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Opinion for Trends in Ecology and Evolution

Title: Re-introducing environmental change drivers in biodiversity-ecosystem functioning research

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Abstract

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 re-introducing environmental change drivers in B-EF research is needed to predict the functioning of ecosystems facing changes in biodiversity. Next, we show how this re-introduction also allows for better control over community composition in B-EF experiments and thus helps to obtain mechanistic insights about how multiple aspects of biodiversity relate to function, and how biodiversity and function relate in food-webs. We also highlight challenges for the proposed re-introduction, and propose 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.

1. Predicting effects on ecosystem functions from changes in biodiversity: a brief history

Various types of environmental change, such as climate change and the deterioration of environmental quality, can profoundly alter multiple facets of biodiversity [1-3]. The past 25 years have seen a rise in different empirical approaches to examine how such changes affect ecosystem functions and services [4, 5]. Many focus on altering biodiversity while observing any corresponding changes in function [6]. These approaches can be first classified based on the nature of the manipulation (Table 1 and 'Glossary'), whether species are added or removed randomly or non-randomly. Random manipulations assume a random extinction or colonization order, while non-random species additions or removals are done based on the (presumed) response of species to environmental change [7], or based on the effects of species on function (e.g. species that function best are removed first) [8]. A second distinction can be based on whether manipulations of biodiversity are direct or indirect. Direct biodiversity manipulations are performed by manually removing or adding species [9], whereas with indirect manipulations, a relevant environmental change is introduced to alter biodiversity [10, 11].

Indirect and non-random manipulations of biodiversity make intuitive sense because they are rooted in a recognition that environmental change drivers are often the cause of biodiversity alterations [3] and that these alterations are non-random [8, 12]. As a consequence, early research on biodiversity and ecosystem functioning ('B-EF research' [6]) often adopted indirect and non-random biodiversity manipulations [10, 11, 13]. However, such approaches were increasingly subject to controversy and disagreement. In his seminal paper, Huston [14] criticized indirect and non-random 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 effects of biodiversity on ecosystem functioning from the many other effects environmental change can have on function ('Glossary'). Non-random 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 [14-16] pushed the field towards direct and randomized biodiversity manipulations (Table 1, [6, 9]). The advantage of this methodological shift was that the causal relationship between biodiversity and ecosystem functioning could be more rigorously tested, and the different effects that biodiversity alterations could have on ecosystem functioning were more readily quantified [17]. However, despite this improvement in methodology, it still remains unclear how either random or direct manipulations of biodiversity can be used to meet two of ecology's main challenges: (1) to support quantitative prediction of the ecological effects of anthropogenic activities [6]; and (2) to unravel the mechanisms linking community structure and composition to ecosystem function [18, 19]. An emerging trend in contemporary B-EF research is to re-introduce non-random and indirect manipulations of biodiversity using environmental change drivers, such as various climate variables, chemical stressors, and nutrient enrichment [20-24]. In the present contribution we submit that this approach (1) is a prerequisite to predicting the functioning of ecosystems facing changes in biodiversity that are caused by environmental change (section 2); and (2) facilitates unravelling mechanistic insight into the connections between community structure and composition to ecosystem function (section 3).

2. The re-introduction of environmental change drivers is needed to predict ecosystem functioning following changes in biodiversity

In many ecosystems, environmental change causes biodiversity declines or increases [25-28]. Experiments that directly and randomly manipulate biodiversity are unlikely to predict function in these ecosystems (Fig. 1, shaded area). This is because biodiversity changes that are non-random with respect to function ('Glossary') will affect ecosystem function more or less than do random biodiversity changes [8, 29]. In addition, environmental change can also alter the effect species have on ecosystem functions by altering (1) per-capita functioning [30, 31], and (2) population density [32, 33]. Depending on the type of environmental change, these alterations can be mostly positive (e.g. nutrient enrichment, [34]), mostly negative (e.g. drought, [35], pollution, [36]), or negative for some species and positive for others (e.g. warming, [37-39]).

Trait-based frameworks are available to predict how non-random effects of environmental change on per-capita functioning, population densities, and biodiversity translate to changes in ecosystem function [8, 29]. 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 (Fig. 1). The shape of this relationship critically depends on (1) whether the responses elicited by the environmental change driver are positive or negative, and (2) the type of non-randomness exerted by the environmental change driver [27, 40] (Box 1). Second, changes in function are expected before any change in species richness is observed (Fig. 1A and D; levels 0-0.1), and – more generally – the variability of ecosystem function within one level of species richness is substantial (Box

1, Box 3, ‘Outstanding questions’). The ensemble of B-EF relationships constructed through direct and random biodiversity manipulation (Fig. 1, shaded area) does not capture the variation in B-EF shapes arising from indirect and non-random biodiversity manipulation, and can both over- (e.g. Fig. 1B) and underestimate variation of function within one biodiversity level (e.g. Fig. 1C).

3. The re-introduction of environmental change drivers can augment mechanistic insight

Many descriptors of biodiversity (richness, community composition and structure), but also total density (community size) and per-capita functioning, can affect ecosystem functions [32, 41, 42]. A main research theme in ecology is to understand their relative importance to function [6, 43]. Using environmental change drivers to indirectly manipulate biodiversity, total density, and per-capita functioning facilitates such studies. This is because different environmental change levels trigger effects on different subsets of these variables (Fig. 1). For example, in Fig. 1A, environmental change levels between 0.25 and 0.7 will all lead to the same species richness, but alter total density and per-capita functioning. In Fig. 1B, effects on richness are always more important than effects on total density or per-capita functioning. In Fig. 1A and D, low levels of change only affect per-capita functioning and total density. 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 functioning is by definition impossible through direct manipulations of biodiversity because it is no descriptor of biodiversity, and always requires some change of environmental conditions. Even community composition, structure, and richness will often be uncontrollable through direct biodiversity manipulations. For example, in the model presented in Fig. 1, persistence of species 0 or dominance by any other species than species 9 is only possible in the continuous presence of an appropriate environmental change driver, i.e. through indirect manipulations. Without this presence, community structure will always converge to the one shown in Box 1 and richness will be 9, even when all 10 species are added to the initial community. Many examples illustrate community compositions and structures that only emerge in the presence of specific environmental change drivers and do not occur in their absence (Table 1).

The relationship between biodiversity and functioning in multi-trophic communities (food-webs) has been an important research theme in ecology since the 1990s [6, 44-46]. For example, the biodiversity of one food-web compartment can drive functions performed by other parts of the food-web [47], or both can be unrelated [48]. Using environmental change drivers to indirectly and non-randomly manipulate biodiversity facilitates such studies. This is because environmental change drivers often target specific food-web compartments so that it becomes possible to experimentally alter biodiversity and related functions of specific food-web compartments and measure corresponding changes in other compartments (Table 1). In addition to the well-known cases of resource addition or manipulation of climate variables, chemical stressors comprise an exceptionally useful group of experimental agents that can be used for both non-random manipulations as well as for manipulations that are random with respect to the effects species have on function. This is illustrated by the many studies that have exposed relatively complex food-webs composed of field organisms (typically primary producers and invertebrate grazers and predators) to concentration series of chemical stressors during several weeks to months (Fig. 2). For example, many pyrethroid insecticides will target arthropod consumers and predators [49, 50], while photosystem-inhibiting herbicides will target specific algal taxa [51, 52]. In contrast, certain biocides such as triphenyltin [53] and narcotic chemicals [54] are examples of chemical substances that exert effects that are random with respect to function. Directly manipulating food-webs to persistently exclude certain trophic levels or functional groups (e.g. small-bodied benthic grazers, specific bacterial communities or algal taxa) will be nearly impossible. Indirect non-random manipulations might therefore be the only solution.

4. Back to the future: methods to connect indirect manipulations of biodiversity with classic B-EF research

Several methods are available that facilitate connecting indirect manipulations of biodiversity to the classic approach of direct, random manipulations (Box 3, ‘Outstanding questions’) [22]. The literature is replete with studies exposing communities to environmental gradients (bottom-right entry in Table 1). 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 (‘Glossary’ contains examples of such effects) using available analytical techniques. One possible way to do so is by applying multivariate statistical techniques, such as structural equation modelling [58, 59] (Box 2). However, sophisticated structural equation models [20, 23] can also be used to partition the effects on function that are not mediated by biodiversity into their constituents (‘Glossary’). In addition, methods based on versions of the Price equation that do not require monoculture data but only need 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 non-random with respect to function from all other effects environmental change can have on function [41].

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, which is rarely done (Table 1). In a first design, we recommend using a well-known environmental change driver to non-randomly manipulate a community, while setting up another treatment where the same community is manipulated directly, but non-randomly in a manner that aims to match the community resulting from the application of the environmental change driver. For example, in Fig. 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. Fig. 1B, ‘resulting B-EF’ panel) could be compared to the one resulting from the direct species removal. If both were not significantly different, this would suggest that the chosen type of environmental change mainly acts upon ecosystem functioning through effects on biodiversity. If B-EF relationships do differ, follow-up studies could examine in more detail the potential mechanisms explaining this difference, for example by inspecting the magnitude of effects on per-capita functioning [24]. However, we recognize that this design can be challenging because, as mentioned in section 3, certain community compositions are impossible to reconstruct without the use of environmental variables. This problem could be addressed by statistically testing if per-capita functioning (functional contribution of a species, e.g. its total biovolume divided by its population density) differs between the direct and indirect biodiversity treatment. If the inferred values of per-capita functioning do not differ between both biodiversity treatments, this suggests that the selected type of environmental change impacts ecosystem functioning through other mechanisms than effects on per-capita functioning.

A second design consists of a factorial experiment where the presence or absence of a direct biodiversity manipulation that aims to match the community composition resulting from the indirect biodiversity manipulation (as discussed in the first design) is crossed with the presence and absence of an environmental change driver [60]. If all the effects of the driver on ecosystem functioning are mediated by biodiversity changes, then 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, then it would suggest non-biodiversity-mediated effects on ecosystem functioning.

5. Challenges of re-introducing environmental change drivers in B-EF research

Although we advocate re-introducing environmental change drivers to B-EF research, there are are at least two challenges that need to be addressed for this to be successful. First, in the approach we advocate, we implicitly assume that environmental change does not affect per-capita species interactions (the α in Box 1). The effects of species interactions on a focal species can only be altered through changes in the density of species with which it interacts. This assumption has been shown to prevail in some systems [61], but not in others [62, 63]. 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 [62, 63]. Such effects can lead to a variety of effects of stress on community composition and ecosystem function, depending on the type of stress factor and species traits [64]. Suttle et al. [65] 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 [66] 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 in per-capita species interactions is needed to predict how the selected environmental change driver affects biodiversity and ecosystem function (Box 3, 'Outstanding questions').

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 [37]), and many responses are non-monotonic, with the sign of the response depending on the level of environmental change (e.g. [67]). In addition, depending on the life history of the considered species, populations can genetically adapt [68], 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 composition can be harder to predict, and therefore more difficult to control, for certain combinations of environmental change drivers and ecosystem types.

6. Opportunities for ecosystem assessment and management

Novel tools for biological monitoring will substantially increase the amount of biodiversity data [69, 70]. 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 [71, 72]. Re-introducing environmental change drivers in B-EF research could help ecosystem managers 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 [21, 73] will be instrumental to ask if knowledge about one type of environmental change can be transposed to other types of environmental change (Box 3, ‘Outstanding questions’). Following ecosystem assessments, predicted changes of ecosystem functions could be used to inform management as well, 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 [74]. We conclude that re-introducing the use of environmental change drivers to B-EF research can reinforce this connection.

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Tables

Table 1: Biodiversity manipulation can occur directly or indirectly and randomly or non-randomly (‘Glossary’). Classic research on biodiversity and ecosystem function (‘Classic B-EF’) has focused on direct and random biodiversity manipulations. We provide four examples of environmental change drivers that cause negative (A and B) or positive (C and D) non-random direct effects in communities. Note that effects in case D are only initial effects, as explained in section 5. Direct non-random manipulations are rare and are proposed in section 4 as a way forward to elucidate the role of biodiversity-mediated effects of environmental change on function. Indirect and random manipulations are rare as well but some chemical stressors can achieve such manipulations. Indirect biodiversity manipulations are by definition non-random with respect to species responses to environmental change.

	Direct	Indirect
Random	Common: Classic B-EF [6, 9]	Rare: Narcotic chemicals decrease survival of all species with lipid bilayers, and therefore manipulate biodiversity randomly with respect to function [54].
Non-random	Rare [7]: Proposed designs (section 4)	Common: A: Drought in streams decreases survival of large-bodied consumers and predators and reduces growth of encrusting green algae [35]. B: Pyrethroid insecticides in ditches decrease survival of arthropod predators [49, 50]. C: Nitrogen enrichment in grasslands increases growth of nitrogen demanding grasses [34]. D: Increased precipitation in grasslands increases growth of nitrogen-fixing forbs [65].

Box 1: Non-random and indirect vs. random and direct biodiversity manipulations. We simulate richness and ecosystem functioning in a community of 10 species responding to a level l of an environmental change driver and contributing to an ecosystem function F:

$$\frac{dN_i}{dt} \cdot \frac{1}{N_i} = \left[\mu_i(l) + \sum_1^{10} \alpha_{i,j} \cdot N_j\right] \qquad \text{(based on [44])}$$

$$F = \sum_1^{10} f_i(l) \cdot N_i^*$$

The $\alpha_{i,j}$ are per-capita effects of species j on species i ($\alpha_{i,j} = \alpha_{j,i} = -0.2$; intraspecific effects $\alpha_{i,i}$ 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 (‘per-capita functioning’) as a function of l:

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

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

where r_i represents the response of species i to environmental change and the division by two ensures per-capita functioning responds more strongly than density [75]. All species have $f_{i,max} = 10$, respond differently to environmental change (Fig. I), have different growth rates (Fig. I) and therefore different competitive strengths (Fig. II).

We manipulated richness indirectly and non-randomly by exposing the community to levels l between 0 (no change) and 1 (100% increase or decrease of μ of the most responsive species), and measured the corresponding F (Fig. 1, colored symbols). When dominants respond most negatively (Fig. 1A), function decreases but richness is higher with than without environmental change because of competitive release of species 0. Thus, environmental change promotes co-existence and richness only decreases at high levels of change. The resulting B-EF relationship is therefore non-monotonic. When environmental change mostly elicits negative responses of subordinates (Fig. 1B), richness decreases already at low levels of change because subordinates (species 1) combine a 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 (Fig. 1C) or positive B-EF relationships (Fig. 1D) emerge from exactly the same mechanisms as in Fig. 1A and 1B.

We also manipulated richness directly and randomly by removing all possible combinations of 1 to 5 species from the community and measuring the corresponding F while setting l=0 (Fig. 1, shaded area, identical for all four scenarios).

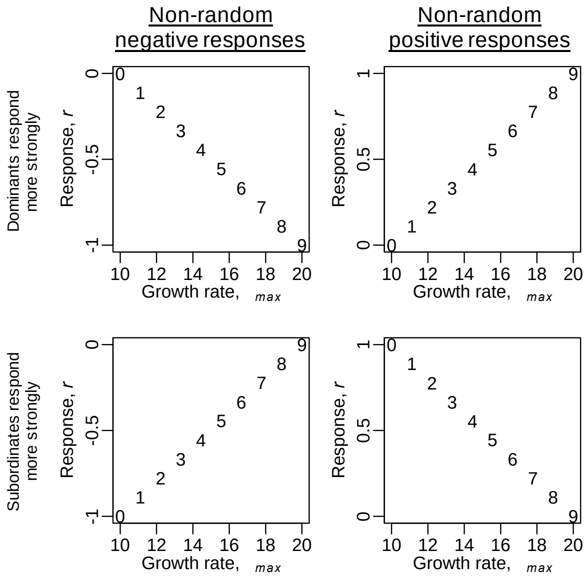

Figure I: Environmental change elicits negative (left panels) or positive responses (right panels) that are strongest for species with high (top row) or low (bottom row) growth rates, i.e. species that are dominant and subordinate in pre-change conditions, respectively (Fig. II). Numbers give species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

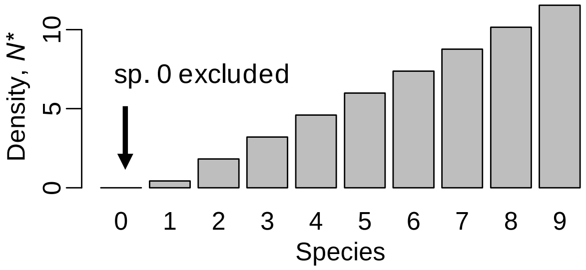

Figure II: Equilibrium densities in absence of environmental change.

Box 2: Separating biodiversity-mediated effects on ecosystem functioning Structural equation models (SEMs) can be used to compare biodiversity-mediated effects on ecosystem functioning with the other effects environmental change can have on function (‘Glossary’). A SEM is described as “the use of two or more structural [cause-effect] equations to model multivariate relationships”, which allows for an intuitive graphical representation of complex causal networks [58, 59]. Most notably, a SEM cannot only be used to isolate biodiversity-mediated effects on ecosystem functioning, but also to investigate the partial contributions of correlated explanatory variables to test alternative hypotheses [58].

For illustrative purposes, we analysed data from a previously published microcosm study evaluating the effects of chemical pollution (a mixture of insecticides) on aquatic invertebrate richness and decomposition in a ditch community [76, 77] with a simple structural equation model. We also present previously published effects of nitrogen and carbon dioxide enrichment on plant richness and biomass production in grasslands [22]. These analyses show that richness-mediated effects are negative for environmental change drivers that have negative effects on richness and that this effect can only partly be compensated by other effects of environmental change. These analyses also show that the relative contribution of both types of effect differs among types of environmental change drivers. Many examples in the literature support the conclusion that cosm studies with chemical agents can be successfully analysed with SEMs, including SEMs with more extended effect pathways [20, 23]. In more replicated experimental setups [58], different biodiversity and community metrics could be tested in parallel to extract the most relevant biodiversity metric causing alterations in ecosystem functioning.

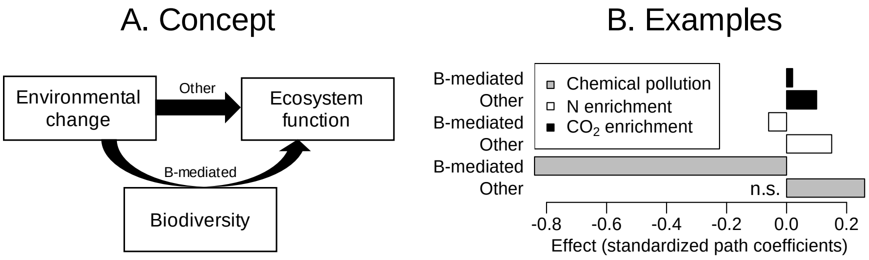

Figure I. A: Environmental change drivers can affect functions by altering biodiversity or through other mechanisms (‘Glossary’) [22]. B: Structural equation models for three environmental change drivers. All effects are significant ($P < 0.05$) except when indicated (n.s.). The variance of diversity and function explained by the model (R^2) for the case of chemical pollution was 68% and 65%, respectively. Effects are standardized path coefficients

[59]. Details on the analysis for the other two drivers can be found in the original publication [22].

Box 3: Outstanding questions

- Model simulations indicate 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?
- Biodiversity-ecosystem functioning research has mostly focused on the effects of random species loss on functions. How do these effects compare to those occuring 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?

Glossary

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 destruction, and chemical stress.

Direct biodiversity manipulation: If biodiversity is manipulated directly, communities with different biodiversity levels are composed, e.g. by taking different subsets of a species pool in case of taxonomic richness.

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 non-random with respect to species responses to environmental change.

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

Non-random biodiversity manipulation: Non-random biodiversity manipulations are done based on known or presumed extinction or colonization orders (non-random with respect to species responses to environmental change), or based on the contribution of species to function (non-random with respect to species effects on ecosystem functions) [78].

Biodiversity-mediated effect of environmental change on ecosystem function: Effects occurring through changes in any aspect of biodiversity (community composition or structure, richness).

Other effects of environmental change on ecosystem function: Effects occurring through mechanisms other than biodiversity changes. Examples include changes of total density (community size), changes of per-capita functioning ($f_i(l)$ in Box 1, e.g. physiological responses to warming), or changes of the bioavailability of macronutrients such as carbon, nitrogen, or phosphorous [79].

Figure legends

Figure 1: Simulations illustrating that indirect and non-random manipulations of biodiversity can result in a multitude of biodiversity-ecosystem function relationships (‘Resulting B-EF’, colours represent a scale from l=0 (yellow) to l=1 (red), the value for l=0 is indicated with a ‘x’ for clarity) by affecting not only richness but also per-capita functioning (average effect across all species) and total density (sum of all species). These effects depend on the level of environmental change (‘level-dependent effects’) and the shape of the resulting B-EF critically depends on whether dominants (A and C) or subordinates (B and D) respond more strongly to environmental change, and on whether the elicited responses are negative (A and B) or positive (C and D). The shaded area indicates the expected B-EF under direct and random biodiversity manipulations.

Figure 2: Chemical stressors can be used to non-randomly and indirectly manipulate biodiversity, as illustrated by 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; Det. represents detrital material and its associated microflora. B: Results for exposure to 50µg/L linuron, a photosystem (‘PS’) inhibitor [51, 52]. C: Results for exposure to 35 µg/L chlorpyrifos, a pyrethroid insecticide [49, 50]. Significant primary responses by 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 coloured and dotted circles indicate whether the effect was positive (increase in abundance - coloured circle larger than dotted circle) or negative (decrease of abundance - coloured circle smaller than dotted circle).

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