

The role of niche complementarity in the strengthening of the diversity-ecosystem functioning relationship over time

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Abstract

1. Species-rich communities exhibit higher levels of ecosystem functioning compared to species-poor ones, and this positive relationship strengthens over time. One proposed explanation for this phenomenon is the reduction of niche overlap among plants or animals, which corresponds to increased complementarity and reduced competition.
2. In order to examine the potential of increased complementarity among plants or animals to strengthen the relationship between diversity and ecosystem functions, we integrated models of bio-energetic population dynamics and food-web assembly. Through the simulation of various scenarios of plant and animal complementarity change, we sought to elucidate the mechanisms underlying the observed increases in (1) primary productivity, (2) control of herbivores by predators, and (3) reduction of herbivore pressure on plants in species-rich communities.
3. Our findings reveal that increased niche complementarity of plants can steepen the diversity-function relationships if it does not increase their intraspecific competition, while increasing complementarity among animals during community assembly can also have a positive effect but with considerable variability.
4. The study highlights the importance of trait variation both among and within species, and the interplay between intra- and interspecific competition strength in shaping the functioning of ecosystems over time. These results offer insights into the mechanisms underpinning the diversity-functioning relationship, and have practical implications for ecosystem management and conservation efforts.

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- 6 2. In order to examine the potential of increased complementarity among plants or animals
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- 17 4. The study highlights the importance of trait variation both among and within species, and
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19 functioning of ecosystems over time. These results offer insights into the mechanisms
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21 ecosystem management and conservation efforts.

22

23 **Keywords:**

24 community assembly, competition, food-webs, herbivory, herbivory control, interspecific,
25 intraspecific, productivity, trophic niche

26

27 **Introduction**

28 An ecosystem's ability to function and thus provide services to humans depends on its
29 biodiversity (Hooper *et al.* 2005; Cardinale *et al.* 2012; Isbell *et al.* 2017). Positive effects of
30 biodiversity, have been reported for primary production (Cardinale *et al.* 2011), herbivory and
31 predation (Ebeling *et al.* 2014; Barnes *et al.* 2020), decomposition (Ebeling *et al.* 2014; Handa *et al.*
32 *al.* 2014), as well as pollination (Gavini *et al.* 2021). Remarkably, these positive diversity-
33 ecosystem functioning relationships tend to establish during community assembly (Cardinale *et al.*
34 *al.* 2007; Meyer *et al.* 2016; Eisenhauer *et al.* 2019). Therefore, they may be weak (Reich *et al.*
35 2012) or absent (Strecker *et al.* 2016) among communities in the first few years of their
36 establishment, becoming considerably more positive in later years (Reich *et al.* 2012; Huang *et al.*
37 *al.* 2018; Wagg *et al.* 2022). Consequently, restored communities may require considerable time
38 for dynamic assembly processes to achieve a functioning level comparable to old natural
39 communities (Moreno-Mateos *et al.* 2020; Resch *et al.* 2021; Bannar-Martin *et al.* 2018;
40 Ladouceur *et al.* 2022). Understanding the mechanisms involved in establishing and steepening
41 the diversity-ecosystem functioning relationship is thus crucial for effective ecosystem
42 management, as they can tip the scales in conservation versus restoration decisions.

43 Competition for resources, such as light or nutrients, is instrumental in understanding the
44 changes in plant community functioning over time (Reich *et al.* 2012). The strength of
45 competition is often characterized by a gradient ranging from niche overlap (strong competition)
46 to complementarity (weak competition or even facilitation) (Barry *et al.* 2019). Plant species
47 grown in diverse plant communities (mixtures) become morphologically more dissimilar than the
48 same species grown in monocultures (Zupping-Dingley *et al.* 2014; Roscher *et al.* 2015). This
49 suggests that species respond to interspecific competition by shifting their niche to reduce
50 overlap with other species, making them more complementary in their use of resources
51 (Eisenhauer *et al.* 2019). However, intraspecific trait variability also allows individuals to escape
52 competition from conspecifics (Jung *et al.* 2010). Avoiding interspecific competition by shifts
53 along a finite niche axis to achieve species complementarity can come at the cost of increasing
54 intraspecific competition. Consequently, plant productivity may decrease even when
55 interspecific variability is high, if individuals of the same species become more clumped in the
56 same area of niche space (Fig. 1a, clumped scenario). Therefore, we expect niche differentiation
57 to have a net positive effect on productivity only if it reduces interspecific competition while
58 maintaining a tolerable level of intraspecific competition (Roscher *et al.* 2015). This requires that
59 species shift their location in niche space relative to each other while maintaining relatively high
60 dispersion of niche positions among their individuals (Fig. 1a, spread-out scenario). Despite
61 evidence that plant populations shift in their heritable traits over time (Zupping-Dingley *et al.*
62 2014) and thus change their niche spectrum, it is unclear how these changes affect the processes
63 underlying the community's diversity-productivity relationship.

64 Moreover, plant diversity-productivity relationships may not only depend on plant-plant
65 interactions, but also on multi-trophic interactions (Schneider *et al.* 2016; Seibold *et al.* 2018;

66 Wang & Brose 2018; Eisenhauer *et al.* 2019; Barnes *et al.* 2020; Albert *et al.* 2022). What
67 becomes increasingly clear is the importance of expanding the focus of the field from primary
68 productivity to functions performed by the consumer community (Poisot *et al.* 2013; Barnes *et*
69 *al.* 2020; Maureaud *et al.* 2020) and the multitrophic control of plant diversity and productivity
70 (Schneider *et al.* 2016; Wang & Brose 2018). This multi-trophic perspective is equally relevant
71 in our effort to understand how community assembly across trophic levels can reshape this
72 relationship over time (Duffy *et al.* 2007). Active dispersal enables consumers to colonize a
73 location, provided they can find resources there (Gravel *et al.* 2011; Bauer *et al.* 2022), but after
74 the early pioneer phase, the food-web they comprise will also be structured by competitive
75 exclusion. Specifically, strong competitors can extirpate species that occupy a similar niche,
76 while new species can succeed in invading the community only if they are sufficiently unique to
77 avoid competition by existing species (Hui *et al.* 2021). In this sense, species' trophic links are a
78 manifestation of their realized niche (Bolnick *et al.* 2011); species that share resources will
79 experience high exploitative competition, while species that share consumers are subject to
80 apparent competition (Holt 1977; Stouffer & Bascompte 2010; Holt & Bonsall 2017). The
81 expected effect of time is, therefore, to restructure the animal community in a way that reduces
82 the similarity of trophic interactions among species, thereby increasing trophic niche
83 complementarity (Poisot *et al.* 2013; Bauer *et al.* 2022) (Fig. 1b, high-complementarity
84 scenario), with potential cascading effects on the plant community. However, the impacts of such
85 multi-trophic restructuring during community assembly processes on the strength of the
86 relationship between plant diversity and primary productivity have remained largely unexplored.
87 As these different competition mechanisms for plants and animals (Fig. 1a, b) are likely to act in
88 concert, discerning their individual contribution to the observed patterns in plant diversity-

89 productivity relationships can be challenging. Therefore, in-silico biodiversity experiments allow
90 us to investigate how the different niche shifts of animal and plant communities during assembly
91 (illustrated in Fig. 1a, b) and their combinations modify the plant diversity-function relationship.
92 Here, we investigated the potential for niche differentiation over time, in both plant and animal
93 communities, to modify the relationship between plant diversity and three key ecosystem
94 functions: primary productivity, herbivory pressure on plants, and herbivore control by predators.
95 We hypothesized that steepening of the diversity-function relationship over time could result
96 from (H1) plant species segregation on a niche axis (reducing interspecific competition) only
97 with niche adaptation (similar levels of intraspecific competition), whereas (H2) niche
98 concentration leading to clumped niches and higher intraspecific competition (Fig. 1a) should
99 reduce ecosystem functioning. Additionally, we expected that (H3) increasing trophic
100 complementarity of animals during assembly, which also decreases competition (Fig. 1b), should
101 also steepen the biodiversity-functioning relationships.

102

103 **Methods**

104 *Regional species pool*

105 We generated a regional pool of 1000 species (250 each of plants, herbivores, omnivores, and
106 predators). Species' body-masses (in grams), here defined as 10^x , where x was sampled from a
107 uniform distribution in $[-9, 3]$. The links from plants to their consumers (herbivores and
108 omnivores) were set according to a nested pattern. First, a 250x500 plant by plant-consumer
109 matrix was generated. Then, every b_{ij} element of the matrix was given a value according to its
110 position in the matrix:

111
$$b_{ij} = \left(\frac{i}{250}\right)^2 + \left(\frac{j}{500}\right)^2 \quad (1)$$

112 This function describes a paraboloid, giving the elements in the matrix' lower right corner higher
 113 values. If $b_{ij} \geq 1$, we set it equal to 1, and used b_{ij}^2 as a probability of a Bernoulli trial, replacing
 114 matrix elements with 0 or 1. The produced matrix was subsequently embedded in the square
 115 matrix that contained all the potential trophic interactions.

116 Predatory interactions were assumed to scale allometrically, adapted from Schneider *et al.*
 117 (2016): the feeding niche of each animal species was defined as the body-mass interval at which
 118 the Ricker function used in Schneider *et al.* (2016) returns values larger than a threshold θ :

119
$$M_{ij} = \begin{cases} 1, & \text{if } \left(\frac{m_j}{m_i R_{opt}} e^{1 - \frac{m_j}{m_i R_{opt}}}\right)^\gamma > \theta \\ 0, & \text{otherwise.} \end{cases} \quad (2)$$

120 Here m_j is the mass of the predator, m_i that of the prey, γ is the width of the Ricker function and
 121 R_{opt} is the optimal predator-prey mass ratio which we set to 3.98 (Brose *et al.* 2006). To produce
 122 a food-web for which allometry does not entirely determine consumption (i.e. non-interval food-
 123 web (Cattin *et al.* 2004)), the resulting interaction matrix was thinned by randomly removing
 124 30% of produced interactions.

125 *Establishment of local communities*

126 Local communities of 2-16 plant species (2, 3, ..., 16) and 40 animal species (300 replicates for
 127 each plant diversity increment) were produced by randomly sampling the regional pool, while
 128 ensuring that all consumer species have at least one resource in the community (following Bauer
 129 *et al.* (2022)). For each community, we generated a plant competition matrix (representing
 130 resource competition), corresponding to a naive community (*sensu* Moorsel *et al.* (2018)) with

131 high niche overlap among species, i.e. the competition that each species experiences from all
132 other species can be as high as the competition from conspecifics (Fig. 1a). The produced food-
133 webs represent early pioneer communities without any shared time allowing for niche
134 differentiation, where consumer occurrence is most contingent on the presence of their resources.
135 Consequently, consumers have unrestricted trophic similarity and, therefore, limited
136 complementarity.

137 *Effect of history on plants*

138 To simulate niche differentiation on plants, we directly manipulated the plant-plant interaction
139 matrix (see *Community dynamics*, below). For each local community, we generated a
140 competition matrix consistent with reduced niche overlap, but without niche spread-out, i.e
141 interspecific competition is reduced but intraspecific competition increases, so the overall
142 competition remains the same. We also generated a competition matrix consistent with reduced
143 niche overlap combined with niche spread-out, such that species compete less with other species
144 but without increased intraspecific competition; therefore the overall competition that a species
145 experiences is reduced.

146 *Effect of history on animals*

147 The communities described above were then exposed to a simulation of turnover, based on a
148 Metropolis-Hastings algorithm. The algorithm sequentially removed animal species from local
149 communities with a probability depending on their linkage similarity to other local species (a
150 proxy of niche overlap), replacing them with random species from the regional pool. If the
151 average Jaccard similarity J' of this new community is larger than the Jaccard similarity J of the

152 community before replacement, then the swap becomes effective. Otherwise, the replacement
153 could still be accepted with probability P :

$$154 \quad P = e^{\left(\frac{J-J'}{J \cdot 0.01}\right)}. \quad (3)$$

155 This algorithm increases the probability of arriving at a community composition of reduced
156 average similarity among local species (Bauer *et al.* 2022), representative of communities
157 structured by history, where competitive exclusion is also at play.

158 The combination of two animal trophic complementarity scenarios (low, high, Fig. 1b) crossed
159 with three plant niche complementarity scenarios (overlapping, clumped, spread-out, Fig. 1a)
160 resulted in six versions of a focal community. Across 15 levels of plant richness (2-16 species)
161 with 300 replicates for each community type, this produced 27,000 simulated food-webs.

162 *Community dynamics*

163 We simulated community dynamics with a bio-energetic model (Delmas *et al.* 2017; Gauzens &
164 Berti 2022). Changes in plant biomass over time are described by

$$165 \quad \frac{dB_i}{dt} = (r_i G_i - x_i) B_i - \sum_j x_j y_j B_j F_{ij}. \quad (4)$$

166 The first term in equation (4) describes biomass gains through growth: B_i is the biomass of
167 species i , r_i is the mass-specific maximum growth rate, G_i is the net growth rate and x_i is the
168 mass-specific metabolic rate, scaled to the growth rate r of the smallest basal species in the
169 regional pool. The second term describes losses to consumption: B_j is the biomass of consumer j ,
170 y_j is the maximum feeding rate of j relative to its metabolic rate and F_{ij} is the per unit biomass
171 feeding rate of species j on species i . The net growth rate of species i is defined as

172
$$G_i = 1 - \frac{s_i}{K_i/N}, \quad (5)$$

173 where K_i is the carrying capacity of species i , and N is the number of plant species in the
 174 corresponding community, ensuring that the total amount of available resources that plants
 175 implicitly compete for, does not change across the plant richness gradient. s_i depends on the
 176 inter- and intraspecific competition for resources a_{ij} :

177
$$s_i = \sum_j a_{ij} B_j, \quad (6)$$

178 The diagonal elements of matrix a correspond to intraspecific competition, while the off-
 179 diagonals to interspecific competition.

180 By manipulating the relative strengths of the a_{ij} elements, we implemented the different plant
 181 competition scenarios described above. While restricting row sums to 1, we set $\sum_j a_{ij} \leq a_{ii}$ for
 182 the overlap scenario, and $\sum_j a_{ij} \ll a_{ii}$ for the clumped scenario. Finally, combining the a_{ii}
 183 values of the former scenario with the a_{ij} values of the later scenario, we produced communities
 184 with an overall decrease of plant competition (spread-out scenario).

185 Changes in animal biomass over time are described by the equation

186
$$\frac{dB_i}{dt} = B_i(x_i y_i \sum_j F_{ji} e_j - x_i) - \sum_j x_j y_j B_j F_{ij}. \quad (7)$$

187 The first term in equation (7) describes biomass gains through consumption (after metabolic
 188 losses x_i), where B_i is the biomass of species i , F_{ji} is the per unit biomass feeding rate of species
 189 i on species j , and e_j is the assimilation efficiency of prey j . The second term describes losses to
 190 consumption as in eq. 4. The multi-prey (for k prey species) functional response F_{ij} of species j
 191 consuming i is described by the equation

192
$$F_{ij} = \frac{w_{ij}B_i^q}{B_0^q + c_j B_j + \sum_k w_{kj} B_k^q}, \quad (8)$$

193 where w_{ij} is j 's relative consumption rate when consuming i . q is the Hill exponent determining
194 the shape of the functional response. B_0 is the half-saturation density, while c_j is the intraspecific
195 interference factor.

196 We simulated community dynamics using the *ATNr* package (Gauzens & Berti 2022), and ran
197 simulations for 40,000 time-steps.

198 *Ecosystem functioning*

199 To assess the effects of complementarity changes among animals and plants on ecosystem
200 functioning, we examined primary productivity at the end of simulations. Herbivory pressure on
201 plants was quantified as the total out-flux of energy from plants to their consumers, per unit of
202 plant biomass. Finally, we quantified herbivore control by predators as the ratio of out-fluxes to
203 in-fluxes of herbivores (after Barnes *et al.* 2020).

204

205 **Results**

206 We initiated our model simulations with communities of 2-16 plant species and 40 animal
207 species. The simulated communities reproduced the expected positive and saturating plant
208 species richness-productivity relationship (Fig. 2a), and a positive relationship between plant
209 species richness and standing plant biomass (Fig. S1).

210 We tested for effects of the two plant niche differentiation processes, concentration and
211 adaptation (see Fig. 1a), on the plant diversity-productivity relationship. An increase in plant

212 complementarity through concentration (i.e. higher intraspecific competition) dampened the
213 diversity-productivity relationship (Fig. 2a, red versus yellow lines). The difference in
214 productivity in a focal community resulting from this complementarity change was, on average,
215 very limited for plant-poor communities (Fig. 2b), and unpredictable in terms of its sign. The
216 probability of being positive was almost as likely as being negative for communities with only
217 two plant species (Fig. 2b, red inlay plot). Communities with more plant species had more
218 pronounced negative differences in productivity (Fig. 2b) that were very consistent for plant-rich
219 communities. The probability of a positive difference was close to zero for eight species or more
220 (Fig. 2b, red inlay plot). Conversely, an increase of plant complementarity through adaptation
221 (i.e. lower interspecific competition with no change of intraspecific competition) produced a
222 pattern of a steeper diversity-productivity relationship (Fig. 2a, green versus yellow lines).
223 Consequently, differences in productivity in a focal community were more consistently positive
224 (Fig. 2b), and of higher magnitude for species-rich communities (Fig. 2b, green line and green
225 inlay plot). Together, these results demonstrate that plant diversity-productivity relationships
226 become shallower or steeper under the plant concentration or adaptation scenarios, respectively.

227 We also tested for effects of increasing complementarity in the trophic links of animal species
228 (i.e. trophic complementarity). An increase in trophic complementarity among animals also
229 contributed to the steepening of the diversity-productivity relationship on average, but this was
230 more pronounced in communities with high plant complementarity and low plant competition
231 (adaptation scenario, Fig. 2a, dashed versus solid green lines). There was considerable variation
232 in the difference in productivity in a focal community as a result of the transition from low to
233 high animal complementarity (Fig. 2c). For plant-poor communities, this difference was as likely
234 to be negative as positive, while among plant-rich communities with low plant competition, the

235 transition led to positive differences in productivity for 3 out of 4 communities (Fig. 2c, inlay
236 plots). Our results show that the impact of increasing animal trophic complementarity on the
237 plant diversity-productivity relationship depends on how plants increase their complementarity.

238 We next considered the effects of plant niche differentiation on the control of herbivores by
239 predators. Control of herbivores had a hump-shaped relationship with plant richness, peaking
240 between 4 and 8 plant species (Fig 3a). The difference in herbivore control by predators was
241 generally positive when communities increased plant complementarity through niche adaptation
242 (Fig. 3b, green line) and generally negative when they did so through concentration (Fig. 3b, red
243 line). Differences in control due to adaptation were again more consistently positive (Fig. 3b,
244 green inlay) and of higher magnitude for plant-rich communities.

245 The transition to higher trophic complementarity among animals had, on average, a positive
246 effect on herbivore control (Fig. 3a, dashed vs solid lines and 3c). Again, there was considerable
247 variation in the difference in control in a focal community as a result of this transition but for 3
248 out of 4 of plant-rich communities the difference was positive (Fig. 3c, inlays), regardless of the
249 plant complementarity scenario that trophic complementarity was combined with.

250 We finally considered the effects of plant and animal complementarity changes on herbivory
251 pressure. Like herbivore control, herbivory peaked in communities with ~4 plant species and
252 declined with increasing plant richness (Fig 4a). The increase of plant complementarity through
253 adaptation led to increased herbivory pressure (Fig. 4b, green line). This difference in herbivory
254 pressure was consistently positive for plant species-rich communities (Fig. 4b green inlay). In
255 contrast, increased plant complementarity through niche concentration had more variable effects
256 on herbivory pressure. The average difference in herbivory pressure was negative for

257 communities with a low to medium number of plant species and was very close to zero for plant
258 species-rich communities and communities with only two plant species (Fig. 4b, red line).
259 Finally, the transition effect from low to high trophic complementarity among animals, while
260 highly variable, was on average that of a reduction of herbivory pressure on plants. This average
261 negative difference in pressure was more pronounced in communities of low to intermediate
262 number of plant species (Fig. 4c) regardless of the plant complementarity scenario. Across the
263 plant richness gradient, approximately 1 in 4 communities had a response against this general
264 trend (Fig. 4c inlays).

265 **Discussion**

266 Simulating complex food-web dynamics, we found that shifts in plant resource niches to reduce
267 interspecific competition only strengthen the diversity-functioning relationship if they do not
268 come at the cost of increased intraspecific competition. The effects of increased complementarity
269 among animals during community assembly are highly variable, yet positive on average.
270 Together, these results indicate an interplay between plant niche shifts and animal community
271 assembly in steepening biodiversity-functioning relationships over time.

272 Across experiments, it has been shown that biodiversity-functioning relationships steepen over
273 time (Reich *et al.* 2012; Meyer *et al.* 2016; Huang *et al.* 2018; Wagg *et al.* 2022). Increases in
274 plant niche complementarity have been suggested to explain this pattern (Zupinger-Dingley *et*
275 *al.* 2014; Eisenhauer *et al.* 2019). Our results demonstrate that temporal changes in biodiversity-
276 functioning relationships largely depend on how increasing niche complementarity is achieved,
277 due to implications for plant competition. If plants respond to interspecific competition by
278 concentrating their niche (Fig. 1a, clumped scenario), thereby experiencing stronger intraspecific

279 competition, the diversity-function relationship is dampened. If plants can avoid interspecific
280 competition by spreading out in niche-space (Fig. 1a, adaptation scenario), thereby maintaining
281 low levels of intraspecific competition, the effect on the diversity-function relationship is
282 generally positive and stronger with increasing plant richness. The importance of intraspecific
283 trait variation for ecological processes has been repeatedly highlighted (Bolnick *et al.* 2011;
284 Violle *et al.* 2012; Des Roches *et al.* 2018) with several studies examining its implications for
285 leaf economics (Anderegg *et al.* 2018; Pichon *et al.* 2022), coexistence (Turnbull *et al.* 2013;
286 Hart *et al.* 2016) and even niche differentiation (Roscher *et al.* 2015, 2018; Rodríguez-Alarcón *et*
287 *al.* 2022). Our results support empirical evidence that the interplay between intra- and
288 interspecific trait variation can be as important as species diversity for some ecosystem processes
289 (Crutsinger *et al.* 2006; Des Roches *et al.* 2018). This underscores the need to examine shifts in
290 the distribution of traits between and within species together (Roscher *et al.* 2015), when seeking
291 explanations for the steepening of biodiversity-function relationships over time.

292 In complex food-webs, changes in plant diversity and productivity can cascade to higher trophic
293 levels and feedback to plants by changes in herbivory (Barnes *et al.* 2020; Galiana *et al.* 2020).
294 To address the importance of these cascading effects, we also studied how top-down herbivore
295 control by predators and herbivory respond to changes in plant diversity and niche segregation.
296 Along the plant diversity gradient, we found that control of herbivores by predators increased
297 sharply from communities with two plant species to those with four to six plant species, before
298 decreasing gradually. In consequence, herbivory strength followed similar trends along this
299 gradient. Accordingly, a reduction of herbivore effects on plants in communities with higher
300 plant diversity has been demonstrated experimentally (Barnes *et al.* 2020). These observed
301 patterns in our model and prior empirical studies find an explanation in classic theory on biomass

302 pyramids along productivity gradients (Oksanen *et al.* 1981; Perkins *et al.* 2022). Increasing
303 plant diversity increases plant biomass but also the biomass of higher trophic levels (Scherber *et*
304 *al.* 2010). This increases herbivore biomass and thus herbivory at lower plant biomass levels
305 (Oksanen *et al.* 1981). Further increases in herbivore and plant biomass generate higher predator
306 biomass (Oksanen *et al.* 1981), leading to increasing dominance of higher trophic levels that
307 control each other by intra-guild predation and dampen trophic cascades (Finke & Denno 2005;
308 Schneider *et al.* 2012; Wang *et al.* 2019). The biomass distribution along the plant diversity
309 gradient thus causes shifts in trophic cascades and energy fluxes to higher trophic levels (Barbier
310 & Loreau 2018; Barnes *et al.* 2020; Galiana *et al.* 2020). This reduces fluxes among lower
311 trophic levels, such as top-down pressure on herbivores and herbivory, with increasing plant
312 diversity. Together, these findings explain the hump-shaped relationship between top-down
313 pressure on herbivores as well as herbivory with plant diversity.

314 Despite increasing knowledge on how energy fluxes and trophic cascades vary with productivity,
315 biomass distributions and plant diversity (Borer *et al.* 2005; Barnes *et al.* 2017; Barnes *et al.*
316 2020; Buzhdygan *et al.* 2020), the question of how dynamic plant niche differentiation modifies
317 them remains unresolved. In our study, the effect of higher complementarity among plant species
318 on herbivore control and herbivory pressure was also conditional on how this complementarity
319 was achieved. Herbivory and predatory herbivore control increase under plant niche adaptation
320 and decrease under concentration. Similar to the effects of plant diversity, these decreases are
321 explained by changes in plant biomass production and the resulting biomass pyramids. Increases
322 in plant productivity under adaptation yield higher fluxes to herbivores and higher trophic levels,
323 whereas the decreased productivity due to strong intraspecific competition under concentration

324 causes decreased fluxes to higher trophic levels. Thus, our results link plant niche differentiation,
325 community biomass patterns, and energy fluxes in a general conceptual framework.

326 Our results confirm that higher complementarity among consumers, arising from ongoing
327 community assembly, leads to better herbivore control, on average. Additionally, if consumers in
328 a community become more complementary over time, herbivory pressure on plants is likely to be
329 reduced. Simultaneously, we demonstrate that the effects of increased complementarity among
330 consumers on ecosystem functioning can vary, so we should not necessarily expect higher
331 herbivore control or reduced herbivory pressure in communities with complementary consumers.
332 While this variability is partly a consequence of the random variability we imposed on food-web
333 parameters, it can also be explained by differences in consumer control via intra-guild predation
334 (Finke & Denno 2005; Wang *et al.* 2019). Therefore, our results suggest a complex interplay
335 between consumer complementarity and the network structures arising during community
336 assembly, generating feedbacks on the biodiversity-functioning relationships.

337 Seabloom *et al.* (2017) demonstrated that when plant communities are embedded in complex
338 food-webs, the effects of plant richness on productivity can be obscured, if biomass is used as a
339 proxy for productivity, due to the partial transformation of plant biomass to animal biomass. In
340 contrast, dynamic models allow us to consider plant productivity directly, while simultaneously
341 examining potential top-down effects of the animal community (Schneider *et al.* 2016). Our
342 results show that the magnitude of animal complementarity effects on plant productivity is
343 context dependent; it is stronger when both animals and plants have complementary niches as in
344 our spread-out scenario whereas it is less pronounced in the presence of high inter- or
345 intraspecific plant competition in the overlapping or clumped scenario, respectively. Similar to
346 the effects of animal complementarity on herbivory and top-down control of herbivores, the

347 effects on primary productivity were quite variable. As network properties that alter top-down
348 control, such as intra-guild predation and modularity, vary with species richness (Riede *et al.*
349 2010), the resulting increased animal complementarity effects on plant diversity-productivity
350 relationships may be idiosyncratic.

351 Our results augment the growing evidence that community assembly is important for ecosystem
352 functioning (Bannar-Martin *et al.* 2018). We show that it can lead to shifts in animal species
353 composition and plant niche distributions, resulting in a steepening of the biodiversity-
354 functioning relationship. This illustrates a fundamental connection between ecosystem
355 functioning and landscape processes that can accelerate or decelerate assembly. For instance,
356 habitat fragmentation and anthropogenic disturbance together with species' dispersal capacities
357 can impede the progress to mature, structured communities with high complementarity (Carrara
358 *et al.* 2012; Arroyo-Rodríguez *et al.* 2013; Hirt *et al.* 2018). Indeed, consumers in disturbed
359 habitats exhibit poor niche specialization (Korotkevich *et al.* 2018), suggesting that disturbance
360 can have a regressive effect on assembly, preventing communities from increasing their
361 ecosystem functioning. In this sense, our model informs our understanding of how such
362 perturbations can impose costs by hindering assembly processes, which reduces ecosystem
363 functionality beyond the direct effects of lower diversity.

364 As a simplifying assumption, we configured plant competition changes allowing plant niche
365 adaptation to be unconstrained by the number of plant species. In reality, however, the capacity
366 of species to avoid overlap within a finite niche space is constrained by niche space filling and
367 thus by the number of coexisting species (Tilman 2004). Therefore, an increase in species
368 richness will eventually lead to saturation of the niche space (Jousset *et al.* 2011; Eisenhauer *et*
369 *al.* 2013). Regarding our approach, one could argue that shifting plant niches to avoid

370 interspecific competition could lead to a spread-out scenario under low plant diversity, whereas
371 this is less likely at high plant diversity, where most of the niche space is occupied and the
372 clumped or overlapping scenarios might be more realistic depending on the relative strength of
373 intra- and interspecific competition. However, given our results, this would imply that primary
374 productivity should increase especially when plant diversity is low with spread-out niches,
375 resulting in a shallower relationship between diversity and productivity. As experimental results
376 point in the opposite direction (Reich *et al.* 2012; Huang *et al.* 2018; Wagg *et al.* 2022), we
377 conclude that the simplifying assumption of modeling niche shifts independently of species
378 richness is unlikely to impact our conclusions.

379 We focused on complementarity-related processes driving the biodiversity-functioning
380 relationship. Alternatively, selection effects may also become stronger over time to steepen the
381 relationship. However, there is mounting evidence that complementarity, rather than selection, is
382 driving the diversity-ecosystem functioning relationship (Loreau and Hector 2001; Cardinale *et*
383 *al.* 2007; Reich *et al.* 2012; Huang *et al.* 2018; Wagg *et al.* 2022; but see Genung *et al.* 2020;
384 Lisner *et al.* 2022). Accordingly, we focused on how complementarity among plants and animals
385 can change the ecosystem functioning relationship. Although selection effects are implicit in our
386 simulations because more productive species have higher survival rates, we refrained from
387 including changes in selection effects over time without a clear hypothesis on their relation to
388 assembly processes. However, if the assembly process correlates with global change factors such
389 as nutrient addition, the overall niche space may become denser (Harpole & Tilman 2007),
390 which could lead to stronger selection effects. Here, we provide a modeling framework that is
391 flexible to include such changes in selection effects during community assembly, for example,

392 related to variations in intrinsic growth rates or asymmetric competition strengths of plants or
393 maximum consumption rates of animals.

394 To achieve generality, we kept our model parameters at a generic level, while future studies
395 could extend our approach to explore specific settings. For example, plant competition, which we
396 modeled with a generic interaction strength matrix, could be replaced by explicitly modeling of
397 differences in plant nutrient uptake, neighbor shading, and space use (Brose *et al.* 2008; Albert *et*
398 *al.* 2022). Similarly, we modeled community assembly by sampling species from a pool without
399 dispersal constraints. This could be replaced by linking dispersal capacity with species' traits and
400 landscape characteristics (Hirt *et al.* 2018; Ryser *et al.* 2021). These examples illustrate how our
401 modeling approach could integrate more explicit ecological processes to differentiate the reasons
402 for the steepening of the diversity-function relationship over time, considering specific
403 community and landscape types.

404 **Conclusions**

405 Our findings reveal that shifts in plant niches that reduce interspecific competition without
406 increasing intraspecific competition provide a mechanism that strengthens the relationship
407 between biodiversity and function. However, they also caution against any narrative that would
408 suggest an uncomplicated relationship between niche complementarity and elevated ecosystem
409 functioning. The restrictions imposed by intraspecific competition on complementarity's
410 potential to act as a direct agent in the steepening of the relationship, highlight the need for
411 empirical studies focusing on trait plasticity (Zuppinge-Dingley *et al.* 2014), explicit
412 comparisons of inter- versus intraspecific trait variation (Roscher *et al.* 2015, 2018) and how
413 their ratio changes over time. Such studies would help settle whether it is mainly niche
414 adaptation or concentration occurring over time and therefore allow us to discern if

415 complementarity is directly responsible for increasing function, or whether any positive
416 complementarity effect is instead mediated by its importance for species persistence.

417 Finally, we note that ecosystems that have reached a high level of functioning in the long process
418 of their assembly history, are not easily replaceable. It is reasonable to expect that species
419 turnover in multitrophic communities will increase complementarity over time, through a process
420 of invasion, competitive exclusion and niche sorting. Despite evidence suggesting that plant
421 communities can follow a predictable assembly (Petermann *et al.* 2010), the high
422 unpredictability of multitrophic complementarity effects on different ecosystem functions shows
423 that restoring an ecosystem after disturbance does not guarantee an assembly trajectory that will
424 invariably lead to a functioning level necessary to provide desired ecosystem services (Arroyo-
425 Rodríguez *et al.* 2017). Integration of ecosystem functioning into nature conservation concepts
426 thus favors old-grown, mature communities over rewilding or reforestation strategies.

427

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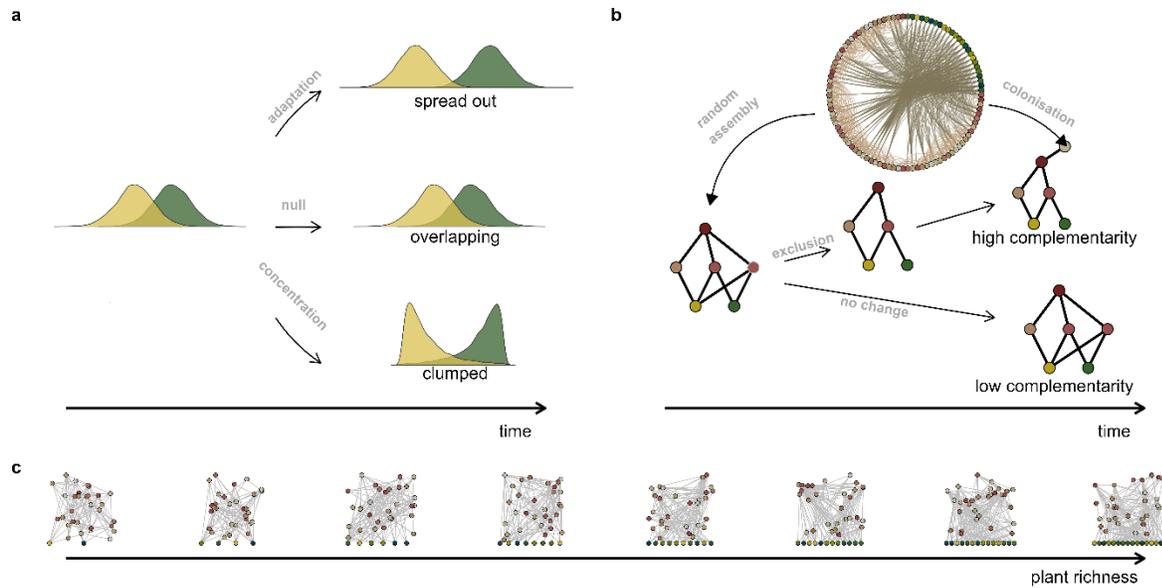
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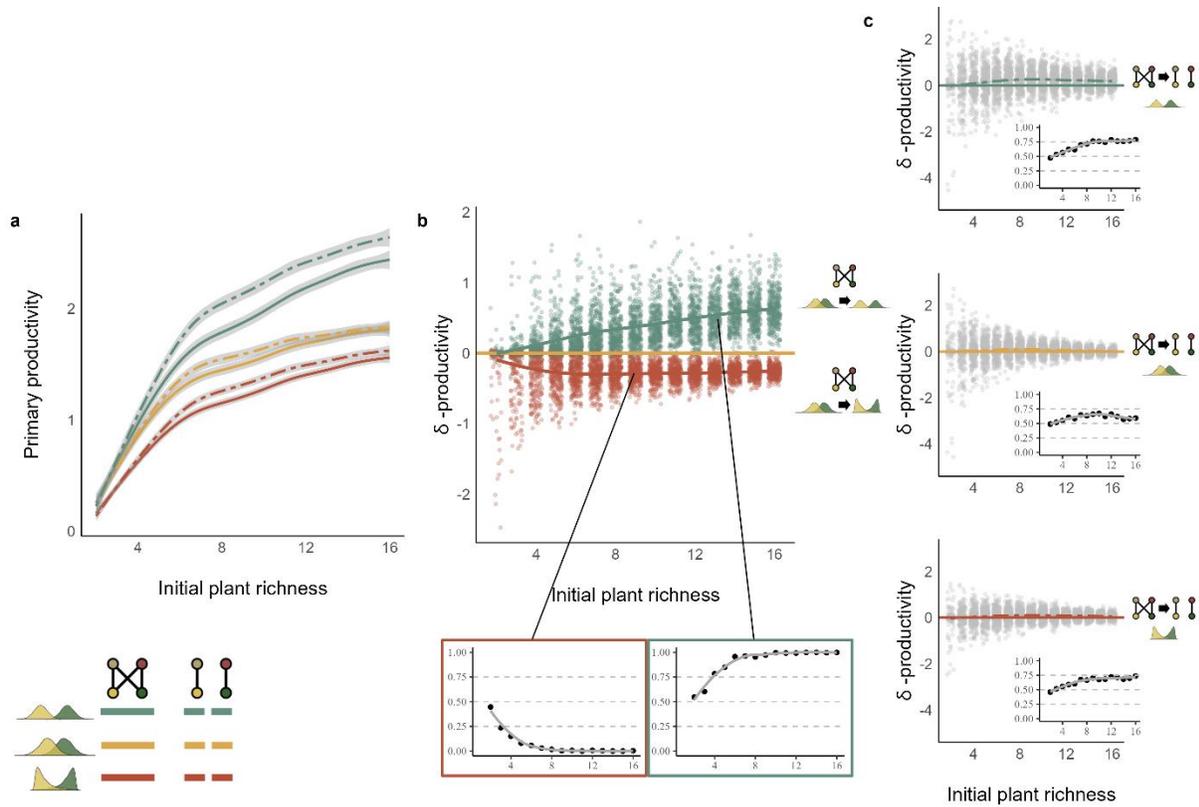
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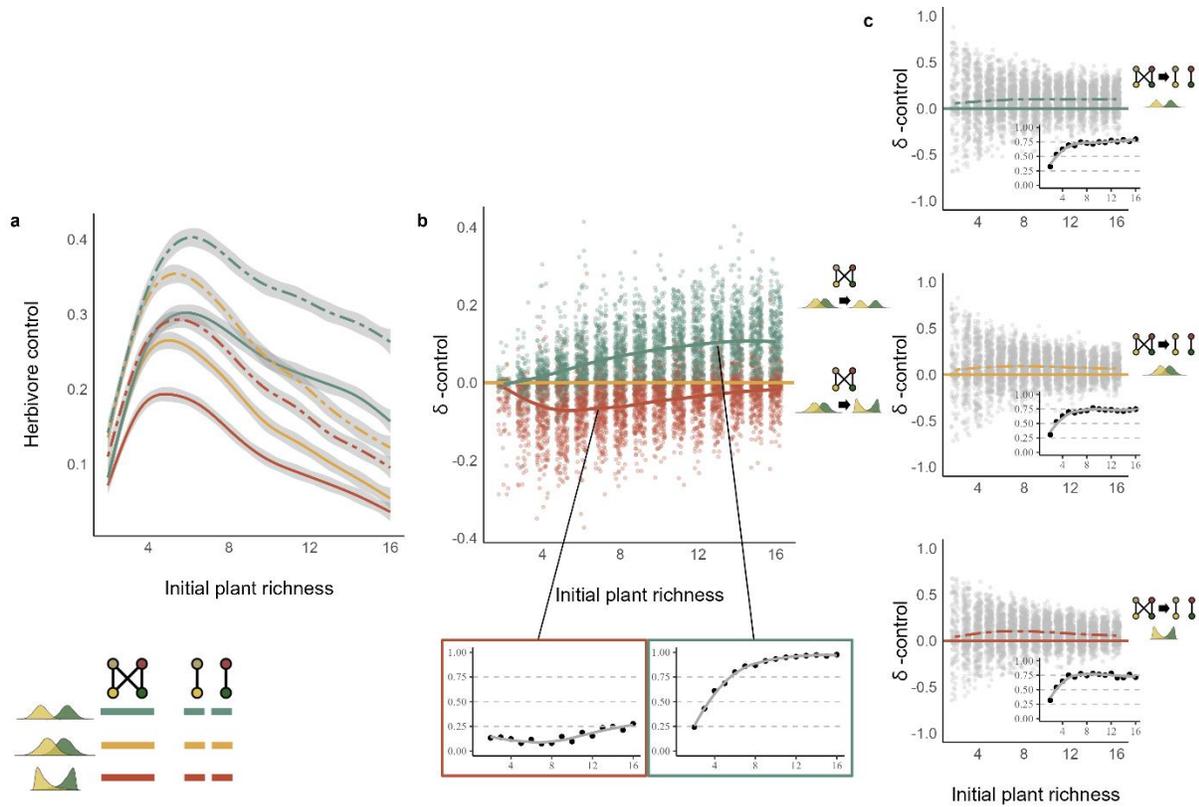
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742 **Figure 1.** (a) Plant species in a community can reduce their niche overlap and therefore
 743 interspecific competition, either through niche concentration or adaptation. (b) In the early
 744 phase of community assembly, consumers may have high trophic similarity (low
 745 complementarity). A turnover process of competitive exclusion and colonisation of new
 746 species can reduce trophic similarity and therefore lead to high trophic complementarity.
 747 (c) These changes can take place in communities that contain a varying number of plant
 748 species.



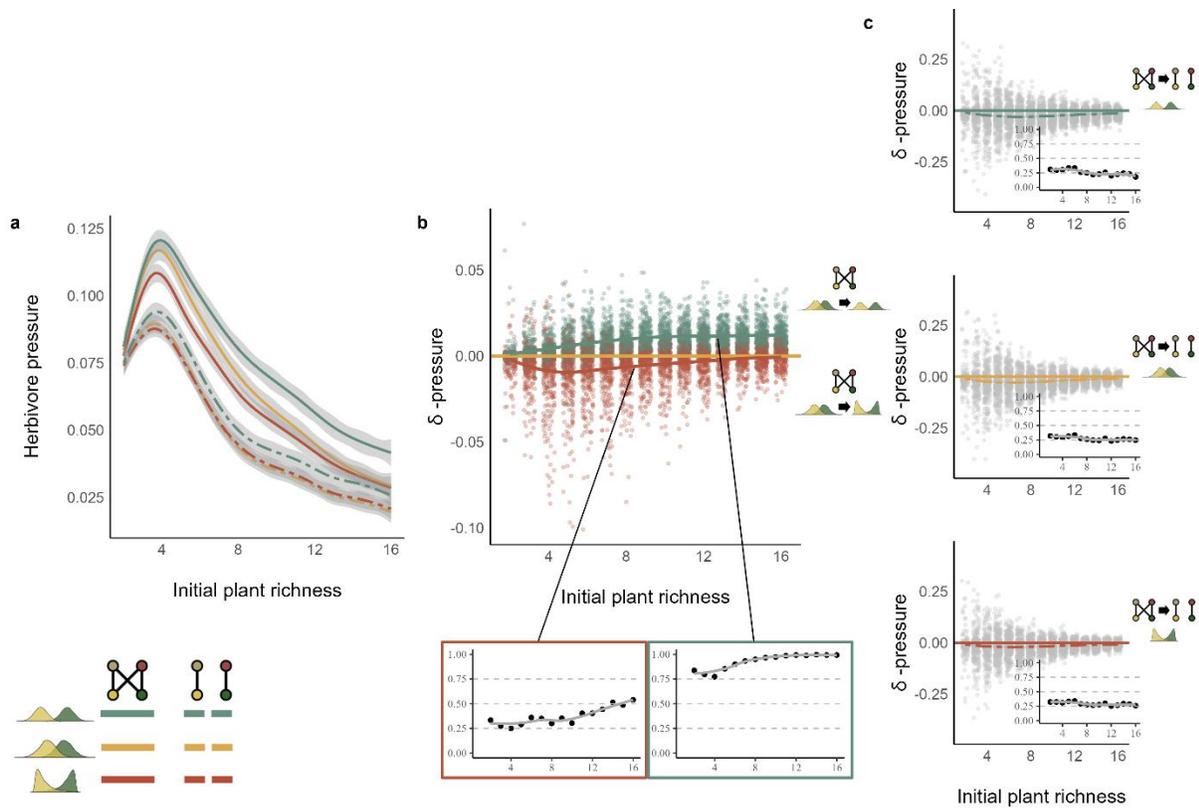
749

750 **Figure 2.** (a) The relationship between plant richness and primary productivity for
 751 communities with different combinations of plant and animal complementarity:
 752 communities with high niche overlap among plants (yellow lines), or reduced niche overlap
 753 either through niche concentration (red lines) or adaptation (green lines). Solid lines for
 754 communities with low animal complementarity and dashed lines for high animal
 755 complementarity. (b) The difference in primary productivity when plant complementarity
 756 increases through concentration (red points) or adaptation (green points). The red and
 757 green inset figures show the proportion of positive changes for each scenario. (c) The
 758 difference in primary productivity as communities transition from low to high animal
 759 complementarity. The colors correspond to the three different plant complementarity
 760 scenarios. Inset figures show the proportion of positive changes for each scenario.



761

762 **Figure 3.** (a) The relationship between plant richness and herbivore control for
 763 communities with different combinations of plant and animal complementarity:
 764 communities with high niche overlap among plants (yellow lines), or reduced niche overlap
 765 either through niche concentration (red lines) or adaptation (green lines). Solid lines for
 766 communities with low animal complementarity and dashed lines for high animal
 767 complementarity. (b) The difference in herbivore control when plant complementarity
 768 increases through concentration (red points) or adaptation (green points). The red and
 769 green inset figures show the proportion of positive changes for each scenario. (c) The
 770 difference in herbivore control as communities transition from low to high animal
 771 complementarity. The colors correspond to the three different plant complementarity
 772 scenarios. Inset figures show the proportion of positive changes for each scenario.



773

774 **Figure 4.** (a) The relationship between plant richness and herbivore pressure for
 775 communities with different combinations of plant and animal complementarity:
 776 communities with high niche overlap among plants (yellow lines), or reduced niche overlap
 777 either through niche concentration (red lines) or adaptation (green lines). Solid lines for
 778 communities with low animal complementarity and dashed lines for high animal
 779 complementarity. (b) The difference in herbivore pressure when plant complementarity
 780 increases through concentration (red points) or adaptation (green points). The red and
 781 green inset figures show the proportion of positive changes for each scenario. (c) The
 782 difference in herbivore pressure as communities transition from low to high animal
 783 complementarity. The colors correspond to the three different plant complementarity
 784 scenarios. Inset figures show the proportion of positive changes for each scenario.