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1 **Opinion for** *Trends in Ecology and Evolution*

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

3 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 improves experimental control over community composition and structure, which helps to obtain mechanistic insight 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 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 different 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 non-randomly (see 'Glossary'). Random manipulations assume a random extinction or colonization order, while non-random manipulations are done 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 (see 'Glossary'). Direct biodiversity manipulations are performed by manually altering species densities [10], whereas with indirect manipulations, a relevant environmental change is introduced to alter biodiversity [11, 12].

Indirect and non-random manipulations of biodiversity make intuitive sense because they are rooted in a recognition that environmental change drivers (see 'Glossary') are often the cause of biodiversity alterations [3] and that these alterations are non-random [9, 13]. As a consequence, early research on biodiversity and ecosystem functioning ('B-EF research' [7]) often adopted indirect and non-random biodiversity manipulations [11, 12, 14]. However, such approaches were increasingly subject to controversy and disagreement. In his seminal paper, Huston [15] 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 biodiversity-mediated effects on ecosystem function from the many other effects environmental change can have on function (see '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 [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 to understand how the data produced using random and/or direct manipulations of

103 biodiversity can be used to meet two of ecology's current challenges: (1) to support

104 quantitative prediction of the ecological effects of anthropogenic activities [7]; and (2) to

105 unravel the mechanisms linking community structure (relative abundances) and composition

106 to ecosystem function [19, 20]. In the present contribution, we submit that re-introducing

107 non-random and indirect manipulations of biodiversity using environmental change drivers

108 [21-25] (1) is a prerequisite to predicting the functioning of ecosystems facing changes in

109 biodiversity that are caused by environmental change (section 2); and (2) facilitates

110 unravelling mechanistic insight into the connections between community structure and

111 composition and ecosystem function (section 3).

112

113 **The re-introduction of environmental change drivers is needed to predict ecosystem**

114 **functioning following changes in biodiversity**

115 In many ecosystems, environmental change causes biodiversity declines or increases [26-29].

116 Experiments that directly and randomly manipulate biodiversity are unlikely to predict

117 function in these ecosystems (Fig. 1, shaded area). This is because biodiversity changes that

118 are non-random with respect to species' contributions to function will affect ecosystem

119 functioning more or less than do random biodiversity changes [9, 30]. In addition,

120 environmental change can alter the effect species have on ecosystem functions by altering (1)

121 per-capita contributions to function [31, 32], and (2) population density [33, 34]. Depending

122 on the type of environmental change, these alterations can be mostly positive (e.g. nutrient

123 enrichment [35]), mostly negative (e.g. drought [36] or pollution [37]), or negative for some

124 species and positive for others (e.g. warming [38-40]).

125

126 Trait-based frameworks are available to predict how non-random effects of environmental

127 change on per-capita contributions to function, population densities, and biodiversity

128 translate to changes in ecosystem function [9, 30]. A simple extension of this framework with

129 species interactions (Box 1) and using richness as a biodiversity indicator illustrates two

130 important points. First, environmental change can cause a variety of B-EF relationships (Fig.

131 1). The shape of this relationship critically depends on (1) whether the responses elicited by

132 the environmental change driver are positive or negative, and (2) the type of non-randomness

133 exerted by the environmental change driver [29, 41] (Box 1). Second, changes in function are

134 expected before any change in species richness is observed (Fig. 1A and D; levels 0-0.1), and

135 – more generally – the variability of ecosystem function within one level of species richness

136 is substantial (Box 1, Box 3, 'Outstanding questions'). The ensemble of B-EF relationships

137 constructed through direct and random biodiversity manipulation (Fig. 1, shaded area) does
138 not capture the variation in B-EF shapes arising from indirect and non-random biodiversity
139 manipulation, and can both over- (e.g. Fig. 1B) and underestimate variation of function
140 within one biodiversity level (e.g. Fig. 1C).

141

142 **The re-introduction of environmental change drivers can augment mechanistic insight**
143 Many descriptors of biodiversity (e.g. richness and evenness, and based on traits, taxonomy,
144 or genes), but also community structure and composition, total density (community size) and
145 per-capita contributions to function, can affect ecosystem functioning [33, 42-45]. A main
146 research theme in ecology is to understand their relative importance to functioning [7, 46,
147 47]. Using environmental change drivers to indirectly manipulate biodiversity, community
148 structure and composition, total density, and per-capita contributions to function facilitates
149 such studies. This is because different environmental change levels trigger effects on
150 different subsets of these variables (Fig. 1). For example, in Fig. 1A, environmental change
151 levels between 0.25 and 0.7 will all lead to the same species richness, but will alter total
152 density and per-capita contributions to function. In Fig. 1B, effects on richness are always
153 more important than effects on total density or per-capita contributions to function. In Fig.
154 1A and D, low levels of change only affect per-capita contributions to function and total
155 density. In general, the fact that different levels of environmental change cause different
156 effects offers greater control over the different mechanisms underlying change of function
157 than do direct manipulations of biodiversity. Controlling per-capita contributions to function
158 is by definition impossible through direct manipulations of biodiversity, since per-capita
159 contribution to function is no descriptor of biodiversity. However, even community
160 composition, structure, and richness will often be uncontrollable through direct
161 manipulations. For example, in the model presented in Fig. 1, persistence of species 0 or
162 dominance by any other species than species 9 is only possible in the continuous presence of
163 an appropriate environmental change driver, i.e. through indirect manipulations. Without this
164 presence, community structure will always converge to the one shown in Box 1, and richness
165 will be 9, even when all 10 species are added to the initial community. Many examples
166 illustrate community compositions and structures that only emerge in the presence of specific
167 environmental change drivers and do not occur in their absence. For example, drought in
168 streams reduces the relative density of large-bodied consumers, predators, and encrusting
169 green algae [36]. Nitrogen enrichment in grasslands increases the relative density of nitrogen
170 demanding grasses [35], while increased precipitation in grasslands increases the relative

171 density of nitrogen-fixing forbs [48]. Even though most of the available studies are based on

172 taxonomic diversity, case studies showing how environmental change drivers can cause loss

173 or gain of genetic diversity are rapidly accumulating [29, 49].

174 The relationship between biodiversity and functioning in multi-trophic communities (food-

175 webs) has been an important research theme in ecology since the 1990s [7, 50-52]. For

176 example, the biodiversity of one food-web compartment can drive functions performed by

177 other parts of the food-web [53], or both can be unrelated [54]. Using environmental change

178 drivers to indirectly and non-randomly manipulate food-webs facilitates studying such links.

179 This is because environmental change drivers often target specific food-web compartments so

180 that it becomes possible to experimentally alter biodiversity and related functions of specific

181 food-web compartments and measure corresponding changes in other compartments. For

182 example, resource enrichment can be used to increase functions performed by basal species

183 groups (e.g. bacterial decomposition, water purification, primary production), while

184 desiccation can be used to target functions performed by non-basal species [36]. In addition

185 to the well-known cases of resource addition or manipulation of climate variables, chemical

186 stressors comprise an exceptionally useful group of experimental agents that can be used for

187 both non-random manipulations as well as for manipulations that are random with respect to

188 the effects species have on function. This is illustrated by the many studies that have exposed

189 relatively complex food-webs composed of field organisms (typically primary producers and

190 invertebrate grazers and predators) to concentration series of chemical stressors during

191 several weeks to months (Fig. 2). For example, many pyrethroid insecticides will target

192 arthropod consumers and predators [55, 56], while photosystem-inhibiting herbicides will

193 target specific algal taxa [57, 58]. Certain biocides such as triphenyltin [59] and narcotic

194 chemicals [60] are examples of chemical stressors that exert effects that are random with

195 respect to the effects species have on function. Directly manipulating food-webs to

196 persistently exclude certain trophic levels or functional groups (e.g. small-bodied benthic

197 grazers, specific bacterial communities or, algal taxa) will be nearly impossible. Indirect non-

198 random manipulations might therefore be the only solution.

199

200 **Back to the future: methods to connect indirect and non-random manipulations with**

201 **classic B-EF research**

202 Most classic B-EF designs focus on the effect of random biodiversity changes on ecosystem

203 function through direct manipulations. To quantify the contribution of such effects to the

204   functioning of ecosystems following environmental change (Box 3, 'Outstanding questions')

205   [23] analysing available data is a useful starting point. The literature is replete with studies

206   exposing communities to environmental gradients. When a sufficient number of change

207   levels has been tested across a sufficiently broad gradient of change, the contributions of

208   biodiversity-mediated effects can be separated from the other effects of environmental

209   change on ecosystem function using available analytical techniques. One possible way to do

210   so is by applying multivariate statistical techniques, such as structural equation modelling

211   [61, 62] (Box 2). However, sophisticated structural equation models [21, 24] can also be used

212   to partition the effects on function that are not mediated by biodiversity into their

213   constituents. In addition, methods based on versions of the Price equation that do not require

214   monoculture data but only need species contributions to function before and after

215   environmental change can be used to separate the effects of species loss and gain that is

216   random and non-random with respect to the effects species have on function from all other

217   effects environmental change can have on function [42].

218

219   Post-hoc analyses are a useful first step to quantify biodiversity-mediated effects on function.

220   However, we recommend combining direct and indirect biodiversity manipulations as

221   separate treatments in a single experiment. In a first design, we recommend using a well-

222   known environmental change driver to non-randomly manipulate a community, while setting

223   up a second treatment where the same community is manipulated directly. Importantly, the

224   direct manipulation should be done in the absence of the environmental change driver but

225   aim to match the community resulting from the application of the environmental change

226   driver, as observed in the first treatment, and should therefore be non-random. For example,

227   in Fig. 1B, applying a level of change of 0.1 would constitute an indirect biodiversity

228   manipulation that excludes species 1. Higher levels would exclude species 2, 3, and so on.

229   Thus, the direct biodiversity manipulation treatments should represent the same gradient of

230   community compositions, by consecutively excluding species 1, 2, 3, and so on. Next, the B-

231   EF relationship resulting from the indirect manipulation (e.g. Fig. 1B, 'resulting B-EF' panel)

232   could be compared to the one resulting from direct species removal. If both were not

233   significantly different, this would suggest that the chosen type of environmental change

234   mainly acts upon ecosystem functioning through compositional effects. If B-EF relationships

235   do differ, follow-up studies could examine in more detail the potential mechanisms

236   explaining this difference, for example by inspecting the magnitude of effects on per-capita

237   contributions to function [25], or by considering effects on community structure. However,

238 we recognize that this design can be challenging because, as mentioned in section 3, certain
239 community compositions are impossible to reconstruct without the use of environmental
240 variables. This problem could be addressed by statistically testing if per-capita contributions
241 to function (functional contribution of a species, e.g. its total biovolume divided by its
242 population density) differ between the direct and indirect biodiversity treatment. If the
243 inferred values of per-capita contributions to function do not differ between both treatments,
244 this suggests that the selected type of environmental change impacts on ecosystem
245 functioning through other mechanisms than effects on per-capita contributions to function.

247 A second design consists of a factorial experiment where the presence or absence of a direct
248 biodiversity manipulation that aims to match the community structure resulting from the
249 indirect biodiversity manipulation is crossed with the presence and absence of an
250 environmental change driver [63]. If all the effects of the driver on ecosystem functioning are
251 mediated by biodiversity changes, then the combination of direct biodiversity manipulation
252 and the environmental change treatment should display the same level of ecosystem
253 functioning as both the direct manipulation alone and the environmental change treatment
254 alone. If this were not the case, then it would suggest non-biodiversity-mediated effects on
255 ecosystem functioning. Interestingly, the same design has been recently proposed by Vellend
256 [64], yet motivated by a different objective. Vellend proposed to use this design to test if a
257 community structure shaped by environmental change maximizes function under that same
258 type of environmental change, a prediction based on the analogy between community
259 ecology and population genetics.

261 **Challenges of re-introducing environmental change drivers in B-EF research**
262 Although we advocate re-introducing environmental change drivers in B-EF research, there
263 are at least two challenges that need to be addressed for successful application. First, in the
264 approach we advocate, we implicitly assume that environmental change does not affect per-
265 capita species interactions (the α in Box 1). In our model, the effects of species interactions
266 on a focal species are only altered through changes in the density of species with which it
267 interacts. This assumption has been shown to prevail in some systems [65], but not in others
268 [66, 67]. Arguably the best-known example of environmental effects on per-capita
269 interactions is the 'stress gradient hypothesis', where there is a shift from competitive (i.e.
270 negative) to facilitative (i.e. positive) interactions as the level of stress increases [66, 67].
271 Such effects can lead to a variety of effects of stress on community structure and composition

272 and ecosystem function, depending on the type of stress factor and species traits [68]. Suttle
273 et al. [48] found that sustained increased precipitation eventually caused negative interactions
274 among plant species that were not apparent before the treatment. In alfalfa communities,
275 Barton and Ives [69] found that reduced precipitation changed interactions between spotted
276 aphids and their ladybeetle predators through dietary shifts of the latter. These examples
277 make clear that species interactions prevailing in the pre-change system cannot always be
278 used to predict the chain of secondary and higher-order effects occurring after the change. In
279 such cases, knowledge about shifts of per-capita species interactions is needed to gain control
280 over community structure and composition in experiments (Box 3, 'Outstanding questions'),
281 and to correctly interpret the observed effects of environmental change on biodiversity and
282 ecosystem functioning.

283

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

295

296 **Opportunities for ecosystem assessment and management**
297 Novel tools for biological monitoring will substantially increase the amount of biodiversity
298 data [70, 71]. However, linking monitored biodiversity trends to ecosystem functions remains
299 a major difficulty for ecosystem assessment, as has been discussed in the framework of
300 several environmental regulations worldwide [72, 73]. Re-introducing environmental change
301 drivers in B-EF research could help ecosystem assessors by realistically translating observed
302 biodiversity trends to trends of ecosystem function for a suite of well-studied environmental
303 change drivers. Studies compiling and comparing different types of environmental change
304 [22, 74] will be instrumental to ask if knowledge about one type of environmental change can
305 be transposed to other types of environmental change (Box 3, 'Outstanding questions').

306   Following ecosystem assessments, predicted changes of ecosystem functions could be used to
307   inform management as well, for example by triggering mitigating measures if needed. In
308   addition, ecosystem managers could propose critical levels of biodiversity change that, when
309   exceeded, lead to unacceptable loss of ecosystem functioning. The connection of B-EF
310   research to applied science has often been debated [75]. Re-introducing the use of
311   environmental change drivers to B-EF research can reinforce this connection.

312

313   **Concluding remarks**

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

321

322   Re-introducing environmental change drivers into B-EF research can be realised by analysing
323   existing data of well-known environmental change drivers and through novel experimental
324   designs. Designs combining direct and indirect biodiversity manipulations constitute a
325   particularly useful research avenue as they allow to directly test how biodiversity,
326   environmental change, and ecosystem function relate. However, unexpected effects of
327   environmental change on per-capita species interactions and the variety of species' responses
328   to such change are two main challenges to the use of environmental change drivers in B-EF
329   research. Opportunities include an improved capacity to assist ecosystem assessment and
330   management, by translating monitored biodiversity trends to trends of ecosystem function,
331   which are rarely monitored. We conclude that re-introducing environmental change drivers in
332   B-EF research is a prerequisite for predicting shifts of ecosystem function in a changing
333   world, facilitates understanding the mechanisms causing these shifts, and strengthens the
334   connections between B-EF research and applied ecology.

335

374

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 [9]:

$$\frac{dN_i}{dt} \cdot \frac{1}{N_i} = \left[\mu_i(l) + \sum_1^{10} \alpha_{i,j} \cdot N_j\right] \qquad \text{(based on [50])}$$

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

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 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 contributions to function responds more strongly than density [76]. 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).

406

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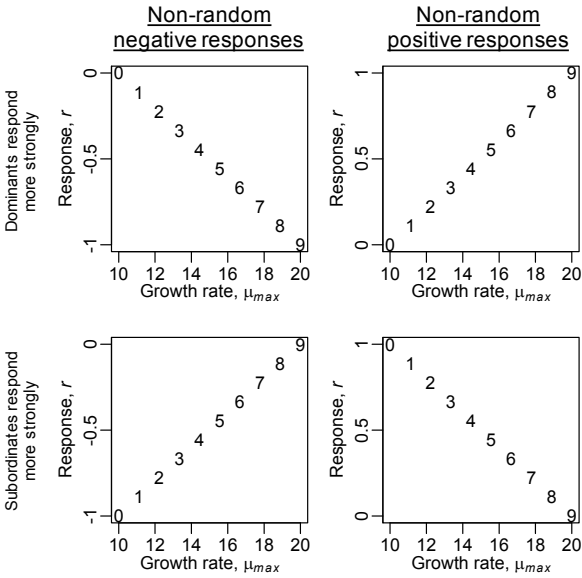
Figure I: Environmental change elicits negative (left panels) or positive responses (right panels) that are strongest for species with high (top row) or low (bottom row) growth rates, i.e. species that are dominant and subordinate in pre-change conditions, respectively (Fig. II). Numbers give species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

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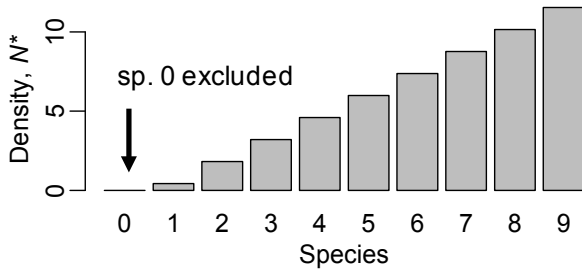
Figure II: Equilibrium densities in absence of environmental change.

425 **Box 2: Separating biodiversity-mediated effects on ecosystem functioning.** Structural

426 equation models (SEMs) can be used to compare biodiversity-mediated effects on ecosystem

427 functioning with the other effects environmental change can have on function. A SEM is

428 described as "the use of two or more structural [cause-effect] equations to model multivariate

429 relationships", which allows for an intuitive graphical representation of complex causal

430 networks [61, 62]. Most notably, a SEM cannot only be used to isolate biodiversity-mediated

431 effects on ecosystem functioning, but also to investigate the partial contributions of correlated

432 explanatory variables to test alternative hypotheses [61].

433 For illustrative purposes, we analysed data from a previously published microcosm study

434 evaluating the effects of chemical stress (a mixture of insecticides) on aquatic invertebrate

435 richness and decomposition in a ditch community [77, 78] with a simple structural equation

436 model. We also present previously published effects of nitrogen and carbon dioxide

437 enrichment on plant richness and biomass production in grasslands [23]. These analyses show

438 that richness-mediated effects on function are negative for environmental change drivers that

439 have negative effects on richness, and that these richness-mediated effects can be partly

440 compensated by other effects of environmental change. Many examples in the literature

441 support the conclusion that environmental change studies can be successfully analysed with

442 SEMs, including SEMs with more extended effect pathways [21, 24]. In more replicated

443 experimental setups [61], different biodiversity and community metrics could be tested in

444 parallel to extract the most relevant biodiversity metric causing alterations in ecosystem
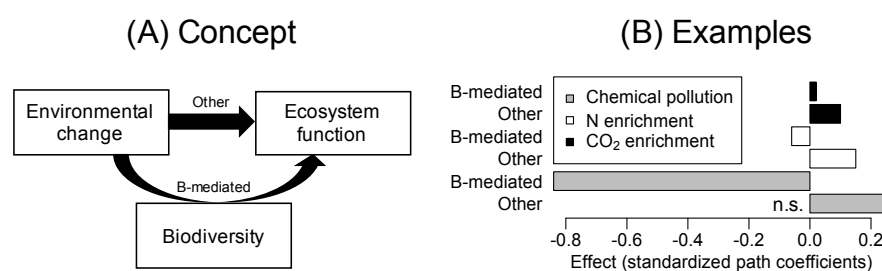
445 functioning.

446

447 Figure I. A: Environmental change drivers can affect functions by altering biodiversity or

448 through other mechanisms [23]. B: Structural equation models for three environmental

449 change drivers. All effects are significant (P < 0.05) except when indicated (n.s.). The

450 variance of diversity and function explained by the model (R^2) for the case of chemical stress

451 was 68% and 65%, respectively. Effects are standardized path coefficients [62]. Details on

452 the analysis for the other two drivers can be found in the original publication [23].

453

454 **Glossary**

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

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

461 **Indirect biodiversity manipulation**: If biodiversity is manipulated indirectly, one applies
462 different levels of an environmental change driver to create a biodiversity gradient. Indirect
463 biodiversity manipulations are by definition non-random with respect to species responses to
464 environmental change.

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

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

472 **Biodiversity-mediated effect of environmental change on ecosystem function:** Effects
473 occurring through changes in any aspect of biodiversity (mostly richness or evenness).

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

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Figure titles and legends

489 Figure 1: Indirect and non-random manipulations of biodiversity can result in a multitude of

490 biodiversity-ecosystem function relationships ('Resulting B-EF', simulated from the model in

491 Box 1; l is the level of environmental change and colours represent a scale from l=0 (yellow)

492 to l=1 (red), the value for l=0 is indicated with a 'x' for clarity). These relationships emerge

493 as a consequence of effects on richness, per-capita contributions to function (average effect

494 across all species), and total density (sum of all species). The strength of these effects

495 depends on l ('level-dependent effects') and the shape of the resulting B-EF critically

496 depends on whether dominants (A and C) or subordinates (B and D) respond more strongly to

497 environmental change, and on whether the elicited responses are negative (A and B) or

498 positive (C and D). The shaded area indicates the expected B-EF under direct and random

499 biodiversity manipulations.

500

501 Figure 2: Chemical stressors can be used to non-randomly and indirectly manipulate food-

502 webs. This is illustrated by empirically observed effects of continuous exposure of freshwater

503 ditch food-webs to chemical stressors in published micro- and mesocosm experiments. A:

504 Predators, herbivores and detritivores are separated into arthropod (Arth) and non-arthropod

505 (Non-arth) species; primary producers are separated into macrophytes (Macro) and algae;

506 Det. represents detrital material and its associated microflora. B: Results for exposure to

507 50µg•L linuron, a photosystem ('PS') inhibitor [57, 58]. C: Results for exposure to 35 µg•L

508 chlorpyrifos, a pyrethroid insecticide [55, 56]. Significant primary responses by the

509 corresponding chemical stressor are shown in red, secondary effects mediated by species

510 interactions are shown in green. White circles indicate that there was no effect. The relative

511 sizes of the coloured and dotted circles indicate whether the effect was positive (increase in

512 abundance - coloured circle larger than dotted circle) or negative (decrease of abundance -

513 coloured circle smaller than dotted circle).

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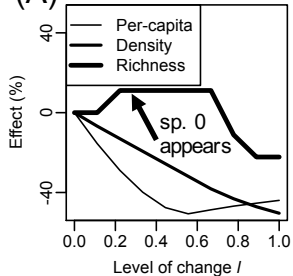703   Limnology and Oceanography 49 (4), 1202-1213.
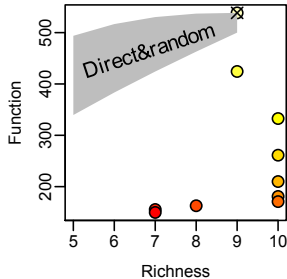704

Non-random negative responses

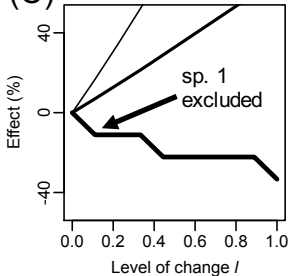**Non-random positive responses**

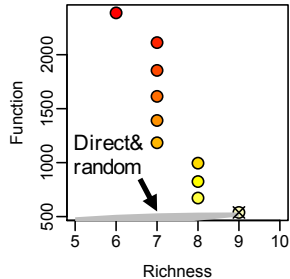Dominants respond more strongly

(A) **Level-dependent effects** — Effect (%) vs Level of change l; Per-capita, Density, Richness; "sp. 0 appears"

Resulting B-EF — Function vs Richness; "Direct&random"

(B) **Level-dependent effects** — "sp. 1 excluded"

Resulting B-EF — "Direct&random"

Subordinates respond more strongly

(C) **Level-dependent effects** — "sp. 1 excluded"

Resulting B-EF — "Direct&random"

(D) **Level-dependent effects** — "sp. 0 appears"

Resulting B-EF — "Direct&random"

(A) Key

Predators
- Arth
- Non-Arth

Detritivores
- Arth
- Non-Arth

Herbivores
- Arth
- Non-Arth

Primary producers
- Detr
- Macro
- Algae
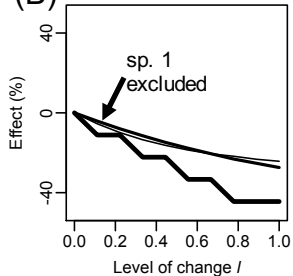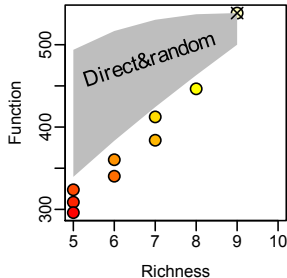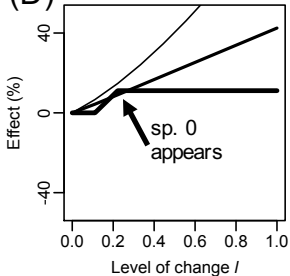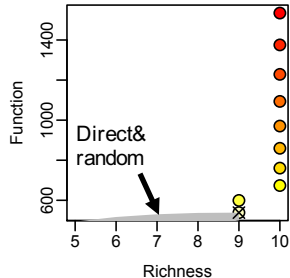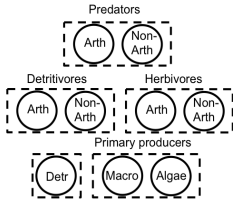
(B) PS inhibitor

(C) Pyrethroid