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Community- and ecosystem-level effects of multiple environmental change drivers

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1 **Title: Community- and ecosystem-level effects of multiple environmental change drivers:**
2 **beyond null model testing**

3 **Running head: From null models to theory-based predictions**

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26 **Abstract:**

27 Understanding the joint effect of multiple drivers of environmental change is a key scientific
28 challenge. The dominant approach today is to compare observed joint effects with predictions
29 from various types of null models. Drivers are said to combine synergistically
30 (antagonistically) when their observed joint effect is larger (smaller) than that predicted by the
31 null model. Here, I argue that this approach does not promote understanding of effects on
32 important community- and ecosystem-level variables such as biodiversity and ecosystem
33 function. I use ecological theory to show that different mechanisms can lead to the same
34 deviation from a null model's prediction. Inversely, I show that the same mechanism can lead
35 to different deviations from a null model's prediction. These examples illustrate that it is not
36 possible to make strong mechanistic inferences from null models. Next, I present an alternative
37 framework to study such effects. This framework makes a clear distinction between two
38 different kinds of drivers (resource ratio shifts and multiple stressors) and integrates both by
39 incorporating stressor effects into resource uptake theory. I show that this framework can
40 advance understanding because of three reasons. First, it forces formalisation of “multiple
41 stressors”, using factors that describe the number and kind of stressors, their selectivity and
42 dynamic behaviour, and the initial trait diversity and tolerance among species. Second, it
43 produces testable predictions on how these factors affect biodiversity and ecosystem function,
44 alone and in combination with resource ratio shifts. Third, it can fail in informative ways. That
45 is, its assumptions are clear, so that different kinds of deviations between predictions and
46 observed effects can guide new experiments and theory improvement. I conclude that this
47 framework will more effectively progress understanding of global change effects on
48 communities and ecosystems than does the current practice of null model testing.

49

50

51 **Null models to study the joint effects of multiple environmental change drivers**

52 Ecosystems today are invariably challenged by a multitude of environmental change drivers
53 (Brook *et al.*, 2008; Crain *et al.*, 2008; Halpern *et al.*, 2015; Halpern *et al.*, 2008; Schäfer *et*
54 *al.*, 2016). Understanding their joint effect is a pressing scientific and societal need (Côté *et*
55 *al.*, 2016; Dupont & Pörtner, 2013; Rudd, 2014). During past years, substantial effort has been
56 put in quantifying such joint effects, with **many** studies focusing at the physiological level
57 (Brennan & Collins, 2015; Gunderson *et al.*, 2016; Häder & Gao, 2015; Sokolova, 2013), while
58 **fewer** have addressed how the effects of individual drivers scale up to affect higher levels of
59 biological organisation such as communities and ecosystems (Garnier *et al.*, 2017).

60

61 The dominant approach to examine effects of multiple drivers is to use null models. These null
62 models predict joint effects based on the effects elicited by the individual drivers. When the
63 observed joint effects are smaller than or greater than those predictions, so-called ‘antagonistic’
64 or ‘synergistic’ effects are concluded, respectively (Crain *et al.*, 2008). A variety of null models
65 exists, each with their own assumptions and limitations (Piggott *et al.*, 2015), and
66 comprehensive overviews exist in the literature (Schäfer & Piggott, 2018). In general, these
67 null models differ in their underlying assumption on how drivers combine to affect the
68 biological variable of interest. The most frequently used null model is additive: it assumes that
69 the effects of the individual drivers add up, correcting for non-independence among drivers if
70 needed. The null model approach is applied to study effects at all levels of biological
71 organisation, going from the individual to the community-level, and are used in both primary
72 studies and meta-analyses (Crain *et al.*, 2008; Darling & Cote, 2008; Jackson *et al.*, 2016;
73 Tolkkinen *et al.*, 2015).

74

75

76 **Null models do not advance comprehension of community and ecosystem-level effects.**

77 The application of null model testing to community- and ecosystem-level effects of multiple
78 drivers has been criticized before (Kroeker *et al.*, 2017; Thompson *et al.*, 2018). Most of these
79 critiques revolve around the fact that drivers combine differently at different levels of
80 biological organisation (Schäfer & Piggott, 2018). For example, additivity of effects at the level
81 of populations does not automatically imply additivity at the community level (Kroeker *et al.*,
82 2017). To remediate this difficulty, the development of new null models has been recently
83 proposed (Thompson *et al.*, 2018). In this opinion, however, I propose an alternative solution:
84 to move away from testing null models on community and ecosystem data. My main argument
85 to do so is that current null model testing at the level of communities and ecosystems does not
86 advance comprehension. While null model testing has certainly facilitated meta-analyses, it
87 has until now not augmented general insight in the mechanisms linking environmental change,
88 multiple drivers, and biodiversity and ecosystem function (De Laender *et al.*, 2016; Griffen *et*
89 *al.*, 2016; Jackson *et al.*, 2016).

90

91 The premise of my argument is that null models can only advance comprehension when
92 deviations from their predictions advance mechanistic insight. That is, deviations from their
93 predictions should point towards implications other than “the null model is incorrect”. An
94 example of a null model advancing comprehension, taken from biodiversity science, is the null
95 model of biodiversity effects on ecosystem function (Baert *et al.*, 2017; Fox, 2005; Loreau &
96 Hector, 2001). This null model is based on a clear and explicit assumption: interactions within
97 species (i.e. among conspecifics) are equal to interactions among species (i.e. among
98 heterospecifics). Given this assumption, it is mathematically inevitable that ecosystem
99 functions stay constant with the number of species in the community. Exactly because of the
100 clarity of the underlying assumption, deviations from the null model’s predictions are

101 informative: they point towards interactions within and between species that are of unequal
102 strength.

103

104 Null models in multiple stressor and environmental change research make clear predictions
105 (e.g. effects add up when the model is additive). However, at the community- and ecosystem-
106 level, it is not clear on which hypothesis these predictions are based (Schäfer & Piggott, 2018).
107 Rather, the hypothesis seems to equal the prediction, which hampers inference and thus
108 scientific progress. Indeed, deviations from null model predictions only imply that the joint
109 effect is, for example, not additive. In what follows, I illustrate this point using classic theory
110 in community ecology and the case of species richness as an example of a community-level
111 variable. I do so by showing that there is no link between the sign and size of the deviations
112 from a null model and the community-level mechanisms causing these deviations. More
113 specifically, I show that the same mechanism can lead to different deviations (antagonism and
114 synergism), but also that the opposite holds true: two inherently different mechanisms can both
115 lead to the same deviation (e.g. antagonism).

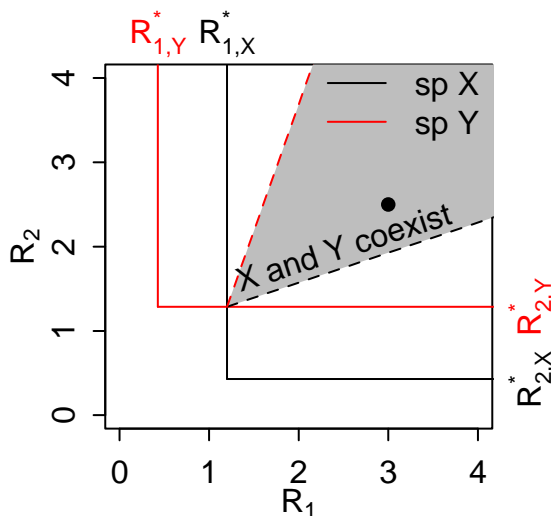
116

117 I consider two species X and Y competing for two essential nutrients R_1 and R_2 , according to
118 resource uptake theory (Chase & Leibold, 2003; Tilman, 1982), assuming Monod uptake and
119 optimal foraging (Tilman, 1982). In this model formulation, a species' competitive ability for
120 R_j is greater when its so-called R_j^* is lower:

121
$$R_j^* = (mK_j)/(r - m) \quad \text{(eq.1)}$$

122 where m, K_j, r represent a species' mortality rate, half-saturation constant for uptake of R_j , and
123 its maximum reproduction rate, respectively. The outcome of competition between X and Y
124 can be graphically determined by plotting the isoclines of both species in the resource plane
125 (solid lines in Fig. 1). An isocline is a line that connects the combinations of R_1 and R_2 at which

126 a species is at equilibrium, and its location is fully defined by the species' R_1^* and R_2^* . Thus, the
 127 two isoclines need to intersect for both species to have equilibrium densities at the same
 128 combination of resource levels. In the example of Fig. 1, there is a trade-off in the ability to
 129 take up nutrients: X is the best competitor for R_2 (R_2^* of X < R_2^* of Y) while Y is the best
 130 competitor for R_1 (R_1^* of Y < R_1^* of X). This trade-off allows the intersection of the two
 131 isoclines. However, this trade-off is a necessary but insufficient condition for coexistence: in
 132 addition, the resource supply point must lie within the coexistence region (in grey in Fig. 1),
 133 which is the region between the consumption vectors of both species (dashed lines in Fig. 1).
 134 Given the assumption of optimal foraging, the consumption vectors are proportional to R^* ; the
 135 per-capita consumption rate of a species on resource i is $\frac{R_i^*}{y_i}$, with y_i the amount of biomass
 136 produced per unit of resource i.



137
 138 Figure 1: A plane of resource levels, containing two isoclines: one for species X (black), and
 139 one for species Y (red). Parameters (m, K_1, K_2, r) are $(0.3, 2.8, 1, 1)$ for species X, and $(0.3, 1,$
 140 $3, 1)$ for species Y. Therefore, R_1^* for X, $R_{1,X}^*=1.20$, $R_{2,X}^*=0.43$, $R_{1,Y}^*=0.43$, and $R_{2,Y}^*=1.29$.
 141 The dashed lines are the two species' consumption vectors according to optimal foraging. The
 142 yield y is the same for both species (0.1). When the supply rate of both resources (dot) falls
 143 within the zone (in grey) delimited by the consumption vectors, coexistence is possible.

144 I consider a first pair of environmental change drivers that both slow down resource uptake:
145 they both increase the half-saturation constant K_2 of species X for R_2 , and therefore R_2^* of X
146 (eq.1), by a certain arbitrarily chosen factor (Fig. 2A-C). They do not affect any other
147 parameters. A variety of mechanisms may underpin such effects. For example, temperature
148 may alter nutrient-uptake proteins in plants (Giri *et al.*, 2017) and light-harvesting pigments in
149 phytoplankton (Chalifour *et al.*, 2014), while ocean acidification can impair ciliary activity in
150 mussels, decreasing feeding (Clements & Darrow, 2018). When present alone (Fig. 2A-B),
151 both drivers do not affect species richness: the new coexistence region still comprises the
152 resource supply point and so both species continue to coexist. However, when both drivers are
153 present (Fig. 2C), the joint effect on species X's competitive ability is too large to maintain
154 coexistence: the coexistence region does no longer contain the resource supply point. Hence,
155 one species will go extinct. Thus, overall, the joint effect of these two drivers on species
156 richness would be categorized as synergistic: the joint effect (a reduction from two to one
157 species) is greater than expected from the single drivers, which have no effect on species
158 richness when applied individually.

159

160 I now consider a second pair of drivers that work via the same mechanism as the first pair: both
161 drivers again slow down resource uptake (Fig. 2D-F). However, in contrast to the first pair of
162 drivers, both drivers now each target one specific species. This could be due to, for example,
163 both species having different physiologies or resource uptake strategies, giving them different
164 sensitivities to different stressors (Clements & Darrow, 2018; McMahon *et al.*, 2012; Mensens
165 *et al.*, 2017). The first driver increases K_2 of species X (Fig. 2D), while the second driver
166 increases K_1 of species Y (Fig. 2E). Again, they do not affect any other parameters. In both
167 cases, the isoclines do not intersect anymore, so one species is excluded. However, when both
168 drivers are present (Fig. 2F), the isoclines do intersect: the two drivers install a new trade-off

169 between the competitive abilities of species X and Y that saves them from extinction. Thus,
170 the joint effect is smaller than expected based on the individual drivers. In a null model
171 framework, this joint effect would be termed ‘antagonistic’. Taken together, the two pairs of
172 drivers (Fig. 2A-C and Fig. 2D-F) illustrate that the same mechanism (a reduction of resource
173 uptake) can lead to both synergistic and antagonistic effects.

174

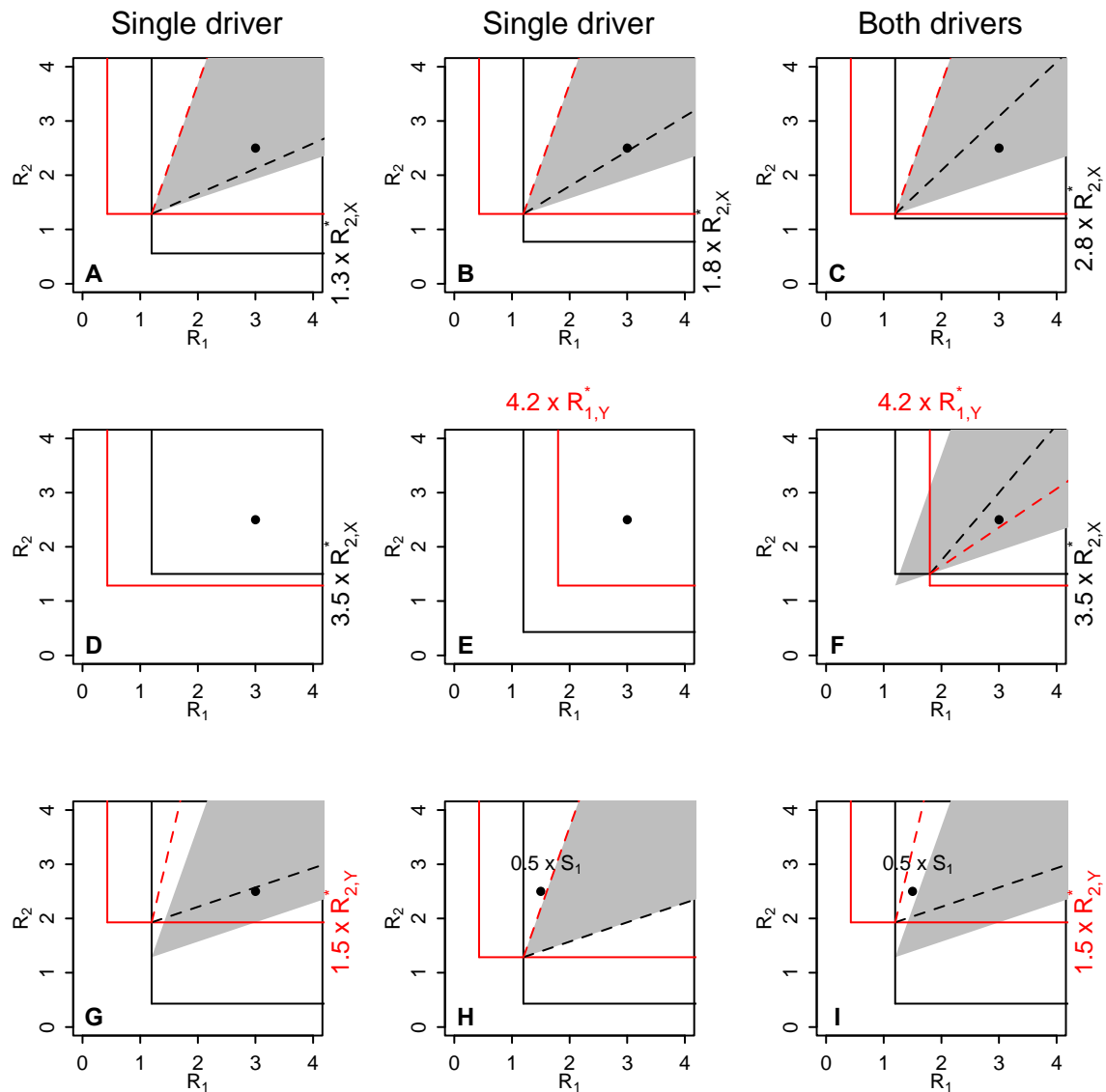
175 I now turn to a third pair of drivers (Fig. 2G-I) that act on different mechanisms than the two
176 first pairs given above. One driver (Fig. 2G) does slow down resource uptake (now it increases
177 K_2 of species Y) and leaves other parameters unchanged, as in the examples given before.
178 However, the other driver corresponds to a decrease in the availability of R_1 (Fig. 2H). The
179 first driver causes extinction of one species by shifting the coexistence region sufficiently up
180 such that it no longer includes the supply point (Fig. 2G). The second driver causes extinction
181 too, by moving the resource supply point outside of the coexistence region (Fig. 2H). When
182 combined, the joint effect of both drivers on richness is zero: both species are able to coexist
183 because the new resource supply point falls into the new coexistence region (Fig. 2I). Thus,
184 the null model approach would classify the joint effect as antagonistic. Taken together, the
185 second and third pair of drivers illustrate that two different mechanisms (Fig. 2F: reductions of
186 resource uptake vs. Fig. 2I: a reduction of resource uptake combined with a resource shift) can
187 both lead to the same deviation from a null model prediction, in this case an antagonistic effect.

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193 Figure 2: As Fig. 1, but now after exposure to one (panels A, B, D, E, G, H) or two
 194 environmental change drivers (columns C, F, I). Every row represents a different pair of
 195 drivers. The coexistence region in absence of change (in grey) is redrawn from Fig. 1 for
 196 comparison, unless when environmental change disrupts the intersection of isoclines and so
 197 removes the coexistence region (D, E). The numbers in black and red indicate the R^* values of
 198 species X and Y after modification by a stressor, respectively. The numbers inside panels H
 199 and I show the magnitude of resource supply shift.

200

201 One could argue that this example only shows that null models do not provide mechanistic
202 insight, while they can still provide practical guidelines on how to manage ecosystems. Null
203 models would allow grouping certain driver combinations that act, for example, synergistically.
204 This information could be used for prioritisation and environmental decision making.
205 However, the model illustration (Fig. 2) also shows that the deviations from null models will
206 critically depend on the level of environmental change. For example, a smaller reduction of the
207 resource uptake in Fig. 2G-I, or a larger reduction of R_1 , would have resulted in different
208 outcomes of how the joint effect is categorized. This illustrates the idea that information
209 obtained from null models cannot be extrapolated beyond the tested ranges of the
210 environmental change drivers (Schäfer & Piggott, 2018). This feature limits the capacity of
211 null models to assist ecosystem management.

212

213 **A new framework for community- and ecosystem-level effects of environmental changes**

214 As illustrated above, the current null model approach does not enhance understanding of
215 community- and ecosystem-level effects of multiple drivers. We therefore need to move away
216 from null model testing and start constructing a mechanistic framework (Griffen *et al.*, 2016;
217 Kroeker *et al.*, 2017), as has been recently initiated at the level of populations (Galic *et al.*,
218 2017; Hodgson *et al.*, 2017) and communities (Thompson *et al.*, 2018). Here, I propose such a
219 framework and show that deviations from its predictions can be informative, exactly because
220 the assumptions underlying the predictions are well-defined.

221

222 As a starting point, I propose to formalise “environmental change”. I postulate that two main
223 types of environmental change are resource supply shifts (Vitousek *et al.*, 1997) and the
224 appearance of multiple abiotic stressors (Steinberg, 2012). The effects of resource supply shifts
225 are a main ingredient of theoretical ecology, and so their effects on community and ecosystem

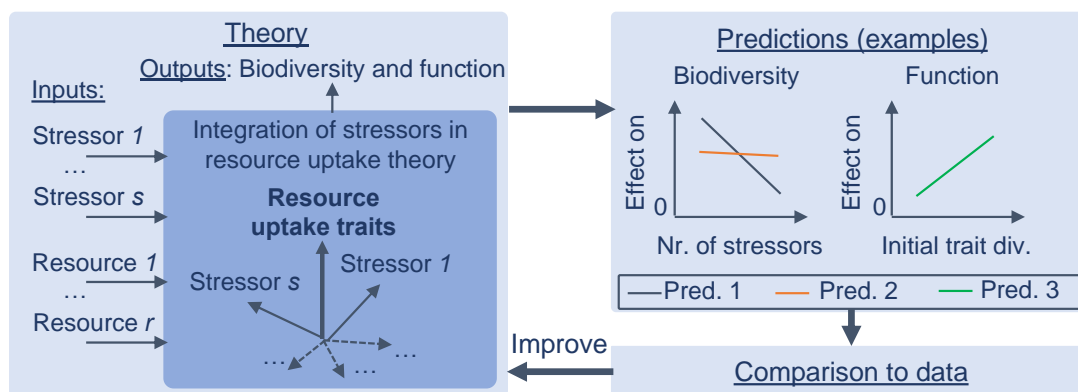
226 variables are well understood. Resource uptake theory (Armstrong & McGehee, 1976; Chase
227 & Leibold, 2003; Harpole *et al.*, 2016; Hillebrand *et al.*, 2014; Huisman & Weissing, 1994;
228 Tilman, 1982) predicts that an imbalance in resource supply, for example caused by changing
229 nutrient loads, leads to biodiversity loss and altered ecosystem function (Loreau, 1998; Loreau,
230 2010) (e.g. as in Fig. 2H). Whether or not resource ratio shifts result in extinctions depends on
231 the resource uptake traits of the species. Here, I define resource uptake traits (hereafter 'traits')
232 as done by Litchman and Klausmeier (2008), i.e. as parameters of a resource uptake model.
233 This definition is broadly applicable across a wide range of community types, including
234 plankton (e.g. Edwards *et al.*, 2013), terrestrial plants (e.g. HilleRisLambers *et al.*, 2012) and
235 animal consumers (Murdoch *et al.*, 2003), because resource uptake models are mathematically
236 similar across community types. These traits mostly include half-saturation constants,
237 conversion efficiencies from resource to biomass, and loss rates (Armstrong & McGehee,
238 1976; Harpole *et al.*, 2016; Hillebrand *et al.*, 2014; Huisman & Weissing, 1994; Tilman, 1982).
239 These traits determine the location of the isoclines in Fig. 1 (e.g. half-saturation constants for
240 nitrogen determine the R_N^*), and therefore predict the outcome of competition at a given
241 resource supply ratio. These traits thus determine how a species will respond to its biotic and
242 abiotic environment and determine its contribution to ecosystem function, which makes them
243 both response and effect traits (Violle *et al.*, 2007).

244

245 Inspired by the early work of Tilman *et al.* (1981), I postulate that integrating multiple stressors
246 into resource uptake theory makes for a comprehensive framework to study community- and
247 ecosystem-level effects of multiple drivers, including stressors and resource shifts.
248 Specifically, I propose to realise this integration by making traits multivariate functions of
249 multiple stressors (Fig. 3). If we know the effects of multiple stressors on such traits we can
250 make educated guesses of how these effects translate to changes of variables at the level of

251 communities (e.g. biodiversity) and ecosystems (e.g. function). Note that the framework allows
 252 stressors to affect multiple traits, contrary to the examples provided in Fig. 2. In addition, we
 253 can readily include the additional influence of resource ratio shifts, since these are by definition
 254 covered by resource uptake theory. In this paper, I illustrate the framework for the case of
 255 competitive communities. However, resource uptake theory is general, and can be extended to
 256 food-webs (Chesson & Kuang, 2008; Murdoch *et al.*, 2003). Importantly, it can also be used
 257 to study community assembly (Koffel *et al.*, 2018; Seabloom *et al.*, 2003) and meta-community
 258 dynamics (Haegeman & Loreau, 2015; Tilman, 1994), allowing the inclusion of invasive
 259 species and habitat fragmentation as environmental change drivers not included in the present
 260 paper.

261



262

263 Figure 3: A proposed framework to study effects of multiple environmental changes on
 264 communities and ecosystems. Integrating multiple stressors into resource uptake theory yields
 265 predictions (pred.) regarding, for example, the influence of the number of stressors and the
 266 initial trait diversity of the exposed community on biodiversity and ecosystem function.
 267 Predictions 1-3 are detailed in the text. Comparing these predictions to experimental data can
 268 expose invalid assumptions underlying the theory, and therefore advances science.

269

270

271 **How the new framework advances comprehension**

272 The proposed framework advances comprehension in three ways: (1) by formalising exposure
273 to multiple stressors using a set of key factors; (2) by producing a multitude of testable
274 predictions on how these factors, alone and in combination with resource ratio shifts, affect
275 communities and ecosystems; and (3) by quantifying and interpreting deviations between these
276 predictions and observed effects.

277

278 I identify five factors that can describe the exposure to a given stressor combination in a formal
279 way. This formalisation facilitates mechanistic progress because these factors are key
280 determinants of community- and ecosystem-level variables such as biodiversity and function.

281 A first and second factor are evidently the number of stressors and stressor response intensity.

282 In line with Steudel *et al.* (2012), I define stressor response intensity (*SRI*) as the community
283 average (i.e. across all species) of the absolute effect of a particular stressor combination on
284 population growth (e.g. biomass or number of individuals) in monoculture:

285
$$SRI = E[|M - M'|/M]$$

286 where E, M, M' represent the expected value operator, monoculture growth in absence of the
287 stressor cocktail and in presence of that cocktail, respectively. Note that *SRI* could also be

288 defined at the level of the traits, representing the community-average effect on traits, and could

289 include information on the sign of the effect in monoculture (i.e. growth stimulation or

290 depression). *SRI* depends on the tolerance of the exposed species and the value of the stressors

291 and is therefore often referred to as ‘effect’ (e.g. Liess *et al.*, 2016; Schäfer & Piggott, 2018).

292 *SRI* and the number of stressors are typically not considered separately in experimental studies

293 (Brennan & Collins, 2015). However, scientific progress demands understanding the

294 contribution of both factors to the net effect. For example, in Fig. 2C, the factor causing

295 extinction is *SRI*, rather than the number of stressors. Indeed, exposing the community to only

296 one of the stressors, but at a higher *SRI*, could have sufficed to cause an extinction. A third
297 factor is selectivity: the degree to which stressors affect all species or only a subset (De Laender
298 *et al.*, 2016). For selective stressors, also co-tolerance plays a role: species can be (in)tolerant
299 to multiple stressors at a time or not (Vinebrooke *et al.*, 2004). For example, in Fig. 2A-C, there
300 is positive co-tolerance, while in Fig. 2D-F, there is negative co-tolerance, with radically
301 different effects on species richness. This formalises the idea that selectivity is important only
302 when it implies greater stress to species with particular traits (Diaz *et al.*, 2013; Newbold *et al.*,
303 2015; Suding *et al.*, 2008). Selective stressors can therefore cause different effects on
304 biodiversity and function than unselective stressors (Mensens *et al.*, 2017; Selmants *et al.*,
305 2012; Spaak *et al.*, 2017). A fourth factor is initial trait diversity among species, which is
306 expected to determine resistance to stressors. Initial trait diversity implying larger niche
307 differences and smaller fitness differences will be better buffered (i.e. more resistant) to
308 stressor effects (Chesson, 2000). A fifth factor is the dynamic behaviour of stressors. Indeed,
309 stressors often fluctuate through time (Gunderson *et al.*, 2016), which can cause different
310 effects on coexistence (Chesson, 1994), and thus on biodiversity and function, than when
311 stressors remain constant through time.

312

313 Defining the five factors allows representing stressor combinations in a standardized way.
314 However, more importantly, we can make general predictions on how these factors matter for
315 the resulting community- and ecosystem-level effects (Fig. 3), and on how these factors
316 combine with resource ratio shifts. These predictions can offer scientists, working on a variety
317 of communities, theory-based and testable predictions that extend beyond the question if
318 effects are, for example, additive. More specifically, for various combinations of the number
319 of stressors, *SRI*, selectivity and co-tolerance, initial trait diversity, and temporal stressor
320 dynamics (constant, or various kinds of fluctuations, as in Jiang & Morin, 2004; Jiang & Morin,

321 2007), various aspects of biodiversity but also two types of ecosystem function (biomass
322 production and resource uptake) can be predicted. Here, as an example, I provide five such
323 predictions, of which three are illustrated in Fig. 3. The exhaustive analysis of how the five
324 factors mentioned above together affect biodiversity and function is not an objective of the
325 present opinion paper. Future theoretical contributions can address this question in full-
326 factorial setups. Rather, I want to illustrate the kind of predictions the framework could
327 produce. Afterwards, I discuss how these could be experimentally tested.

328

329 Prediction 1 postulates that, for selective stressors exhibiting negative co-tolerance (each
330 stressor only affects one species), the effect on species richness decreases with the number of
331 stressors. This is because, with an increasing number of stressors, but a constant *SRI*, an
332 increasing number of species will be affected but to a smaller extent. When *SRI* is low, this
333 will not affect the trade-offs that maintain composition and sustain function. When *SRI* is high,
334 this can lead to new trade-offs being installed (e.g. Fig. 2F). Note that, for both low and high
335 *SRI*, effects on biomass production can occur, leading to stressor effects on function in absence
336 of effects on richness (Spaak *et al.*, 2017). Prediction 2 postulates that lower stressor selectivity
337 results in smaller effects of the number of stressors on biodiversity and function. For example,
338 when stressors are completely unselective, every stressor should affect every species to exactly
339 the same extent. The number of stressors causing this effect is irrelevant. In the opposite case,
340 when stressors are very selective, i.e. every stressor affects a different species, the number of
341 affected species equals the number of stressors. A higher number of stressors thus means that
342 more species are affected, but to a lesser extent (again, since *SRI* needs to stay constant).
343 Prediction 3 postulates that the effects of selective stressors on function increase with initial
344 trait diversity. For example, when initial trait diversity is small (all species have very similar
345 trait values), small levels of selective stress can suffice to disrupt coexistence, leading to

346 diversity loss. However, since tolerant and sensitive species have very similar trait values,
347 tolerant species will rapidly compensate for the lost biomass of the sensitive species and
348 changes of function will be minor. When initial trait diversity is high, selective stress will be
349 less likely to cause exclusion but effects on function can be more substantial because of a loss
350 of functional complementarity. Prediction 4 postulates that fluctuations of stressors matter less
351 when the number of stressors is low. This is because, when resource supply does not fluctuate,
352 affecting few types (a consequence of the current example of high stressor selectivity) is less
353 likely to cause large changes in resource levels. This reduces the covariation between
354 environmental and competition effects on species' growth. Coexistence theory learns that this
355 makes fluctuation-dependent coexistence mechanisms less important (Chesson, 1994). Finally,
356 Fig. 2I illustrates prediction 5: stressors that reduce resource uptake can make community
357 composition less resistant to resource ratio shifts. Indeed, the two stressors reduced the
358 coexistence area, meaning that smaller shifts of resource ratio are needed to disrupt coexistence
359 and cause extinction.

360

361 I propose testing predictions like those listed above using two approaches. A first approach
362 could focus on 'high-level' predictions that transcend the specificities of model systems. Such
363 high-level predictions exist in other research fields. Examples include the increase of
364 ecosystem function with the number of functionally different species (Cardinale *et al.*, 2011),
365 the effects of niche dimensionality on species diversity (Harpole *et al.*, 2016), and the effect of
366 dispersal on regional biodiversity (Mouquet & Loreau, 2003). The proposed framework could
367 be exploited to identify predictions about the effects of the number of stressors, *SRI*, and
368 selectivity that are robust to other parameter settings. Monoculture experiments would then
369 suffice to quantify *SRI* and selectivity for a given community composition exposed to a given
370 stressor combination: resource uptake traits need not be measured. Thus, by selecting the right

371 combination of species and stressors, one can experimentally test high-level predictions on
372 how these factors, alone and combined with resource ratio shifts, affect biodiversity and
373 function.

374

375 A second approach is far more labour intensive and requires growing species in monoculture,
376 at various resource supply and stressor levels, to infer their traits and how these change with
377 stress. These data can then predict the outcome of competition at various combinations of
378 stressors and resource ratio shifts. Comparing these predictions to the actual outcome of
379 competition experiments is the strongest possible test of the theory. This approach is
380 conceptually similar to the work by Tilman *et al.* (1981) for the case of a single stressor,
381 temperature. However, the amount of work needed to apply this approach to multiple stressors
382 restricts this approach to microbial systems tested using high-throughput protocols (Altermatt
383 *et al.*, 2015), and makes it inapplicable to species with longer life cycles. Still, this approach
384 can lead to considerable progress in two ways. First, it would yield insight into which facets of
385 global change most disturb trade-offs that sustain biodiversity and functions in microbial
386 systems (Litchman *et al.*, 2015). Second, it would add environmental stress as a new dimension
387 to the classic topic of resource enrichment and niche dimensionality (Borer *et al.*, 2014;
388 Cardinale *et al.*, 2009; Harpole *et al.*, 2016; Hillebrand *et al.*, 2014).

389

390 One useful ingredient of the existing null model approach is the fact that it makes clear
391 predictions. Assessing the capacity and limitations of predictive capacity is indeed a central
392 goal in ecology and environmental science (Houlahan *et al.*, 2017; Petchey *et al.*, 2015).
393 However, the new framework I propose here allows studying not only predictive capacity but
394 also what drives predictive capacity, again because the assumptions are clear and are different
395 from the predictions. Thus, observations deviating from theoretical predictions (e.g.

396 predictions 1-5 listed above) point at invalid assumptions and thus expose areas of theory
397 improvement, advancing science. For example, the theoretical approach I propose assumes that
398 the interaction type does not change with *SRI*: resource competition is always the only
399 interaction type. The only way stressors can change community dynamics is by changing
400 resource uptake traits, and thus potentially competitive outcome. Regardless of the *SRI*, species
401 always interact indirectly by relying on the same resources; they never interact directly. Thus,
402 when species interaction types change profoundly with *SRI* we can expect theoretical
403 predictions to become increasingly erroneous (Barton & Ives, 2014; Mulder *et al.*, 2001; Suttle
404 *et al.*, 2007). More specifically, the stress gradient hypothesis postulates that competitive (i.e.
405 negative) interactions would switch to facilitative (i.e. positive) interactions (Olsen *et al.*, 2016)
406 as environmental change intensifies (i.e. the environment gets ‘harsher’, or *SRI* increases) (He
407 & Bertness, 2014; Hines *et al.*, 2015; Maestre *et al.*, 2009; Mulder *et al.*, 2001). Thus, in
408 community types where predictive capacity drops with *SRI*, more detailed studies could be set
409 up to examine interaction types along stressor gradients. In an experimental study,
410 Vanellander *et al.* (2009) found that the marine diatom *Cylindrotheca closterium* grew better
411 in medium containing substances leaked by other diatom species than in fresh medium. In a
412 modelling study, Baert *et al.* (2016) inferred from experimental data that such facilitative
413 interactions could be the exception rather than the rule in a similar community type evaluated
414 along a pesticide gradient.

415

416 Another example of how the proposed theory could deviate from observed joint effects is
417 through the influence of time. Again, the theory is very clear on how time is considered: it
418 assumes traits to change instantly with the stressor level (Fig. 3). Community dynamics are
419 therefore purely driven by external fluctuations in *SRI*, by the rate at which ecological
420 interactions propagate these fluctuations to population growth, and by consumer-resource

421 dynamics internal to the system (Chesson, 1994; Huisman & Weissing, 1999). Thus, one can
422 expect a reduced predictive capacity when long-term effects on traits occur, e.g. due to
423 evolution or slow transgenerational plasticity (Doebeli & Ispolatov, 2014; Litchman *et al.*,
424 2015). This is because, in this case, the resulting long-term effects on biodiversity and function
425 will be unpredictable from short-term responses of traits to environmental change (Feckler *et*
426 *al.*, 2018; Turcotte & Levine, 2017). Microbial systems are well-suited to study such effects in
427 realistic time frames, as one can study adaptation of single strains to new environmental
428 conditions or altered fluctuation regimes, due to novel mutations or horizontal gene transfer
429 (Brennan & Collins, 2015; Collins *et al.*, 2014; Litchman *et al.*, 2015). For phytoplankton, such
430 events have been found to be more prevalent when the number of environmental drivers is
431 greater (Brennan *et al.*, 2017). Thus, when the predictive capacity of the proposed theory (Fig.
432 3) decreases with the number of generations and does so more when the number of drivers is
433 higher, this could stimulate studies on, for example, the adaptation of resource uptake traits.

434

435 Both examples given here of how the proposed theory could misjudge the effects of the number
436 and kind of drivers on communities and ecosystems align with the idea that science benefits
437 from ‘breaking models’ when these models have formal assumptions (Thiele & Grimm, 2015).
438 Indeed, this practice not only identifies follow-up studies on facilitation and trait adaptation
439 but will also lead to extensions of the theory. Resource uptake theory can be extended with
440 equations for exudate production and uptake (Van den Meersche *et al.*, 2004), and for long-
441 term trait change. As a starting point for long-term trait change, one could consider approaches
442 from quantitative genetics, allowing to make various assumptions on the direction and rate of
443 trait adaptation along gradients of environmental change (Barabás & D'Andrea, 2016; Chevin
444 *et al.*, 2010; Schreiber *et al.*, 2011).

445

446 **Conclusions**

447 In order to advance understanding of how multiple drivers of environmental change affect
448 communities and ecosystems, we need to move away from testing null models: they lack a
449 mechanistic basis and deviations from, or correspondence to, observations can therefore not
450 advance insight. Here, I propose to base predictions on ecological theory and interpret
451 deviations from observations as an essential step to meet the scientific and societal challenge
452 of understanding global change effects. The approach I advocate here can probably be
453 generalized to other organizational levels, because quantitative frameworks are available to
454 predict physiological effects of multiple stressors at the individual and population level,
455 including bio-energetic models (Sokolova, 2013) and dynamic energy budget models coupled
456 with individual-based models (Galic *et al.*, 2017; Goussen *et al.*, 2016).

457 At present, there is a tendency to label deviations from additivity as ‘ecological surprises’
458 (Brook *et al.*, 2008; Crain *et al.*, 2008; Darling & Cote, 2008; Thompson *et al.*, 2018), implying
459 they are not to be expected (‘surprising’) on the basis of ecological science. However,
460 synergistic and antagonistic effects can be expected from basic ecological science and are
461 therefore no ecological surprises (Fig. 2 and Halstead *et al.*, 2014). The proposed framework
462 provides better guidance as to which driver combinations provoke truly surprising effects, i.e.
463 effects that are not expected from one of ecology’s most established theories but triggered by
464 emergent processes such as stress-induced facilitation and trait adaptation.

465

466 **Figure captions**

467 Embedded in the text.

468

469 **Figures**

470 Embedded in the text.

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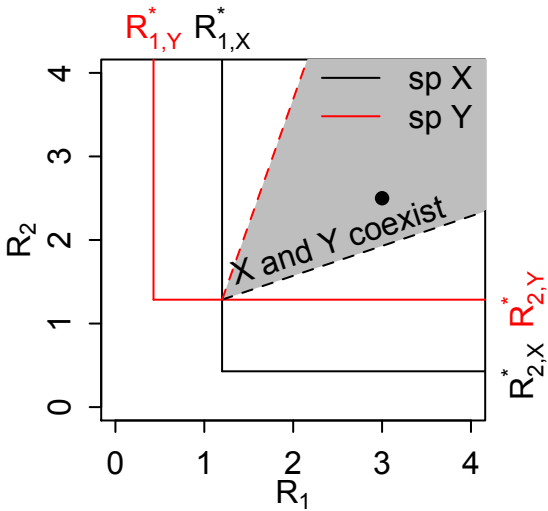
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Single driver

Single driver

Both drivers

