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1 **Species extinctions strengthen the relationship between biodiversity and resource use**
2 **efficiency**

3

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16

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19 **Abstract**

20 Evidence from terrestrial ecosystems indicates that biodiversity relates to ecosystem functions
21 (BEF), but this relationship varies in its strength, in part, as a function of habitat connectivity and
22 fragmentation. In primary producers, common proxies of ecosystem function include
23 productivity and resource use efficiency. In aquatic primary producers, macroecological studies
24 have observed BEF variance, where ecosystems with lower richness show stronger BEF
25 relationships. However, aquatic ecosystems are less affected by habitat fragmentation than
26 terrestrial systems and the mechanism underlying this BEF variance has been largely overlooked.
27 Here, we provide a mechanistic explanation of BEF variance using a trait-based, numerical model
28 parameterized for phytoplankton. Resource supply in our model fluctuates recurrently, similar
29 to many coastal systems. Our findings show that following an extinction event, the BEF
30 relationship can be driven by the species that are the most efficient resource users. Specifically,
31 in species-rich assemblages, increased redundancy of efficient resource users minimizes the risk
32 of losing function following an extinction event. On the other hand, in species-poor assemblages,
33 low redundancy of efficient resource users increases the risk of losing ecosystem function
34 following extinctions. Furthermore, we corroborate our findings with what has been observed
35 from large-scale field studies on phytoplankton.

36 **Introduction**

37 For decades, research has shown that biodiversity influences ecosystem functioning (Cardinale
38 et al. 2011, 2012, Hooper et al. 2012, Tilman et al. 2012), coined simply as the BEF relationship.
39 The mechanisms governing the strength of the BEF relationship are complex. For example,
40 heterogeneous landscapes comprised of well-connected patches, i.e., metacommunities
41 (Staddon et al. 2010; Bogoni et al. 2017), tend to show weaker relationships between biodiversity
42 and productivity. This occurs because dispersal processes such as immigration, pollination and
43 scattering of seeds from surrounding patches provides functional compensation in species-poor
44 patches (Chase and Ryberg 2004; Godbold et al. 2011). In addition, biodiversity effects on local
45 productivity are reduced when grazers are able to move through heterogeneous landscapes
46 (France and Duffy 2006). Conversely, when landscapes become fragmented the benefits of
47 connectivity are lost. Moreover, isolated, species-poor patches have lower probability to include
48 a very productive species (sampling effect), compared to species-rich patches. Consequently,
49 stronger BEF relationships are more likely to be observed in fragmented landscapes (Liu et al.
50 2018, and references therein). This habitat-connectivity/fragmentation conceptual model makes
51 for an excellent framework of understanding for BEF relationship variance in terrestrial
52 ecosystems. However, the lack of spatial structure often characterizing marine systems calls for
53 a different framework for understanding the BEF relationship therein.

54 Aquatic ecosystems tend to show the same variance in the strength of the observed BEF
55 relationship (Ptacnik et al. 2008; Olli et al. 2014) as in heterogeneous landscapes. However, in
56 aquatic systems, spatial heterogeneity and habitat fragmentation may not be as prominent

57 drivers as the aqueous medium can be easily homogenized with wind and/or tidal-driven mixing
58 and dissipation of turbulence. In the absence of metacommunity effects on localized biodiversity,
59 however, speciose aquatic systems are still observed. This is because biodiversity-sustaining
60 mechanisms that are independent of dispersal may play a more important role in aquatic
61 systems. These mechanisms include fluctuating resource supplies (Kilham and Kilham 1980;
62 Smayda 1980; Tilman 1982; Sommer 1989), existence of complementary life-history traits
63 between competitors leading to neutrality (Roelke and Eldridge 2008; Chust et al., 2013), lumpy-
64 coexistence (Scheffer and van Nes 2006; Sakavara et al. 2018) or intransitivity (Huisman and
65 Weissing 1999; Schippers 2001), host-pathogen cycles with host specificity (Bratbak et al. 1993,
66 Fuhrman 1999, Mayali et al. 2008), and predator-prey cycles with grazing preferences (Gaul and
67 Antia 2001, Katechakis et al. 2002, Winder et al. 2012), to name a few. For these reasons,
68 conceptual models independent of habitat-connectivity/fragmentation should be advanced to
69 provide frameworks of understanding for BEF relationship variance in aquatic ecosystems.

70 As mentioned above, fluctuating resource supplies can alter the outcome of phytoplankton
71 competition, affecting succession, biodiversity and biomass (Kilham and Kilham 1980; Smayda
72 1980; Tilman 1982; Sommer 1989). These fluctuations can also lead to recurrent limitation of
73 different nutrients (temporal switching as to which nutrient limits productivity most). This is
74 commonly observed in coastal ecosystems (e.g. Caraco 1988; Webb 1988; Moore et al 2013),
75 with evidence from Chesapeake Bay (Fisher et al 1992), Baltic lagoons (Pilkaitytė and Razinkovas
76 2007), Mediterranean gulfs (Tamvakis et al 2012), the Pearl River estuary in Hong Kong (Yin 2002;
77 Yin et al 2004), to name a few. This temporal switching in the limiting nutrient occurs because
78 coastal ecosystems have multiple nutrient sources whose influence varies over the course of a

79 year, where sources include terrestrial runoff (sometimes from multiple watersheds),
80 groundwater inflows and oceanic mixing.

81 Transitions from limitation of one nutrient to another can be abrupt or gradual, and this mode of
82 switching also influences phytoplankton succession, biodiversity and productivity (Roelke and
83 Spatharis 2015a,b, Sakavara et al. 2018). Abrupt transitions might occur in systems characterized
84 by episodic rainfall events and associated runoff (Tamvakis et al. 2012; Roelke et al. 2013; Roy et
85 al. 2013; Morse et al. 2014), or wind-driven vertical mixing events (Lares et al. 2009; Hu et al.
86 2011; Chen et al. 2013). On the other hand, gradual transitions might occur in systems
87 characterized by protracted wet seasons, by annually occurring periods of upwelling (Anabalón
88 et al. 2014; Zhou et al. 2014), or by in-stream reservoirs that buffer the effect of episodic runoff
89 (Magilligan and Nislow 2005; Poff et al. 2007). In addition, these larger temporal scale
90 fluctuations, occurring over an annual cycle, might also be punctuated by stochastic, short-lived
91 nutrient loading events (Spatharis et al. 2007). Since resource fluctuations affect species
92 competition, they are also likely to be an important mediator of the BEF relationship; yet we lack
93 a clear understanding of this mechanism.

94 Aquatic systems that experience resource fluctuations (e.g., coastal systems) could be more
95 unpredictable and thus more prone to stochastic species extinctions (e.g. Lotze et al. 2006).
96 When assessing the impact of extinctions on ecosystem functions, it is important to consider the
97 life-history traits of extinct species relative to the extant species (Isbell et al. 2011; Cardinal et al.
98 2012; Strong et al. 2015). In the case of high functional redundancy, it is predicted that extant
99 species will replace or compensate for extinct species (Brown et al. 2001; Hooper et al. 2005). On

100 the other hand, a species' extinction may lead to a more pronounced impact on ecosystem
101 function when increased trait diversity is not accompanied by high functional redundancy
102 (Mouillot et al. 2013).

103 For phytoplankton, an important trait that summarizes a species' competitive ability is its ability
104 to exploit resources, also known as its R^* (Tilman 1982). When R^* and cell quota are considered,
105 a species' resource use efficiency can be discerned. To illustrate, when considering fluctuation of
106 two limiting resources, a two-dimensional resource trade-off space would be defined by those
107 species with the lowest R^* for each resource (Roelke and Spatharis 2015a, b). These species carry
108 the most important function in the assemblage. We hypothesize that the absence of these
109 species (e.g., following an extinction event) will affect ecosystem function the most when
110 functional redundancy is low. Low functional redundancy is anticipated when species richness is
111 low. Conversely, we anticipate high functional redundancy when species richness is high, and
112 hypothesize that ecosystem function will be less affected by extinctions. If our hypotheses are
113 true, then we expect stronger BEF relationships (i.e. a more positive slope in statistically
114 significant relationships) when assemblages have experienced extinctions compared to those
115 assemblages which have not experienced extinctions.

116 In the current research, we explore the effects of resource supply fluctuations and species
117 extinctions on the steepness of the relationship between species richness and resource use
118 efficiency (RUE). We employ a mechanistic model depicting multiple species competing for two
119 limiting resources. To increase the realism of our research we allowed simulated phytoplankton
120 assemblages to self-organize under environmentally plausible resource fluctuation regimes. By

121 examining the traits of species that have been selected for under these regimes, we were able to
122 elucidate mechanisms underpinning relationships between species richness and RUE. This
123 approach further enabled a trait-based exploration of extinction effects under scenarios of
124 environmental stochasticity and fluctuation mode of the resource supply. Recurrent resource
125 supply fluctuations enabled the co-existence of species that could exploit the whole range of the
126 available resources. Extinction events focusing on species at the extremes of the resource trade-
127 off space, and possible ensuing extinction cascades, enabled the detection of their impact on the
128 richness-RUE relationship. To demonstrate the relevance of our findings to real world
129 phytoplankton assemblages, our results were compared with large-scale phytoplankton studies
130 reported in the literature (Ptacnik et al. 2008; Olli et al. 2014).

131 **Methods**

132 *Overview*

133 We employed an assemblage organization technique in our simulation experiments that involved
134 starting with species-rich pools, imposing environmental conditions for an extended period, then
135 considering only surviving species as members of assemblages (see Roelke and Eldridge 2008).
136 For the remainder of the manuscript, these assemblages are referred to as 'intact'. We recorded
137 characteristics of these intact assemblages such as richness, biomass, and resource use efficiency
138 (RUE), as well as the life-history traits of the surviving species. We then forced extinction of one
139 species within each of the intact assemblages, allowed the assemblages to re-organize (which
140 sometimes involved species extinction cascades), then recorded the assemblage characteristics

141 again. For the remainder of the manuscript, these re-organized assemblages are referred to as
142 'compromised'.

143 As the driver of environmental variability, we focused only on resource supply fluctuations. Six
144 experimental scenarios were explored (Figure 1b-g). For the first scenario, we considered a
145 fluctuation mode whereby the concentrations of two limiting resources in the supply, recurrently
146 and abruptly reversed half way through the annual cycle. In the second scenario, the two limiting
147 resources in the supply again recurrently fluctuated asynchronously over a period of a year, but
148 now in a gradual manner. To simulate stochastic events leading to smaller temporal scale
149 variability in nutrient inputs (e.g. short-period nutrient pulses) the abrupt and gradual nutrient
150 supply fluctuation scenarios were run with the addition of either 0-20% (low) or 0-80% (high)
151 noise intensities in the resource supply. Thus, the third and fourth environmental scenarios
152 comprised abrupt and gradual nutrient supply fluctuations with low noise, and the fifth and six
153 environmental scenarios comprised abrupt and gradual nutrient supply fluctuations with high
154 noise.

155 In all, we tested 12 scenarios, i.e., the six environmental scenarios described above where each
156 intact assemblage emerged through assemblage organization from a species rich pool, and
157 another six scenarios where a compromised assemblage emerged following an extinction event
158 from the intact assemblage. For each environmental scenario 300 assemblages were generated.
159 Thus, there were 1800 intact assemblages and 1800 compromised assemblages explored in this
160 research, totally 3600 assemblages.

161 *Mathematical model*

162 The model used is described in detail in Roelke and Spatharis (2015a, b). It is an adaptation of a
163 well-known mathematical model previously used for depicting population dynamics and
164 assemblage composition of primary producers, i.e., plants and algae (Leon and Tumpson 1975;
165 Tilman 1982; Grover 1997), where multiple growth-limiting resources were represented. The
166 model was structured to simulate a phytoplankton assemblage where new resources arrived with
167 inflow, and loss of cells and ambient nutrients occurred through hydraulic flushing.

168 For each coexisting phytoplankton species, population demographics were simulated using an
169 equation of the form:

170
$$\frac{dN_i}{dt} = \mu_i N_i - v N_i \quad , \quad i = 1 \dots 300 \quad (1)$$

171 where N_i is the population density (cells liter⁻¹) of species i , μ is the specific growth rate (d⁻¹) of
172 species i , and v is the hydraulic flushing (d⁻¹). When growth rate μ is equal to the flushing rate v
173 the assemblage is considered at steady-state.

174 For the two limiting resources, dynamics of the resource concentrations were simulated using an
175 equation of the form:

176
$$\frac{dR_j}{dt} = v \left(R_{source_j} - R_j \right) - \sum_{i=1}^n Q_{ji} \mu_i N_i \quad , \quad j = 1, 2 \quad \text{and} \quad i = 1 \dots 300 \quad (2)$$

177 where R_{source_j} is the varying concentration i.e. abrupt or gradual reversals in the supply of
178 resource j , R_j is the concentration of each growth-limiting resource j , Q_{ji} is the cellular content

179 of the resource j for each species i , n is the number of coexisting species at any given time step,
180 and other parameters were the same as previously described.

181 Specific growth rate for each species i was determined using the Monod equation and Liebig's
182 "Law of the Minimum" following the form:

$$183 \quad \mu_i = \mu_{max} \left(\min \left[\frac{R_j}{R_j + K_{ji}} \right] \right) \quad , \quad j = 1, 2 \quad \text{and} \quad i = 1 \dots 300 \quad (3)$$

184 where μ_{max} is the maximum specific growth rate for species i (d^{-1}), R_j is the concentration of each
185 growth-limiting resource j , and K_{ji} is the half-saturation coefficient of species i for limiting
186 resource j . A function 'min' was used to determine which resource was limiting growth at each
187 time step of the simulation.

188 It is worth noting here that although this Monod approach to representing plankton assemblages
189 (and plant communities) is widely used, Monod based models do not represent reality as well as
190 other models. Specifically, changes in resource concentrations do not "instantaneously" affect
191 phytoplankton growth rates. Instead, changes in resource concentrations influence nutrient
192 uptake rates (Dugdale 1967), which are in turn linked to reproductive rate through intracellular
193 resource pools, or cell quotas (Droop 1973, 1974, 1975, 1983). Computationally, however, it is
194 challenging to solve numerically simulated assemblages comprising several species and with
195 multiple limiting resources (Roelke et al. 1999, Roelke 2000, Eldridge and Roelke 2010, 2011).
196 Attempting to use a Dugdale/Droop type model comprised of 300 species, and performing 3,600
197 such simulations, each spanning 15 years (which is done in this research, see below), is beyond
198 the scope of this research. It is further noted here, however, that Monod-based models give near

199 equivalent results to cell-quota based models as systems asymptotically approach equilibrium
200 (Burmester 1979).

201 Differential equations were solved numerically using ordinary differential equation solving
202 routines that were part of a commercial software package (The Math Works, Inc.). The routines
203 were based on fourth-order Runge-Kutta procedures and used a variable time step that was
204 based on a local error tolerance set at 10^{-6} .

205 *Parameterization of initial species-rich pool*

206 Phytoplankton assemblages were generated using a numerical procedure that involved
207 modelling the population dynamics of a species-rich pool of 300 species under fluctuating
208 resource supply conditions. Parameterization of the initial species pool was based on known
209 relationships of species traits (see also Roelke and Spatharis 2015a, b). Specifically, the half-
210 saturation coefficients for the two resources presented a trade-off, preventing any single species
211 from being a superior competitor for both resources. Thus, a species that was a good competitor
212 for one resource would be a poor competitor for the other resource, and a species being an
213 intermediate competitor for one resource would also be an intermediate competitor for the
214 other resource (Tilman 1982; Vincent et al. 1996). This trade-off promoted multiple species co-
215 existence through relative non-linearity (Chesson 1994; Gravel et al. 2011). To achieve this,
216 parameter K_{1i} was selected randomly from a uniform distribution in the range 0.04–1 and then
217 parameter K_{2j} was calculated based on the applied trade-off. When in units of μM , the applied
218 range on K_{ji} represents what is typically observed for phytoplankton half-saturation coefficients
219 (Reynolds 2006; Grover et al. 1999). Further, the half-saturation coefficient K_{ji} was proportional

220 to a species cellular resource content Q_{ji} (Huisman et al. 2001). The value of Q_{ji} was set equal to
221 K_{ji} , using units of $10^{-6} \mu\text{M cell}^{-1}$, thus representing typical cellular resource content Q_{ji} measured
222 in phytoplankton (Grover et al. 1999; Reynolds 2006). More details on the species pool
223 parameterization are provided in Roelke and Spatharis (2015a, b).

224 To generate the initial species-rich pool, for each of the replicates for each scenario (see below),
225 we further defined a relationship between the 300 interacting species which competed for the 2
226 resources. To do this we used the parameter R_{ji}^* which is directly related to the ability of species
227 i to exploit resource j and is defined as

$$228 \quad R_{ji}^* = \frac{\nu K_{ji}}{\mu_{max} - \nu} \quad , j = 1, 2 \quad \text{and} \quad i = 1 \dots 300 \quad (4)$$

229 As the maximum growth rate μ_{max} and the flushing rate ν were the same for all species, R_{ji}^* was
230 directly proportional to K_{ji} . Since K_{ji} was defined as a species-specific constant, its knowledge
231 enabled the determination of unique, invariable R_{ji}^* values for each species i (Tilman 1982;
232 Sommer 1989). The relationship between the competitive ability of the 300 species for the two
233 resources was defined within a two-dimensional resource trade-off space by following a
234 downward-curved distribution (see representative assemblage in Figure 1a). This relationship
235 was established using experimental data on phosphorus-silicate and nitrate-silicate trade-offs
236 (Huisman and Weissing 2001). This procedure is detailed in Roelke and Spatharis (2015a, b).

237 Initial population densities for each species were the same for all simulations, i.e., $N_i = 0.1$ ($\times 10^6$
238 cells liter $^{-1}$). Initial resource concentrations depended on the initial concentrations in the
239 resource supply (see next section) and varied between 2 and 20 μM . Parameter constants

240 included total flushing and maximum specific growth rate, which were $v = 0.25 \text{ d}^{-1}$ and $\mu_{max} = 2$
241 d^{-1} respectively. All parameterizations were within the range of what is typically observed for
242 phytoplankton assemblages and pelagic environments (Grover et al. 1999; Reynolds 2006; Baker
243 et al. 2009; Roelke and Eldridge 2010).

244 The simulated period over which assemblages organized was 15 years. By this time, the modeled
245 assemblages had asymptotically approached a recurring succession sequence within a year.
246 Using only model results from the 15th year of the simulation, we summed the population
247 densities from eight time points (days 1, 91, 110, 183, 219, 274, 329, 365). When over this
248 simulated year, a population summed $<0.01 \times 10^6 \text{ cells liter}^{-1}$, the species was considered as
249 competitively excluded from the assemblage. This decision was based on real world limitations
250 using microscopy to enumerate plankton, where species not observed could be regarded as part
251 of a 'hidden flora', thus not accounted for in any studies. The surviving species after these 15
252 years were considered members of either the intact or compromised assemblages. In this way,
253 we consider our assemblages as "self-organized".

254 *Fluctuations in the resource supply*

255 Three hundred replicates were available for each of the six scenarios of annually fluctuating
256 resource supply (i.e., 300 intact assemblages for each scenario), where fluctuations of the two
257 resources were asynchronous. The asynchronous fluctuations ensured an alternating resource
258 limitation. Furthermore, resource fluctuations allowed multiple species co-existence through a
259 temporal storage effect (Chesson 1994; Gravel et al. 2011). The first scenario considered an
260 abrupt resource supply reversal, where nutrient concentrations suddenly switched every 182

261 days (Figure 1b). The second scenario considered a gradual change, where the first resource
262 progressively increased from day 1 to day 182, while the second resource progressively
263 decreased during this time period, and then progressively changed back to their initial values
264 (Figure 1c). The other four scenarios were meant to add more realism to the aforementioned
265 resource reversals by randomly adding stochasticity in the form of two different ranges of noise
266 to the resource supply concentrations: a lower range from 0-20% noise (Figure 1d, e) and a higher
267 range of 0-80% noise (Figure 1f, g). An annual noise pattern was created that was different for
268 each of the simulated 15 years for each of the 300 replicates for each simulation. To create this
269 noise pattern, a number was randomly generated from a uniform distribution in the range of -
270 0.2 to 0.2 (for the ± 0 -20% noise) or -0.8 to 0.8 (for the ± 0 -80% noise) and was multiplied with the
271 resource supply concentration. To further adjust the periodicity of the occurrence of the noise
272 on resource concentration, another random number was generated over the range 0 to 14,
273 corresponding to the period in days. In total, 1800 intact assemblages are reported on here. The
274 magnitude of 0-80% noise and the applied period range generated dynamic (and erratic) nutrient
275 concentrations in the resource supply similar to that observed in many rivers discharging into
276 estuaries and bays (see Roelke and Spatharis 2015a, b).

277 *Extinctions*

278 The effect of extinctions was then tested on each of the 1800 intact assemblages (Figure 1b-g).
279 We forced targeted extinctions of a species that was positioned at the edge of the resource trade-
280 off space (e.g. species 3 or 9 in Figure 1h) as it accumulated the highest biomass (Figure 2a) and
281 was thus expected to have an impact in the total biomass. These targeted extinctions allowed

282 the exploration of the importance of these species on the richness-RUE relationship. Species with
283 intermediate competitive abilities, which were placed in the middle of the resource trade-off
284 space (e.g. species 5, 4 and 10 in Figure 1h), accumulated low biomass (Figure 2c) and were thus
285 not expected to have any impact on ecosystem function (Hooper et al. 2005). Once the extinction
286 was induced, the assemblages re-organized for another 15 years, accounting for possible
287 extinction cascades (which occurred occasionally). When over the 15th simulated year, a
288 population summed $<0.01 \times 10^6$ cells liter⁻¹, the species was considered as competitively excluded
289 from the assemblage. In this way, 1800 compromised assemblages (one for each intact
290 assemblage) emerged.

291 *Assemblage characteristics*

292 The measured assemblage characteristics included biomass, species richness, breadth of
293 resource gradient used, and resource use efficiency RUE. For each characteristic, the measure
294 corresponded to its average during the last simulated year. The resource gradient is calculated
295 as the R_j^* range (i.e. $R_{j^*max} - R_{j^*min}$). RUE has been traditionally calculated as the ratio of
296 productivity per unit of resource (Sheriff et al. 1995). Studies on field phytoplankton have
297 reported RUE as the ratio of biomass to the limiting nutrient – usually total phosphorus (Ptacnik
298 et al. 2008). In the present study, since the limiting nutrient alternated, we used the ratio of time
299 averaged biomass to the averaged minimum R^* in an assemblage, which was directly
300 proportional to the time-averaged concentration of the limiting nutrient.

301 *Statistics*

302 The regression line between species richness and RUE followed the equation

303
$$\ln(\text{RUE}) = \alpha \ln(S_k) + b \quad , \quad k = 1 \dots 12 \quad (5)$$

304 Where, α is the slope of the regression line, S_k is species richness in the k^{th} scenario and b is the
305 intercept, as in Ptacnick et al (2008). The model was applied within each one of the six resource
306 supply scenarios (Figure 1b-g) for both intact and compromised assemblages. In order to quantify
307 the slope of the lines we additionally report the coefficients and the p-values associated with t-
308 tests that indicate significant departures of the slope coefficient from zero.

309 **Results**

310 Considering all scenarios tested, the assemblage organization in the abrupt resource supply
311 reversal scenarios and the 0-80% noise scenarios had the lowest number of species and the
312 highest RUE (Figure 2). Species were distributed along the entire resource trade-off space,
313 irrespective of noise levels and mode of resource supply reversal (e.g. Figure 1h). Towards the
314 extremes of the resource trade-off space, surviving species were either solitary (e.g. species 3 in
315 Figure 1h) or formed a cluster comprised of species with similar life history traits (see species 7,
316 9 and 13 in Figure 1h). These competitively similar species, although co-existing, presented a
317 difference in biomass ranging over four orders of magnitude (see the same species 7, 9 and 13 in
318 Figure 3a, b). Species, whose life-history traits placed them in the middle of the resource trade-
319 off space, generally had a lower biomass compared to species placed in the extremes. Overall, in
320 a yearly succession, species with lower R^* s for one resource (i.e. higher competitive ability for

321 the resource) presented population maxima during periods of limitation for this resource (e.g.,
322 last annual cycle of the 15-year period, Figure 3).

323 The effect of extinction on biomass and resource use was variable because it depended on
324 whether the extinct species was part of a cluster of species with redundant traits or not. When
325 the extinct species was part of a cluster (e.g. species 9 Figure 1h), other species compensated for
326 its loss thus the assemblage biomass remained unchanged (e.g., last annual cycle of the 15-year
327 period after extinction, Figure 4b). The resource breadth used was also not affected, as shown in
328 Figure 5a-c, where compromised assemblages (grey points) are positioned with intact
329 assemblages (black points). When the extinct species was not part of a cluster (e.g. species 3
330 Figure 1h), other species did not compensate for its loss resulting in a decrease in the biomass
331 produced (e.g., last annual cycle of the 15-year re-organization period, Figure 4a). The resource
332 breadth used was also diminished, as shown in Figure 5a-c, where compromised assemblages
333 (grey points) are positioned 'to the left' of intact assemblages (black points), indicating that the
334 amount of resource in the extreme of the resource space remained unutilized. When resource
335 supply reversal was gradual, a species extinction lead to a more pronounced reduction of the
336 breadth of resource gradient used when stochasticity (i.e. noise) was considered in the resource
337 supply (Figure 6a-c).

338 When extinction concerned a species that was a member of a cluster of species of similar R^* , the
339 extinction had no effect on the RUE (gray points at the same level with black points in Figure 5d-
340 f and 6d-f). When extinction concerned a solitary species (i.e. not member of a cluster of species
341 with similar R^*) then the extinction had a negative effect on the RUE of the assemblage

342 irrespective of the mode of the resource supply reversal or supply noise level (gray points lower
343 than black points in Figure 5d-f and 6d-f). This negative effect on the assemblage RUE lead to a
344 positive richness-RUE relationship observed across all scenarios including compromised
345 assemblages. On the other hand, in the intact assemblages, before any extinction event, the
346 richness-RUE relationship was either weak (positive or negative) or non-existing (table 1, Figure
347 5d-f and 6d-f). Noise in the resource supply was not a prerequisite for a positive richness-RUE
348 relationship. The slope of the richness-RUE relationship was the steepest in the scenario where
349 there was: 1) a 0-80% noise level in the resource supply; 2) there were abrupt transitions in the
350 resource supply reversal; and 3) an extinction occurred (Figure 5f, Table 1).

351 **Discussion**

352 Our findings suggest that in phytoplankton, a diversity-ecosystem functioning relationship under
353 fluctuating resource supply is driven by species positioned at the edge of the resource trade-off
354 space. The slope of the relationship was steeper (stronger BEF) when such species became extinct
355 in assemblages that experienced an abrupt resource supply reversal and high stochasticity. These
356 conditions led to the least diverse assemblages. The occurrence of all three of the above
357 conditions could be expected in dynamic systems, such as coastal ecosystems. These systems
358 could receive nutrient pulses that follow a random pattern based on rainfall and terrestrial runoff
359 that could import pollutants (e.g. pesticides) and lead to species extinctions (Relyea 2005).

360 In the present approach, we consider the life history traits of the phytoplankton species after
361 assemblage organization. These traits are representative of each species' competitive ability for
362 resource use (Tilman 1982). Resource fluctuations cause a continuous shifting of the ratio of the

363 two resources, thus creating multiple niches and enabling the coexistence of species along the
364 resource trade-off space (Tilman 1982; Sommer 1989; Sakavara et al. 2018). Therefore, both the
365 temporal storage effect (temporal variability on resources) and relative non-linearity (trade-off
366 between species competitive abilities) promoted species co-existence during an annual cycle in
367 our system (Chesson 1994; Gravel et al. 2011).

368 The closer the surviving species are spaced within the defined resource trade-off space, the more
369 similar they are in their competitive abilities. Clusters formed by competitively similar species
370 increase the functional redundancy in the assemblage (Scheffer and van Nes 2006, Sakavara et
371 al. 2018). These clusters are more likely to form with increased species richness. Species that are
372 superior competitors for a given resource are placed in the extremes of the resource trade-off
373 space (Roelke and Spatharis 2015a, b). The lower the needs of these species for a resource (lower
374 R^* values), the further they expand the resource trade-off space exploited by the assemblage. As
375 a consequence, more resource is being converted to biomass, increasing the RUE of the
376 assemblage. This is more evident under abrupt resource supply reversal, where prolonged
377 periods of limitation for one resource benefit species with high competitive abilities for that
378 resource, placed at the extremes of the resource trade-off space. An increase in species richness
379 under this mode of reversal would thus lead to higher numbers of species with high competitive
380 abilities for either resource that significantly contribute in the total biomass and resource use.
381 Species with intermediate competitive abilities, which are placed in the middle of the resource
382 trade-off space, contribute less to the total ecosystem RUE. This initial finding sets the
383 mechanistic basis for explaining observed patterns on the richness-RUE relationship.

384 Our results suggest that if all co-existing species are exploiting the full capacity of the
385 environment, such as in the case of our intact assemblages, a positive steep richness-RUE
386 relationship does not occur. This is consistent with recent modelling studies suggesting that when
387 functional diversity is based on the species' resource requirements, it does not strongly affect
388 productivity (Vallina et al. 2017). This finding is also reminiscent of the terrestrial habitat
389 connectivity/fragmentation conceptual model discussed earlier, where an intact landscape (i.e.,
390 not fragmented) provides compensatory mechanisms to local patches leading to weak BEF
391 relationships (Liu et al. 2018). In aquatic ecosystems, compensatory mechanisms, such as spatial
392 averaging, could lead to increased phytoplankton productivity in connected patches (Smeti et al
393 2016).

394 Our results also suggest that loss of a species at the edge of the resource trade-off space strongly
395 changes the slope of the richness-RUE relationship. Therefore, we advocate that assemblages in
396 which species cannot exploit the edge of the resource space will present a stronger richness-RUE
397 relationship (Figure 7). The absence of these species could be attributed to extinction events. In
398 addition, an extinction event could trigger an extinction cascade, as our study shows. This was
399 particularly evident during abrupt resource supply fluctuations. This is more pronounced in
400 species poor assemblages, where a species at the extreme of the resource trade-off space is
401 isolated. This was the case in the assemblages under abrupt resource supply reversal and high
402 stochasticity level, which supported the lower number of species before the extinction event and
403 presented the steepest slope after the extinction event. This finding is again reminiscent of the
404 terrestrial habitat connectivity/fragmentation conceptual model, where a compromised
405 landscape (i.e., fragmented) does not provide compensatory mechanisms to local patches

406 leading to strong BEF relationships (Liu et al. 2018). However, in a species rich assemblage,
407 clusters of functionally redundant species placed at the extremes of the resource trade-off space
408 will result in higher ecosystem stability since, after an extinction event, the rest of the species
409 will compensate for the loss (Yachi and Loreau 1999; Brown et al 2001; Fonseca and Ganade
410 2001-Figure 7).

411 The way species losses and community change affect ecosystem functions depends on multiple
412 factors. In phytoplankton, species with different growth strategies and thus functional traits
413 could cause a different shift in the BEF relationship if they go extinct. For example, growth
414 strategists tend to accumulate higher biomass at high resource concentrations than storage
415 strategists (e.g. Papanikolopoulou et al. 2018); thus, the extinction of a growth strategist would
416 cause a more pronounced effect on ecosystem functions than the extinction of a storage
417 strategist. In addition, eutrophication could be an ecosystem property that leads to community
418 changes (e.g. Bužančić et al. 2016), and thus to ecosystem function changes, as more eutrophic
419 ecosystems become light limited and worse light competitors could go extinct. Phytoplankton
420 species are also the base of the food web, therefore the edibility of a species by higher level
421 organisms could greatly affect the pathway through which the phytoplankton assemblage
422 change, thus affecting ecosystem functions (Roelke 2018).

423 Species richness in the present study was not manipulated (i.e. we did not explicitly set the
424 number of species) as is usually the case in experimental studies testing for diversity-ecosystem
425 functioning relationships. However, our approach resembled more field approaches, where
426 assemblages of different sites in a specified region were used to demonstrate such relationships

427 (e.g. Ptacnik et al. 2008, Lehtinen et al. 2017). Furthermore, our results are directly comparable
428 to and consistent with such large-scale field observations, that report steeper positive richness-
429 RUE relationships in less diverse regions (e.g. coastal sites in the Baltic Sea) compared to more
430 diverse regions (e.g. Scandinavian lakes – Ptacnik et al. 2008, Olli et al. 2014). We suggest that in
431 the less diverse regions, resources remain unexploited due to the absence of species at the edge
432 of the resource trade-off space, possibly due to their extinction, a mechanism that could explain
433 the observed difference in steepness of the BEF relationship.

434 Our results could be important for ecosystem management, or at least provide a better
435 understanding of ecosystem responses to anthropogenic activities, as they show clear
436 differences between sudden and gradual resource supply transitions. Activities such as reservoir
437 construction in watersheds can result in hydraulically less dynamic systems, that is, smaller inflow
438 events and protracted periods marginally above historical baseline flows (Magilligan and Nislow
439 2005, Poff et al. 2007). In turn, downstream aquatic systems could shift from sudden resource
440 supply transitions to gradual with these altered flows. The question of how such human activities
441 and resulting alterations to inflows and nutrient loading might influence phytoplankton
442 succession and assemblage characteristics is worth exploring as continued impoundment
443 construction is ongoing in many watersheds globally (Winemiller et al. 2016). Our findings
444 suggest that BEF relationships may be weakened in such systems.

445 **Conclusions**

446 In the present study, we investigated realistic scenarios of environmental variability, such as
447 resource fluctuations and stochasticity, jointly considering species life history traits such as μ_{max}

448 and K_s (both reflected on R^*) to identify the mechanisms driving the BEF relationship in
449 phytoplankton. The added realism renders our results comparable to large-scale field studies,
450 enabling the mechanistic explanation of the trends so far observed. Our findings highlight the
451 importance of the surviving species life history traits in driving the steepness of the BEF
452 relationship under resource supply fluctuations in aquatic systems. The loss of species that can
453 most efficiently exploit the available resources, that is, species positioned at the edges of the
454 resource trade-off gradient, could change the RUE and therefore strengthen the BEF relationship.

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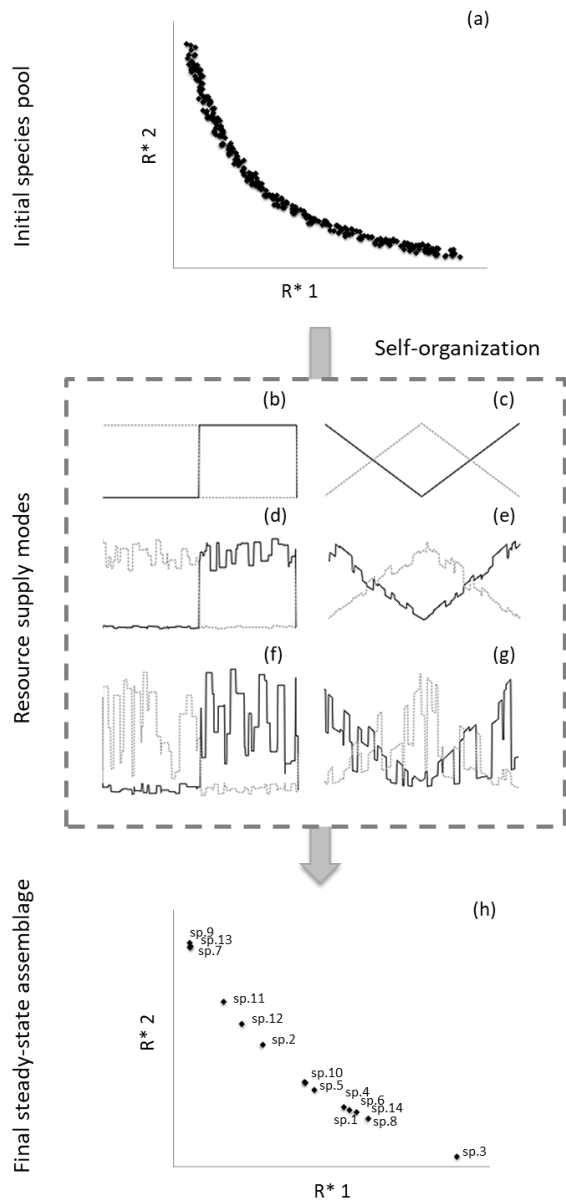
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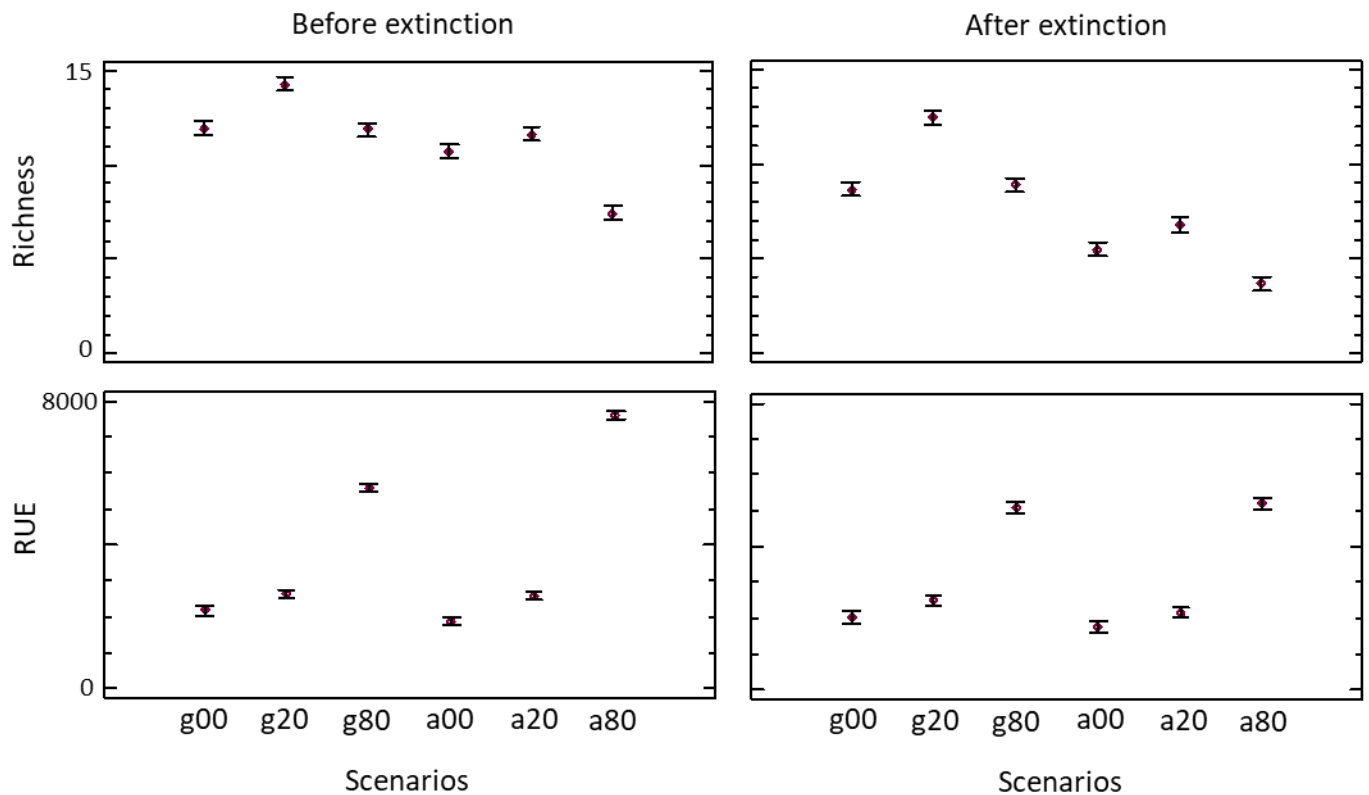
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685 regulated on water quality (nutrients, dissolved oxygen, and phytoplankton biomass) in three
686 contrasting waters of Hong Kong. *Environ. Monit. Assess.* 186, 1705–1718.



688

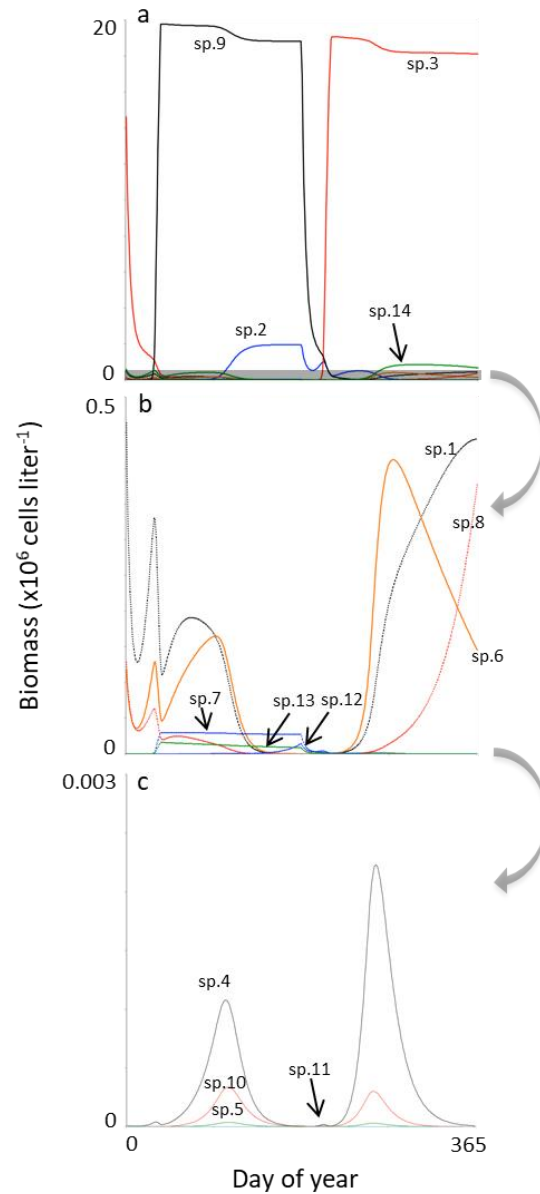
689 Figure 1. A species-rich assemblage of 300 species (a) underwent assemblage organization for 15
 690 years under each of the four resource supply scenarios (b-g). The abrupt resource supply reversal
 691 shifted from a resource supply of 2 and 20 μM for resources 1 and 2 to a resource supply of 20
 692 and 2 μM respectively with an abrupt transition on day 182. We accounted for three levels of

693 stochasticity in the resource supply: no noise (b), 0-20% noise (d) and 0–80% noise (f). The gradual
 694 resource supply reversal also shifted from a resource supply of 2 and 20 μM for resources 1 and
 695 2 to a resource supply of 20 and 2 μM respectively, but with a slow change that reversed direction
 696 on day 182. Again, three levels of stochasticity in the resource supply were considered: no noise
 697 (c), 0-20% noise (e) and 0–80% noise (g). By the end of the assemblage organization process fewer
 698 species remain and the R^* s of a representative phytoplankton assemblage is shown in panel (h).
 699 The numbers on panel (h) coincide with the species in Figures 2 and 3.



700

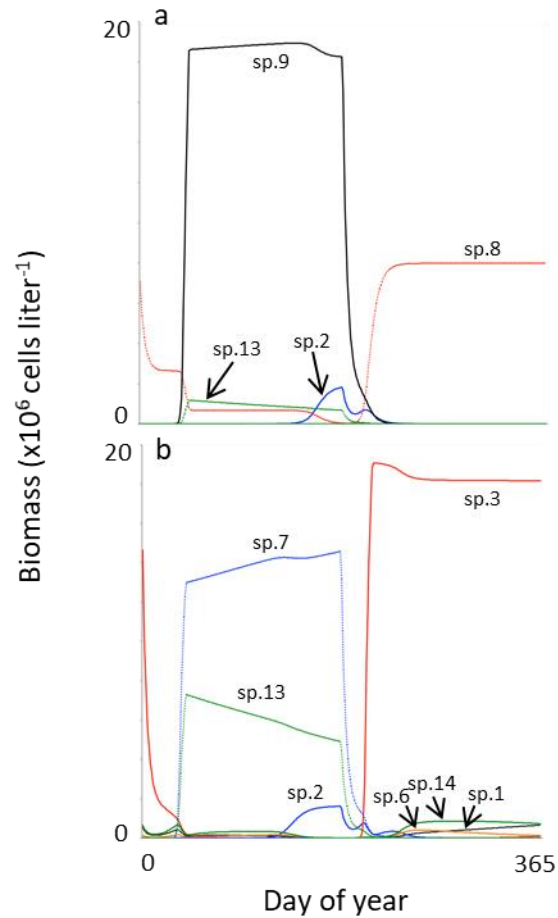
701 Figure 2. Richness and RUE in all tested scenarios of all 300 assemblages before and after
 702 experiencing an extinction event. g- gradual resource supply reversal, a- abrupt resource supply
 703 reversal, 00- 0 noise, 20-0-20% noise, 80-0-80% noise, n=300.



704

705 Figure 3. Representative population dynamics and composition of an intact assemblage during
 706 the last annual cycle of the 15-year organization period (i.e., just before experiencing an
 707 extinction event), when resource supply reversal was abrupt, showing dominant (a),
 708 subdominant (b) and rare (c) species. The species numbers correspond to those in Figure 1h.

709



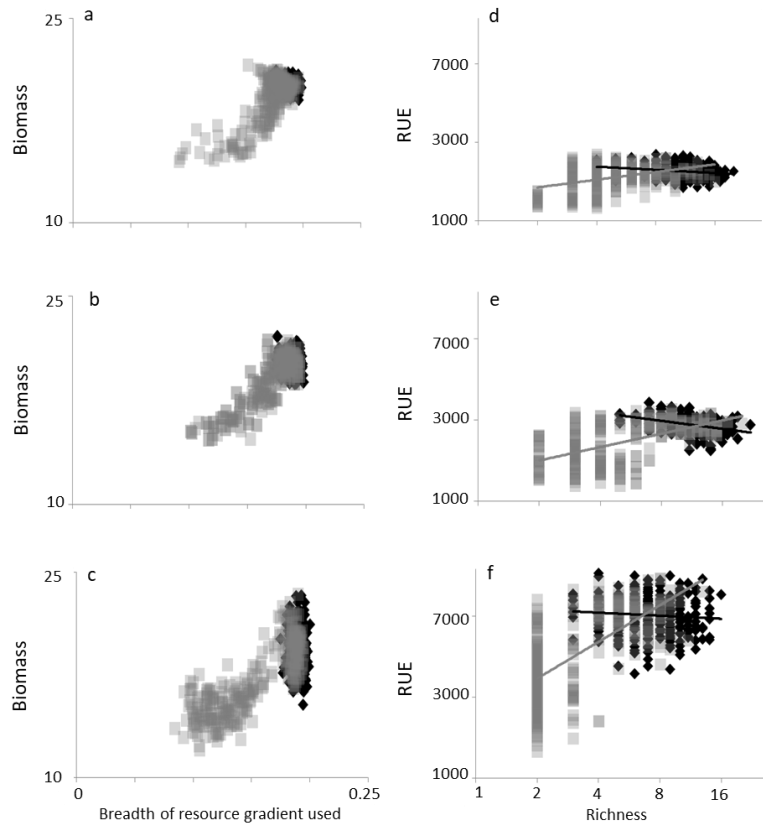
710

711 Figure 4. Representative population dynamics and composition of a compromised assemblage
 712 during the last annual cycle of the 15-year re-organization period (after the initial extinction of
 713 one species and following potential extinction cascades). Here, extinctions involved: a species
 714 with an extreme R^* for resource 2 (sp.3 from Figure 1) where no members of the assemblage
 715 were competitively similar (a); a species with an extreme R^* for resource 1 (sp.9 from Figure 1)
 716 where there were members of the assemblage that were competitively similar (b).

717

718

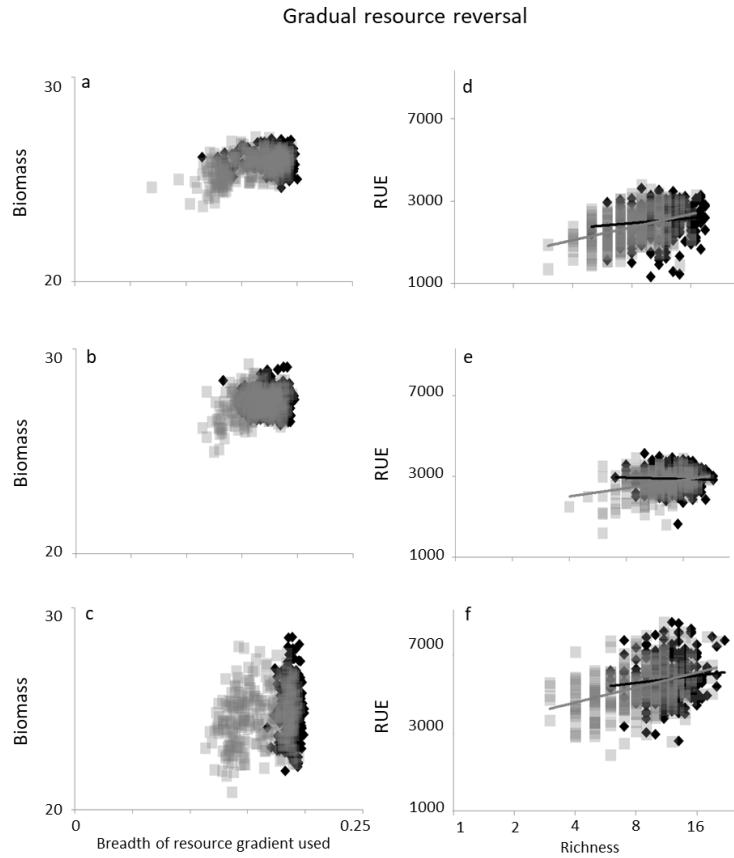
Abrupt resource reversal



719

720 Figure 5. Attributes of intact assemblages during the last year of the 15-year organization period
 721 (black markers and lines), and attributes of compromised assemblages during the last year of the
 722 15-year re-organization period (i.e., the same intact assemblages but following an initial
 723 extinction of one species, and potential cascading extinctions - gray markers and lines) under the
 724 abrupt resource supply reversal without noise (a, d), with 0-20% noise (b, e) and with 0-80% noise
 725 (c, f) in the supply resource concentrations. Shown are the time-averaged biomass and the
 726 breadth of the resource gradient used by the assemblages (a-c). Also shown are linear fit models
 727 (see Table1 for coefficients) between richness and RUE (d- f - both axes are in log scale).

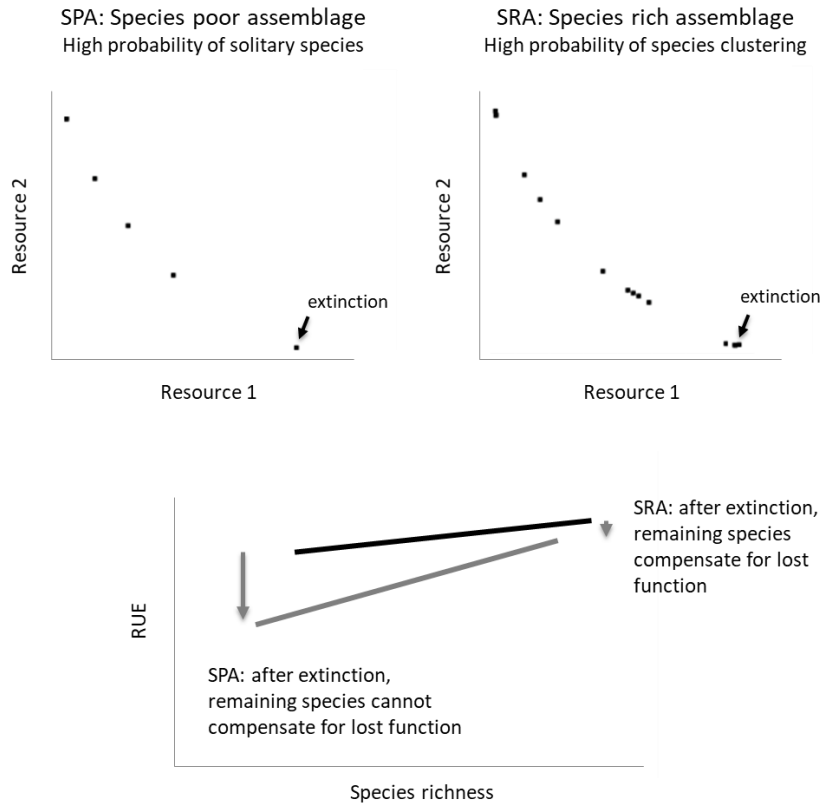
728



729

730 Figure 6. Attributes of intact assemblages during the last year of the 15-year organization
 731 period (black markers and lines), and attributes of compromised assemblages during the last
 732 year of the 15-year re-organization period (i.e., the same intact assemblages but following an
 733 initial extinction of one species, and potential cascading extinctions - gray markers and lines)
 734 under the gradual resource supply reversal without noise (a, d), with 0-20% noise (b, e) and
 735 with 0-80% noise (c, f) in the supply resource concentrations. Shown are the time-averaged
 736 biomass and the breadth of the resource gradient used by the assemblages (a-c). Also shown
 737 are linear fit models (see Table1 for coefficients) between richness and RUE (d-f - both axes are
 738 in log scale).

739



740

741 Figure 7. Conceptual framework of the mechanism explaining the change in the steepness (drop
 742 of the slope) of the assemblages compromised by an extinction event. Upper panels show the
 743 species spanning along the resource trade-off space. Arrows indicate the species that goes
 744 extinct.

745 Table 1. Regression coefficients for richness in a regression model predicting resource use
 746 efficiency (RUE) when seasonal transitions in resource supply were abrupt or gradual, with intact
 747 or with extinction events assemblages, and without (deterministic) and with (stochastic) noise in
 748 the resource supply concentrations. The slope coefficient a and the intercept coefficient b is as
 749 in Ptacnik et al (2008). p-values associated with t-tests that indicate significant departures from
 750 zero : * <0.05, ** <0.01, *** <0.001.

		$\ln(\text{RUE}_i) = \alpha \ln(S_i) + b$					
Scenario		Coefficients					
Resource supply reversal	Assemblage state	Intercept	Slope	Intercept	Slope	Intercept	Slope
		b	α	b	α	b	α
		No noise		0-20% noise		0-80% noise	
Abrupt	Intact	7.67 ***	-0.06***	8.19 ***	-0.14 ***	9.02 ***	-0.05
	With extinction	7.23 ***	0.14 ***	7.25 ***	0.24 ***	7.68 ***	0.65 ***
Gradual	Intact	7.45 ***	0.09*	7.94 ***	-0.02	8.26 ***	0.14 *
	With extinction	7.11 ***	0.23***	7.45 ***	0.15 ***	7.91 ***	0.28 ***

751