactions | Horizontal, e.g. facilitation competition [26] ^a | Biodiversity effects could be due to facilitation within trophic level | Vertical; biodiversity loss from one trophic level [27,60,90] ^a , [54] ^b | Consumer extinctions can either amplify or buffer the effects of producer extinction | Vertical biodiversity loss within the food web [57] ^a , [54] ^b | Multiple extinctions at various trophic levels can affect a given ecosystem function either synergistically or antagonistically | Vertical and horizontal; inclusion of indirect effects (such as trophic cascades) |
| Theoretical models | | | | | | | |
| Predicting B-EF relations | The effect of species richness on one process [28] ^b | Models show that species identity and biodiversity simultaneously influence ecosystem functioning | Single trait of a species and influences of one environmental factor [78] ^a | Model can be used to predict the productivity of an assemblage consisting of different functional groups | (i) Multiple traits, responses and drivers; frequency dependence and functional complementarity [39] ^a (ii) Effect of species richness on biomass within 2–3 trophic levels [67,68] ^a | (i) Model can be used to simultaneously predict sampling and complementarity effect (ii) Model can predict biomass of lower trophic levels | Model includes multiple traits, processes and trophic interactions |

^aExample of a classical paper.^bExample of a summary (review, meta-analysis, etc.).

assemblages and processes. Connected to this are problems associated with the methodologies used to measure both response (i.e. process rates) and predictor (i.e. biodiversity) variables. Further, there are still many other considerable gaps in our understanding of how organisms shape ecosystem processes together and which interactions have to be taken into account to understand B-EF relationships.

In recent years, several studies [17–19] have diverged from the approaches used in the earlier, pioneering B-EF research. These early studies typically focussed on species richness as the measure of biodiversity, measured only single process rates and focussed on competitive or facilitative interactions within guilds. By contrast, the newly emerging studies have moved the emphasis toward considering alternative metrics of biodiversity (e.g. functional groups), multiple processes and interactions within the wider ecological network (e.g. food web). It is becoming

increasingly apparent that these three topics have to be addressed if B-EF research is to become a predictive science that can forecast the effects of species loss in the complex, multitrophic systems that we encounter in nature. Consequently, the consideration of traits, multiple processes and multitrophic interactions is now rapidly coming to the fore in B-EF research (Table 1).

In this paper, we review these new developments, identify gaps in our current knowledge and suggest how these could be dealt with in the future. Within this new B-EF context, some key questions are: at which level of organisation should we measure biodiversity (i.e. do we use gene, trait, species, etc. level as the relevant entity)? How do these entities interact and shape ecosystem functioning? How can different processes be evaluated to assess the effects of biodiversity on overall ecosystem functioning? One consequence of this modified B-EF focus is that biodiversity is not a synonym for species richness

Box 1. Additive and nonadditive effects in B-EF experiments

Many statistical methods employed in B-EF studies use comparisons between mono- and polycultures [28]. Effect of entity (species, functional group, etc.) diversity can be tested statistically by estimating whether the effect of the entity is the same in monoculture as it is in polyculture. If this is the case, then effects of entities are purely additive. For illustration, we will consider a mix of leaf-eating invertebrates (diversity as predictor) and their potential effect on the food resource (response). It is possible that each entity (e.g. each species) always feeds on the same amount of leaf material, irrespective of how many and which other entities are present; that is, their effects are additive.

In a wider B-EF context, additive mechanisms mean that polycultures will perform best when those organisms that perform well in monoculture are present and especially when these entities are abundant (sampling effect). Also, it implies that the maintenance of one or more processes simply depends on whether those entities are present that sustain them and whether they are present in sufficient numbers. When entities drive different processes and those are measured simultaneously, it is possible that the most diverse assemblage enhances overall functioning. This is a case of comple-

mentarity, where additive mechanisms operate. For example, we might observe more leaf mass loss in leaf-eater polyculture compared to monoculture averages due to species feeding on different parts of a leaf. However, the effect in polyculture can be predicted from the individual monocultures and it is hence an additive mechanism.

However, when organisms interact and their performances depend on each other (in a positive [facilitation] or negative way), then nonadditive effects can be observed and this is another instance of complementarity. Using the example of leaf-eating invertebrates, we could imagine that the feeding of a particular species is enhanced through the feeding activity of another one.

To demonstrate whether additive mechanisms operate, it is important to correct for abundance. B-EF experiments tend to be designed to hold either biomass or abundance constant, and in the latter case this results in fewer individuals of each entity in polyculture compared to monoculture (e.g. for three entities: 12, 6+6 and 4+4+4 individuals in mono-, duo- and triculture, respectively). Hence, the statistical test has to account for reduced numbers of individuals in polyculture, because an entity will not only perform according to its traits but also depending on its abundance.

(see definition of biodiversity in the Glossary), and in acknowledgement of this we will refer to different biodiversity entities (e.g. functional groups or species) throughout this paper.

Biodiversity-ecosystem functioning research: the story so far

Observations about potential B-EF relationships can be traced back at least as far as Darwin, who referred to an experiment on the performance of different species and mixtures of grasses and herbs in *The Origin of Species* [20,21]. However, the first studies to investigate B-EF relations explicitly were performed in the early 1990s (see Ref. [22] and references therein). This research described potential outcomes of the effects of changing biodiversity on certain measurable ecosystem processes. Conceptually, they used bivariate graphs, with species richness as the biodiversity measure and predictive variable on the x-axis and the predicted ecosystem process on the y-axis. In the so-called redundancy model, the process rate (e.g. primary production) saturates above a certain species richness threshold, but declines below this point as species are lost (see Ref. [23] for more detail and a summary of other models). This saturation effect has received considerable attention because it implies that species can be redundant (i.e. replaceable) for functioning [4]. This has indeed been found to be the case for some processes and systems (e.g. for leaf breakdown by stream fungi or invertebrates [24,25]).

Many B-EF studies focussed on linking empirical observations with concepts such as complementarity and sampling effects (e.g. [26–29]). A comparison of mono- and polycultures assembled using different biodiversity entities (e.g. different species) illustrates these two concepts: when polycultures perform better than monoculture (on average), this can be as a result of the best-performing entity being present in the polyculture. This has been called the sampling or selection effect, and here effects of entities are additive and they do not interact (Box 1). A recent meta-analysis of aquatic and terrestrial studies showed that within broad trophic groups (producers, her-

bivores, detritivores and predators), resource use was not significantly different in the most species-rich assemblage compared to the most productive single species, which points toward the ubiquity of sampling effects. However, some studies have shown that polycultures can perform significantly better than individual monocultures. For example, predatory crabs feed on more prey when they are in polyculture and their densities are high [30]. This effect must be a result of the different species facilitating or complementing one another. To demonstrate these effects, individual treatments are compared (as opposed to using averages), and it is tested whether a polyculture's performance is the sum of 'complementing' parts or even exceeds the sum of its parts. Facilitation is explained by nonadditive mechanisms, whereas complementarity can be driven by both additive and nonadditive effects (Box 1). Descriptions of complementarity effects are rarer than those of selection effects, but complementarity has been proposed to be both common and to increase in importance over time [29].

These concepts have challenged more recent B-EF research to uncover the mechanisms behind them. For example, in most examples where a sampling effect has been demonstrated, it remains unclear which attributes make a certain entity (e.g. species) perform better than others. However, some insights are now emerging as to how some particular facilitation effects might arise. For example, species-rich assemblages of caddisfly larvae create optimal water flow because of their different body shapes and this enhances the feeding success of the assemblage as a whole [26]. The principal questions here are whether sampling and complementarity effects can be observed over different scales and levels of observation (e.g. time or across subsections of the food web) and whether the interpretation of B-EF relations depends on the particular measures used to define both biodiversity and ecosystem functioning.

Increasingly, studies are expanding B-EF measures (toward using traits and considering multiple response variables) with the aim of addressing these gaps in our knowledge. In parallel, other studies are addressing

Box 2. Evolutionary change, speciation and ecosystem functioning

Until recently, B-EF research has rarely considered the possibility of evolutionary change. However, the variation in traits observed between individuals and between species is a product of natural selection. Trait variation also dictates the rate at which ecological interactions change in response to altered density or to the introduction or removal of species from given ecological networks (see Ref. [73]). Mounting evidence suggests that genetic differences mediate species' interactions over even small temporal and spatial scales [74], and act to change the dynamics, strength and number of species' interactions. If such adaptation is common, then an ecosystem's resilience is related to the ability of its constituent species to adapt to changes in the environment and to the density of their congenitors [75]. Most research in this issue relates to abiotic environmental gradients: few data are available on responses to biotic gradients, which are determined by interactions between species, arguably the vast majority of ecological gradients [76,77].

The widespread observation of adaptive divergence in fitness traits also means that species vary in their role in different ecosystems within their ranges, and this variability will differ between taxa. For example, larger populations might contribute more to ecosystem functioning than small populations, not just because they transfer more energy but also because they harbour more genetic diversity

(both in a single population and throughout their geographical range). Consequently, they are more likely to be resilient to environmental change or species loss. A recent analysis considered this explicitly in a multispecies context [78], and such an approach could also be extended to include within-species variation.

Differences in the way speciation occurs mean that systematic differences might exist between taxa in the functional or genetic diversity they harbour (see Ref. [79] and references therein). This lack of equivalence could obscure or generate B-EF relations, and it is possible that robust ecological patterns can only be observed at higher taxonomic scales than the species level. Species that form owing to niche splitting or character displacement under competition within trophic levels might also harbour more equivalent amounts of genetic and functional diversity, compared to species that form without strong diversifying selection. The extent to which competition is a major structuring force in ecological communities is still hotly debated [80–82]. Alternatively, competitive exclusion might take a long time, perhaps on the same timescale as species extinction. In temporally stable ecosystems, redundancy might therefore be much lower, generating stronger B-EF correlations. Data on this issue could be provided by studying the persistence of ecological patterns following taxonomic inflation (e.g. [83]).

multitrophic interactions in ecological networks within a B-EF context. These topics are the main focus of our review, but we would like to stress that these are by no means the only important topics of current B-EF studies and theory. Evolutionary change (Box 2), nontrophic interactions (e.g. [31]), the role of dominance (see [32]), the sequence of species loss [33,34] and the importance of expanding scales of time and space in experiments (e.g. [15]) are all receiving increasing attention in B-EF research.

The use of traits in biodiversity metrics

B-EF research is increasingly moving away from its traditional focus on taxonomic diversity toward a more functional, trait-based perspective (e.g. [19,35,36]). Essentially, much of the research interest now lies in understanding what organisms do, and how many 'types' are needed to maintain ecosystem functioning, rather than which and how many species are present. This means that instead of assessing taxon richness, an assemblage is characterised based on functional traits, which are those

Box 3. On using individuals and species in trait-based B-EF measures

To date, most B-EF research has focussed on species as the level of observation. Therefore, the effects of intraspecific variation on certain ecosystem processes have largely been ignored.

Species averages

B-EF studies dealing with functional diversity typically assign traits to species based on averages. Examples for species-averaged traits are: maximum or average body size, lifespan, mode of reproduction and so forth. When processes (e.g. secondary production) are measured over longer time periods, traits such as number of offspring or clutch size will be important, which are characteristics of the species [72]. Species averages might also be the most appropriate unit for experiments involving species without large ontogenetic shifts and this includes bacteria, many protists and fungi, and microscopic metazoans (e.g. meiofauna).

The individual as the level of observation

Individuals will be the level of observation when studying intraspecific variation in more detail and when assessing functional diversity within a species. Interactions in ecological networks occur between individuals [84], and food web theory is now increasingly moving toward focussing on individual traits and behaviour [85]. For example, size structure within food webs becomes more evident when data on individuals are used as opposed to species averages [84,86], and some have argued that using species averages impairs our ability to find the mechanisms that underlie interactions [86]. A good example of this is provided by the ingestion rate of consumers: this is often largely a function of body mass rather than taxonomic identity and is manifested at the individual level, yet it will be a key driver of many ecosystem processes (e.g. [24]). In a B-EF context, the individual

approach is especially meaningful for studies involving species with ontogenetic niche shifts, that is where young individuals show different traits to older ones. Examples of traits assigned to individuals include body size, per-capita interaction strength or consumption rate.

Feasibility of using individuals

B-EF studies will require information both on individuals and on the species as a whole, depending on the processes measured, time-scales and questions addressed. The 'new' individual-level approach can be less labour intensive than a species average one, as many marine studies show, where researchers use size bins and trophic height, rather than species richness, to characterise biotic assemblages [86].

Individuals, body size and biomass

In studies on bacteria, protists and animals, it is important to know the size of the individuals within the biodiversity entity (e.g. species or functional group). The performance of an entity will not only depend on its traits but also on the metabolic rates of the individuals. This means that it is important to know whether the total biomass is composed of small or large individuals, because the former will exhibit higher process rates for a given unit of mass (e.g. [87]). This aspect also has to be taken into account when performance in monoculture is used to calculate metrics such as the joint measure of ecosystem processes (e.g. the one suggested by Gamfeldt *et al.* [52]). In cases of higher plants, or in those circumstances where individuals are difficult to define (as in algal colonies, fungal mats, etc.), it might be desirable to know biomass production rather than biomass, as this will indicate the underlying metabolic rates.

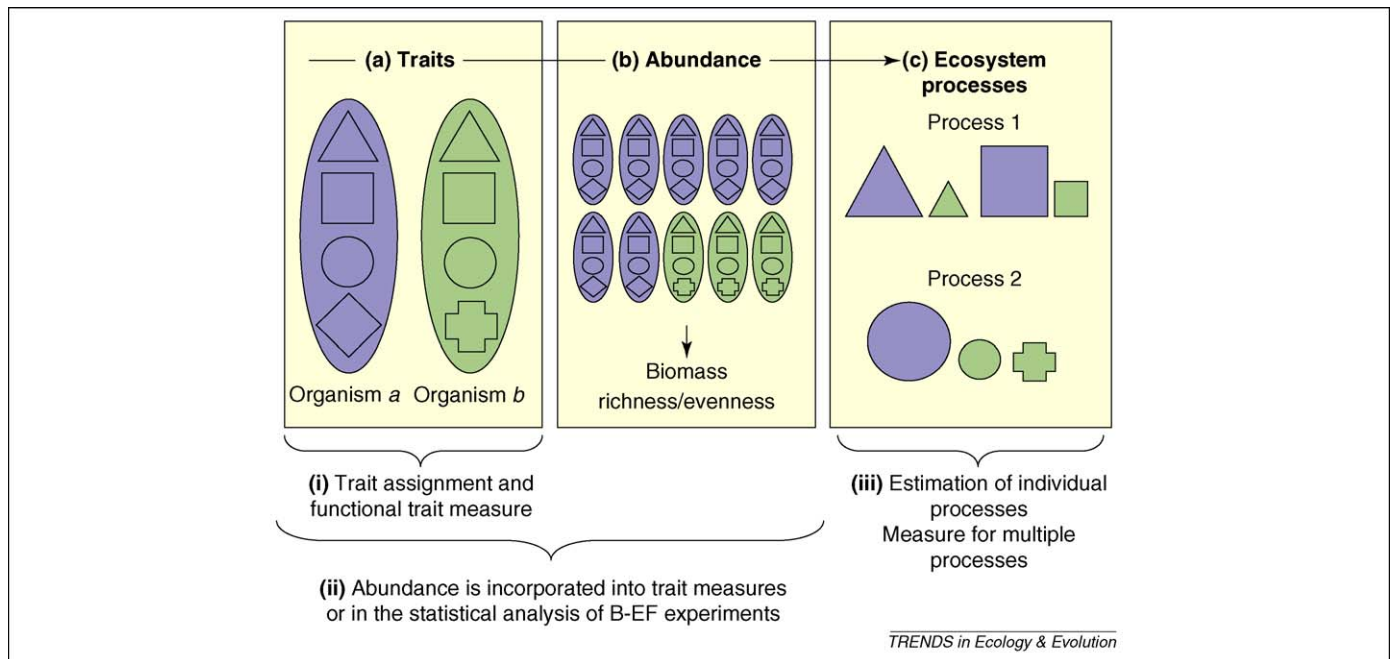


Figure 1. Measuring traits and multiple processes. **(a)** Traits are assigned to organisms (individual or species average level). Example shows two organisms with three common (represented by triangle, square and circle) and one unique trait (diamond and cross for organisms *a* and *b*, respectively). **(b)** Abundance of the organisms then determines the biomass, richness and evenness of traits represented in an assemblage. **(c)** Individual ecosystem processes depend on the traits represented by the assemblage and abundance (i.e. biomass, richness, evenness). The example shows process 1, which is driven by two traits. The process rate is dominated by organisms from entity *a* (in blue), as they have the highest abundance. Organisms *a* and *b* are redundant because both could regulate the process, if they have sufficient biomass. Process 2 is determined by two traits. Organism *a* does not dominate, as the process also depends on a trait they do not possess (provided by organism *b*, in green).

components of the organisms' phenotypes that determine their effects on processes [19] and their response to environmental factors [2]. Examples of functional traits assigned to organisms in B-EF studies include the area, weight and thickness of macroalgal fronds [35] or the preferences of pollinating bees for flowers of a particular height and the within-flower behaviour of bees [36] (see Box 3 for more examples).

One of the reasons behind this change in emphasis is the growing number of studies which show that species richness or identity has little or no effect on ecosystem processes (e.g. [25]; see Ref. [8]). These findings imply that at least some species are redundant within an assemblage because their loss is in some way compensated for. This redundancy might be an artefact related to the time and spatial scales of observation [37] or a real phenomenon. Certainly, there can be severe consequences if an entire functional group of seemingly redundant species is lost in an ecosystem. Many researchers have argued that the functional diversity of an assemblage is a more suitable predictor of ecosystem functioning than is taxonomic richness [38]. For example, plant ecologists have shown repeatedly that functional diversity, rather than species diversity *per se*, enhances ecosystem processes (see Ref. [38] and references therein).

Another, less discussed (but see Refs [19,39]) reason for using a trait-based rather than a species-based biodiversity measure relates to intraspecific variation. An individual's ability to perform (e.g. to use resources) is determined by its functional traits, and these can vary within a species (and be similar among species). Hence, a trait-based classification of individuals within a given natural assemblage should reflect its potential for performance more accu-

ately than does species richness (Figure 1; Box 3). However, to date, the units that have been used for trait assignment are species and not individuals (Box 3).

Fundamental to a functional approach is, however, how organisms can be classified and grouped in terms of their traits. Trait assignment is mostly done at the species level, where trait information is available for certain animals (e.g. [40]) and especially plants (see Ref. [41] and references therein), and much of this is held in databases (e.g. [42] and references therein). However, information is often missing for many organisms and for trait assignment within species. Here, traits could be identified from monocultures [43,44] and other observations [19].

To date, it is still under discussion which metrics are most appropriate for measuring functional diversity, and researchers have used both discontinuous and continuous measures. Three of the most common methods (discussed in Ref. [19]) are grouping species into discrete groups (e.g. [2]), assigning distances between species in trait space (e.g. resulting in a dendrogram in which species are clustered based on some measure of similarity; e.g. [45]) and the size of dendrogram that results from clustering species (e.g. [46]). Whether the assignment of *a priori* functional groups (e.g. the grass-forb-legume classification scheme [41]) is meaningful in a B-EF context is open to question [41]. The fact that individuals (or species) can have shared, but not necessarily fully overlapping, traits means that it is often difficult to assign them to independent groups. This suggests that a multivariate statistical approach that captures traits on a continuous scale (e.g. dendrograms) might be the most appropriate method for this purpose (measures of 'functional diversity' reviewed by Ref. [19], and see Refs [47–49]).

Choosing the appropriate measure of functional diversity and selection of traits will, of course, depend on the particular aims of any given study and the process(es) measured [19]. Addressing this point, some recent studies calculated different functional measures and compared their predictive power for different processes [48,49]. To gauge the value of any classifications, it is necessary to verify them statistically, for example by comparing *a priori* created groups with those formed randomly (e.g. through a bootstrap method [19,50]). When discrete functional groups are used, it is also possible to assign species into groups *a posteriori* via best-fit functional groups [41].

Ecosystem functioning measures: multiple processes

Although a few of the earliest B-EF studies measured multiple processes simultaneously (e.g. [51]), the vast majority of research to date has focussed on a single response variable per study. Two recent meta-analyses have questioned the validity of this approach, because species typically contribute to more than one process at the same time [17,52] (this also applies to individuals) and overall ecosystem functioning is sustained by multiple processes. Importantly, the number of species (or traits) needed to maintain ecosystem functioning increases with the number of processes measured because progressively more species (or traits) are required to sustain multiple processes.

It is important, therefore, to measure multiple response variables simultaneously and, ideally, to combine their individual values in a single metric that captures overall ecosystem functioning [17,52]. It might seem surprising then that this point has, as far as we are aware, only been addressed in two studies to date. However, finding a meaningful measure for multiple processes is not trivial and simply using an average can be inappropriate because one process does not necessarily compensate for another [52]. In fact, different processes can even act antagonistically or show other forms of interdependence.

When identifying 'multiprocess' metrics, we encounter some of the same principles involved in defining multiple-trait measures. The correlated nature of many processes and their temporal variability suggests a nondiscrete measure, which we lack at present. However, because many B-EF studies could potentially quantify several processes simultaneously (at a single point in time), a useful joint measure might be calculated assuming nonoverlapping responses. Here, four basic criteria have to be met. First, individual processes have to be defined and, second, the level at which they are sufficiently sustained has to be established. In addition, the principal processes contributing to ecosystem functioning have to be measured, and finally the processes have to be weighted, that is their relative importance to overall functioning has to be quantified.

Gamfeldt *et al.* [52] have recently introduced a multiprocess metric that satisfies the first two criteria outlined above. They defined overall functioning to be sustained when all individual processes are working above an acceptable threshold, which they set at 50% of that achieved by the best-performing monoculture. Their approach is therefore based on the premise that effects of entities and species should be additive in polyculture. By contrast,

Hector and Bagchi [17] used information on polycultures. Starting with a full model that contained a main effect for the presence and absence of every species for a given polyculture, they then removed each species from the model in turn. They calculated the Akaike information criterion to compare polyculture performance and the effects of the loss of particular species on the process measured.

Although both studies have assumed nonoverlapping processes and might not satisfy all four rules outlined above, they clearly demonstrate that as more processes are considered, the scope for redundancy is reduced. Therefore, the true effects of biodiversity on ecosystem functioning might be far greater than would appear from studying a single process. This is a potentially critical finding because if redundancy declines as an increasing portion of total functioning is captured, then the consequences of species loss could be far more serious than we have assumed to date.

Integrating B-EF and food web theory

Traditionally, most B-EF studies have focussed on primary producers or on single consumer guilds and the species interactions within these groups: that is, horizontal, rather than vertical, biodiversity has been manipulated (but see Refs [18,53,54]). However, all individuals within an ecosystem are connected via vertical and horizontal linkages, for example within the food web. A more integrated view that takes a true system-level perspective is now starting to emerge in B-EF research, by also considering vertical interactions within the wider ecological network. Using this network metaphor, most previous studies have focussed on effects of particular nodes rather than considering the potential importance of the links (i.e. interactions) between them (but see Refs [55–59]).

In addressing the effects of vertical diversity on B-EF relations, some recent studies have manipulated consumer richness and composition and explored how these changes had indirect effects on processes that are driven by species at the base of the food web. For example, experiments with plants and their herbivores have shown that increasing consumer diversity often enhances the total abundance or production at that level, while suppressing the abundance of the primary producers below [12,27]. A new approach has been to focus on combined effects of biodiversity within and between adjacent trophic levels [55,56,60,61] by manipulating the richness of more than one trophic level (e.g. of plants, herbivores and predators [54]). In the case where top-down control is prevalent, both theory and experiments have shown that ecosystem properties are most strongly affected by altering predator diversity [62,63]. For instance, when predators interact negatively via intraguild predation or interference, increasing predator diversity is predicted to reduce their total impact on prey [62,64].

When it comes to the number of trophic links an individual or species has, the degree of generalisation versus specialisation of consumers has a strong impact on B-EF relationships [53,57,58]. For example, an analysis of host–parasitoid food webs showed that the presence of generalist and omnivorous species at higher trophic levels was key for controlling outbreaks of potential pests,

Box 4. Trophic cascades and B-EF relations in multitrophic systems

Trophic cascades can affect ecosystem functioning via biodiversity change, and are mediated by the patterning of interaction strengths and the level of predator generalism within the food web [18,53,54,57,60,88]. Six different scenarios are shown which depict simplified modules that are observed in natural food webs (Figure 1): (a)–(c) correspond to compartmentalised webs (i.e. discrete food chains), and (d)–(f) to semi-reticulate ones, in which food chains are linked by generalist consumers. Two species (or functional groups) lumping individuals with similar traits and trophic position) per trophic level (nodes) are considered, and their diameter corresponds to numerical abundance (or biomass). Arrows point from prey to predator and line thickness corresponds to biomass flux or interaction strength. Slight differences in the configuration of interaction strengths exist: all are weak in (a) and (d), there is a mix of weak and strong interactions in the remaining webs, but with different positions for each. Predator 5 within the red square is the species that is lost from the system. Changes in the abundance of primary consumers 1 and 2, following the extirpation of the predator, are shown as the diameter of the grey nodes beneath the dashed lines.

Extinction of the predator in (a) results in a small decrease in the abundance of producer 1 mediated by a small increase in the herbivore feeding on 1. The trophic cascade is very faint here, owing to the weak interactions in the food chain. The same extinction in (b) results in a considerable decrease in producer 1 abundance mediated by a large increase in herbivore population the predator here was controlling herbivore population more intensively than in (a). However, despite strong interactions being present in (c), they have no effect on producer 1 following predator extinction because they are positioned within a different food chain.

Predator generalism in (d)–(f) produces reticulated food webs. In these webs, biodiversity loss has less pronounced effects on primary production than is the case for their compartmentalised counterparts (a–c). In both (d) and (f), no change is observed after extinction, because predator 6 compensates the loss of predator 5 by consuming more individuals of herbivore 3. A slightly different result would

be observed if density compensation were neglected. In (e), predator 6 also compensates the effect of extinct predator 5, but such compensation is assumed to be constrained: it cannot fully compensate the strong interaction that predator 5 had on herbivore 3 populations.

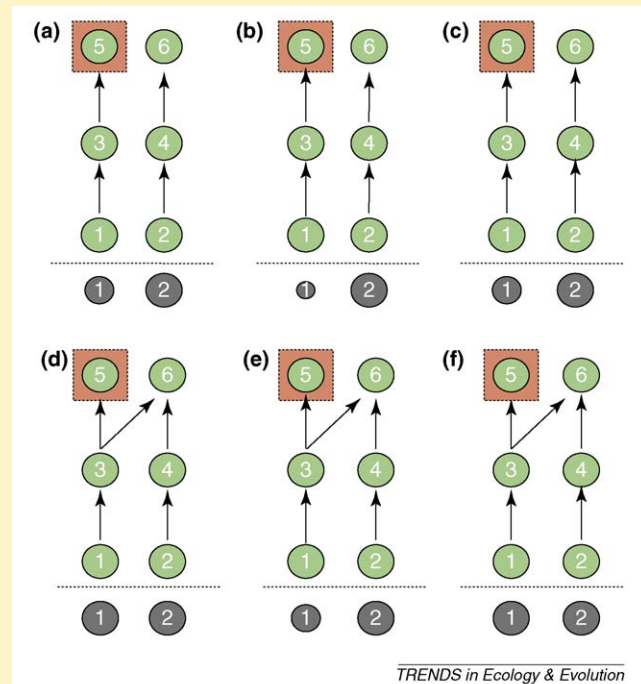


Figure 1. Examples of how trophic cascades can affect ecosystem functioning.

because the parasitoids interacted most strongly with the dominant herbivore [53]. Therefore, the addition or removal of species within high trophic levels can have contrasting effects on food resources, depending on whether they are strongly or weakly linked (Box 4).

One largely unexplored topic involves trophic interactions across multiple food web compartments (e.g. food resource, primary and secondary consumers). Here, biodiversity effects are potentially manifested through changes in the configurations of interaction strength within the food web: for example, if one consumer–resource link becomes stronger, the effects of this can ramify quickly through the network of interconnected species [65], Box 4).

Multitrophic interactions are expected to make B-EF relationships more complex and nonlinear, in contrast to the monotonic changes predicted for simplified systems with a single trophic level [58]. Across the trophic network, the degree of diversity can be related to food web connectance (the proportion of links that are realised), which in turn determines how the loss of species affects properties of the assemblage or ecosystem functioning [58]. The success of recent efforts to incorporate food web theory into B-EF research is likely to motivate further investigations that manipulate biodiversity within food webs in a more explicit manner.

Implications and future directions

Biodiversity comes in many forms and, when exploring its effects on ecosystem functioning, we have to apply

appropriate measures, which might involve the combination of different measures in certain cases. For example, classifications such as species richness or a measure of genetic variability can be combined with a trait-based biodiversity metric (e.g. [66]). As traits can vary within a species, the most successful approach might be one that is based on individuals rather than the traditional focus on species averages (Box 3). Generally, important attributes of species or functional groups in terms of their performance are their biomass and production (Box 3; Figure 1), which are determined by the number of organisms and their individual body masses. This highlights the importance of incorporating abundance and evenness when assessing or modelling biodiversity effects. Predictive B-EF models have to consider the absolute and relative abundance of organisms possessing specific traits, as has been done recently [39,44]. Including abundance and evenness in B-EF experiments can be achieved by incorporating them into the trait-based measure of functional diversity [48] as outlined above. Alternatively, they can be accounted for by careful experimental design and statistical analyses. As an example for the latter approach, if we know the effect of an entity in monoculture at a specific density, we could predict its effect in polyculture by applying a linear model which accounts for density effects.

The fact that more than one process contributes to ecosystem functioning demonstrates the importance of measuring multiple response variables when estimating the effects of biodiversity and calls for the use of a joint

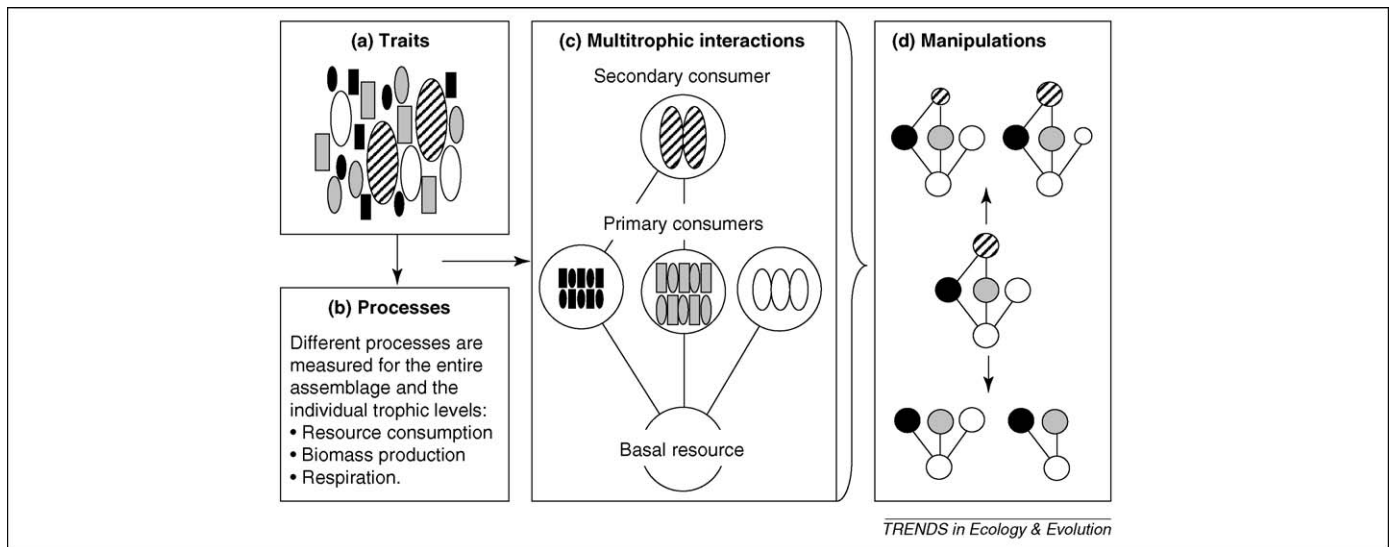


Figure 2. Example for an experiment incorporating traits, multiple functions and food web dynamics. **(a)** The B-EF experiment uses an assemblage of animals (two species [rectangles and ovals] with individuals differing in size [four size classes, represented by the colour and the area of each rectangle or oval]) and a basal food resource (not shown). Biodiversity is measured as species richness and number of traits (size classes). **(b)** The processes measured as responses to diversity could include resource consumption, biomass production and respiration, and their joint measure of ecosystem functioning can be calculated (e.g. after Ref. [52]). **(c)** Biodiversity is measured as body size classes, with individuals assigned to a potential trophic position on the basis of their size and diet. Species 1 (oval) shifts from feeding on the basal resource to being predatory in its largest size class, but can only feed on individuals that are small enough. **(d)** Biodiversity is manipulated by either removing individuals at random from different groups, which results in lower abundance or biomass (represented by nodes smaller in diameter; top panel) or from a particular size class (i.e. removing an entire group; lower panel). In the latter example, large individuals are removed to mimic scenarios that are commonly observed under current global change.

measure [52]. In this context, it should be noted that many studies focussing on primary production have already been using joint measures, but that these differ from those highlighted here, such as net primary production (which is gross primary production minus autotrophic respiration). In general, data on interdependent processes collected over time would require a continuous measure, which has yet to be developed. Many ecosystem processes are interdependent (e.g. carbon sequestration and primary production), but for pragmatic reasons we might have to classify them as discrete until we are able to model their interdependence.

Experiments addressing horizontal and vertical biodiversity effects can integrate food web theory by focussing on the number, distribution and strength of interactions. As the number of possible diversity combinations increases exponentially with the number of species (or other entities) within the food web, the challenge is whether we can find consistent trends in their relationship with ecosystem functioning. One approach is to use simplified model systems, for example where up to six nodes and two to three discrete trophic levels are considered. These types of abstractions have already produced testable models, such as those that predict plant and herbivore biomass as functions of producer and consumer species richness [67] or those that can predict biomass dynamics within three trophic levels [68]. Within this context, trophic cascades provide a useful example because they demonstrate how additive, synergistic or antagonistic effects can arise by changing vertical diversity and the configuration of interactions (Box 4).

How can we address this demand for including multiple traits, processes and multitrophic interactions into the already complex world of B-EF research? Clearly it depends on the questions being asked as to whether we want to

address traits, multiple processes and multitrophic interactions in B-EF experiments and whether we want to address them simultaneously. However, to approach more realistic B-EF scenarios, we have to consider and ultimately combine these emerging perspectives in future studies. This approach is not necessarily more data intensive than traditional studies (Figure 2), but it does represent a change of focus. Nonetheless, in many instances it can be tested with existing data sets, such as the (mostly terrestrial) studies that have estimated an array of processes. These could be revisited and analysed by applying existing measures [17,52] based on an assumption of nonoverlapping processes. Regarding traits, future experiments could hold species identity constant, but alter traits and functional diversity (e.g. by using different combinations of size classes within and across species) to demonstrate whether species provide unique contributions to ecosystem processes. The experimental setup here is still manageable, for example by using three species and two size classes (as a proxy trait measure) within species while measuring their effect on one or more processes, such as their food consumption and biomass production (Figure 2). Equally feasible are multitrophic B-EF experiments that expand their focus from measuring predominantly biomass as the only ecosystem property (as done previously [67,68]) toward measuring basal resource consumption or respiration.

By using a multitrophic perspective combined with a trait-based approach (Figure 2), we could start to address the consequences of losing individuals with specific traits that are especially sensitive to particular perturbations. For instance, habitat loss or overfishing affects principally large-bodied organisms disproportionately [33,69,70]. It is possible to simulate and manipulate experimentally the disappearance of large individuals from a food web and its consequences on multiple functions.

In summary, there are several novel approaches that can now be employed to address the seemingly more complex B-EF context in both experiments (Figure 2) and models (Table 1). These new perspectives will help to reveal how changes in biodiversity will affect the functioning of complex, natural ecosystems by considering the true multifaceted nature of both the drivers and the responses of B-EF relations.

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