
How community adaptation affects biodiversity–ecosystem functioning relationships

Aubree Flora ^{1,*}, David Patrice ², Jarne Philippe ², Loreau Michel ³, Mouquet Nicolas ⁴, Calcagno Vincent ¹, Chase Jonathan

¹ Université Côte d'Azur INRAE CNRS ISA 06900 Sophia Antipolis, France

² Centre d'Ecologie Fonctionnelle et Evolutive CNRS Université de Montpellier Université Paul Valéry Montpellier - IRD - EPHE 1919 route de Mende 34293 Montpellier Cedex 5, France

³ Centre for Biodiversity Theory and Modelling, Theoretical and Experimental Ecology Station CNRS and Paul Sabatier University Moulis 09200, France

⁴ MARBEC CNRS-IFREMER-IRD-University of Montpellier Montpellier 34095, France

* Corresponding author : Flora Aubree, email address : flora.aubree@inrae.fr

Abstract :

Evidence is growing that evolutionary dynamics can impact biodiversity–ecosystem functioning (BEF) relationships. However the nature of such impacts remains poorly understood. Here we use a modelling approach to compare random communities, with no trait evolutionary fine-tuning, and co-adapted communities, where traits have co-evolved, in terms of emerging biodiversity–productivity, biodiversity–stability and biodiversity–invasion relationships. Community adaptation impacted most BEF relationships, sometimes inverting the slope of the relationship compared to random communities. Biodiversity–productivity relationships were generally less positive among co-adapted communities, with reduced contribution of sampling effects. The effect of community-adaptation, though modest regarding invasion resistance, was striking regarding invasion tolerance: co-adapted communities could remain very tolerant to invasions even at high diversity. BEF relationships are thus contingent on the history of ecosystems and their degree of community adaptation. Short-term experiments and observations following recent changes may not be safely extrapolated into the future, once eco-evolutionary feedbacks have taken place.

Keywords : Adaptive dynamics, eco-evolutionary dynamics, invasion, productivity, species interactions, species traits, stability

44 Introduction

45 Diversity, most classically defined as the number of constituent species in a com-
46 munity, plays an essential role in many aspects of ecosystem functioning (Hooper
47 *et al.*, 2005, 2012; Isbell *et al.*, 2011). Understanding how species composition affects
48 ecosystem properties is a fundamental question in basic and applied ecology, and
49 renewed practical importance given the accelerating biodiversity crisis (Pimm *et al.*,
50 2014).

51 Observational data, controlled experiments and theoretical developments have
52 converged in identifying ecosystem properties that exhibit systematic responses to
53 diversity. Three types of so-called biodiversity-ecosystem functioning (BEF) rela-
54 tionships are most commonly described, even though all three are seldom considered
55 in the same study. (i) First, the biodiversity-productivity relationship, historically
56 investigated in grassland communities (Tilman *et al.*, 1996; Loreau & Hector, 2001),
57 has been explored in several other taxa and ecosystems (Abramsky & Rosenzweig,
58 1984; Naeem *et al.*, 1994; Hooper *et al.*, 2005; Gamfeldt *et al.*, 2015). It is often
59 assumed that more diverse ecosystems are more productive, in agreement with the-
60 oretical predictions (Loreau, 1998; Tilman, 1999). (ii) Second, biodiversity-stability
61 relationships have also received a lot of attention (Elton, 1958; Tilman, 1999; Mc-
62 Cann, 2000), both theoretically (May, 1973; Loreau & Mazancourt, 2013) and ex-
63 perimentally (Gross *et al.*, 2014; Renard & Tilman, 2019). The intuitive view that
64 diverse ecosystems are more stable in the face of environmental fluctuations ap-
65 peared contradicted by early theoretical models suggesting the opposite (McCann,
66 2000). In fact, predictions may differ importantly depending on the type of sta-
67 bility metric, with negative relationships expected at the level of individual species
68 (dynamical stability: May, 1973; Tilman *et al.*, 1996; Ives & Carpenter, 2007), and
69 positive relationships expected for aggregate metrics (ecosystem stability: May, 1973;
70 Tilman *et al.*, 1996; Ives *et al.*, 1999; Barabás & D’Andrea, 2016; Pennekamp *et al.*,
71 2018). (iii) Last, biodiversity-invasion relationships have also attracted much atten-

72 tion, since native diversity has long been regarded as a key attribute determining
73 the susceptibility of communities to invasions. It is generally considered that more
74 diverse ecosystems should be less susceptible to invasions, and should suffer from
75 fewer adverse impacts (e.g. secondary extinctions) following an invasion (Levine,
76 2000; Hector *et al.*, 2001; Davis, 2009).

77 Ecosystem functioning is driven, beyond the sheer number of species, by com-
78 munity composition in terms of key functional trait (Gagic *et al.*, 2015). Com-
79 munities with the same diversity, but different trait compositions, might possess
80 different functioning characteristics. Communities probably harbor very different
81 traits depending on whether they are recent assemblages drawn from the regional
82 pool, or if species have adapted to the local environment and to the other species,
83 through various mechanisms including plasticity, niche-construction and evolution
84 (Kylafis & Loreau, 2011; Hendry, 2016; Meilhac *et al.*, 2020). In particular, evol-
85 utionary changes may be important on ecological timescales (Davis *et al.*, 2005;
86 Hendry, 2016), and there is mounting evidence that species can adapt rapidly to
87 environmental changes and to the presence of competitors or predators (Thompson,
88 1998; Faillace & Morin, 2016; Kleynhans *et al.*, 2016; Hart *et al.*, 2019; Meilhac
89 *et al.*, 2020). By altering species trait composition, such community adaptation
90 may impact the existence, magnitude and shape of BEF relationships.

91 Even though BEF studies are traditionally conducted from an ecological per-
92 spective, long term grassland experiments (Reich *et al.*, 2012; Meyer *et al.*, 2016)
93 and microbe experiments (Bell *et al.*, 2005) found that biodiversity-yield relation-
94 ships change through time. The most recent studies have explicitly highlighted a role
95 of evolution in modifying biodiversity-yield relationships: in grasslands (Zuppinger-
96 Dingley *et al.*, 2014; van Moorsel *et al.*, 2018) and with microbes, using experimental
97 evolution (Fiegna *et al.*, 2014, 2015). However, results have proven quite variable,
98 prompting a plea for more theoretical investigations (Fiegna *et al.*, 2015).

99 Here we propose a theoretical evaluation of the consequences community adapta-

tion may have for BEF relationships. We use a general modeling approach to address the three types of BEF relationships highlighted above (biodiversity-productivity, biodiversity-stability, and biodiversity-invasion). We compare two contrasted types of communities: (i) random communities, in which only ecological processes control species trait composition, with no evolutionary dynamics, and (ii) co-adapted communities, in which species traits composition have further been shaped by microevolution (species adaptation to the environment and to other species). Specifically, species have adjusted their traits and are at (co)evolutionary equilibrium (Christiansen, 1991). Real-life communities would harbour various degrees of co-adaptation in between these two limiting cases. Recently-founded or perturbed ecosystems, such as artificially assembled communities, are probably closer to the random case. In contrast, ecosystems that have long remained in relatively constant conditions, such as primary old-growth forests, may be closer to co-adapted communities.

As species coexistence and eco-evolutionary dynamics depend on the type of ecological interactions (Mouquet *et al.*, 2002; Chave *et al.*, 2002; Calcagno *et al.*, 2017), we model communities governed by four contrasted scenarios of ecological interactions, representative of classical coexistence mechanisms (Doebeli & Dieckmann, 2000; Calcagno *et al.*, 2017): two scenarios based on resource competition (one symmetric, one asymmetric), one life-history trade-off scenario, and a trophic chain scenario. In each case, several functioning metrics are computed to evaluate BEF relationships. This general approach allows to evaluate the extent to which the consequences of community adaptation are general or depend on particular types of metrics and ecological interactions.

We report clear influences of community adaptation on each of the three BEF relationships investigated, highlighting how co-adaptation impacts species trait distribution and, in turn, functioning properties. Although conclusions may depend importantly on the type of ecological interaction scenario considered, general predictions regarding the consequences of community adaptation are formulated, and

128 discussed in light of available experimental evidence.

129 **Material and methods**

130 ECOLOGICAL SCENARIOS AND TRAITS

131 In natural ecosystems species are engaged in various interactions, within the same
132 trophic level (horizontal interactions) and among different trophic levels (vertical
133 interactions), at different spatio-temporal scales. The dominant form of species in-
134 teraction may differ across communities (Chave *et al.*, 2002), and some studies have
135 argued that generalist predation, exploitative competition and simple three-species
136 food chains compose the common backbone of interaction networks (Mora *et al.*,
137 2018). To reflect this diversity, we here considered a set of four contrasted ecolo-
138 gical scenarios (Fig. 1a), based on classical species coexistence models, and spanning
139 the range from completely horizontal symmetric interactions to completely vertical
140 asymmetric interactions. The first two scenarios describe competition for resources.
141 The *Niche* scenario is a classical model of symmetric competition along an axis of
142 niche differentiation (Doebeli & Dieckmann, 2000; Calcagno *et al.*, 2017). The *Body-*
143 *size* scenario introduces interference and asymmetric competition, based on *e.g.* size
144 differences (Rummel & Roughgarden, 1985; Doebeli & Dieckmann, 2000). The third
145 scenario (*LH-tradeoff*) models a life-history trade-off, describing the strongly asym-
146 metric competition between species good at colonizing empty habitat and species
147 locally dominant, along a competitive hierarchy (Tilman, 1994; Calcagno *et al.*,
148 2006, 2017). Last, the fourth (*Trophic*) scenario describes a size-structured trophic
149 chain, based on the model introduced by Loeuille & Loreau (2005).

150 In each interaction scenario, species are characterized by one key trait, denoted
151 x (Fig. 1a). In the *Niche* scenario, the trait represents niche position along the
152 continuum of resources, and interspecific competition thus decreases with trait dif-
153 ference (niche differentiation). In the *Body-size* scenario, the trait is body size:

154 species with similar size compete more intensely, and bigger species have a com-
 155 petitive advantage over smaller ones. In the *LH-tradeoff* scenario, species trait is
 156 the colonization rate: species with greater trait value are more apt at colonizing
 157 empty patches, but also more susceptible to be competitively displaced from occu-
 158 pied patches (Calcagno *et al.*, 2006). Last, in the *Trophic* scenario, species trait is
 159 body mass: body mass influences growth and metabolic rates, and species preferen-
 160 tially consume species that are smaller, with some optimal mass difference (Loeuille
 161 & Loreau, 2005).

162 After appropriate reformulations (Supporting information (S.I.) Section 1), all
 163 models can be set in the common Lotka-Volterra form:

$$\frac{dn_i}{dt} = n_i r(x_i) \left(1 - \sum_j \frac{n_j a(x_i, x_j)}{k(x_i)} \right) \quad (1)$$

164 with n_i the abundance of species i , that denotes, depending on scenario, either a
 165 number of individuals (*Niche*), a biomass (*Body-size* and *Trophic*) or a fraction of
 166 occupied sites (*LH-tradeoff*).

167 The three functions included in equation (1) allow to describe species demo-
 168 graphy and inter-specific interactions: $r(x_i)$ is the intrinsic growth rate of species
 169 i that governs the ecological timescale; $a(x_i, x_j)$ is the impact that a variation in
 170 species j abundance has on the per capita growth rate of species i , normalized by
 171 the intra-specific interaction (see S.I., Section 1.1); and $k(x_i)$, usually called the
 172 carrying capacity, quantifies the resistance to density dependence of species i . In
 173 all scenarios but the *Trophic* one, it is also the equilibrium abundance reached by
 174 the species if growing alone in the community, or in other words the mono-culture
 175 abundance (Loreau & Hector, 2001). The shape of the functions for each scenario
 176 differ in important ways, as represented in Fig. 1a. See S.I. Section 1 for a complete
 177 description of each scenario.

178 Evolution would often favor certain trait values that are better adapted to the
 179 current habitat; this is described by the mono-specific abundance function $k(x)$,

180 which defines the optimum trait value, as represented by the red dots in Fig. 1a. The
181 relationship between trait value and mono-specific abundance may have an inter-
182 mediate optimum (*Niche*, *Body-size* and *Trophic*) or be open-ended (*LH-tradeoff*),
183 see red dots positions in Fig.1a. Sometimes, inter-individual interactions and com-
184 petition may counteract evolution towards optimal trait values, in particular in the
185 *LH-tradeoff* scenario, in which evolution effectively results in traits with comparat-
186 ively low mono-specific abundances (Calcagno *et al.*, 2017).

187 Species traits, through functions r , k and a , determine species interactions and
188 overall ecosystem and evolutionary dynamics. Note that we consider here species
189 that coexist stably and have distinct ecological traits. For each scenario, one or
190 two parameters controlling the shape of the functions were systematically varied
191 to ensure that conclusions were robust to parameter changes (all details and the
192 parameter ranges explored are provided in S.I., Section 2).

193 In the *Niche* scenario, we varied the width of the competition function (Fig.
194 1a) keeping the width of the mono-specific abundance function constant (Doebeli
195 & Dieckmann, 2000). In the *Body-size* scenario, we varied both the width of the
196 competition function and its skew (level of competitive asymmetry; see Rummel
197 & Roughgarden, 1985; Doebeli & Dieckmann, 2000). In the *LH-tradeoff* scenario,
198 we varied the intensity of the tradeoff, and the level of competitive preemption
199 (Calcagno *et al.*, 2006). Finally, in the *Trophic* scenario, we varied the level of
200 interference competition and the width of the consumption function (Loeuille &
201 Loreau, 2005). In the figures, for clarity, only three contrasted and representative
202 parameter sets are presented per scenario.

203 RANDOM AND CO-ADAPTED COMMUNITIES

204 The process of community formation is sketched Fig. 1b. For diversity levels (N)
205 between 1 and 10, sets of species were drawn randomly from a regional pool. The
206 ecological equilibrium with N species was computed from equation (1), and the

207 community was retained if all species persisted at equilibrium (see S.I. Section 3
 208 for details). This was repeated until obtaining, for each diversity level, 1,000 such
 209 random communities. The distribution of species trait values in the regional pool
 210 was chosen to minimize information content (maximum entropy; Jaynes, 1957), while
 211 being representative of typical trait values expected for the corresponding ecological
 212 scenario and parameter set. This is a generic approach but, of course, there are many
 213 ways in which diversity gradients can be generated in nature and experiments. We
 214 tried alternative methods to assemble random communities, and conclusions were
 215 little affected (see S.I. Section 3). For some scenarios and parameter sets, no feasible
 216 community could be found beyond some diversity level, in which case we stopped
 217 at the highest feasible level.

218 Whereas random communities are only constrained by ecological processes (re-
 219 gional pool and local competitive exclusion), co-adapted communities met the addi-
 220 tional constraint that species traits are at (co)evolutionary equilibrium ("evolution-
 221 ary filter"; Fig. 1b). We computed, for each species in a community, the selection
 222 gradient (Christiansen, 1991), defined as

$$\nabla(x_i) = \left. \frac{ds(x_m)}{dx_m} \right|_{x_m=x_i} \quad (2)$$

223 where $s(x_m)$ is the fitness (growth-rate) of a rare phenotype x_m . Note that fitness is
 224 density- and frequency-dependent and varies with community composition (species
 225 trait and abundances).

226 If $\nabla(x_i) > 0$, selection acts to increase the trait value, whereas if $\nabla(x_i) < 0$
 227 smaller values are selected for. When all selection gradients are simultaneously
 228 cancelled in a community, species have attained an evolutionary attractor and are at
 229 equilibrium with respect to first-order selection (Christiansen, 1991). This approach
 230 assumes heritable trait variation and sufficiently small phenotypic variance within
 231 each species. We thus generated, for each scenario, parameter set and diversity level,
 232 all possible co-adapted communities (most often, only one), in the sense of eq. (1)

233 and (2). See S.I. Section 3 for detailed methods.

234 BIODIVERSITY-FUNCTIONING RELATIONSHIPS

235 For each generated community, we computed several properties of interest (Fig. 1c;
236 full list in S.I. Section 4) to investigate the three BEF relationships. We present
237 results based on the properties describe hereafter, as conclusions were similar based
238 on the others. First, community productivity (Tilman, 1999; Loreau & Hector,
239 2001) was measured as the species average rate of production (positive contribu-
240 tion to growth rate) in the community. Second, ecological stability was assessed
241 in two ways. We computed the classical asymptotic resilience (May, 1973; Arnoldi
242 *et al.*, 2016), *i.e.* asymptotic rate of return to equilibrium of the community after
243 a perturbation, and the community stability (May, 1973; Ives *et al.*, 1999), *i.e.* the
244 inverse of the coefficient of variation of total community abundance under sustained
245 environmental noise. Finally, to study the response to invasions, we also used two
246 properties. The first is the resistance to invasion (Elton, 1958; Hector *et al.*, 2001),
247 *i.e.* the probability that a random alien species, introduced at low abundance, fails
248 to establish in the community. The second was the tolerance to invasion (Elton,
249 1958), *i.e.* the proportion of species that, following a successful invasion, were not
250 driven to extinction. Details on the mathematical computation of each metric are
251 presented in S.I. Section 4.

252 For each metric, diversity level, scenario and parameter set, we computed the
253 average value over the 1,000 random communities, and over the few (or, most often,
254 the unique) co-adapted communities. To ensure that average differences represented
255 large effect sizes, we further computed the percentile, in the distribution of values
256 over random communities, corresponding to the value of co-adapted communities.
257 Our results showed that co-adapted communities often lie in the tail of the distribu-
258 tion of random communities, for all metrics (see S.I. Section 5). Average differences
259 between co-adapted and random communities were thus large relative to the vari-

260 ability of random communities. For this reason we only present average values in
261 the Figures.

262 The above metrics were correlated to species richness to produce BEF rela-
263 tionships and compare random and co-adapted communities. Since the impacts of
264 co-adaptation are mediated by changes in trait values, we compared the structure
265 of co-adapted and random communities. We then computed the average absolute
266 difference in trait space between the two, as a measure of the strength of the evol-
267 utionary filter. We summarized trait compositions using two additional quantities
268 (Fig. 1c). The first was the minimum distance to the optimal trait value (red dots
269 in Fig. 1a), that reflects how well the better performing species is adapted to the
270 habitat. The second was the average trait interval between species (trait range di-
271 vided by number of species minus one), that indicates how “packed” species are in
272 trait space. More details are provided in S.I. Section 4.

273 Results

274 BIODIVERSITY-PRODUCTIVITY

275 Random and co-adapted communities differed in productivity at low diversity levels,
276 but at higher diversity levels, differences were more modest (Fig. 2). Moreover, in
277 all scenarios except the *LH-tradeoff*, the effect of community adaptation was to in-
278 crease productivity. Those two observations explain the quantitative differences in
279 biodiversity-productivity relationships between random and co-adapted communit-
280 ies.

281 Qualitatively, co-adaptation affected the biodiversity-productivity relationship
282 in all four scenarios (Fig. 2). The impact could be as spectacular as a slope inver-
283 sion. For instance, the *LH-tradeoff* scenario, unlike the other scenarios, generated
284 mildly negative biodiversity-productivity relationships in random communities (see
285 also Loreau, 2010), while in co-adapted communities, they switched to markedly

286 positive for all parameter sets (Fig. 2c). Conversely, the *Trophic* scenario generated
287 a classical positive biodiversity-productivity relationship in random communities,
288 but the relationships switched to negative in co-adapted communities (with oscillations
289 between odd and even diversity levels, caused by trophic cascades; Fig. 2d).
290 The possibility of such inversions of biodiversity-production relationships has, to the
291 best of our knowledge, never been reported so far.

292 In the remaining scenarios, those based on resource competition, biodiversity-
293 productivity relationships were always positive – at least slightly – irrespective of
294 co-adaptation (Fig. 2a,b). However, the shape of the relationships differed markedly
295 between random and co-adapted communities: the increase in productivity with
296 diversity was close to linear or gradually slowed down with diversity, whereas in
297 co-adapted communities, the relationships saturated very quickly, reaching almost
298 maximum productivity at low diversity levels and then plateauing, especially in the
299 *Body-size* scenario (Fig. 2b).

300 SPECIES TRAIT COMPOSITION

301 As shown in Fig. 3, random and co-adapted communities exhibited systematic differ-
302 ences in their trait composition and structure. The specifics differed across ecological
303 scenarios, but general trends can be identified. First, random communities are gen-
304 erally less packed than co-adapted ones, as can be seen by the slopes lower than one
305 in Fig. 3), indicative of broader trait ranges in random communities. Second, the
306 difference was maximal at low diversity and tended to vanish as diversity increases.
307 Increasing diversity made random and co-adapted communities converge to similar
308 trait distributions on average (aligning on line $x = y$ in Fig. 3), with one exception
309 in the *Trophic* scenario. As a result, the impact of community adaptation on com-
310 munity structure, i.e. the strength of the evolutionary filter, globally declined with
311 the number of species (insert panels in Fig. 3).

312 More specifically, in random communities, the chance to find a highly perform-

313 ing species inevitably increased with the number of species, so that the minimum
314 trait distance to the optimum decreased with diversity in all scenarios (Fig. 4a-d).
315 Concomitantly, the average distance between species decreased sharply with species
316 richness (Fig. 4e-h), reflecting the greater species packing. In contrast, a close-to-
317 optimal species was always present in co-adapted communities (constant minimum
318 distance to optimum trait Fig. 4a,b,d), except for the *LH-tradeoff* scenario in which
319 evolution did not drive species to the optimum trait (Fig. 4c). Community adapta-
320 tion also made the level of species packing virtually constant irrespective of species
321 number (Fig. 4e-h; see also Fig. 3).

322 BIODIVERSITY-STABILITY

323 Asymptotic resilience, in all four ecological scenarios, declined with diversity (Fig. 5a-
324 d). Moreover, the biodiversity-stability relationships were similarly negative, regard-
325 less of community adaptation, even though co-adapted communities were generally
326 more stable than random ones.

327 Ecosystem stability, was also higher overall in co-adapted than in random com-
328 munities (Fig. 5e-h). However, unlike asymptotic resilience, it had different re-
329 sponses to diversity depending on ecological scenario. It increased with species
330 richness in the two scenarios based on resource competition (*Niche* and *Body-size*),
331 but decreased with species richness in the *LH-tradeoff* and *Trophic* scenarios. In all
332 cases, unlike asymptotic resilience, the variation of ecosystem stability with species
333 richness was strongly affected by co-adaptation, and the patterns were quite consist-
334 ent with those observed for total productivity (Fig. 2), except for the *LH-tradeoff*.

335 BIODIVERSITY-INVASION

336 Resistance to invasion (Fig. 6a-d) presented consistent trends in the four ecological
337 scenarios. First, it increased with species richness, reflecting classical expectations.
338 Second, co-adapted communities were generally more resistant to invasion than ran-

339 dom ones, at any species richness level, reflecting the concentration of species around
340 trait optima, which leaves only more peripheral niches available for potential invas-
341 ive species. This difference was also quite in line with common expectations, but it
342 could vanish, or even reverse for some parameter values, in the *LH-tradeoff* scenario
343 (Fig. 6c). Overall, the biodiversity-invasion relationships were thus similar regard-
344 less of co-adaptation.

345 The effects of co-adaptation were much more dramatic and consistent when look-
346 ing at tolerance to invasion (Fig. 6e-g), with a pronounced interaction between the
347 effects of diversity and community adaptation. In random communities tolerance
348 to invasion steeply declined with species richness, meaning that successful inva-
349 sions were more and more harmful (in terms of diversity loss) as diversity increased
350 (Fig. 6e-g). In contrast, co-adapted communities were in all cases more tolerant
351 to invasion than random communities: they retained their almost perfect tolerance
352 to invasion as diversity increases, the biodiversity-invasion relationship being essen-
353 tially flat.

354 Discussion

355 Natural and anthropized ecosystems present tremendous variation in their diversity
356 and composition (species richness and trait values), and also in the degree to which
357 component species are adapted to the local environmental conditions and to one
358 another, here referred to as community adaptation. While it is clear that diversity
359 is an important determinant of ecosystem functioning, we still know little about how
360 the level of community adaptation might impact BEF relationships (Fiegna *et al.*,
361 2015; Hendry, 2016). In this study we addressed this question with a general model-
362 ling approach, systematically comparing random and co-adapted communities with
363 respect to three BEF relationships (biodiversity-productivity, biodiversity-stability
364 and biodiversity-invasion) and across four classical scenarios of ecological interac-

365 tions.

366 We found that community adaptation had an impact on all BEF relationships,
367 but that the nature and extent of the impact depend on both the metrics and the
368 scenarios considered for species interactions. Overall, the biodiversity-productivity
369 and biodiversity-invasion relationships were strongly impacted by community ad-
370 aptation, while the biodiversity-stability relationships were much less so. Indeed,
371 co-adapted communities, at any species richness, tended to be more dynamically
372 stable in terms of asymptotic resilience than random ones, but there was little
373 interaction with diversity: BEF relationships looked qualitatively very similar in
374 random and co-adapted communities. This suggests that the connection between
375 diversity and dynamical stability is a rather universal property in such systems
376 of interacting species, largely insensitive to the details of species interactions and
377 to community adaptation. Co-adapted communities were more dynamically stable,
378 which likely reflects the fact that co-adaptation brings traits closer to optimal values
379 (Fig. 4a-d), entailing faster returns to equilibrium (see also Loeuille, 2010). Consist-
380 ent with this interpretation, the only case where co-adapted communities were on
381 average less dynamically stable than random ones occurred at low diversity in the
382 *LH-tradeoff* (Fig. 5c), a case where co-adaptation pushes traits away from the op-
383 timum (Fig. 1a and 3). When looking at ecosystem stability (May, 1973; Ives *et al.*,
384 1999; Arnoldi *et al.*, 2016), BEF relationships differed more importantly between
385 co-adapted and random communities, but these differences closely mirrored those
386 observed for biodiversity-productivity relationships (Fig. 5e-h). This suggests that
387 variation in ecosystem stability were linked to variation in total productivity and
388 the total biomass of species, but, beyond that, were little impacted by community
389 adaptation in a direct manner (see Ives *et al.*, 1999), especially for the *Niche*, *Body-*
390 *size* and *Trophic* scenarios. Consistent with this interpretation, overall Spearman
391 correlation coefficients between productivity and ecosystem stability were, across all
392 communities, 0.97, 0.97, 0.65 and 0.79 for the *Niche*, *Body-size*, *LH-tradeoff*, *Trophic*

393 scenarios, respectively.

394 Biodiversity-productivity relationships were both quite variable across ecological
395 scenarios and strongly impacted by community adaptation. The impact could be
396 as pronounced as a slope inversion between random and co-adapted communities,
397 with switches from positive to negative (*Trophic* scenario; Fig. 2d) or from negative
398 to positive (*LH-tradeoff* scenario; Fig. 2c). In all cases, changes in the shape of
399 biodiversity-productivity relationships were mostly driven by low diversity levels, at
400 which co-adapted communities differed importantly for random ones, while at higher
401 diversity levels community adaptation had modest impact on average (Fig. 2). The-
402 oretical (Mazancourt *et al.*, 2008) and experimental (terHorst *et al.*, 2018; Scheuerl
403 *et al.*, 2020) studies have found that biodiversity inhibits the evolution of species
404 traits (but see Jousset *et al.* (2016), and our *Trophic* scenario; Fig. 3d). This can
405 be attributed to the strong constraints on species trait distributions in rich com-
406 munities, due to species interactions and persistence conditions (ecological filter),
407 which leaves adaptive evolution much less room to alter species traits. As a result,
408 co-adapted and random communities are more and more similar as the number of
409 species increases, i.e. the strength of the evolutionary filter decreases (see Fig. 3: its
410 presence makes less and less of a difference for ecosystem functioning.

411 In most ecological scenarios (*Niche*, *Body-size* and *Trophic*), co-adapted com-
412 munities at low diversity levels were more productive than random ones on average
413 (Fig. 2a,b,d). Therefore, community adaptation weakened the positive biodiversity-
414 productivity relationships observed in random communities, making those shallower,
415 or even reversing them to negative (*Trophic*). In the *LH-tradeoff* scenario, low
416 diversity co-adapted communities were on the contrary less productive than ran-
417 dom ones, so that the effect of community adaptation was opposite: co-adapted
418 communities exhibited a positive biodiversity-functioning relationships, whereas a
419 slightly negative relationship is predicted in random communities (see also Loreau,
420 2010).

421 The qualitative effect of community adaptation on biodiversity-productivity re-
422 lationships could thus be determined, to a large extent, from the overall direction
423 of selection in isolated species (monocultures), either towards higher productivity
424 (*Niche*, *Body-size*, *Trophic* scenarios), weakening positive relationships or switching
425 them to negative, or towards lower productivity (*LH-tradeoff* scenario), switching
426 negative relationships to positive.

427 Community adaptation also affected the mechanisms underlying biodiversity-
428 productivity relationships. In the two scenarios describing competition for resources
429 (*Niche* and *Body-size*) and in the *Trophic* scenario, low diversity co-adapted com-
430 munities were more productive because adaptive evolution favoured traits that were
431 close to the optimum (Fig. 4a,b,d). At higher diversity levels, more and more spe-
432 cies were kept farther away from the optimal trait value, and thus intrinsically less
433 productive. Such a change in the intrinsic productivity of species as diversity in-
434 creases is often called a “selection effect” (Loreau & Hector, 2001), but here, following
435 Zuppinge-Dingley *et al.* (2014), we will call it a “sampling effect” to avoid confusion.
436 In random communities, this sampling effect was positive, as usually expected, and
437 contributed importantly to the positive biodiversity-productivity relationship: richer
438 communities were more likely, by chance, to harbor species that were intrinsically
439 more productive in the habitat (Fig. 4a,b,d, blue curves). In co-adapted communit-
440 ies, the sampling effect was much reduced or entirely absent, owing to the effect of
441 co-adaptation explained above. In contrast, the average trait distance between ad-
442 jacent species (the level of niche packing) declined sharply with diversity in random
443 communities, but much less so in co-adapted communities (Fig. 4e-h). Therefore,
444 the level of species trait complementarity was less sensitive to diversity with com-
445 munity adaptation. Altogether, this suggests positive biodiversity-productivity re-
446 lationships should be more driven by complementarity effects, and less by sampling
447 effects, in co-adapted communities compared to random communities.

448 There is good experimental evidence that biodiversity-productivity relationships

449 do change over time. In grassland experiments, the positive biodiversity-productivity
450 relationships were reported to become steeper (Reich *et al.*, 2012), or sometimes flat-
451 ter (Meyer *et al.*, 2016, for most of its biomass-related metrics), over several years. A
452 study of decomposing microbial communities observed a decline in productivity and
453 a flattening of the biodiversity-productivity relationship over several days (Bell *et al.*,
454 2005). Several of these studies (Bell *et al.*, 2005; Reich *et al.*, 2012; Meyer *et al.*,
455 2016) deal with short timescales and are not directly relevant to address community
456 adaptation, since observed changes are generally attributed to transient ecological
457 mechanisms, such as below-ground feedbacks or resource depletion. Direct compar-
458 ison with our results, in which transient dynamics have been sorted out, is thus
459 difficult. Fortunately, more recent analyses of the longest grassland experiments
460 have looked for, and found, evidence of character displacement and evolution of
461 niche differentiation, even on relatively short timescales (Zuppinge-Dingley *et al.*,
462 2014; van Moorsel *et al.*, 2018). This suggests that the evolutionary effects ana-
463 lyzed in this work might have begun to play a role. Interestingly, it was observed
464 that biodiversity-productivity relationships assembled from co-selected species were
465 higher at low diversity, but saturated faster with diversity, thus being more con-
466 cave (van Moorsel *et al.*, 2018). This is strikingly reminiscent of our predictions in
467 the standard “resource competition” scenarios (*Niche* and *Body-size*; see Fig. 2a,b).
468 Furthermore, it was found that species evolving in mixed assemblages (thus ap-
469 proaching a state of community adaptation) elicited more complementarity effects,
470 and less sampling effects, than assemblages of non-co-adapted species (Zuppinge-
471 Dingley *et al.*, 2014). This too is quite consistent with our findings. In a more direct
472 approach, Fiegna *et al.* (2014, 2015) used experimental evolution to demonstrate
473 that biodiversity-productivity relationships are impacted by co-adaptation in bac-
474 teria. They further showed that these changes involved an evolutionary component
475 in species interactions, not just of individual species performances, even though the
476 overall impact on biodiversity-productivity relationships was quite variable among

477 experiments. These studies thus clearly support a role for community adaptation in
478 the dynamics of BEF relationships as highlighted here.

479 Regarding the biodiversity-invasion relationships (Fig. 6), the effects of com-
480 munity adaptation were much more consistent across ecological scenarios than for
481 biodiversity-productivity relationships. Resistance to invasion increased, and toler-
482 ance to invasion decreased, with diversity under all scenarios, which conforms well
483 to general expectations (Levine, 2000; Hector *et al.*, 2001; Davis, 2009). The impact
484 of community adaptation was moderate for resistance to invasion (probability of
485 establishment) but spectacular for tolerance to invasion (number of secondary ex-
486 tinctions) (Fig. 6e-h), highlighting that different invasion properties can behave quite
487 differently. Indeed, resistance to invasion was only slightly impacted by community
488 adaptation, the latter generally increasing invasion resistance, but with almost no
489 interaction with diversity. In contrast, biodiversity-tolerance relationships markedly
490 differed with community adaptation (Fig. 6e-h): while tolerance to invasion gradu-
491 ally decreased with species diversity in random communities, it remained virtually
492 constant with community adaptation.

493 This can be understood in terms of changes in species trait distributions. In
494 co-adapted communities, species traits were more concentrated around the optimal
495 trait (Fig. 3 and Fig. 4e-h orange curves) and more evenly spaced (see S.I. Section
496 6 Fig S2), so that successful invaders tended to occupy peripheral niches at either
497 tail of the trait distribution, which did not cause resident extinctions. However, this
498 is not the case in random communities in which an invader might find vacant niche
499 space anywhere along the trait spectrum, possibly very close to a resident species,
500 thus potentially excluding the latter and triggering further secondary extinctions.

501 Beyond BEF relationships, these results have interesting implications for com-
502 munity assembly dynamics. With the possibility of species (co)evolution, invasion
503 resistance and tolerance would both increase in between species colonization events.
504 In other words, successful invasions would be rarer, but also more constructive in

505 terms of community assembly: invaders would more often add to the community
506 without driving many resident species extinct. With trait co-evolution, assembly
507 trajectories should therefore be less eventful (fewer invasions and fewer extinctions),
508 and more steadily progressing or "efficient", compared to pure invasion-assembly.
509 Although this prediction deserves further exploration, it nicely complements some
510 earlier studies of community assembly (Rummel & Roughgarden, 1985).

511 Unfortunately, empirical evidence is even scarcer regarding the role of community
512 adaptation for invasion properties than for productivity. Most studies focus on
513 documenting the impact of invasions on the evolutionary dynamics of communities,
514 not the other way round; yet, evolutionarily immature (e.g. insular) communities or
515 recently assembled ecosystems such as anthropized habitats are known to be more
516 sensitive to invasions than old species assemblages. Although this is suggestive of a
517 protective role of co-evolution, the diversity-invasion relationship is difficult to relate
518 to evolutionary history, as most long-co-evolved communities are highly diverse while
519 recently assembled ones are usually species-poor (David *et al.*, 2017).

520 Our approach was a first attempt at combining eco-evolutionary theory and BEF-
521 relationships. It could be extended and improved in several ways. One important
522 simplification was the assumption of one single trait that structures communities
523 and is subject to evolution. It would be interesting to describe species interactions
524 as governed by multiple traits, which is probably more realistic and might result in
525 more complex eco-evolutionary dynamics (Vasconcelos & Rueffler, 2020). Similarly,
526 we assumed no upper limit on the amount of phenotypic change a species can un-
527 dergo. Trait changes between random and co-adapted communities may sometimes
528 be quite large, especially at low diversity levels (Fig. 3). However, since genetic
529 variation is usually not infinite, species responses to selection can be constrained.
530 Such limits on evolution would probably weaken some of the reported effects, even
531 though preliminary analyses suggest that results are quite robust to this (see S.I.
532 Fig. S3 Section 7).

533 Overall our work highlights some potentially important consequences of evolu-
534 tionary dynamics for biodiversity-functioning relationships. Through its action on
535 species trait values, community adaptation can profoundly change the expected re-
536 lationship between diversity and various ecosystem functioning properties, even in
537 qualitative terms. This occurs because of the differential magnitude and direction
538 of species trait evolution in poor versus rich communities, so that the ecological
539 impact of species number interacts with the evolutionary history of communities.
540 Therefore, BEF relationships derived from short-term experiments or observed fol-
541 lowing recent habitat perturbations might not be safely extrapolated into the future,
542 once eco-evolutionary feed-backs have played out. This may have consequences for
543 our understanding and prediction of the way ecosystems respond to species loss
544 and environmental perturbations, and for ecosystem management and restoration.
545 Eco-evolutionary theory definitely calls for more long-term and evolution-oriented
546 studies of BEF relationships.

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554 References

- 555 Abramsky, Z. & Rosenzweig, M.L. (1984) Tilman's predicted productivity–diversity rela-
556 tionship shown by desert rodents. *Nature*, **309**, 150–151.
- 557 Arnoldi, J.F., Loreau, M. & Haegeman, B. (2016) Resilience, reactivity and variability:
558 A mathematical comparison of ecological stability measures. *Journal of Theoretical*
559 *Biology*, **389**, 47–59.
- 560 Barabás, G. & D'Andrea, R. (2016) The effect of intraspecific variation and heritability on
561 community pattern and robustness. *Ecology Letters*, **19**, 977–986.
- 562 Bell, T., Newman, J.A., Silverman, B.W., Turner, S.L. & Lilley, A.K. (2005) The contribu-
563 tion of species richness and composition to bacterial services. *Nature*, **436**, 1157–1160.
- 564 Calcagno, V., Mouquet, N., Jarne, P. & David, P. (2006) Coexistence in a metacommunity:
565 the competition–colonization trade-off is not dead. *Ecology Letters*, **9**, 897–907.
- 566 Calcagno, V., Jarne, P., Loreau, M., Mouquet, N. & David, P. (2017) Diversity spurs
567 diversification in ecological communities. *Nature Communications*, **8**, 15810.
- 568 Chave, J., Muller-Landau, H.C. & Levin, S.A. (2002) Comparing classical community
569 models: theoretical consequences for patterns of diversity. *The American Naturalist*,
570 **159**, 1–23.
- 571 Christiansen, F.B. (1991) On Conditions for Evolutionary Stability for a Continuously
572 Varying Character. *The American Naturalist*, **138**, 37–50.
- 573 David, P., Thébault, E., Anneville, O., Duyck, P.F., Chapuis, E. & Loeuille, N. (2017)
574 Chapter one - Impacts of invasive species on food webs: a review of empirical data.
575 *Networks of Invasion: A Synthesis of Concepts* (eds. D.A. Bohan, A.J. Dumbrell &
576 F. Massol), vol. 56 of *Advances in Ecological Research*, pp. 1 – 60. Academic Press.
- 577 Davis, M.B., Shaw, R.G. & Etterson, J.R. (2005) Evolutionary responses to changing
578 climate. *Ecology*, **86**, 1704–1714.
- 579 Davis, M.A. (2009) *Invasion Biology*. OUP Oxford.
- 580 Doebeli, M. & Dieckmann, U. (2000) Evolutionary Branching and Sympatric Speciation
581 Caused by Different Types of Ecological Interactions. *The American Naturalist*, **156**,
582 S77–S101.
- 583 Elton, C. (1958) *Ecology of invasions by plant and animals*. Chapman and Hall, London.
- 584 Faillace, C.A. & Morin, P.J. (2016) Evolution alters the consequences of invasions in ex-
585 perimental communities. *Nature Ecology & Evolution*, **1**, 0013.
- 586 Fiegna, F., Moreno-Letelier, A., Bell, T. & Barraclough, T.G. (2014) Evolution of species
587 interactions determines microbial community productivity in new environments. *The*
588 *Isme Journal*, **9**, 1235–1245.
- 589 Fiegna, F., Scheuerl, T., Moreno-Letelier, A., Bell, T. & Barraclough, T.G. (2015) Satur-
590 ating effects of species diversity on life-history evolution in bacteria. *Proceedings of the*
591 *Royal Society B-Biological Sciences*, **282**, 20151794.

- 592 Gagic, V., Bartomeus, I., Jonsson, T., Taylor, A., Winqvist, C., Fischer, C. & et al.
593 (2015) Functional identity and diversity of animals predict ecosystem functioning better
594 than species-based indices. *Proceedings of the Royal Society B: Biological Sciences*, **282**,
595 20142620.
- 596 Gamfeldt, L., Lefcheck, J.S., Byrnes, J.E.K., Cardinale, B.J., Duffy, J.E. & Griffin, J.N.
597 (2015) Marine biodiversity and ecosystem functioning: what's known and what's next?
598 *Oikos*, **124**, 252–265.
- 599 Gross, K., Cardinale, B.J., Fox, J.W., Gonzalez, A., Loreau, M., Wayne Polley, H. & et al.
600 (2014) Species richness and the temporal stability of biomass production: a new analysis
601 of recent biodiversity experiments. *The American Naturalist*, **183**, 1–12.
- 602 Hart, S.P., Turcotte, M.M. & Levine, J.M. (2019) Effects of rapid evolution on species
603 coexistence. *Proceedings of the National Academy of Sciences USA*, **116**, 2112–2117.
- 604 Hector, A., Dobson, K., Minns, A., Bazeley-White, E. & Hartley Lawton, J. (2001) Com-
605 munity diversity and invasion resistance: an experimental test in a grassland ecosystem
606 and a review of comparable studies. *Ecological Research*, **16**, 819–831.
- 607 Hendry, A.P. (2016) *Eco-evolutionary Dynamics*. Princeton University Press.
- 608 Hooper, D.U., Chapin III, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S. & et
609 al. (2005) Effects of biodiversity on ecosystem functioning: a consensus of currents
610 knowledge. *Ecological Monographs*, **75**, 3–35.
- 611 Hooper, D.U., Adair, E.C., Cardinale, B.J., Byrnes, J.E.K., Hungate, B.A., Matulich, K.L.
612 & et al. (2012) A global synthesis reveals biodiversity loss as a major driver of ecosystem
613 change. *Nature*, **486**, 105–108.
- 614 Isbell, F., Calcagno, V., Hector, A., Connolly, J., Harpole, W.S., Reich, P.B. & et al. (2011)
615 High plant diversity is needed to maintain ecosystem services. *Nature*, **477**, 199–202.
- 616 Ives, A.R., Gross, K. & Klug, J.L. (1999) Stability and variability in competitive com-
617 munities. *Science*, **286**, 542–544.
- 618 Ives, A.R. & Carpenter, S.R. (2007) Stability and diversity of ecosystems. *Science*, **317**,
619 58–62.
- 620 Jaynes, E.T. (1957) Information theory and statistical mechanics. *Phys. Rev.*, **106**, 620–
621 630.
- 622 Jousset, A., Eisenhauer, N., Merker, M., Mouquet, N. & Scheu, S. (2016) High functional
623 diversity stimulates diversification in experimental microbial communities. *Science Ad-
624 vances*, **2**, e1600124.
- 625 Kleynhans, E.J., Otto, S.P., Reich, P.B. & Vellend, M. (2016) Adaptation to elevated CO₂
626 in different biodiversity contexts. *Nature Communications*, **7**, 12358.
- 627 Kylafis, G. & Loreau, M. (2011) Niche construction in the light of niche theory. *Ecology
628 Letters*, **14**, 82–90.
- 629 Levine, J.M. (2000) Species diversity and biological invasions: relating local process to
630 community pattern. *Science*, **288**, 852–854.

- 631 Loeuille, N. (2010) Influence of evolution on the stability of ecological communities. *Ecology*
632 *Letters*, **13**, 1536–1545.
- 633 Loeuille, N. & Loreau, M. (2005) Evolutionary emergence of size-structured food webs.
634 *Proceedings of the National Academy of Sciences USA*, **102**, 5761–5766.
- 635 Loreau, M. (1998) Biodiversity and ecosystem functioning: a mechanistic model. *Proceed-*
636 *ings of the National Academy of Sciences USA*, **95**, 5632–5636.
- 637 Loreau, M. (2010) *From populations to ecosystems*. Princeton University Press. ISBN
638 978-0-691-12269-4.
- 639 Loreau, M. & Hector, A. (2001) Partitioning selection and complementarity in biodiversity
640 experiments. *Nature*, **412**, 72–76.
- 641 Loreau, M. & Mazancourt, C.d. (2013) Biodiversity and ecosystem stability: a synthesis
642 of underlying mechanisms. *Ecology Letters*, **16**, 106–115.
- 643 May, R.M. (1973) Stability in randomly fluctuating versus deterministic environments. *The*
644 *American Naturalist*, **107**, 621–650.
- 645 Mazancourt, C.D., Johnson, E. & Barraclough, T.G. (2008) Biodiversity inhibits species'
646 evolutionary responses to changing environments. *Ecology Letters*, **11**, 380–388.
- 647 McCann, K.S. (2000) The diversity-stability debate. *Nature*, **405**, 228–233.
- 648 Meilhac, J., Deschamps, L., Maire, V., Flajoulot, S. & Litrico, I. (2020) Both selection
649 and plasticity drive niche differentiation in experimental grasslands. *Nature Plants*, **6**,
650 28–33.
- 651 Meyer, S.T., Anne, E., Nico, E., Lionel, H., Helmut, H., Alexandru, M. & et al. (2016)
652 Effects of biodiversity strengthen over time as ecosystem functioning declines at low and
653 increases at high biodiversity. *Ecosphere*, **7**, e01619.
- 654 van Moorsel, S.J., Hahl, T., Wagg, C., De Deyn, G.B., Flynn, D.F.B., Zuppinger-Dingley,
655 D. & Schmid, B. (2018) Community evolution increases plant productivity at low di-
656 versity. *Ecology Letters*, **21**, 128–137.
- 657 Mora, B.B., Gravel, D., Gilarranz, L.J., Poisot, T. & Stouffer, D.B. (2018) Identifying
658 a common backbone of interactions underlying food webs from different ecosystems.
659 *Nature Communications*, **9**, 2603.
- 660 Mouquet, N., Moore, J.L. & Loreau, M. (2002) Plant species richness and community
661 productivity: why the mechanism that promotes coexistence matters. *Ecology Letters*,
662 **5**, 56–65.
- 663 Naeem, S., Thompson, L.J., Lawler, S.P., Lawton, J.H. & Woodfin, R.M. (1994) Declining
664 biodiversity can alter the performance of ecosystems. *Nature*, **368**, 734–737.
- 665 Pennekamp, F., Pontarp, M., Tabi, A., Altermatt, F., Alther, R., Choffat, Y. & et al.
666 (2018) Biodiversity increases and decreases ecosystem stability. *Nature*, **563**, 109–112.
- 667 Pimm, S.L., Jenkins, C.N., Abell, R., Brooks, T.M., Gittleman, J.L., Joppa, L.N. & et
668 al. (2014) The biodiversity of species and their rates of extinction, distribution, and
669 protection. *Science*, **344**, 1246752.

- 670 Reich, P.B., Tilman, D., Isbell, F., Mueller, K., Hobbie, S.E., Flynn, D.F.B. & et al. (2012)
671 Impacts of biodiversity loss escalate through time as redundancy fades. *Science*, **336**,
672 589–592.
- 673 Renard, D. & Tilman, D. (2019) National food production stabilized by crop diversity.
674 *Nature*, **571**, 257–260.
- 675 Rummel, J.D. & Roughgarden, J. (1985) A theory of faunal buildup for competition com-
676 munities. *Evolution*, **39**, 1009–1033.
- 677 Scheuerl, T., Hopkins, M., Nowell, R.W., Rivett, D.W., Barraclough, T.G. & Bell, T.
678 (2020) Bacterial adaptation is constrained in complex communities. *Nature Communi-*
679 *cations*, **11**, 754.
- 680 terHorst, C.P., Zee, P.C., Heath, K.D., Miller, T.E., Pastore, A.I., Patel, S. & et al. (2018)
681 Evolution in a community context: trait responses to multiple species interactions. *The*
682 *American Naturalist*, **191**, 368–380.
- 683 Thompson, J.N. (1998) Rapid evolution as an ecological process. *Trends in Ecology &*
684 *Evolution*, **13**, 329–332.
- 685 Tilman, D. (1994) Competition and Biodiversity in Spatially Structured Habitats. *Ecology*,
686 **75**, 2–16.
- 687 Tilman, D. (1999) The ecological consequences of changes in biodiversity: a search for
688 general principles. *Ecology*, **80**, 1455–1474.
- 689 Tilman, D., Wedin, D. & Knops, J. (1996) Productivity and sustainability influenced by
690 biodiversity in grassland ecosystems. *Nature*, **379**, 718–720.
- 691 Vasconcelos, P. & Rueffler, C. (2020) How Does Joint Evolution of Consumer Traits Affect
692 Resource Specialization? *The American Naturalist*, **195**, 331–348.
- 693 Zuppinge-Dingley, D., Schmid, B., Petermann, J.S., Yadav, V., De Deyn, G.B. & Flynn,
694 D.F.B. (2014) Selection for niche differentiation in plant communities increases biod-
695 iversity effects. *Nature*, **515**, 108–111.

Figures

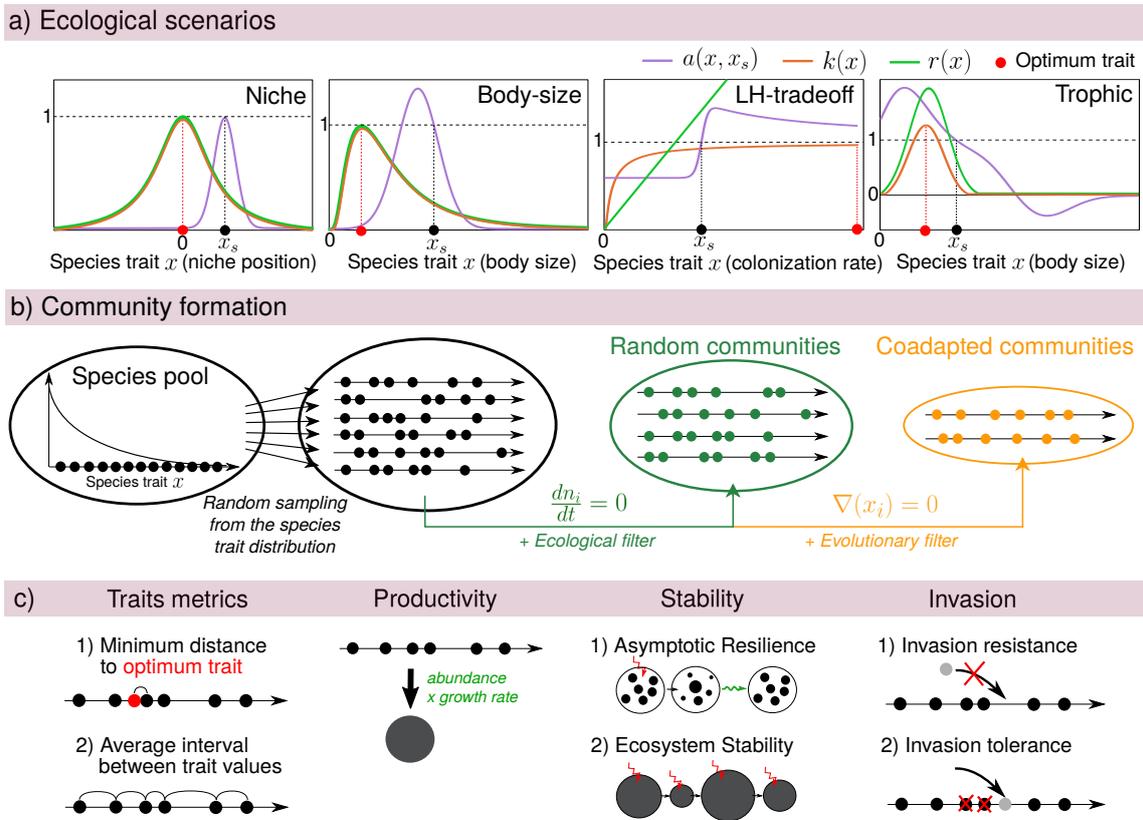


Fig. 1

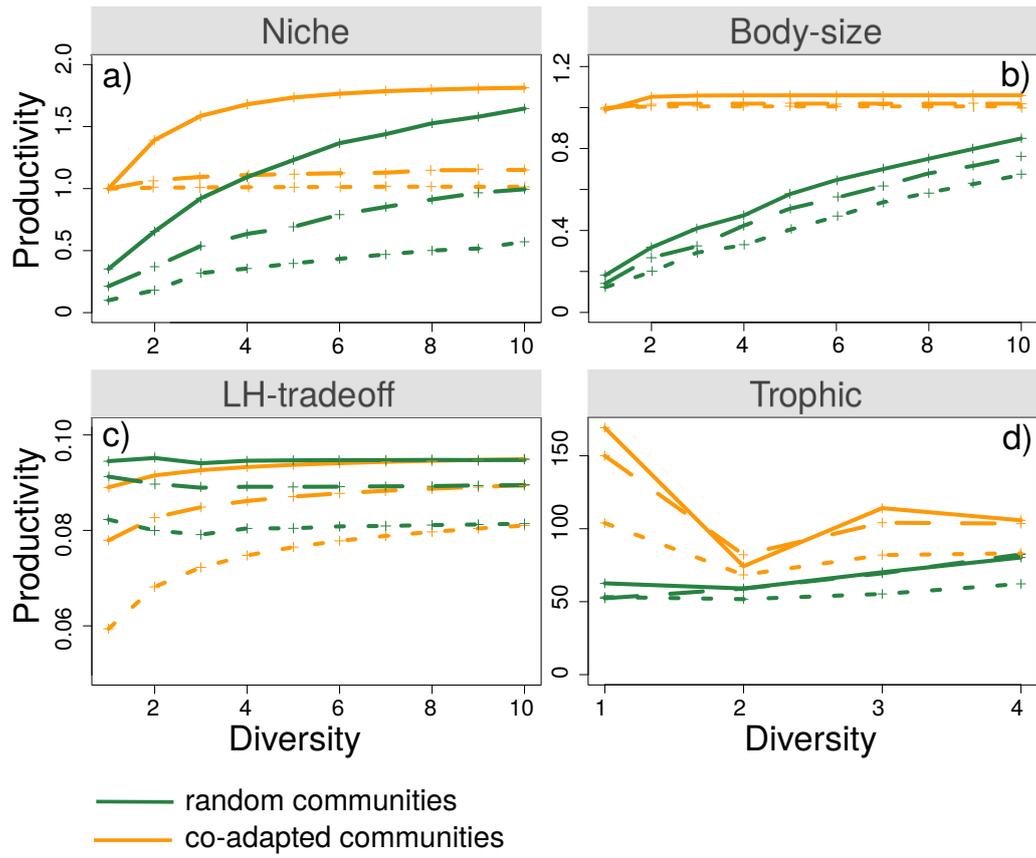


Fig. 2

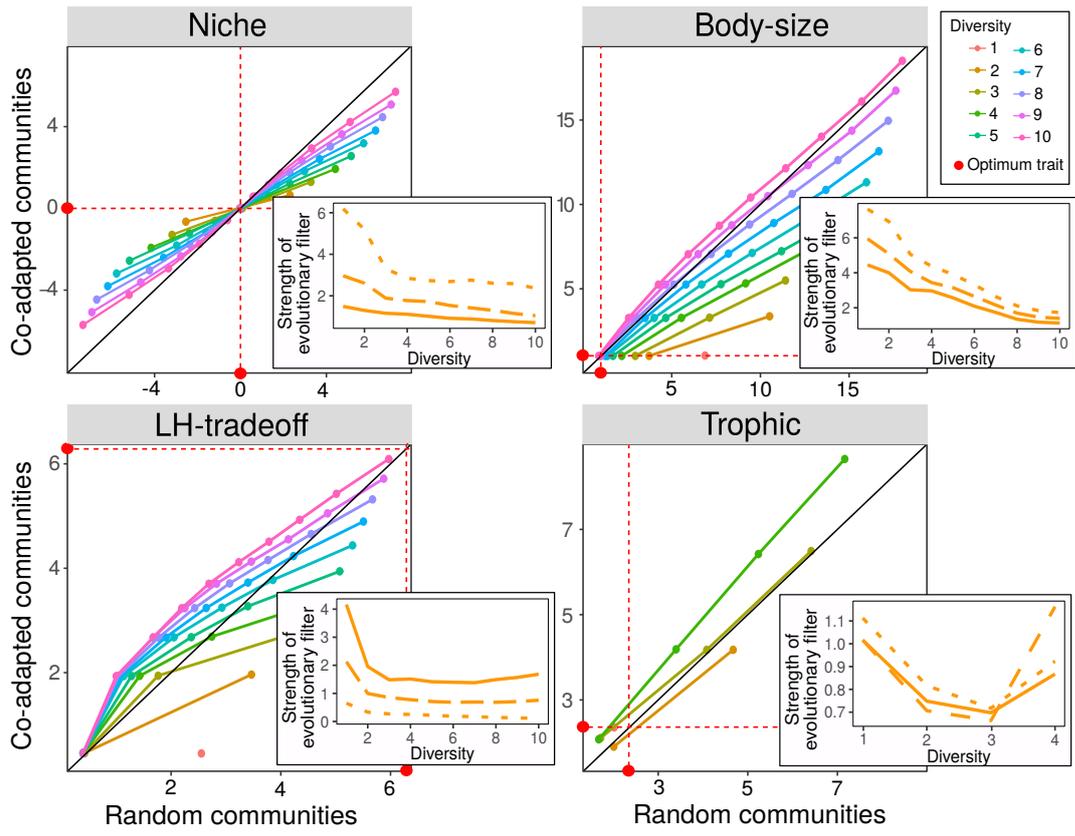


Fig. 3

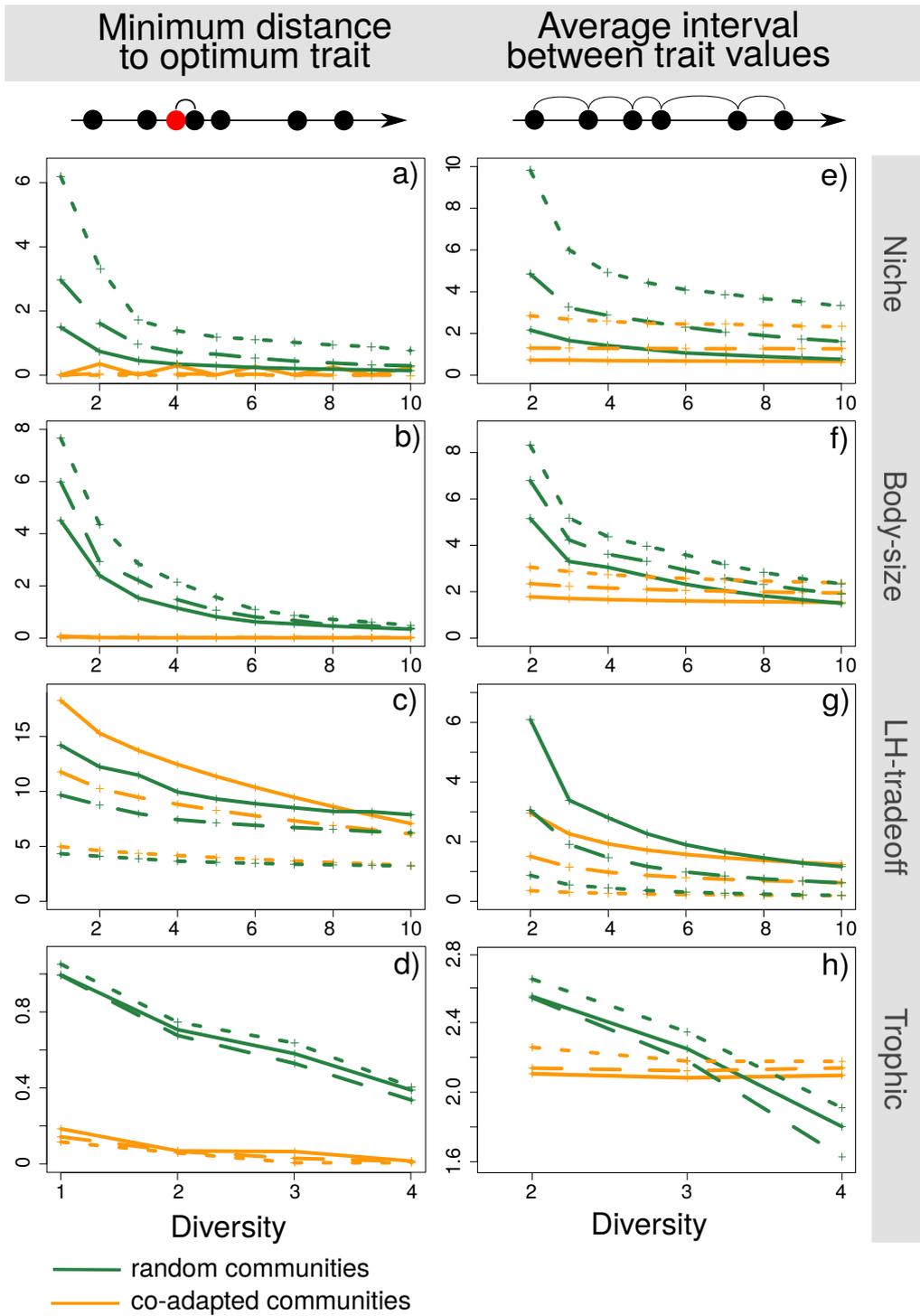


Fig. 4

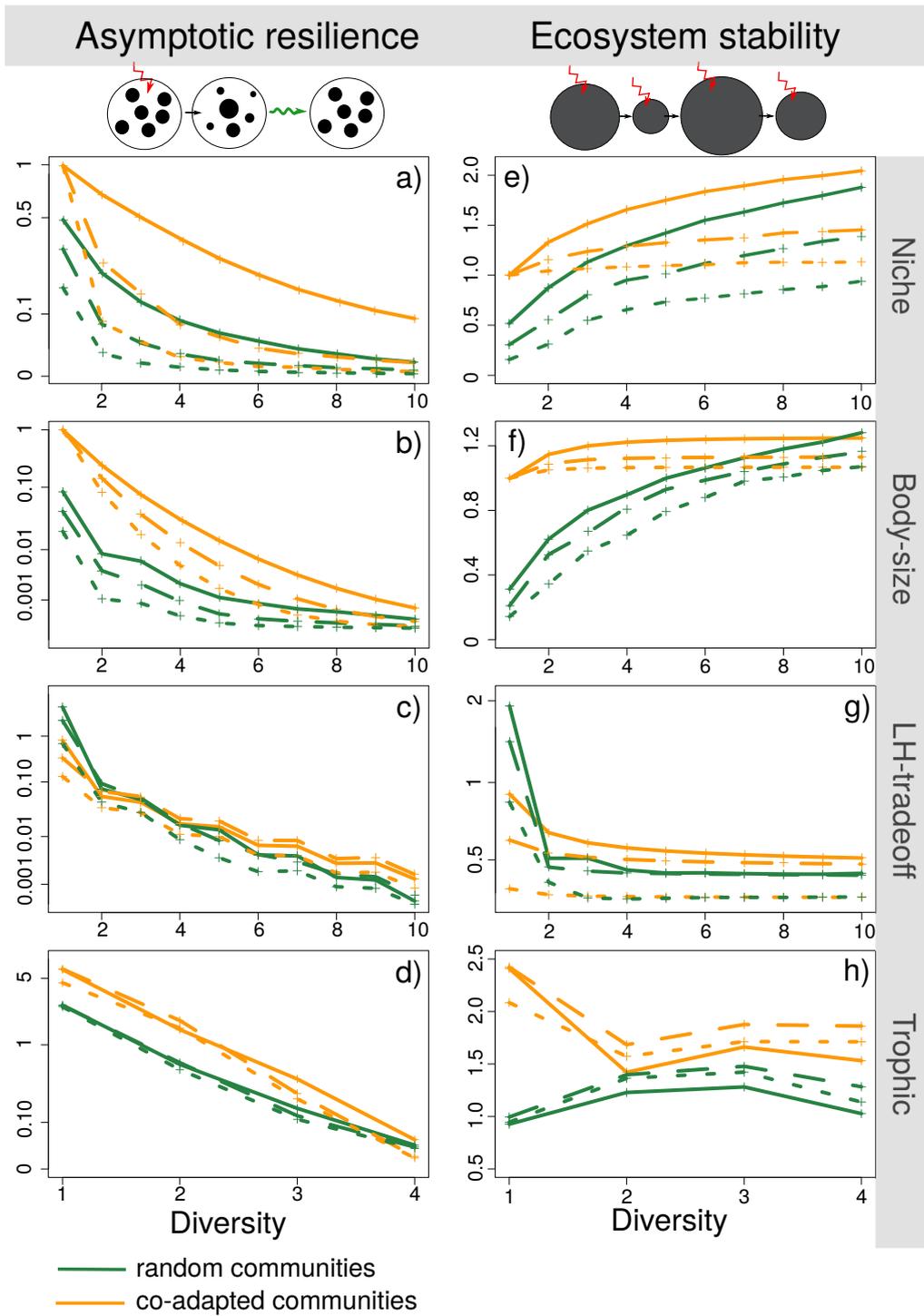


Fig. 5

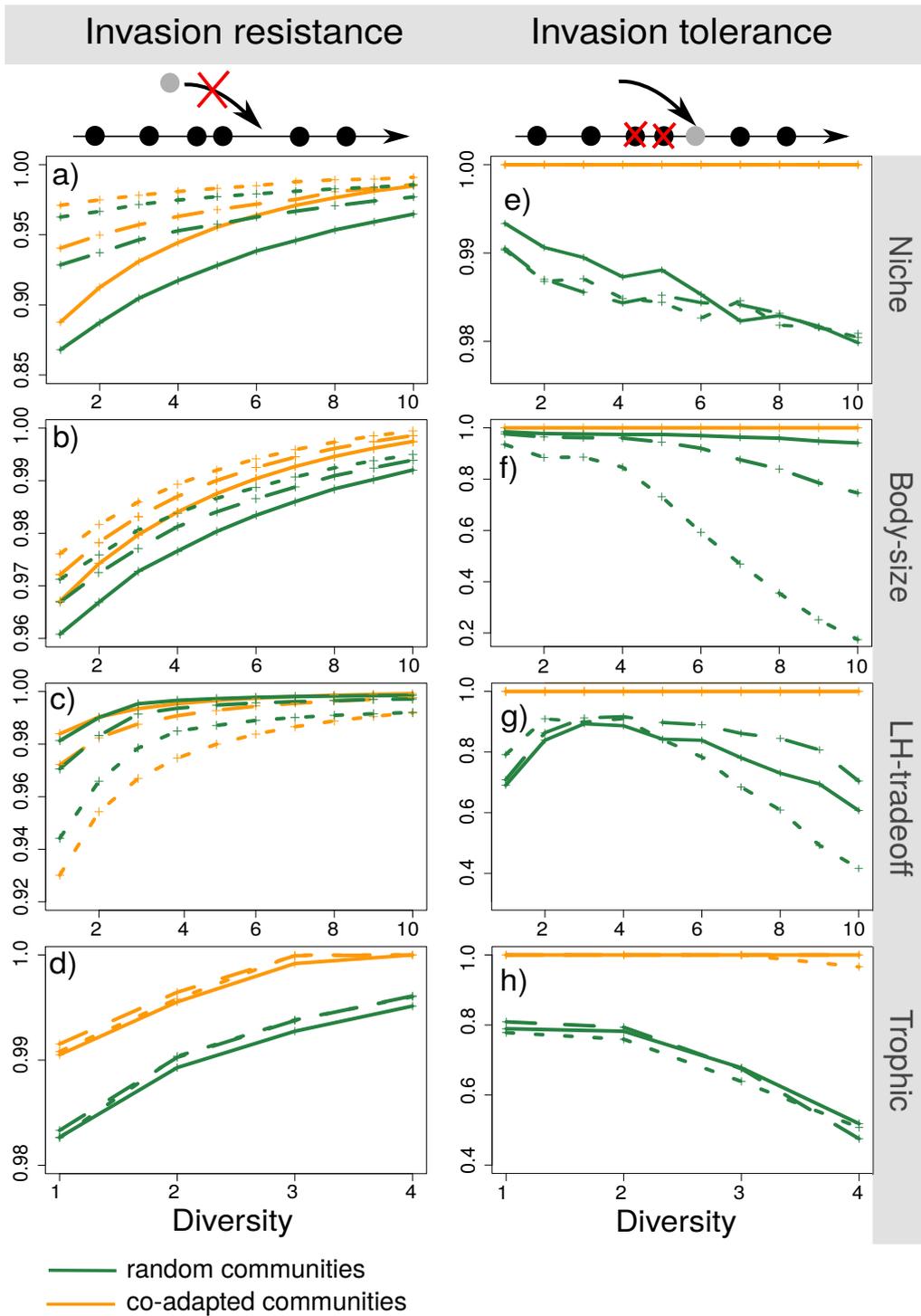


Fig. 6

697 Captions

698 **Fig. 1** (a) Ecological parameters for the four scenarios considered: intrinsic growth
699 rate $r(x)$ (green), mono-specific abundance $k(x)$ (orange) and competitive impact
700 $a(x, x_s)$ (purple) of species x_s over species x as a function of species trait x for the
701 four scenarios. By definition the intra-specific competition is $a(x_s, x_s) = 1$. Red dots
702 indicate the optimum ecological trait, *i.e.* trait that maximizes mono-specific abund-
703 ances. (b) Community formation. Species are sampled from a species pool within a
704 given distribution. An ecological filter is then applied so that only the ecologically
705 existing communities are kept (with no null abundance), and form the random com-
706 munities. Then, species evolution towards their evolutionary equilibrium filters out
707 some species, leading to co-adapted communities. (c) For each community (random
708 or co-adapted), we measure two species trait metrics (minimum distance to optimum
709 trait, and average interval between trait values) and the three types of functioning
710 properties: (i) productivity measured by species abundances time species growth
711 rates, (ii) stability, with asymptotic resilience (return rate to equilibrium) and eco-
712 system stability (reflecting changes in abundances over time), and (iii) response to
713 invasion, with invasion resistance (probability of non-establishment of a foreign spe-
714 cies) and tolerance to invasion (probability of non resident extinction following an
715 invasion).

716 **Fig. 2** Productivity as a function of diversity under the the four scenarios and
717 the two community adaptation levels. Three sets of parameters are used for each
718 scenario, represented by the three different line types. Parameter values are given in
719 S.I. Section 2 together with other explored parameter sets (not shown for the sake
720 of clarity). Each point represents an average over 1000 random communities or the
721 only or few co-adapted communities.

722

723 **Fig. 3** Comparative structures of random and co-adapted communities, in the four
724 ecological scenarios. For each diversity level, species were ranked by trait value, and
725 trait values at each species rank were averaged over all communities. The average
726 trait values at each species rank in co-adapted communities was plotted against the
727 corresponding values in random communities, and connected with colored lines for
728 each diversity level (see legend). As a consequence, lines close to the first diagonal
729 indicate very similar trait compositions in the two community types. Slopes smaller
730 than one indicate greater trait dispersion in random than in co-adapted communit-
731 ies, while slopes greater than one indicate the opposite. Only one parameter set was
732 showed in each scenario (the one corresponding to the wide dotted lines in other
733 figures), for clarity, as patterns are similar in other parameter sets. Optimal trait
734 values (see Fig. 1) are also shown on both axes (red dots). In inserts, we represented
735 the strength of the evolutionary filter as a function of diversity, for all three para-
736 meter sets (each with a different line type). This was computed as the absolute trait
737 difference between random and co-adapted communities, per species rank, averaged
738 over all ranks and all communities.

739 **Fig. 4** Minimum distance to optimum trait (a-d) and average interval between trait
740 values (e-h) as a function of diversity under the four scenarios and the two types of
741 communities. Three sets of parameters are used for each scenario, represented by
742 the three different line types. Parameter values are given in S.I. Section 2 together
743 with other explored parameter sets (not shown for the sake of clarity). Each point
744 represents an average over 1000 random communities or the only or few co-adapted
745 communities.

746 **Fig. 5** Asymptotic resilience (a-d) and ecosystem stability (e-h) as a function
747 of diversity under the four scenarios and the two community adaptation levels.
748 Asymptotic resilience is represented in log-scale, which does not modify the inter-
749 pretation on co-adaptation effect and allows to better visualize the consequences of

750 co-adaptation. Three sets of parameters are used for each scenario, represented by
751 the three different line types. Parameter values are given in S.I. Section 2 together
752 with other explored parameter sets (not shown for the sake of clarity). Each point
753 represents an average over 1000 random communities or the only or few co-adapted
754 communities.

755 **Fig. 6** Probability that a foreign species does not get installed into a community,
756 i.e. resistance to invasion (a-e), and proportion of resident species that do not
757 undergo a secondary extinction, i.e. tolerance to invasion (f-j), as a function of
758 diversity, under the four scenarios and the two community adaptation levels. Three
759 sets of parameters are used for each scenario, represented by the three different line
760 types. Parameter values are given in S.I. Section 2 together with other explored
761 parameter sets (not shown for the sake of clarity). Each point represents an average
762 over 1000 random communities or the only or few co-adapted communities.

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Supporting Information

How community adaptation affects biodiversity-ecosystem functioning relationships

Flora Aubree, Patrice David, Philippe Jarne,
Michel Loreau, Nicolas Mouquet, & Vincent Calcagno.

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1 Modelling of the four ecological scenarios

Preliminary remark: the first three ecological scenarios are models that have already been used and presented in several earlier works, such as Calcagno *et al.* (2017). More information on these can thus be found in the latter reference; only the main elements will be provided here, for easier reading. The fourth scenario is a new model derived from, and almost identical to, the size-structured trophic chain model introduced by and studied by simulation methods in Loeuille & Loreau (2005). Therefore we will provide here its mathematical derivation.

1.1 NICHE SCENARIO

This scenario represents the tendency of species to exploit different parts of a resource spectrum (Dieckmann & Doebeli, 1999; Calcagno *et al.*, 2017). It models a symmetric competition along a continuum of resources, such as a range of seed sizes for granivorous birds. Trait x here represents the average position of a species along that gradient, *i.e.* mean niche position (*e.g.* mean beak size). The model is usually directly formulated under a Lotka-Voltera form represented by equation (1):

$$\frac{dn_i}{dt} = r_i n_i f_i = r_i n_i \left(1 - \sum_j \frac{n_j a_{i,j}}{k_i} \right) \quad (1)$$

where $a_{i,j} = a(x_i, x_j)$ is the impact that a variation in species j abundance has on the per capita growth rate of species i ($\frac{1}{n_i} \frac{dn_i}{dt}$), normalized by the intra-specific interaction (so that $a_{i,i} = 1$). The closer species traits (*i.e.* the more similar resources species consume), the stronger competitive impact between them. It results that the competition is a decreasing function of the trait difference between two species, taking maximum value 1 when the two species have identical niche position. Function $a(x_i, x_j)$ is following general practice taken to be Gaussian with width s_a .

$$a(x_i, x_j) = \exp \left(\frac{-(x_i - x_j)^2}{s_a^2} \right) \quad (2)$$

The carrying capacity function $k_i = k(x_i)$ describes the distribution of resources available along the resource gradient, and is classically supposed to have a symmetric dome-shaped distribution centered on some optimal trait value (0 for convenience). Following Calcagno *et al.* (2017), in order to avoid some degenerate mathematical properties we use a Lorentzian function of width s_k

$$k(x) = \frac{1}{1 + x^2/s_k^2} \quad (3)$$

Last, $r_i = r(x_i)$ is the intrinsic growth rate of species i that governs the ecological timescale, and is taken to be proportional to the mono-specific abundance $r(x) = k(x)$. The shape of the three functions presented above are represented in Fig. 1a in the main article.

59 Parameter s_a is varied in the simulation, over the range presented in section 2, while
 60 parameter s_k has been kept constant equal to 1.

61 1.2 BODY-SIZE SCENARIO

62 This second scenario (Rummel & Roughgarden, 1985) is an extension of the *niche*
 63 model in which asymmetric competition between species is used instead of symmetric
 64 competition. In this case, species trait can represents for instance species body size. It
 65 is represented by the same equation (1), with different competitive, carrying capacity
 66 and intrinsic growth rate functions. As in Calcagno *et al.* (2017), we use a log-normal
 67 carrying capacity function:

$$k(x) = \exp(-\log(x)^2) \quad (4)$$

68 and an asymmetric Gaussian competitive function:

$$a(x_i, x_j) = \exp(d^2/s_a^2) \exp\left(\frac{-(x_i - x_j + d)^2}{s_a^2}\right) \quad (5)$$

69 with s_a controlling the competitive function width, and d the level of asymmetry. The
 70 intrinsic growth rate is also taken proportional to function k : $r(x) = k(x)$. The form
 71 of those functions are represented in Fig. 1a in the main article.

72 Parameters s_a and d are varied in the simulation, over the range presented in section
 73 2.

74 1.3 LIFE HISTORY TRADE-OFF SCENARIO

75 This scenario rests on a patch-occupancy model describing the competition between
 76 species in a meta-community, arranged in a competitive hierarchy. There is a trade-off
 77 between colonization ability at the regional scale and competitive dominance at a local
 78 scale (Calcagno *et al.*, 2006, 2017).

79 The patch-occupancy equation given in Calcagno *et al.* (2006) can easily be rewritten
 80 under the same Lotka-Volterra form as in the two first scenarios (eq. 1) as detailed in
 81 Calcagno *et al.* (2017). The corresponding three functions $a(x_i, x_j)$, $k(x)$ and $r(x)$ are
 82 represented Fig. 1a of the main article and are defined as:

$$a(x_i, x_j) = 1 + x_j \frac{\eta(x_j - x_i)}{x_i - \eta(x_i - x_j)} \quad (6)$$

$$k(x_i) = N - \mu/x_i \quad (7)$$

$$r(x_i) = x_i N - \mu \quad (8)$$

83 with η a logistic function relating the probability to win competition for a patch and
 84 the difference in colonization abilities; see Calcagno *et al.* (2017) for the full derivation.

85 Parameters α (trade-off intensity, *i.e.* the steepness of the logistic function η) and
 86 γ (the preemption level, *i.e.* the maximum value of function η) were both varied,
 87 over the range presented in section 2. Parameters N (total amount of patches in the
 88 metacommunity) and μ (patch extinction rate) were kept fixed to $N = 1$ and $\mu = 0.1$.

89 1.4 TROPHIC SCENARIO: DERIVATION OF THE LOTKA-VOLTERRA FORM

90 This scenario presents a vertical trophic interaction, with species arranged in a trophic
 91 chain structured by body mass. Body mass is thus the species trait x . This model is
 92 taken from Loeuille & Loreau (2005) and reads:

$$\frac{1}{n_i} \frac{dn_i}{dt} = f(x_i) \sum_{j=0} \gamma(x_i - x_j) n_j - m(x_i) - \sum_{j=1} \beta(x_i - x_j) n_j - \sum_{j=1} \gamma(x_j - x_i) n_j \quad (9)$$

93 with n_i the biomass of species i . Index $i = 0$ corresponds to the basal resource, and
 94 its trait x_0 does not evolve. The first term in the right-hand side corresponds to the
 95 consumption by species i of species lower into the trophic chain, and fourth term of the
 96 consumption of species i by species higher in the chain. The consumption rate function
 97 $\gamma(x_i - x_j)$ is a Gaussian of width (standard deviation) s , and taking maximum value
 98 when species biomasses differ by some interval d .

$$\gamma(x_i - x_j) = \frac{\gamma_0}{s\sqrt{2\pi}} \exp\left(\frac{-(x_i - x_j - d)^2}{s^2}\right)$$

99 for $x_i > x_j$. Birth function f depends on species size. The second term of equation
 100 (9) is mortality rate, also depending on species size. Following Loeuille & Loreau
 101 (2005), the size dependence of the birth and mortality rates reads $f(x_i) = f_0 x_i^{-0.25}$ and
 102 $m(x_i) = m_0 x_i^{-0.25}$. Finally, the third term corresponds to competition by interference
 103 between species of similar size. Function β is the competition by interference rate. It
 104 is a gaussian of width s_a and height b (competition intensity):

$$\beta(x_i - x_j) = b \exp\left(-\frac{(x_i - x_j)^2}{s_a^2}\right)$$

105 This model is a consumer-resource model with an abiotic compartment, but using
 106 a mass balance hypothesis, *i.e.* $\sum_{j=0} n_j = N_{tot}$, (mass conservation: Leibold, 1996), it
 107 can be, as the previous scenarios, reformulated under the Lotka-Volterra form (equation
 108 1). Starting from the original equation (9):

$$\frac{1}{n_i} \frac{dn_i}{dt} = f(x_i) \sum_{j=0} \gamma(x_i - x_j) n_j - m(x_i) - \sum_{j=1} \beta(x_i - x_j) n_j - \sum_{j=1} \gamma(x_j - x_i) n_j$$

109 in the first sum, we separate the first term ($j=0$) from the other ones ($j>0$):

$$\frac{1}{n_i} \frac{dn_i}{dt} = f(x_i)(\gamma(x_i - x_0)n_0 + \sum_{j=1} \gamma(x_i - x_j)n_j) - m(x_i) - \sum_{j=1} \beta(x_i - x_j)n_j - \sum_{j=1} \gamma(x_j - x_i)n_j$$

110 we then introduce the mass-balance constraint $n_0 = N_{tot} - \sum_{j=1} n_j$ and get, after a few
111 rearrangements:

$$\begin{aligned} \frac{1}{n_i} \frac{dn_i}{dt} = & f(x_i)\gamma(x_i - x_0)(N_{tot} - \sum_{j=1} n_j) \\ & + f(x_i) \sum_{j=1} n_j \gamma(x_i - x_j) - m(x_i) - \sum_{j=1} \beta(x_i - x_j)n_j - \sum_{j=1} \gamma(x_j - x_i)n_j \end{aligned}$$

112 we rearrange to get all the term summing over j together:

$$\begin{aligned} \frac{1}{n_i} \frac{dn_i}{dt} = & f(x_i)\gamma(x_i - x_0)N_{tot} - m(x_i) \\ & + \sum_{j=1} n_j [f(x_i)(\gamma(x_i - x_j) - \gamma(x_i - x_0)) - \beta(x_i - x_j) - \gamma(x_j - x_i)] \end{aligned}$$

113 and finally we factorize by $f(x_i)\gamma(x_i - x_0)N_{tot} - m(x_i)$ and get:

$$\begin{aligned} \frac{1}{n_i} \frac{dn_i}{dt} = & (f(x_i)\gamma(x_i - x_0)N_{tot} - m(x_i)) * \\ & \left(1 - \frac{\sum_{j=1} n_j [f(x_i)(\gamma(x_i - x_0) - \gamma(x_i - x_j)) + \beta(x_i - x_j) + \gamma(x_j - x_i)]}{f(x_i)\gamma(x_i - x_0)N_{tot} - m(x_i)} \right) \end{aligned}$$

114 which can be recognized as a Lotka-Volterra form with

$$r(x_i) = f(x_i)\gamma(x_i - x_0)N_{tot} - m(x_i) \quad (10)$$

115 so that:

$$\frac{1}{n_i} \frac{dn_i}{dt} = r(x_i) \left(1 - \frac{\sum_{j=1} n_j [f(x_i)(\gamma(x_i - x_0) - \gamma(x_i - x_j)) + \beta(x_i - x_j) + \gamma(x_j - x_i)]}{r(x_i)} \right)$$

116 and using the hypothesis that $a_{i,i} = 1$, we have:

$$\frac{a(x_i, x_i)}{k(x_i)} = \frac{1}{k(x_i)} = \frac{f(x_i)(\gamma(x_i - x_0) - \gamma(0)) + \beta(0) + \gamma(0)}{r(x_i)}$$

117 so that:

$$k(x_i) = \frac{r(x_i)}{f(x_i)(\gamma(x_i - x_0) - \gamma(0)) + \beta(0) + \gamma(0)} \quad (11)$$

118 Equation (9) now writes:

$$\frac{1}{n_i} \frac{dn_i}{dt} = r(x_i) \left(1 - \frac{\sum_{j=1} n_j [f(x_i)(\gamma(x_i - x_0) - \gamma(x_i - x_j)) + \beta(x_i - x_j) + \gamma(x_j - x_i)]}{k(x_i) (f(x_i)(\gamma(x_i - x_0) - \gamma(0)) + \beta(0) + \gamma(0))} \right)$$

119 so that function $a(x_i, x_j)$ writes:

$$a(x_i, x_j) = \frac{f(x_i)(\gamma(x_i - x_0) - \gamma(x_i - x_j)) + \beta(x_i - x_j) + \gamma(x_i - x_j)}{f(x_i)(\gamma(x_i - x_0) - \gamma(0)) + \beta(0) + \gamma(0)} \quad (12)$$

120 Those three functions are represented Fig. 1a in the main article. In this scenario,
 121 following Loeuille & Loreau (2005), we set $m_0 = 0.1$, $s_a = 1.5$, $\gamma_0 = 1$, $f_0 = 0.3$, $d = 2$,
 122 $x_0 = 0$ and we varied b (interference intensity) and s (consumption function width).
 123 Parameter values explored are given in section 2 below.

2 Parameter sets explored and those plotted in the main article figures

In each scenario, key parameters were varied in order to ensure that conclusions are robust to parameters changes.

- In the *Niche* scenario, the width s_a of the symmetric competition function $a(x_i, x_j)$ was varied from 0.5 to 1.5. In this scenario what matters is only the ratio of s_a over s_k , hence the two parameters need not be both varied. A value $s_a = 1$ thus means that the widths of the competition kernel and of the carrying capacity functions are identical ($s_a = s_k$).
- In the *Body-size* scenario, the width of the competition function (s_a) and the level of competitive asymmetry (d) were varied respectively from 1.2 to 2.4 and from 0.1 to 0.3.
- In the *LH-tradeoff* scenario, the preemption level (γ) and the trade-off intensity (α) were respectively varied from 0.3 to 0.7 and from 2 to 12.
- In the *Trophic* scenario, the level of competition by interference (b) and the width of the consumption function (s) were varied respectively from 0.10 to 0.19 and from 1.0 to 1.6.

The parameter ranges presented above have been explored from the minimum to the maximum value. For clarity, in the main article, only three curves corresponding to parameter combinations yielding representative and contrasted patterns were selected and shown in figures. The parameter combinations corresponding to each curve in Figures 2-5 are provided in table S1.

Legend	Niche	Body-size	LH-tradeoff	Trophic
—	$s_a = 0.5$	$s_a = 1.2, d = 0.1$	$\alpha = 2, \gamma = 0.3$	$s = 1.0, b = 0.10$
- - -	$s_a = 0.9$	$s_a = 1.5, d = 0.1$	$\alpha = 4, \gamma = 0.7$	$s = 1.0, b = 0.13$
- - - - -	$s_a = 1.5$	$s_a = 1.8, d = 0.1$	$\alpha = 12, \gamma = 0.7$	$s = 1.2, b = 0.10$

Table S1 Parameter sets used in the main text for the four scenarios. Legend line types refers to the line types used in the figures.

3 Algorithm of community formation

Co-adapted communities We assume that each species is characterized by its mean trait value x and possesses some (small) heritable variance around the latter. In these conditions, the direction and intensity of natural selection on the species trait can be determined by the selection gradient around the species trait value (Christiansen, 1991). The selection gradient is computed at the first derivative of the fitness (exponential rate of increase) of a rare variant with respect to its trait value, evaluated at the trait value of the focal species. The fitness of a rare variant with trait value x_m is defined as, from equation (1):

$$F(x_m) = \lim_{n_m \rightarrow 0} \left(\frac{1}{n_m} \frac{dn_m}{dt} \right) = r(x_m) \left(1 - \sum_j \frac{n_j a(x_m, x_j)}{k(x_m)} \right), \quad (13)$$

where all species are at their respective equilibrium abundance (Christiansen, 1991; Metz *et al.*, 1995). The selection gradient for the i -th species in the community is thus:

$$\nabla(x_i) = \left. \frac{dF(x_m)}{dx_m} \right|_{x_m=x_i} \quad (14)$$

If the selection gradient is positive, adaptive evolution pushes the trait value towards higher values, and if the gradient is negative, the trait moves to lower values, at a speed approximately proportional to the value of the gradient. Fitness and selection gradient are frequency- and density-dependent and change with the composition of the entire community. If the system reaches a state where the selection gradient cancels for all species, then directional evolution ceases and the community has reached a (co)evolutionary equilibrium (Christiansen, 1991; Abrams *et al.*, 1993). Note that at such an equilibrium individual species may be at an evolutionary maximum or at an evolutionary minimum. Evolutionary minima may under appropriate circumstances and inheritance modes favor the splitting of a species into two novel lineages (evolutionary branching) and thus an increase in the number of evolving lineages (Metz *et al.*, 1995; Dieckmann & Doebeli, 1999; Calcagno *et al.*, 2017). Since in this work we systematically consider all diversity levels, we can remain agnostic to second-order selection and to the specific history of transitions among diversity levels (that might involve branchings, invasions and extinctions). We just need to identify, for every diversity level, all feasible co-evolutionary equilibria, characterized by:

$$\nabla(x_i) = 0 \quad i \in [1, \dots, s] \quad (15)$$

For computational efficiency, for each ecological scenario and diversity level, we first identify the different coevolutionary equilibria that are attractors by iterating the adaptive dynamics of traits (defined by the selection gradient (14)) forward in time, starting from 100 random species trait values. From these we identify the one or several coevolutionary equilibria. Then, by continuation, we track these equilibria continuously through the range of parameter values, together with potential bifurcations (changes in

179 the number or nature of equilibria). This provides an exhaustive list of coevolutionary
 180 equilibria for all parameter combinations.

181 **Random communities** To assemble random communities, we randomly drew each
 182 species trait value, independently, from a common probability distribution. The latter
 183 distribution can be regarded as characterizing the available regional pool of species and
 184 trait values. This species pool distribution was chosen in order to allow all feasible
 185 trait values and to be as “random” as possible: specifically, it was chosen to minimize
 186 information content, using the maximum entropy principle (Jaynes, 1957). For each
 187 scenario, we first specified the support of the distribution, *i.e.* the range of possible
 188 values for species traits. We then specified only one additional constraint, for each
 189 parameter set: the mean trait value, that had to be representative of the species typ-
 190 ically expected for the given parameter set. Specifically, it was taken to be equal to
 191 the mean trait value λ that would be observed in the full (saturated) community. In
 192 practice, the co-adapted communities with maximum diversity levels were used as good
 193 approximations of the saturated communities. This constraint ensured that there is no
 194 systematic (average) difference between the random species trait values and the traits
 195 that are expected in the current environment, and thus to generate communities that
 196 remain of similar nature across parameter sets. This also allows to perform comparis-
 197 ons between co-adapted and random communities that are not biased by the fact that
 198 species in random communities would be, intrinsically, ill-adapted. Of course, with only
 199 one constraint on the mean value, max-entropy random distributions were quite broad
 200 and all trait values had a fair chance to be picked.

201 In the *Body-size*, *LH-tradeoff* and *Trophic* scenarios, species trait values x could
 202 take values in $]0, +\infty[$, and the entropy-maximizing distributions were thus exponential
 203 distributions of mean λ defined as explained above. In the *Niche* scenario, trait values
 204 can spread over $] - \infty, +\infty[$ and the model is by construction symmetric around $x = 0$.
 205 Thus the random trait distribution was a double exponential, centered on zero, and with
 206 width defined by the average deviation from zero observed in the saturated community.
 207 Values for λ are given in table S2. Remark that we also used a much more classical and
 208 simpler approach consisting in using uniform distributions for random traits, between
 209 some arbitrary defined minimum and maximum values. Results were similar, and are
 210 thus not qualitatively dependent on the precise random distributions used.

Legend	Niche	Body-size	LH-tradeoff	Trophic
—	1.52	7.63	7.35	5.10
- - -	3.35	9.65	3.71	5.15
- - - - -	6.48	11.9	1.17	5.33

Table S2 Mean trait values λ of the saturated communities, taken to define the entropy-maximising distributions. See table S1 for the correspondence between legend line types and the parameter sets used in the main text.

211 In practice, for each parameter set and diversity level (N), random communities
212 were formed by picking N traits from the species pool defined in the previous para-
213 graphs. The ecological equilibrium obtained from equation (1) was computed, and the
214 community was retained (ecological filter) if all N species persisted at equilibrium with
215 a positive abundance (*i.e.* had abundance above a threshold value of 10^{-5}). The pro-
216 cess was repeated until 1,000 such communities were obtained. Remark that co-adapted
217 communities (as defined in the previous section) are always a specific subset of random
218 communities, characterized by the additional constraint (15), as illustrated in Fig. 1 of
219 the main article.

220 **4 Metrics used to quantify diversity-functioning re-**
 221 **lationships**

222 For each BEF relationship, we computed several alternative metrics that may be used to
 223 quantify the corresponding ecosystem function. Several metrics gave identical or similar
 224 conclusions, and for clarity we retained only one or two metrics per BEF relationship
 225 that are more commonly used. A summary of all metrics can be found in Table S3
 226 to inform the reader that no different conclusion could be drawn from those various
 227 metrics. Then, in the following, for each BEF relationships, we describe the metric(s)
 228 effectively used for the results presented in the main text.

BEF relationship	Metrics	References
Production	Total abundance	(1)
	Productivity*	(1)
Stability	Asymptotic resilience*	(2) (3)
	Stochastic invariability	(3)
	Initial Resilience	(3)
	Ecosystem stability*	(4) (5)
	Robustness	(6)
	Robustness heterogeneity	(6)
Invasion	Deterministic invasion probability	(7) (8)
	Stochastic invasion probability*	(7) (8)
	Proportion of the invader	(7)
	Mean impact of an invader on abundances	(7)
	Proportion of species non extinct*	(7)

* Metrics retained in the main article

Table S3 Metrics measured on the two types of communities for different parameter sets. Metrics in bold types are the one plotted and analyzed in the main article. Each are representative of their categories of relationships. (1) Tilman *et al.* (1996) ; (2) May (1973a) ; (3) Arnoldi *et al.* (2016) ; (4) May (1973b) ; (5) Ives *et al.* (1999) ; (6) Barabás & D’Andrea (2016) ; (7) Elton (1958) ; (8) Hector *et al.* (2001)

229 4.1 PRODUCTIVITY

230 Community productivity is the summed productivity of each of the N component spe-
 231 cies.

$$\Pi = \sum_{i=1}^N n_i g_i \quad (16)$$

232 with g_i the per capita production rate of species i in its community whose expression
 233 depends on the ecological interaction and community composition.

234 For the *Niche* and *Body-size* scenarios, there is no explicit production rate since the
 235 models are directly formulated in Lotka-Volterra form. We made the simple choice of
 236 using the intrinsic growth-rate r_i as the metric per capita productivity so that :

$$\Pi_{Niche} = \sum_i n_i r_i$$

$$\Pi_{Body} = \sum_i n_i r_i$$

237 For the *LH-tradeoff* scenario, we consider the colonization of empty sites ($N - \sum_j n_j$)
 238 as a contributions to productivity. This leads to the per capita productivity:

$$g_{i,LH} = n_i x_i (N - \sum_j n_j)$$

239 and the total productivity is the sum over all species i :

$$\Pi_{LH} = \sum_i n_i g_{i,LH} = \sum_i n_i x_i (N - \sum_j n_j)$$

240 Finally for the *Trophic* scenario, the net growth rate is straightforward, simply
 241 referring to consumption by specie i of lower size species.

$$\Pi_{chain} = \sum_i n_i \left(f(x_i) \sum_{j=0} \gamma(x_i - x_j) n_j \right)$$

242

243

244 4.2 STABILITY

245 Asymptotic resilience is taken as a measure of species stability (May, 1973a; Arnoldi
 246 *et al.*, 2016). It refers to the asymptotic return speed of the slowest species to equilib-
 247 rium after an external abundance perturbation.

$$R_\infty = -\Re(\lambda_m(J)) \tag{17}$$

248 with $\lambda_m(J)$ the highest eigen value of the Jacobian matrix J of the ecological system
 249 whose coefficient are given by (18).

$$J_{i,j} = \frac{\partial}{\partial n_j} \left(\frac{dn_i}{dt} \right)^* \tag{18}$$

250 To get a measure of the all community stability, we consider the community variance,
 251 namely in the variance of the sum of abundances. This measure differs from individual

252 direction stability metrics such as the asymptotic resilience. The sum of abundances can
 253 return faster to its equilibrium value after a perturbation, even if species abundances
 254 are still fluctuating into the community. It is commonly expected (even if not general
 255 and depending on metrics) that species stability has more often a negative relationship
 256 with diversity while community stability tends to get a positive one. Mathematically,

$$\text{var}(N_T) = \sum_i \text{var}(n_i) + \sum_{i,j,j \neq i} \text{cov}(n_i, n_j)$$

257 with $N_T = \sum_{i=1}^S n_i$ the sum of each species abundance for a community with S species.
 258 The variance-covariance matrix B is involved into the equilibrium distribution for pop-
 259 ulation fluctuation in a stochastic environment (May, 1973b) and is the solution of the
 260 Lyapunov matrix equation (19) (see also Wang *et al.* (2015) for a similar derivation):

$$D = 1/2(BA + A^T B) \quad (19)$$

261 with $A = N^{-1} J N$ and N the diagonal matrix containing the equilibrium abundances of
 262 each species whose coefficients are $N_{i,i} = n_i^*$. A^T is A transpose, and D the matrix con-
 263 taining $D_{i,j}$ coefficient which are the overall covariance between white-noise fluctuations
 264 in the stochastic differential equation of species i and the one of species j :

$$\frac{dn_i}{dt} = r_i n_i \left(1 - \sum_j \frac{n_j a_{i,j}}{k_i} \right) + \sum_k \rho_{i,k} \gamma_k(t) n_k \quad (20)$$

265 with $\rho_{i,k}$ measuring the covariance between the environmental fluctuation for species i
 266 and for species j , and $\gamma_k(t)$ is environmental stochasticity in the growth rate of pop-
 267 ulation k at time t , taken as a white noise random fluctuation with variance σ^2 . $D_{i,j}$
 268 coefficients are the diffusion coefficient involved in the Fokker-Planck equation, which
 269 is the differential equation for the probability of transition in between two states of the
 270 system. In our case, we choose to put a perturbation in a white-noise form that has
 271 no inter-species dependence: $\rho_{i,i} = 1$ ($\forall i$) and $\rho_{i,k} = 0$ ($\forall i \neq k$), and D is a diagonal
 272 matrix. All individuals get the same amount of perturbation, so that each species is
 273 perturbed with an intensity that depends on its abundance. More precisely, the variance
 274 imposed on a given species is proportional to the squared of its abundance: $D_{i,i} = \sigma^2 n_i^2$.
 275 This derivation assumes sufficiently small perturbations around the equilibrium to get
 276 a local linearization of the system. To solve the continuous Lyapunov matrix equation
 277 (19), we use the *lyap()* function from Scilab. We then sum all the elements from the
 278 variance-covariance matrix B , and divide this sum by σ^2 (the variance of perturbation
 279 received by each individual, *e.g.* we normalize by the per individual perturbation). The
 280 coefficient of variation CV is defined by:

$$CV = \frac{\sqrt{\frac{\sum_{i,j} B_{i,j}}{\sigma^2}}}{N_T} \quad (21)$$

281 And the community stability metrics is defined by the inverse of CV . Actually, in the
 282 calculation, the value of sigma has no importance because we finally divide by the same
 283 quantity. We take it equal to 1.

284

285 4.3 RESPONSE TO INVASION

286 Two aspects of ecological invasion are considered: (i) the resistance to invasion and
 287 (ii) the tolerance to invasion. Resistance to invasion is defined as the probability that
 288 an alien species (randomly drawn from the regional pool and introduced at low initial
 289 abundance) does not successfully establishes in the community. The probability P_{instal}
 290 that this alien species establishes is:

$$P_{instal} = \int_{x_{min}}^{x_{max}} p_x(x_e) H_{st}(x_e) dx_e \quad (22)$$

291 with $p_x(x_e)$ the trait distribution probability, $H_{st}(x_e) = \begin{cases} \frac{s(x_e)}{b(x_e)} & \text{if } s(x_e) > 0 \\ 0 & \text{if not} \end{cases}$, x_e the
 292 trait of the foreign species which is trying to invade, $b(\cdot)$ the growth rate and $s(\cdot)$ the
 293 fitness function. The trait distribution probability is the same used to form the random
 294 communities (see section 3). Resistance to invasion is then defined by

$$R_{inv} = 1 - P_{instal}$$

295 Tolerance to invasion T_{inv} (eq. 23) is defined by the proportion of species, following
 296 a successful invasion, that are not driven to extinction by the invader:

$$T_{inv} = \frac{N_{final}}{N_{init}} \quad (23)$$

297 with N_{init} the number of species into the community right after the invasion, thus
 298 including the invasive species, and N_{final} the number of species into the community
 299 once ecological equilibrium has been recovered.

300 4.4 METRICS FOR TRAIT COMPOSITION

301 4.4.1 Trait composition representation

302 We sort communities by trait values, and calculate the average trait per rank over the
 303 1000 random communities (or few co-adapted communities when needed). For each
 304 diversity level with N specie, we thus obtain N random averaged trait, and N co-
 305 adapted averaged trait. Values obtained for co-adapted and random traits are plotted
 306 one against the other in Fig. 3 of the main article.

307 **4.4.2 Strength of evolutionary filter**

308 The strength of evolutionary filter is defined with trait difference in between random
309 and co-adapted communities. We sort communities by trait values. Then, for each
310 random community with N species, we calculated the trait difference between random
311 and co-adapted trait per rank, and we made the average over all N species ranks

$$\frac{1}{N} \sum_{i=1}^N |x_{i,coadapt} - x_{i,random}|$$

312 where i denotes the rank and $x_{i,coadapt}$ (resp. $x_{i,random}$) is the trait value for the i^{th} co-
313 adapted (resp.random) species. In the case of multiple co-adapted communities (*Niche*
314 scenario), we calculated the difference to the closest co-adapted community (which is
315 likely to be the evolutionary attractor corresponding to this random community).

316 **4.4.3 Minimum distance to the optimum trait**

317 In the *Niche*, *Body-size*, *TF-tradeoff* scenarios, the optimum trait value x_o is defined as
318 the trait corresponding to the maximum of function $k(x)$. In the *TF trade-off* scenario,
319 the trait value maximizing function $k(x)$ is infinite. We thus take as optimal value x_o
320 the 95th percentile of the species pool distribution defined for the community formation.
321 The minimum trait distance to the optimum is defined as:

$$\min_{i=1}^{N-1} (|x_i - x_o|)$$

322 **4.4.4 Average interval between species trait values**

323 The average interval between species traits is the average two-by-two trait distance:

$$\sum_{i=1}^{N-1} \frac{|x_{i+1} - x_i|}{N - 1}$$

324 with x_i the trait of species i and N the number of species into the community.

325 **5 Magnitude of the difference between random and** 326 **co-adapted communities**

327 In order to ascertain that co-adapted communities can be considered as different from
328 random communities, we measured the percentile of the metric for random communities
329 in which the mean value of the metric for co-adapted communities is (Fig. S1). In all
330 cases, co-adapted values stand above the 8th decile or below the 2nd decile of the
331 random values distribution, for at least part of the BEF relationship. This indicates
332 that co-adapted communities are quite atypical, relative the variability within random
333 communities.

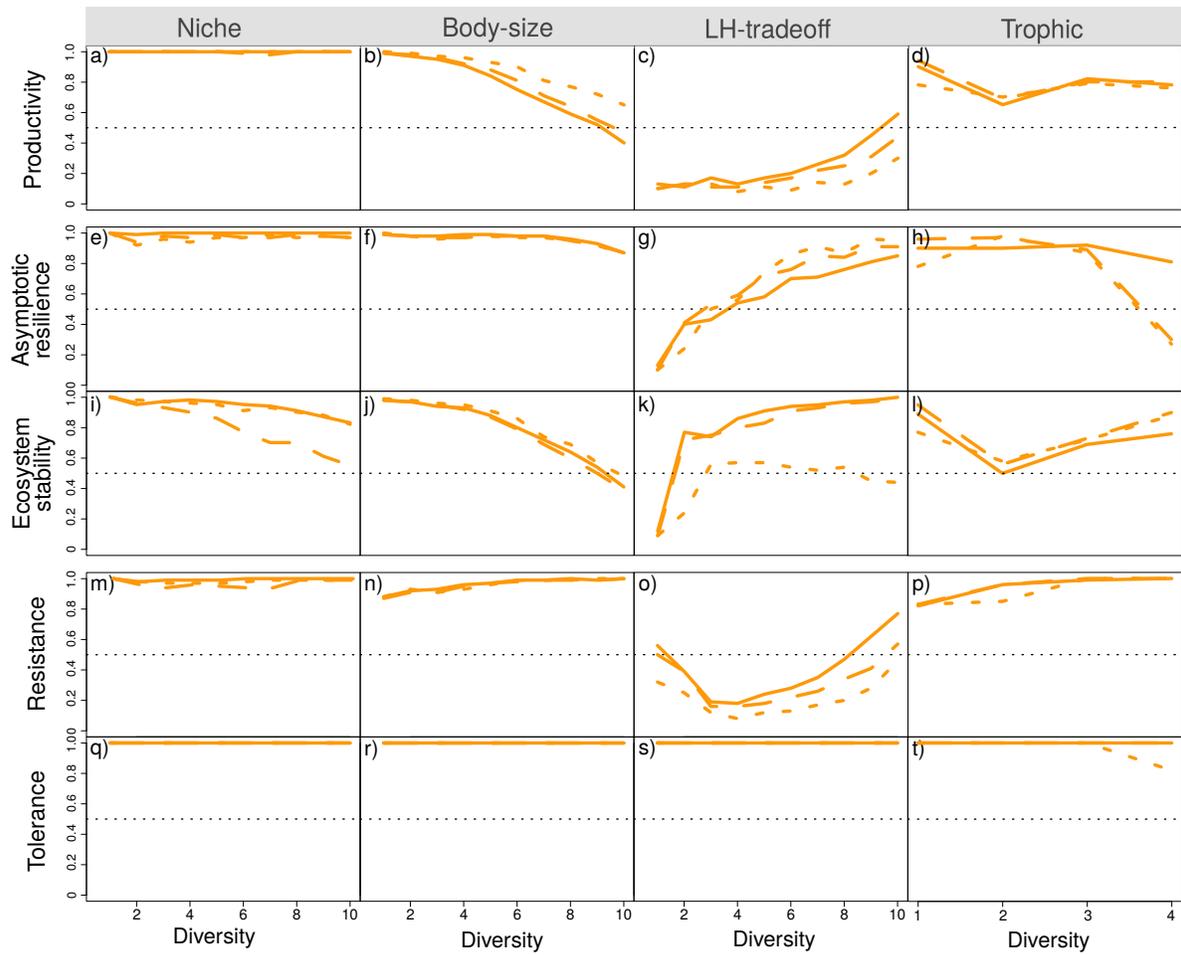


Fig. S1 Quantile Q_c of the metric for random communities in which the mean value of the metric for co-adapted communities is. It is measured for the four scenarios and 5 metrics explored (productivity a-d, asymptotic resilience e-h, ecosystem stability i-l, resistance m-p and tolerance q-t). The closest Q_c to 0.5, the more similar co-adapted and random communities regarding this metric. When Q_c is larger (resp. lower) than 0.5, the metric for co-adapted communities is larger (resp. lower) than for random communities. Ecological interaction parameters set are varied in each scenario (three different line types). Parameters values are given paragraph 2, together with other explored parameters sets (not shown for readability reasons).

335 **6 Coefficient of variation of the average interval**
 336 **between trait values**

337 In the main article, the average interval between trait values is plotted against diversity
 338 (Fig. 4e-h), but it does not give information about how evenly might be distributed
 339 traits among a particular community. To get this information, we plotted the coefficient
 340 of variation of the average interval between trait values (Fig. S2). Species traits in co-
 341 adapted communities are found more evenly distributed (lower coefficient of variation
 342 at any single diversity level) than in random communities.

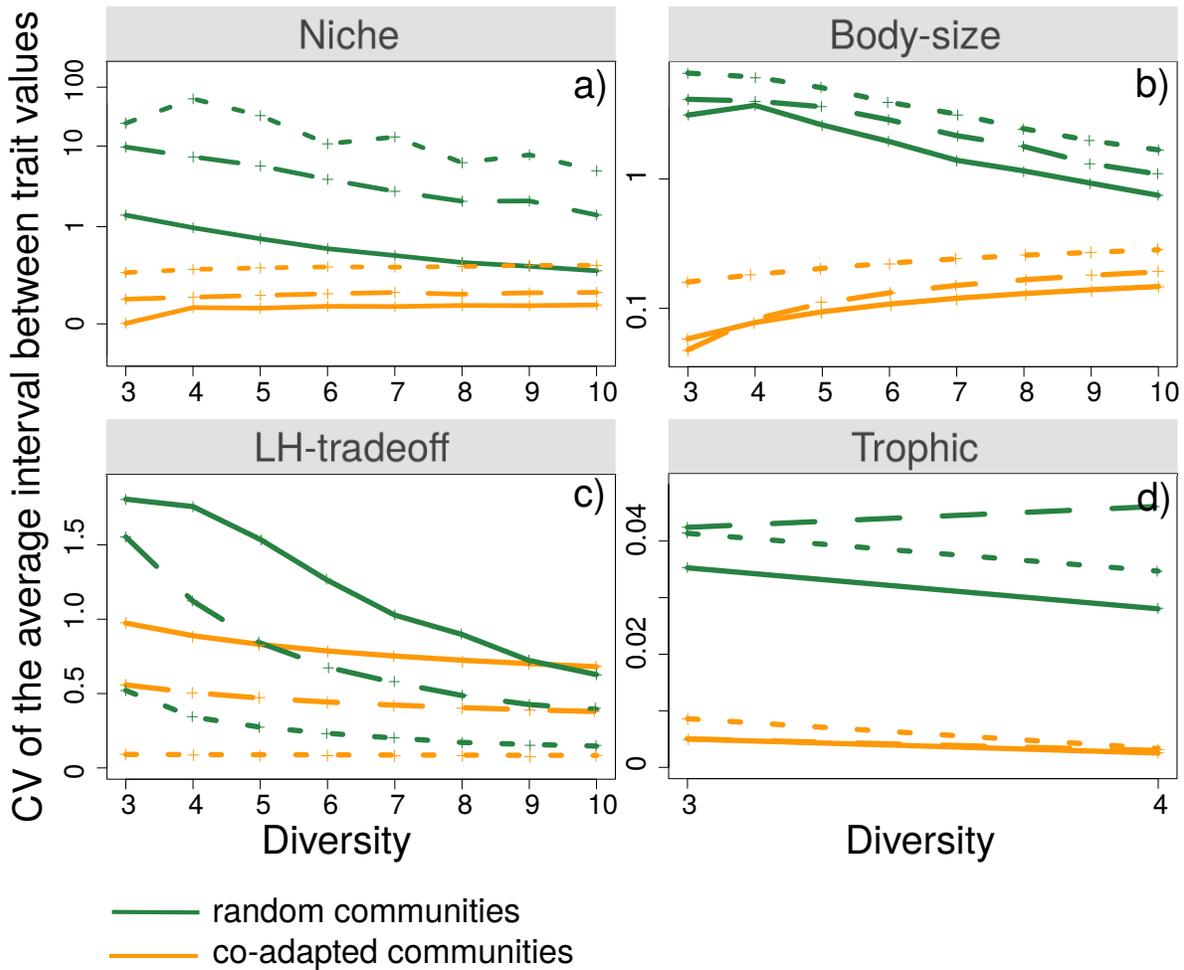


Fig. S2 Coefficient of variation of the average interval between trait values in the four ecological scenarios. The smaller the value, the more evenly distributed are species traits. Ecological interaction parameter sets are varied in each scenario (three different line types). Parameters values are given paragraph 2, together with other explored parameters sets (not shown for readability reasons).

343 7 Results with a limit on possible trait change

344 The model assumes possible unbounded changes of species traits, implying either suf-
345 ficient mutational supply or some kind of infinitely additive alleles. However, genetic
346 variation is usually not infinite, and the response to selection could at some point slow
347 down or stop. To investigate this point, we have sub-sampled the random communities,
348 excluding the ones where at least one species would have to undergo too much trait
349 change to reach the co-adapted state. More precisely, we have defined a maximum trait
350 displacement x_{max} , which corresponds to the amount of change such that the inter-
351 action strength of evolved individuals with ancestral individuals would fall to 1%. In
352 other words, this means that traits can only undergo changes that keep individuals in a
353 similar ‘niche’ as their ancestors, in the sense that they retain non-negligible interaction
354 strength. In practice, this also prevents a species from evolving more than the typical
355 trait interval existing between coexisting species, in species-rich communities. Having
356 retained only the communities with no species further from x_{max} , we recomputed all
357 the metrics for the *Niche* scenario, with the new set of communities (Fig. S3).

358 As expected, the difference between co-adapted and random communities tends to
359 erode. Low diversity levels are more impacted as random species were more likely
360 to stand far from the evolutionary point (see also Fig. 3 in the main text). It fol-
361 lows that, for instance, the patterns for biodiversity-production relationships is less
362 pronounced (Fig. S3f compared to Fig. S3a). Interestingly, the pattern for invasion
363 tolerance (Fig. S3j) is not affected at all, presumably because the largest differences are
364 observed at high diversity, where a restriction on evolutionary change has little import-
365 ance. In all cases, we still observe the general trends and differences that sustain our
366 conclusions. Even though a limit on the amount of evolutionary change allowed would
367 weaken the reported effects, it appears that the general messages are rather robust to
368 this.

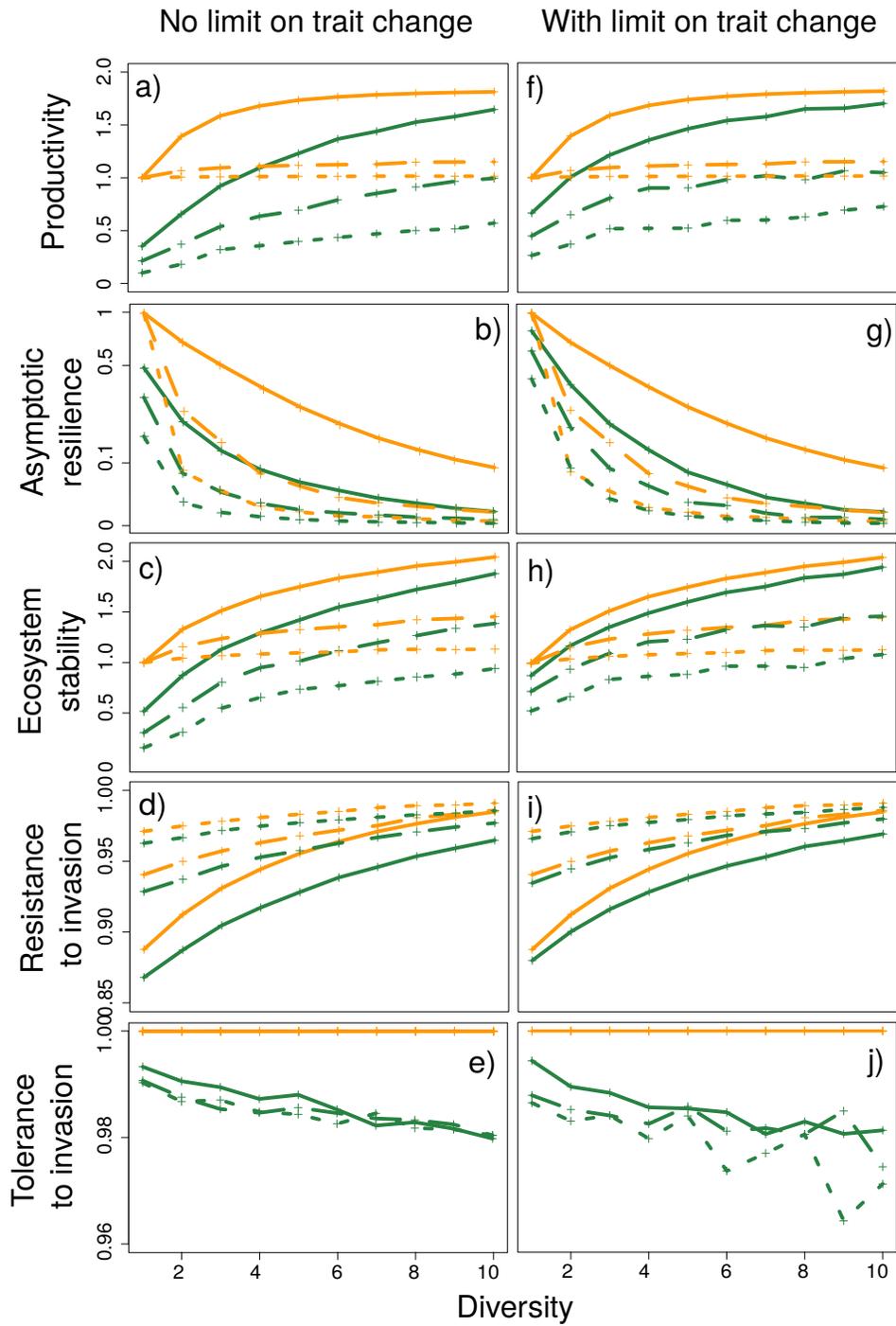


Fig. S3 The five explored metrics for *Niche* scenario, (a-e) when all random communities are considered, and (f-j) when restricting random communities to be not too far in trait space to co-adapted ones. Parameters values (different lines type) are given paragraph 2.

References

- 369
370 Abrams, P.A., Matsuda, H. & Harada, Y. (1993) Evolutionarily unstable fitness maxima and
371 stable fitness minima of continuous traits. *Evolutionary Ecology*, **7**, 465–487. ISSN 1573-
372 8477.
- 373 Arnoldi, J.F., Loreau, M. & Haegeman, B. (2016) Resilience, reactivity and variability: A
374 mathematical comparison of ecological stability measures. *Journal of Theoretical Biology*,
375 **389**, 47–59.
- 376 Barabás, G. & D’Andrea, R. (2016) The effect of intraspecific variation and heritability on
377 community pattern and robustness. *Ecology Letters*, **19**, 977–986.
- 378 Calcagno, V., Mouquet, N., Jarne, P. & David, P. (2006) Coexistence in a metacommunity:
379 the competition–colonization trade-off is not dead. *Ecology Letters*, **9**, 897–907.
- 380 Calcagno, V., Jarne, P., Loreau, M., Mouquet, N. & David, P. (2017) Diversity spurs diversi-
381 fication in ecological communities. *Nature Communications*, **8**, 15810.
- 382 Christiansen, F.B. (1991) On Conditions for Evolutionary Stability for a Continuously Varying
383 Character. *The American Naturalist*, **138**, 37–50.
- 384 Dieckmann, U. & Doebeli, M. (1999) On the origin of species by sympatric speciation. *Nature*,
385 **400**, 354–357.
- 386 Elton, C. (1958) *Ecology of Invasions by Plant and Animals*. Chapman and Hall, London.
- 387 Hector, A., Dobson, K., Minns, A., Bazeley-White, E. & Hartley Lawton, J. (2001) Community
388 diversity and invasion resistance: An experimental test in a grassland ecosystem and a
389 review of comparable studies. *Ecological Research*, **16**, 819–831.
- 390 Ives, A.R., Gross, K. & Klug, J.L. (1999) Stability and Variability in Competitive Communit-
391 ies. *Science*, **286**, 542–544.
- 392 Jaynes, E.T. (1957) Information Theory and Statistical Mechanics. *Phys. Rev.*, **106**, 620–630.
- 393 Leibold, M.A. (1996) A Graphical Model of Keystone Predators in Food Webs: Trophic Reg-
394 ulation of Abundance, Incidence, and Diversity Patterns in Communities. *The American*
395 *Naturalist*, **147**, 784–812.
- 396 Loeuille, N. & Loreau, M. (2005) Evolutionary emergence of size-structured food webs. *Pro-*
397 *ceedings of the National Academy of Sciences*, **102**, 5761–5766.
- 398 May, R.M. (1973a) Qualitative stability in model ecosystems. *Ecology*, **54**, 638–641.
- 399 May, R.M. (1973b) Stability in randomly fluctuating versus deterministic environments. *The*
400 *American Naturalist*, **107**, 621–650.
- 401 Metz, J.A.J., Geritz, S.A.H., Meszina, G., Jacobs, F.J.A. & Heerwaarden, J.S.v. (1995) Adapt-
402 ive Dynamics: A Geometrical Study of the Consequences of Nearly Faithful Reproduction.
403 IIASA Working Paper, WP-95-099, IIASA, Laxenburg, Austria.

- 404 Rummel, J.D. & Roughgarden, J. (1985) A theory of faunal buildup for competition com-
405 munities. *Evolution*, **39**, 1009–1033.
- 406 Tilman, D., Wedin, D. & Knops, J. (1996) Productivity and sustainability influenced by
407 biodiversity in grassland ecosystems. *Nature*, **379**, 718–720.
- 408 Wang, S., Haegeman, B. & Loreau, M. (2015) Dispersal and metapopulation stability. *PeerJ*,
409 **3**, e1295.