

Opinion

Reintroducing Environmental Change Drivers in Biodiversity–Ecosystem Functioning Research

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For the past 20 years, research on biodiversity and ecosystem functioning (B-EF) has only implicitly considered the underlying role of environmental change. We illustrate that explicitly reintroducing environmental change drivers in B-EF research is needed to predict the functioning of ecosystems facing changes in biodiversity. Next we show how this reintroduction improves experimental control over community composition and structure, which helps to provide mechanistic insight on how multiple aspects of biodiversity relate to function and how biodiversity and function relate in food webs. We also highlight challenges for the proposed reintroduction and suggest analyses and experiments to better understand how random biodiversity changes, as studied by classic approaches in B-EF research, contribute to the shifts in function that follow environmental change.

Predicting Effects on Ecosystem Functions from Changes in Biodiversity: A Brief History

Various types of environmental change, such as climate change, habitat fragmentation, or chemical pollution, can profoundly alter multiple facets of biodiversity [1–4]. The past 25 years have seen a rise in various empirical approaches to examine how such changes affect ecosystem functions and services [5,6]. Many focus on altering biodiversity while observing corresponding changes in function [7]. These approaches can be first classified based on the nature of the manipulation: whether species densities are altered randomly or nonrandomly. **Random manipulations** (see [Glossary](#)) assume a random extinction or colonization order, while **non-random manipulations** are performed based on the (presumed) response of species to environmental change [8] or based on the effects of species on function (e.g., species with a greater effect on function are removed first) [9]. A second distinction can be based on whether manipulations of biodiversity are direct or indirect. **Direct biodiversity manipulations** are performed by manually altering species densities [10], whereas for **indirect manipulations** a relevant environmental change is introduced to alter biodiversity [11,12].

Indirect and nonrandom manipulations of biodiversity make intuitive sense because they are rooted in a recognition that **environmental change drivers** are often the cause of biodiversity

Trends

In the 1990s critiques on early biodiversity–ecosystem function (B-EF) research pushed the field towards direct and random biodiversity manipulations.

This evolution allowed the establishment of causal relationships between ecosystem functioning and biodiversity, a main research gap at that time.

A main research gap today is to predict and mechanistically understand shifts of ecosystem functioning following real-world biodiversity shifts caused by different types of environmental change.

Data from direct and random biodiversity manipulations do not predict the functioning of ecosystems that experience biodiversity shifts as these shifts are often nonrandom and combine with a series of other effects such as changes in *per capita* functioning and density.

Environmental change drivers are useful as they offer experimental control over: (i) the relative magnitude of the different facets of biodiversity change; and (ii) food web composition. These two features facilitate inference of the mechanisms connecting environmental change with ecosystem functioning.

alterations [3] and that these alterations are nonrandom [9,13]. As a consequence, early B-EF research [7] often adopted indirect and nonrandom biodiversity manipulations [11,12,14]. However, such approaches were increasingly subject to controversy and disagreement. In his seminal paper, Huston [15] criticized indirect and nonrandom biodiversity manipulations for difficulties in separating 'true' biodiversity effects from the effects of 'hidden treatments'. Huston argued that by indirectly altering biodiversity using an environmental variable, researchers precluded partitioning the **biodiversity-mediated effects on ecosystem function** from the many **other effects that environmental change can have on function**. Nonrandom manipulations were also shown to suffer from inherent bias, because results were highly dependent on the chosen order of species removal or addition. Collectively, the critiques by Huston and others [15–18] pushed the field towards direct and random biodiversity manipulations [7,10]. The advantage of this methodological shift was that the causal relationship between biodiversity and ecosystem functioning, a main research gap at that time, could be more rigorously established. Today, however, a main research gap in ecology is understanding how the data produced using random and/or direct manipulations of biodiversity can be used to meet two of ecology's current challenges: (i) to support quantitative prediction of the ecological effects of anthropogenic activities [7]; and (ii) to unravel the mechanisms linking community structure (relative abundances) and composition to ecosystem function [19,20]. In this Opinion article, we submit that reintroducing nonrandom and indirect manipulations of biodiversity using environmental change drivers [21–25]: (i) is a prerequisite to predicting the functioning of ecosystems facing changes in biodiversity that are caused by environmental change (second section); and (ii) facilitates the unraveling of mechanistic insight into the connections between community structure and composition and ecosystem function (third section).

Reintroduction of Environmental Change Drivers Is Needed to Predict Ecosystem Functioning Following Changes in Biodiversity

In many ecosystems environmental change causes biodiversity declines or increases [26–29]. Experiments that directly and randomly manipulate biodiversity are unlikely to predict function in these ecosystems (Figure 1, shaded area). This is because biodiversity changes that are nonrandom with respect to species' contributions to function will affect ecosystem functioning more or less than do random biodiversity changes [9,30]. In addition, environmental change can alter the effect species have on ecosystem functions by altering: (i) *per capita* contributions to function [31,32]; and (ii) population density [33,34]. Depending on the type of environmental change, these alterations can be mostly positive (e.g., nutrient enrichment [35]), mostly negative (e.g., drought [36], pollution [37]), or negative for some species and positive for others (e.g., warming [38–40]).

Trait-based frameworks are available to predict how nonrandom effects of environmental change on *per capita* contributions to function, population densities, and biodiversity translate to changes in ecosystem function [9,30]. A simple extension of this framework with species interactions (Box 1) and using richness as a biodiversity indicator illustrates two important points. First, environmental change can cause a variety of B-EF relationships (Figure 1). The shape of this relationship critically depends on: (i) whether the responses elicited by the environmental change driver are positive or negative; and (ii) the type of nonrandomness exerted by the environmental change driver [28,41] (Box 1). Second, changes in function are expected before any change in species richness is observed (Figure 1A,D, levels 0–0.1) and – more generally – the variability of ecosystem function within one level of species richness is substantial (Box 1) (see Outstanding Questions). The ensemble of B-EF relationships constructed through direct and random biodiversity manipulation (Figure 1, shaded area) does not capture the variation in B-EF shapes arising from indirect and nonrandom biodiversity manipulation and can both overestimate (e.g., Figure 1B) and underestimate (e.g., Figure 1C) variation of function within one biodiversity level.

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Box 1. Nonrandom and Indirect versus Random and Direct Biodiversity Manipulations

We simulate richness and ecosystem functioning in a community of ten species responding to a level l of an environmental change driver and contributing to an ecosystem function F [9]:

$$\frac{dN_i}{dt} \cdot \frac{1}{N_i} = [\mu_i(l) + \sum_{j=1}^{10} a_{ij} \cdot N_j] \quad [I]$$

(based on [50])

$$F = \sum_{i=1}^{10} f_i(l) \cdot N_i^* \quad [II]$$

a_{ij} are *per capita* effects of species j on species i ($a_{ij} = a_{ji} = -0.2$; intraspecific effects a_{ii} are set to -1). N_i is the density of species i (asterisks denote equilibrium densities); $\mu_i(l)$ and $f_i(l)$ are growth rates and *per capita* contributions to F as a function of l :

$$\mu_i(l) = \mu_{i,max} \cdot (1 + r_i \cdot l) \quad [III]$$

$$f_i(l) = f_{i,max} \cdot (1 + r_i/2 \cdot l) \quad [IV]$$

where r_i represents the response of species i to environmental change and the division by two ensures that *per capita* contributions to function responds more strongly than density [76]. All species have $f_{i,max} = 10$, respond differently to environmental change (Figure 1), have different growth rates (Figure 1), and therefore have different competitive strengths (Figure 1).

We manipulated richness indirectly and nonrandomly by exposing the community to level l between 0 (no change) and 1 (100% increase or decrease of μ of the most responsive species) and measured the corresponding F (see Figure 1 in main text, colored symbols). When dominants respond most negatively (Figure 1A), function decreases but richness is higher with than without environmental change because of competitive release of species 0. Thus, environmental change promotes coexistence and richness decreases only at high levels of change. The resulting B-EF relationship is therefore non-monotonic. When environmental change mostly elicits negative responses of subordinates (Figure 1B), richness decreases at low levels of change because subordinates (species 1) combine low density, which makes them inherently prone to competitive exclusion, with a large negative response. In this case a monotonic positive B-EF relationship emerges. When environmental change elicits positive responses, negative (Figure 1C) or positive (Figure 1D) B-EF relationships emerge from exactly the same mechanisms as in Figure 1A,B.

We also manipulated richness directly and randomly by removing all possible combinations of one to five species from the community and measuring the corresponding F while setting $l = 0$ (Figure 1, shaded area; identical for all four scenarios).

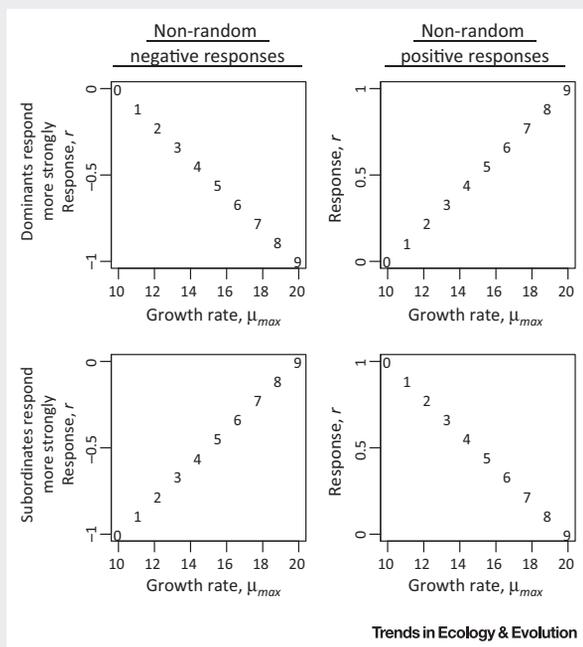


Figure 1. Environmental change elicits negative (left panels) or positive (right panels) responses that are strongest for species with high (top row) or low (bottom row) growth rates [i.e., species that are dominant and subordinate under pre-change conditions, respectively (Figure 1)]. Numbers give species identity.

Glossary

Biodiversity-mediated effect of environmental change on ecosystem function:

effects occurring through changes in any aspect of biodiversity (mostly richness or evenness).

Direct biodiversity manipulation: if biodiversity is manipulated directly, communities with different biodiversity levels are composed, for example, by taking different subsets of a species pool in the case of richness.

Environmental change driver: an environmental variable that exhibits long-term changes, often as a result of anthropogenic activities. Examples include nutrient deposition, climate warming, habitat fragmentation, and chemical pollution.

Indirect biodiversity manipulation: if biodiversity is manipulated indirectly, one applies different levels of an environmental change driver to create a biodiversity gradient. Indirect biodiversity manipulations are by definition nonrandom with respect to species responses to environmental change.

Nonrandom biodiversity

manipulation: nonrandom biodiversity manipulations are performed based on known or presumed extinction or colonization orders (nonrandom with respect to species' responses to environmental change) or based on the contribution of species to function (nonrandom with respect to species' effects on ecosystem functions).

Other effects of environmental change on ecosystem function:

effects occurring through mechanisms other than biodiversity changes. Examples include changes of community composition or structure, of total density (community size), of *per capita* contributions to function [$f_i(l)$ in Box 1; e.g., physiological responses to warming], and of the bioavailability of macronutrients such as carbon, nitrogen, or phosphorous [79].

Random biodiversity

manipulation: if biodiversity is manipulated randomly, community composition or structure is varied within a diversity level. By doing so, one can statistically control for effects of community composition or structure on ecosystem function.

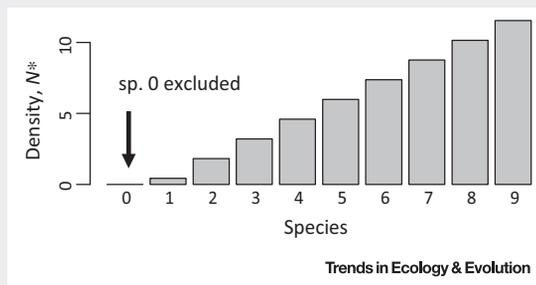


Figure II. Equilibrium Densities in the Absence of Environmental Change.

Reintroduction of Environmental Change Drivers Can Augment Mechanistic Insight

Many descriptors of biodiversity (e.g., richness and evenness, based on traits, taxonomy, or genes), but also community structure and composition, total density (community size), and *per capita* contributions to function, can affect ecosystem functioning [33,42–45]. A main research theme in ecology is to understand their relative importance to functioning [7,46,47]. Using environmental change drivers to indirectly manipulate biodiversity, community structure and composition, total density, and *per capita* contributions to function facilitates such studies. This is because different environmental change levels trigger effects on different subsets of these variables (Figure 1). For example, in Figure 1A environmental change levels between 0.25 and

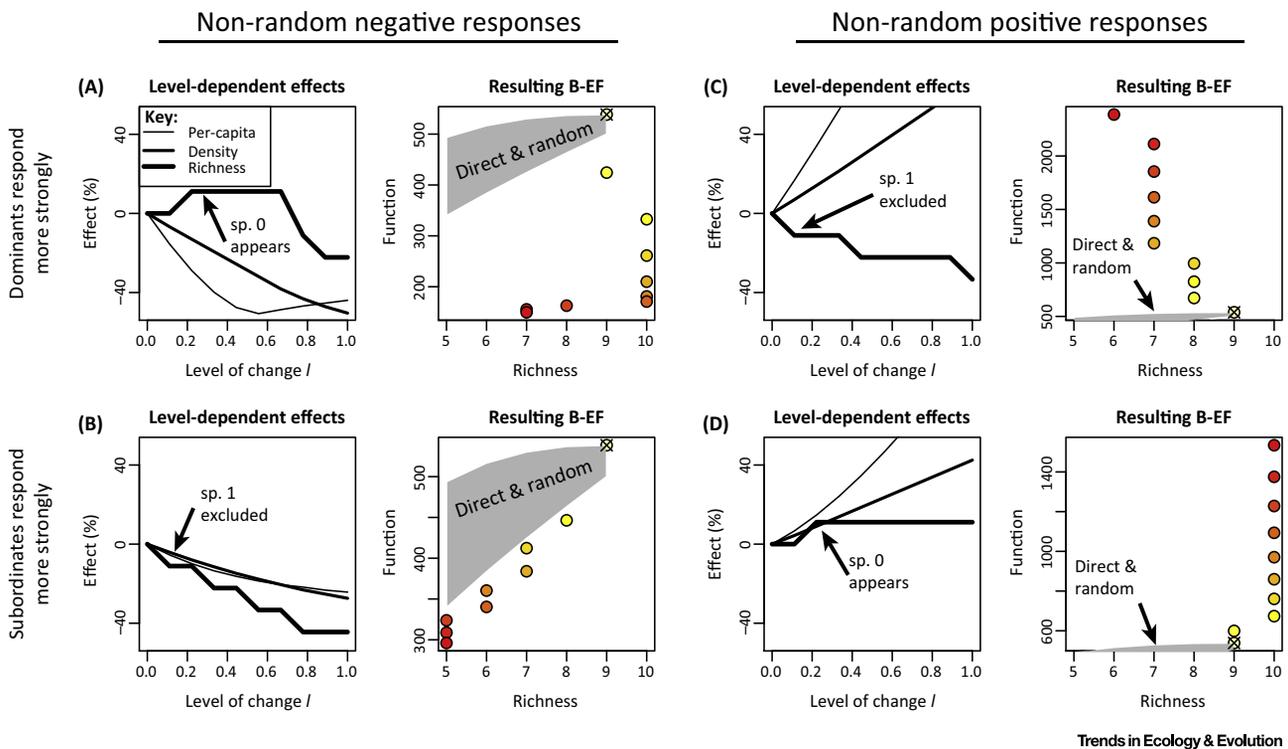


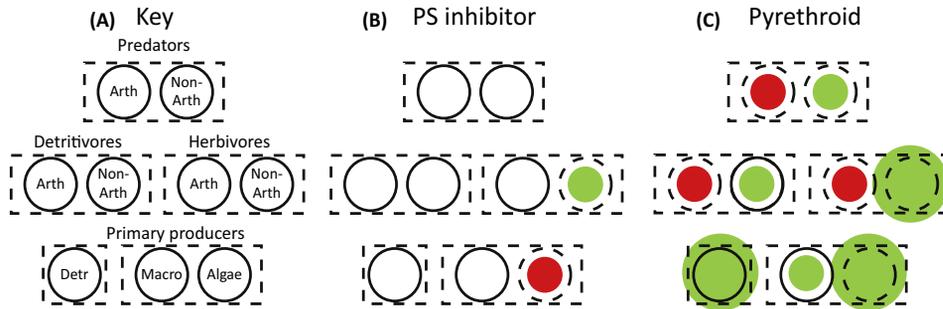
Figure 1. Indirect and Nonrandom Manipulations of Biodiversity Can Result in a Multitude of Biodiversity–Ecosystem Function (B-EF) Relationships. Resulting B-EF simulated from the model in Box 1; l is the level of environmental change and colors represent a scale from $l = 0$ (yellow) to $l = 1$ (red); the value for $l = 0$ is indicated with ‘ \times ’ for clarity. These relationships emerge as a consequence of effects on richness, *per capita* contributions to function (average effect across all species), and total density (sum of all species). The strength of these effects depends on l (level-dependent effects) and the shape of the resulting B-EF critically depends on whether dominants (A,C) or subordinates (B,D) respond more strongly to environmental change and on whether the elicited responses are negative (A,B) or positive (C,D). The shaded area indicates the expected B-EF under direct and random biodiversity manipulations.

0.7 will all lead to the same species richness but will alter total density and *per capita* contributions to function. In Figure 1B effects on richness are always more important than effects on total density or *per capita* contributions to function. In Figure 1A,D low levels of change affect only *per capita* contributions to function and total density. In general, the fact that different levels of environmental change cause different effects offers greater control over the different mechanisms underlying change of function than do direct manipulations of biodiversity. Controlling *per capita* contributions to function is by definition impossible through direct manipulations of biodiversity, since *per capita* contribution to function is not a descriptor of biodiversity. However, even community composition, structure, and richness will often be uncontrollable through direct manipulations. For example, in the model presented in Figure 1, persistence of species 0 or dominance by any species other than species 9 is possible only in the continuous presence of an appropriate environmental change driver (i.e., through indirect manipulations). Without this presence, community structure will always converge to that shown in Box 1 and richness will be 9, even when all ten species are added to the initial community. Many examples illustrate community compositions and structures that emerge only in the presence of specific environmental change drivers and do not occur in their absence. For example, drought in streams reduces the relative density of large-bodied consumers, predators, and encrusting green algae [36]. Nitrogen enrichment in grasslands increases the relative density of nitrogen-demanding grasses [35], while increased precipitation in grasslands increases the relative density of nitrogen-fixing forbs [48]. Although most of the available studies are based on taxonomic diversity, case studies showing how environmental change drivers can cause loss or gain of genetic diversity are rapidly accumulating [28,49].

The relationship between biodiversity and functioning in multitrophic communities (food webs) has been an important research theme in ecology since the 1990s [7,50–52]. For example, the biodiversity of one food web compartment can drive functions performed by other parts of the food web [53] or the two can be unrelated [54]. Using environmental change drivers to indirectly and nonrandomly manipulate food webs facilitates the study of such links. This is because environmental change drivers often target specific food web compartments so that it becomes possible to experimentally alter the biodiversity and related functions of specific food web compartments and measure corresponding changes in other compartments. For example, resource enrichment can be used to increase functions performed by basal species groups (e.g., bacterial decomposition, water purification, primary production) while desiccation can be used to target functions performed by non-basal species [36]. In addition to the well-known cases of resource addition or manipulation of climate variables, chemical stressors are an exceptionally useful group of experimental agents that can be used for both nonrandom manipulations and manipulations that are random with respect to the effects that species have on function. This is illustrated by the many studies that have exposed relatively complex food webs comprising field organisms (typically primary producers and invertebrate grazers and predators) to concentration series of chemical stressors over several weeks to months (Figure 2). For example, many pyrethroid insecticides will target arthropod consumers and predators [55,56] while photosystem-inhibiting herbicides will target specific algal taxa [57,58]. Certain biocides such as triphenyltin [59] and narcotic chemicals [60] are examples of chemical stressors that exert effects that are random with respect to the effects that species have on function. Directly manipulating food webs to persistently exclude certain trophic levels or functional groups (e.g., small-bodied benthic grazers, specific bacterial communities, algal taxa) will be nearly impossible. Indirect nonrandom manipulations might therefore be the only solution.

Back to the Future: Methods to Connect Indirect and Nonrandom Manipulations with Classic B-EF Research

Most classic B-EF designs focus on the effect of random biodiversity changes on ecosystem function through direct manipulations. To quantify the contribution of such effects to the



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Figure 2. Chemical Stressors Can Be Used to Nonrandomly and Indirectly Manipulate Food Webs. This is illustrated by the empirically observed effects of continuous exposure of freshwater-ditch food webs to chemical stressors in published micro- and mesocosm experiments. (A) Predators, herbivores, and detritivores are separated into arthropod (Arth) and non-arthropod (Non-Arth) species; primary producers are separated into macrophytes (Macro) and algae; Detr. represents detrital material and its associated microflora. (B) Results for exposure to 50 $\mu\text{g/l}$ linuron, a photosystem (PS) inhibitor [57,58]. (C) Results for exposure to 35 $\mu\text{g/l}$ chlorpyrifos, a pyrethroid insecticide [55,56]. Significant primary responses to the corresponding chemical stressor are shown in red; secondary effects mediated by species interactions are shown in green. White circles indicate that there was no effect. The relative sizes of the colored and broken circles indicate whether the effect was positive (increase in abundance – colored circle larger than broken circle) or negative (decrease of abundance – colored circle smaller than broken circle).

functioning of ecosystems following environmental change (see Outstanding Questions) [23], analysis of available data is a useful starting point. The literature is replete with studies exposing communities to environmental gradients. When a sufficient number of change levels has been tested across a sufficiently broad gradient of change, the contributions of biodiversity-mediated effects can be separated from the other effects of environmental change on ecosystem function using available analytical techniques. One possible way to do so is by applying multivariate statistical techniques such as structural equation modeling [61,62] (Box 2). However, sophisticated structural equation models (SEMs) [21,24] can also be used to partition the effects on function that are not mediated by biodiversity into their constituents. In addition, methods based on versions of the Price equation that do not require monoculture data but only species contributions to function before and after environmental change can be used to separate the effects of species loss and gain that is random and nonrandom with respect to the effects species have on function from all other effects that environmental change can have on function [42].

Post hoc analyses are a useful first step to quantify biodiversity-mediated effects on function. However, we recommend combining direct and indirect biodiversity manipulations as separate treatments in a single experiment. In a first design, we recommend using a well-known environmental change driver to nonrandomly manipulate a community while setting up a second treatment where the same community is manipulated directly. Importantly, the direct manipulation should be performed in the absence of the environmental change driver but should aim to match the community resulting from the application of the environmental change driver as observed in the first treatment and should therefore be nonrandom. For example, in Figure 1B applying a level of change of 0.1 would constitute an indirect biodiversity manipulation that excludes species 1. Higher levels would exclude species 2, 3, and so on. Thus, the direct biodiversity manipulation treatments should represent the same gradient of community compositions by consecutively excluding species 1, 2, 3, and so on. Next, the B-EF relationship resulting from the indirect manipulation (e.g., Figure 1B, Resulting B-EF panel) could be compared with that resulting from direct species removal. If the two were not significantly different, this would suggest that the chosen type of environmental change mainly acts on ecosystem functioning through compositional effects. If B-EF relationships do differ, follow-up

Box 2. Separating Biodiversity-Mediated Effects on Ecosystem Functioning

SEMs can be used to compare biodiversity-mediated effects on ecosystem functioning with the other effects that environmental change can have on function. A SEM is described as ‘the use of two or more structural [cause–effect] equations to model multivariate relationships’, which allows an intuitive graphical representation of complex causal networks [61,62]. Most notably, a SEM can be used not only to isolate biodiversity-mediated effects on ecosystem functioning but also to investigate the partial contributions of correlated explanatory variables to test alternative hypotheses [61].

For illustrative purposes, we analyzed data from a previously published microcosm study evaluating the effects of chemical stress (a mixture of insecticides) on aquatic invertebrate richness and decomposition in a ditch community [77,78] with a simple SEM (Figure 1). We also present previously published effects of nitrogen and carbon dioxide enrichment on plant richness and biomass production in grasslands [23]. These analyses show that richness-mediated effects on function are negative for environmental change drivers that have negative effects on richness and that these richness-mediated effects can be partly compensated by other effects of environmental change. Many examples in the literature support the conclusion that environmental change studies can be successfully analyzed with SEMs, including SEMs with more extended effect pathways [21,24]. In more replicated experimental setups [61], different biodiversity and community metrics could be tested in parallel to extract the most relevant biodiversity metric causing alterations in ecosystem functioning.

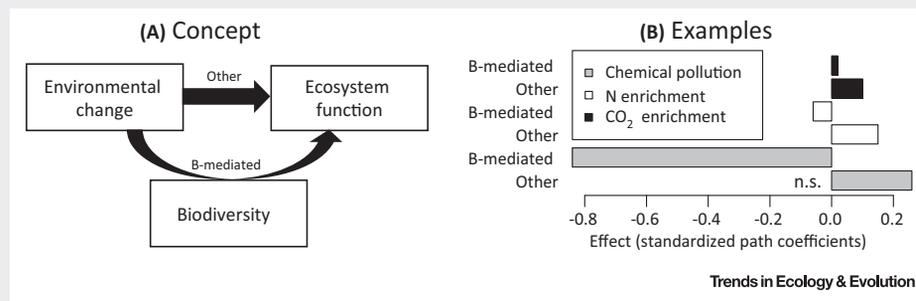


Figure 1. (A) Environmental change drivers can affect functions by altering biodiversity or through other mechanisms [23]. (B) Structural equation models for three environmental change drivers. All effects are significant ($P < 0.05$) except when indicated (n.s.). The variances of diversity and function explained by the model (R^2) for the case of chemical stress were 68% and 65%, respectively. Effects are standardized path coefficients [62]. Details of the analysis of the other two drivers can be found in the original publication [23].

studies could examine in more detail the potential mechanisms explaining this difference; for example, by inspecting the magnitude of effects on *per capita* contributions to function [25] or by considering effects on community structure. However, we recognize that this design can be challenging because, as mentioned in the third section, certain community compositions are impossible to reconstruct without the use of environmental variables. This problem could be addressed by statistically testing whether *per capita* contributions to function (the functional contribution of a species; e.g., its total biovolume divided by its population density) differ between the direct and indirect biodiversity treatments. If the inferred values of *per capita* contributions to function do not differ between the two treatments, this suggests that the selected type of environmental change impacts ecosystem functioning through mechanisms other than effects on *per capita* contributions to function.

A second design comprises a factorial experiment where the presence or absence of a direct biodiversity manipulation that aims to match the community structure resulting from the indirect biodiversity manipulation is crossed with the presence and absence of an environmental change driver [63]. If all of the effects of the driver on ecosystem functioning are mediated by biodiversity changes, the combination of direct biodiversity manipulation and the environmental change treatment should display the same level of ecosystem functioning as both the direct manipulation alone and the environmental change treatment alone. If this were not the case, this would suggest non-biodiversity-mediated effects on ecosystem functioning. Interestingly, the same design has been recently proposed by Vellend [64], although motivated by a different objective.

Vellend proposed to use this design to test whether a community structure shaped by environmental change maximizes function under that same type of environmental change, a prediction based on the analogy between community ecology and population genetics.

Challenges of Reintroducing Environmental Change Drivers in B-EF Research

Although we advocate reintroducing environmental change drivers in B-EF research, there are at least two challenges that need to be addressed for successful application. First, in the approach we advocate we implicitly assume that environmental change does not affect *per capita* species interactions (*a* in Box 1). In our model the effects of species interactions on a focal species are altered only through changes in the density of species with which it interacts. This assumption has been shown to prevail in some systems [65] but not in others [66,67]. Arguably the best-known example of environmental effects on *per capita* interactions is the ‘stress-gradient hypothesis’, where there is a shift from competitive (i.e., negative) to facilitative (i.e., positive) interactions as the level of stress increases [66,67]. Such effects can lead to various effects of stress on community structure and composition and ecosystem function, depending on the type of stress factor and species traits [68]. Suttle *et al.* [48] found that sustained increased precipitation eventually caused negative interactions among plant species that were not apparent before the treatment. In alfalfa communities, Barton and Ives [69] found that reduced precipitation changed interactions between spotted aphids and their ladybeetle predators through dietary shifts of the latter. These examples make clear that species interactions prevailing in the pre-change system cannot always be used to predict the chain of secondary and higher-order effects occurring after the change. In such cases, knowledge about shifts of *per capita* species interactions is needed to gain control over community structure and composition in experiments (see Outstanding Questions) and to correctly interpret the observed effects of environmental change on biodiversity and ecosystem functioning.

Second, we have discussed environmental change drivers eliciting either positive or negative responses that change monotonically as the level of environmental change increases and stay constant through time. However, many environmental change drivers can elicit positive responses in some species but negative responses in others (e.g., temperature [38]) and many responses are non-monotonic, with the sign of the response depending on the level of environmental change (e.g., [47]). In addition, depending on the life history of the considered species, populations can genetically adapt [49], which can alter their response to environmental change through time. While these features do not threaten the general principle of our thesis, they do indicate that community structure and composition can be harder to interpret and predict, and therefore more difficult to control in experiments, for certain combinations of environmental change drivers and ecosystem types.

Opportunities for Ecosystem Assessment and Management

Novel tools for biological monitoring will substantially increase the amount of biodiversity data [70,71]. However, linking monitored biodiversity trends to ecosystem functions remains a major difficulty for ecosystem assessment, as has been discussed in the framework of several environmental regulations worldwide [72,73]. Reintroducing environmental change drivers in B-EF research could help ecosystem assessors by realistically translating observed biodiversity trends to trends of ecosystem function for a suite of well-studied environmental change drivers. Studies compiling and comparing different types of environmental change [22,74] will be instrumental in asking whether knowledge about one type of environmental change can be transposed to other types of environmental change (see Outstanding Questions). Following ecosystem assessments, predicted changes of ecosystem functions could also be used to inform management; for example, by triggering mitigating measures if needed. In addition, ecosystem managers could propose critical levels of biodiversity change that, when exceeded,

lead to unacceptable loss of ecosystem functioning. The connection of B-EF research to applied science has often been debated [75]. Reintroducing the use of environmental change drivers to B-EF research can reinforce this connection.

Concluding Remarks

We have identified two reasons why environmental change drivers should be reintroduced in B-EF research. First, the amount of ecosystem function loss or gain following biodiversity change depends on the type of underlying environmental change driver. Second, environmental change drivers can serve as experimental agents to control various aspects of biodiversity and community composition and structure. These features facilitate the study of to what extent changes in ecosystem function are caused by biodiversity change and which aspects of biodiversity are most important to ecosystem function.

Reintroducing environmental change drivers into B-EF research can be realized by analyzing existing data for well-known environmental change drivers and through novel experimental designs. Designs combining direct and indirect biodiversity manipulations constitute a particularly useful research avenue as they allow direct testing of how biodiversity, environmental change, and ecosystem function relate. However, unexpected effects of environmental change on *per capita* species interactions and the variety of species' responses to such change are two main challenges to the use of environmental change drivers in B-EF research. Opportunities include an improved capacity to assist ecosystem assessment and management by translating monitored biodiversity trends to trends of ecosystem function, which are rarely monitored. We conclude that reintroducing environmental change drivers in B-EF research is a prerequisite for the prediction of shifts of ecosystem function in a changing world, facilitates understanding of the mechanisms causing these shifts, and strengthens the connections between B-EF research and applied ecology.

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Outstanding Questions

Theory indicates that environmental change can affect function without changing richness, but how important are such effects in real ecosystems? How do effects on function at invariant richness vary among ecosystems?

B-EF research has mostly focused on the effects of random species loss on functions. How do these effects compare with those occurring following environmental change?

How does environmental change alter *per capita* species interactions and how does this affect our capacity to manipulate biodiversity using environmental change drivers?

How can knowledge about a selection of well-studied environmental change drivers be used to manage ecosystems exposed to other types of environmental change?

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