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The future of complementarity: disentangling causes from consequences

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Abstract: Evidence suggests that biodiversity supports ecosystem functioning. Yet, the mechanisms driving this relationship remain unclear. Complementarity is one common explanation for these positive biodiversity–ecosystem functioning relationships. Yet, complementarity is often indirectly quantified as overperformance in mixture relative to monoculture (e.g., ‘complementarity effect’). This overperformance is then attributed to the intuitive idea of complementarity or, more specifically, to species resource partitioning. Locally, however, several unassociated causes may drive this overperformance. Here, we differentiate complementarity into three types of species differences that may cause enhanced ecosystem functioning in more diverse ecosystems: (i) resource partitioning, (ii) abiotic facilitation, and (iii) biotic feedbacks. We argue that disentangling these three causes is crucial for predicting the response of ecosystems to future biodiversity loss.

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1 **Title:** The future of complementarity: Disentangling causes from consequences

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41 **Abstract**

42 Evidence suggests that biodiversity supports ecosystem functioning. Yet, the mechanisms
43 driving this relationship remain unclear. Complementarity is one common explanation for these
44 positive biodiversity-ecosystem functioning relationships. Yet, complementarity is often
45 indirectly quantified as overperformance in mixture relative to monoculture (*e.g.*,
46 ‘complementarity effect’). This overperformance is then attributed to the intuitive idea of
47 complementarity or more specifically to species resource partitioning. However, locally, several
48 unassociated causes may drive this overperformance. Here, we differentiate complementarity
49 into three types of species differences that may cause enhanced ecosystem functioning in more
50 diverse ecosystems: 1. resource partitioning, 2. abiotic facilitation, and 3. biotic feedbacks. We
51 argue that disentangling these three causes is crucial for predicting the response of ecosystems to
52 future biodiversity loss.

53 **The confusion over complementarity**

54 Global biodiversity is declining at unprecedented rates [1,2]. Yet, biodiversity is crucial
55 for maintaining **ecosystem functioning** (see glossary) and ecosystems' ability to deliver goods
56 and services (reviewed by [3,4]). Complementarity is often invoked to explain this enhanced
57 ecosystem functioning in diverse plant communities [5,6]. The intuitive idea behind this concept
58 is that plant species are complementary if they fit together like puzzle pieces. Each species
59 (puzzle piece) adds, at least partially, to total community functioning.

60 Yet, complementarity is currently used as both a cause of enhanced ecosystem
61 functioning in diverse communities and a consequence of some community process (Figure
62 1,[7]). For example, in biodiversity–ecosystem functioning research, it is common to calculate
63 measures of overproduction such as the '**complementarity effect**'. These measures of
64 overproduction are statistical measures that demonstrate whether the performance of plant
65 species mixtures exceeds their expected performance based on the monocultures of their
66 component species [8]. These measures (Figure 1, right side) answer the question: do mixtures
67 perform better than monocultures? The complementarity effect and other measures of
68 overproduction of mixtures document the consequence (i.e enhanced ecosystem functioning) but
69 not the underlying mechanistic cause [7]. Yet, these measures of overproduction in mixture are
70 often interpreted as evidence for complementarity in the colloquial sense as a cause or more
71 specifically for **resource partitioning**. In a review of 137 studies that calculated a
72 complementarity effect (see Table 1 for search terms and methods), we found that 63% of studies
73 conflated the complementarity effect (consequence) with complementarity (cause) already in the
74 abstracts of the papers. Often, this interpretation is further misconstrued as evidence that species
75 partition resources (*e.g.*, [3,6,7,9]). Indeed, 30% of studies that conflated complementarity with

76 the complementarity effect explicitly interpreted the complementarity effect as evidence that
77 species partitioned resources in the abstract. This use of complementarity obscures the
78 contribution of other causes that are not linked with the colloquial definition of complementarity
79 and overemphasizes the contribution of resource partitioning to enhanced ecosystem functioning
80 in more diverse mixtures.

81 In fact, several causes drive overproduction in mixture including resource partitioning,
82 **abiotic facilitation**, and **biotic feedbacks** (Figure 1, left side, [8,10]). Here, we formally
83 integrate these three sets of species differences into complementarity. We review the evidence
84 that these causes may drive enhanced ecosystem functioning in more diverse mixtures. Further,
85 we argue that disentangling the causes of complementarity helps us to predict how ecosystems
86 will respond to future biodiversity loss.

87

88 **A revised view of complementarity: from cause to consequence**

89 We define complementarity as differences between species, functional groups, or
90 genotypes that may (but need not) enhance ecosystem functioning. For simplicity, we refer
91 throughout to ‘species’ but other taxonomic levels may be equally relevant. In keeping with this
92 definition, species in any given community can differ from one another in three ways: 1. Species
93 differ in the **resources** that they use (resource partitioning). 2. Species differ in their ability to
94 alter their environment to benefit other species (abiotic facilitation). 3. Species differ in their
95 biotic interactions with other trophic levels (biotic feedbacks). Species in any given community
96 can differ in more than one of these ways. These differences form our preconditions for local
97 plant diversity to enhance ecosystem functioning. Furthermore, these differences only enhance
98 ecosystem functioning if — on average — they increase the performance of mixtures relative to

99 the performance of monocultures (Box 1). Below, we review the current research on resource
100 partitioning, abiotic facilitation, and biotic feedbacks, and the evidence that they enhance
101 ecosystem functioning in plant communities (Table 1). We also discuss classic examples which
102 may be the result of several of these causes combined such as nitrogen fixation by legumes (Box
103 2).

104

105 *Resource partitioning*

106 Resource partitioning occurs when species use different portions of the available resource
107 pool (cause). The result of resource partitioning is that the existing resource pool is more
108 completely used in higher-diversity communities compared to monocultures (consequence,
109 Figure 2.A, yellow line). In plant communities, resource partitioning happens across space (*e.g.*
110 rooting depth, [11]), time (*e.g.* phenology of nutrient uptake, [12]), chemical form (*i.e.*
111 Nitrate(NO_3^-); Ammonium(NH_4^+) and organic Nitrogen (N), [13]), or all of these combined
112 [14].

113

114 *Spatial partitioning*

115 Quantifying spatial resource partitioning between plants generally relies on two
116 approaches: 1) documenting space filling above- or belowground or 2) measuring resource
117 uptake from different areas within the canopy or the rooting zone. Several studies demonstrate
118 that plants more fully utilize vertical aboveground space with increasing diversity [15–20].
119 Belowground, this **pattern** is less clear. Indeed, several studies [21,22] found that plants allocate
120 belowground biomass to deeper layers with increasing diversity. Yet others [23–26] found that
121 plants are more likely to aggregate biomass in the topsoil with increasing diversity.

122 Belowground, isotope tracers may provide better evidence of spatial resource partitioning than
123 root distribution [25,27–29]. However, like studies of belowground biomass allocation, resource
124 tracer studies show mixed [12,25] and largely non-significant [25,27,28] evidence for spatial
125 resource partitioning of common soil resources in space.

126

127 *Temporal partitioning*

128 Communities composed of groups of plants with distinct phenology often have enhanced
129 ecosystem functioning relative to communities composed of species with similar phenology, *e.g.*
130 if early- and late-season species are present. For example, Kahmen *et al.* [12] found that the
131 uptake of nitrogen by different plant species varied across time (indicating the potential for
132 resource partitioning), but that this variation was not associated with increased total N uptake.
133 Alternatively, Jesch *et al.* [28] found no evidence that plant species partition water, nitrogen, or
134 potassium across the growing season (also demonstrated by [14,30]).

135

136 *Chemical form*

137 Ashton *et al.* [13] found strong evidence that grassland species partitioned forms of
138 nitrogen when in **competition** with a dominant species which took up the most available
139 chemical form of nitrogen. von Felten *et al.* [25] also found evidence that species partitioned
140 different forms of nitrogen (cause). However, increased partitioning of nitrogen forms was not
141 associated with enhanced ecosystem functioning (consequence).

142

143 Overall, even when there is some evidence that species differ in their spatial or temporal
144 use of resources [21,25], studies often fail to correlate this evidence of resource partitioning

145 (cause) with enhanced ecosystem functioning (consequence,[21,22]). Thus, these studies provide
146 only limited support for the role of resource partitioning in complementarity — evidence tying
147 the cause to the consequence of enhanced ecosystem functioning in grasslands is limited (but see
148 [21,22] where evidence of spatial resource partitioning is linked to enhanced ecosystem
149 functioning in mixture).

150

151 *Abiotic facilitation*

152 Abiotic facilitation occurs when a plant species benefits another plant species via changes
153 to the abiotic properties of the environment, such as its microclimate, soil chemical properties, or
154 soil physical properties (reviewed by [31,32], [33] for arid environments, [34] for agricultural
155 systems). Abiotic facilitation may cause enhanced ecosystem functioning when species receive a
156 benefit from being in high-diversity systems relative to low-diversity systems (Figure 2.B, blue
157 line). Here, we limit abiotic facilitation to plant–plant interactions. Thus, we exclude nitrogen
158 fixation (and similar cases) from this category, because non-plant interaction partners mediate
159 both the nitrogen fixation and the transfer of this nitrogen to other members of the community
160 (for the role of nitrogen-fixation in biodiversity–ecosystem functioning see Box 2). There are
161 two non-mutually-exclusive ways in which plants likely facilitate each other: 1) plants may
162 enrich the resource pool for neighboring plants, or 2) plants may mediate physical **stress**

163

164 *Resource enrichment*

165 Some plants make resources available to the community which were previously
166 unavailable. We call this abiotic facilitation via resource enrichment. Abiotic facilitation via
167 resource enrichment differs from resource partitioning in that specific plant traits *enlarge the*

168 *resource pool* for the whole plant community. In contrast to resource partitioning where different
169 plant species together *use the available resource pool* more completely.

170 For example, some plant species exude enzymes or organic acids that promote mineral
171 weathering and thereby enlarge the existing resource pool of plant-available soil nutrients
172 (cause). Other members of the plant community may benefit from this increased availability of
173 nutrients as well [34–36]. Another example where plants may enrich the local environment is
174 through hydraulic lift. Plants with deep roots may draw water up from a depth where it was
175 previously inaccessible [37]. These species then make the water available to plants with shallow
176 roots. Hydraulic lift occurs in both woody [38] and herbaceous [39] communities (cause), but
177 this has not yet been connected to enhanced growth of shallow rooted neighbors in biodiversity–
178 ecosystem functioning experiments in grasslands [40](consequence).

179

180 *Physical stress buffering*

181 Plants may provide a barrier against physical stress for other members of their
182 community. For example, Steudel *et al.* [41] found that high temperatures were better buffered in
183 high-diversity communities. Plant species may ameliorate the microclimate for other members of
184 their community by physically mediating wind, heat, or photoinhibition [32]. Milcu *et al.* [42]
185 demonstrated that this was likely in higher-diversity systems which had proportionally lower
186 evaporation and sensible heat flux (see also [43] for natural grasslands).

187

188 Overall, plants can enrich local resource availability and provide a buffer to physical
189 stress simultaneously across diversity gradients [32,44]. However, evidence to date does not

190 directly relate these effects to enhanced ecosystem functioning with higher diversity in grassland
191 plant species (consequence, but see [45] for non-vascular plant species).

192

193 *Biotic feedbacks from other trophic levels*

194 Increasing plant diversity may alter the strength of interactions between plants and other
195 trophic levels (reviewed by [46]). We refer to these interactions as biotic feedbacks from other
196 trophic levels. Biotic feedbacks from other trophic levels may enhance ecosystem functioning in
197 two ways: 1) species differ in their enemies (consumers/herbivores, pests and pathogens). The
198 negative interactions between plant and enemy may create strong conspecific negative **density**
199 **dependence**. This negative density dependence leads to reduced plant performance at low
200 diversity relative to high diversity (Figure 2.A, pink line, [47]). 2) Species differ in their
201 mutualists, these mutualists may also benefit other species (positive biotic feedbacks, Figure 2.B,
202 blue line). If the benefit of mutualists increases with increasing diversity (cause), then ecosystem
203 functioning increases with diversity (consequence, reviewed in [46]).

204

205 *Negative biotic feedbacks*

206 Plant species differ in both above- and belowground enemies (cause). When enemies are
207 sufficiently species-specific, plants are suppressed when they occur among members of their
208 own species in a negative density-dependent manner [48,49]. This monoculture suppression
209 means that ecosystem functioning of diverse communities is enhanced relative to these poorly
210 performing monocultures (consequence). Several studies now demonstrate that enemies in
211 grassland ecosystems can be species-specific and that their damage decreases with increasing
212 diversity (reviewed in [50,51]). Belowground, plant–soil feedback experiments (reviewed in

213 [52,53]) often find that negative feedback from soil enemies (cause) through negative density
214 dependence contributes to enhanced ecosystem functioning (consequence) [54–56]. For example,
215 Hendriks *et al.* [57] found that soil inoculated with species-specific soil biota caused
216 monocultures to underperform relative to mixtures. Seabloom *et al.* [58] found that removing
217 aboveground enemies (cause) increased overall biomass production by a constant proportion
218 across a biodiversity gradient, leading to a greater increase in aboveground biomass production
219 in higher-diversity communities (consequence).

220

221 *Positive biotic feedbacks*

222 If the positive effect of other non-plant species increases with increasing diversity,
223 positive biotic feedbacks between plants and other species (including their mutualists) may also
224 enhance ecosystem functioning (reviewed belowground in [46,53], above and belowground in
225 [59]). However, few studies have linked non-resource related mutualists to ecosystem
226 functioning. We include these resource-related mutualists such as mycorrhizae and rhizobia in
227 the overlap between resource partitioning, abiotic facilitation, and biotic feedbacks (see Box 2).
228 However, aboveground, Ebeling *et al.* [60] demonstrated that pollinator communities increased
229 in diversity with increasing plant diversity and that this increased the stability of plant flowering.

230 Overall, there is strong evidence that the release of negative biotic feedbacks with
231 increasing plant diversity (cause) enhances ecosystem functioning (consequence)[55]. However,
232 there is little evidence that positive biotic feedbacks enhance ecosystem functioning alone (but
233 see Box 2).

234

235 **The future of complementarity**

236 Many studies report the presence of resource partitioning, abiotic facilitation, or biotic
237 feedbacks. Yet, few quantify the contribution of these causes to enhanced ecosystem functioning
238 (but see [21,22,25,28]). Quantifying how each of these causes individually contributes to
239 ecosystem functioning may allow us to better predict the consequences of biodiversity loss in
240 three ways. First, the consequences of biodiversity loss for ecosystem functioning may differ
241 between these causes. Second, the relative importance of these causes likely changes with
242 ecological context. Third, biodiversity may be more important for ecosystem functioning when
243 several causes combine (Figure 2).

244

245 *The ecological consequences of understanding underlying causes*

246 If resource partitioning between species enhances ecosystem functioning, then species
247 loss may have no effect on overall ecosystem functioning or may decline proportionally to the
248 contribution of the species lost. That is, the amount of functioning lost is the contribution of the
249 species lost to functioning. This change in ecosystem functioning likely depends on the ability of
250 the other species in a community to compensate for the functioning of the species lost via
251 adjustments to their resource partition via plasticity [61]. For example, if species partition
252 resources by depth and the deepest rooting species goes extinct, another species may compensate
253 for the lost species by growing deeper roots and the community overall resource uptake will stay
254 the same [62]. If the remaining species are unable to compensate for the lost species then the lost
255 species' ecosystem functioning contribution is lost [61].

256 Alternatively, if abiotic facilitation between species enhances ecosystem functioning then
257 the loss of facilitators may disproportionately decrease ecosystem functioning. That is, if a
258 facilitator is lost, their contribution to ecosystem functioning is lost as is the amount that other

259 species over-perform because of their presence. Under extreme circumstances, if the whole
260 community depends on a single facilitator then the community may collapse [61]. In less
261 extreme cases, the extinction of a facilitator reduces the abundance and performance of other
262 species because they were dependent upon the resources or stress amelioration provided by the
263 facilitator [61]. Even in this less extreme case, over several generations, facilitator loss can
264 accelerate species loss in addition to reducing ecosystem functioning.

265 If feedbacks from biotic interaction partners enhance ecosystem functioning then the loss
266 of individual plant species depends on the type of interaction and whether the interaction is lost
267 or only the species [63]. For example, if the species lost contributes a species-specific enemy
268 then the loss to ecosystem functioning will likely equal the contribution of the species lost.
269 Alternatively, removing the enemies may increase overall ecosystem functioning, especially in
270 terms of total biomass production [58]. If a system loses a species-specific herbivore, total
271 biomass production may increase as species are released from herbivore pressure [58,64].
272 However, this increase in productivity may be accompanied by plant species loss. Less
273 competitive species may be outcompeted by species that are now released from enemy pressure.
274 This competition accelerates species loss even while dominant species maintain productivity
275 [65]. Alternatively, if the plant species that is lost contributes an important mutualist, the species'
276 contribution is lost as is the amount that the population overperformed as a result of the species.
277 [63,66]. For example, if a legume that provides nitrogen to the surrounding plants via its rhizobia
278 is lost, the contribution of the legume is lost as is the amount that ecosystem functioning was
279 increased due to the rhizobia's contribution to the local resource pool (Box 2).

280

281 *Ecological context matters*

282 Resource partitioning, abiotic facilitation, and biotic feedbacks are likely most relevant in
283 different ecological contexts. These differences in relevance may contribute to variation in
284 biodiversity-ecosystem functioning relationships across landscapes and between ecosystems. In a
285 meta-analysis of forest and grassland biodiversity experiments, Guerrero-Ramirez *et al.* [67]
286 found that forests and grasslands had variable biodiversity–productivity relationships that
287 depended on environmental factors. In one grassland, reduced monoculture performance over
288 time drove biodiversity–productivity relationships suggesting that abiotic facilitation via stress
289 amelioration or negative biotic feedbacks caused enhanced ecosystem functioning. In six other
290 grasslands increased mixture performance over time drove biodiversity–productivity
291 relationships suggesting that abiotic facilitation via resource enrichment, positive biotic
292 feedbacks, or resource partitioning caused enhanced ecosystem functioning. Further, soil
293 characteristics such as soil organic carbon content, soil pH, sand and clay content, soil bulk
294 density, cation exchange capacity, and volumetric water content at wilting point explained over
295 40% of these differences between sites. This context dependence suggests that not all causes are
296 equally likely in all ecological contexts (see also [68]). In particular, three **ecological gradients**
297 may influence the likelihood and relative importance of these different causes: resource
298 availability, abiotic stress, and enemy abundance/specificity.

299 Resource availability may change plant community reliance on abiotic facilitation via
300 resource addition and resource partitioning. When resources are severely limiting, abiotic
301 facilitation via resource addition is likely to enhance ecosystem functioning. Without resource
302 limitation, plants are unlikely to profit from the enhanced resource availability from abiotic
303 facilitation via resource addition with increasing diversity. Further, unless plants are not in

304 competition for resources, resource partitioning is likely to be more beneficial when resources
305 are limiting [69].

306 Abiotic stress likely magnifies the contribution of abiotic facilitation via stress
307 amelioration to enhanced ecosystem functioning [44,70,71]. The stress-gradient hypothesis
308 suggests that as environments become more stressful, abiotic facilitation via stress amelioration
309 becomes more important. In the biodiversity–ecosystem functioning context, this increased
310 reliance on abiotic facilitation via stress amelioration means that high-diversity communities will
311 suffer less in stressful conditions. There is some evidence that species can ameliorate the abiotic
312 stress of flooding [72], heavy-metal contamination [73], and drought [45]. Under less stressful
313 conditions resource partitioning may contribute more than abiotic facilitation to enhanced
314 ecosystem functioning. Similarly, positive feedback from biotic interaction partners is likely to
315 be more beneficial under resource limitation and stress.

316 An enemy abundance/specificity gradient will likely amplify the contribution of negative
317 biotic feedbacks to biodiversity–ecosystem functioning relationships. Plant–soil feedback
318 experiments and aboveground enemy removals elucidate a strong and consistent contribution of
319 enemies to enhanced ecosystem functioning [55–58]. A gradient of enemy types (specialist to
320 generalist) or enemy abundance is likely to similarly provide evidence that species-specific
321 enemies reduce monoculture performance. This gradient may be particularly relevant across
322 latitude where changes in the strength and abundance of biotic interactions may contribute to
323 latitudinal gradients in diversity [74]. This continental gradient in enemies may alter
324 biodiversity–ecosystem functioning relationships across continental scales [75,76].

325

326 *When causes combine to enhance ecosystem functioning*

327 When biodiversity enhances ecosystem functioning, it need not occur via any one
328 mechanism alone. Rather, it may be more realistic to assume that resource partitioning, abiotic
329 facilitation, and biotic feedbacks occur simultaneously in many systems. As a consequence,
330 ecosystem functioning represents the **net response** of the ecosystem to combinations of these
331 causes, and the individual effects of the causes are masked. Several studies now implicate
332 multiple causes simultaneously. For example, Seabloom *et al.* [58] experimentally removed
333 insects, foliar fungi, and soil fungi from plots at Cedar Creek Ecosystem Science Reserve. The
334 biodiversity–productivity relationship changed as a result of this removal but was still present.
335 This result implies that enemies are not the only cause of enhanced ecosystem functioning at this
336 site. Similarly, Guerrero-Ramirez *et al.* [67] found that both enhanced functioning in mixture and
337 reduced functioning in monoculture over time drove biodiversity–productivity relationships
338 simultaneously at three grassland sites. This pattern again suggests that several causes are
339 responsible. We hypothesize that when any cause that reduces the average performance of
340 species in monoculture combines with any cause that increases their average performance in
341 mixture, the slope of the biodiversity–ecosystem functioning relationship will increase (Figure
342 2). This increase in slope means that diversity may be proportionally more important for
343 ecosystem functioning under these circumstances.

344

345 **Concluding remarks and future perspectives**

346 For plant communities, complementarity is one of the most commonly invoked drivers
347 behind enhanced ecosystem functioning with increasing biodiversity. Yet, its current usage
348 obscures the individual contributions of resource partitioning, biotic feedbacks, and abiotic
349 facilitation to enhanced ecosystem functioning. The extent to which these different causes

350 contribute to enhanced ecosystem functioning in higher-diversity systems is unclear.
351 Disentangling these components is essential to predicting biodiversity–ecosystem functioning
352 relationships across ecological contexts and under predicted accelerating species loss.

353 We suggest that there are several avenues via which biodiversity ecosystem functioning
354 research should begin to disentangle these components (see also Outstanding Questions). First,
355 improved theoretical work that incorporates more than one cause of enhanced ecosystem
356 functioning simultaneously will help to refine predictions for how these different causes may
357 interact. Theoretical work on biodiversity-ecosystem functioning relationships has focused
358 primarily on complementarity causes in isolation (*e.g.*, [55,77,78]). Theoretical models that
359 incorporate multiple complementarity causes simultaneously are necessary to refine predictions
360 for how the different causes of complementarity may interact.

361 Second, we suggest that combining ecological gradients across resources, stress, and
362 enemies will enhance differences between resource partitioning, abiotic facilitation, and biotic
363 feedbacks and allow them to be more easily quantified (after [79]). For example, monocultures
364 may perform more poorly than mixtures due to negative feedback from species-specific pests
365 and pathogens (biotic feedback) or because other species mediate environmental stress (abiotic
366 facilitation). Along a diversity gradient without species-specific enemies (enemy gradient) under
367 stress (stress gradient) but with ample resources (resource availability gradient), if plants perform
368 more poorly in monoculture than in mixture the most likely driver is abiotic facilitation via stress
369 amelioration. Experimental work that utilizes these gradients will help to elucidate how these
370 three sets of species differences interact to enhance ecosystem functioning across ecological
371 contexts.

372 Finally, further synthesis work from long-term grassland biodiversity experiments may
373 also contribute to a better understanding of the causes of complementarity. Many BEF
374 experiments have now been established for over a decade. These long-term datasets provide
375 particular power to determine whether monocultures are declining or mixtures performing better
376 (*e.g.*, [67]). Further, these long-term datasets span natural climatic and resource gradients (*e.g.*,
377 [3,80]). Long-term data from these experiments of measures like leaf area index [81], resource
378 uptake [28], or soil porosity [72] combined with the natural climatic variation inherent in time
379 series data may be particularly useful. For example, during a drought, if monocultures perform
380 more poorly than the mean performance over time and this effect is linked to a lower leaf area
381 index in these monocultures then abiotic facilitation via stress amelioration likely enhances
382 ecosystem functioning under these circumstances.

383

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388 for this manuscript.

389 **Glossary**

390 **Abiotic facilitation** — occurs when an increase in the abundance of one species
391 increases the relative performance of a different species via changes to the abiotic
392 environment.

393 **Biotic feedbacks** — here narrowly defined as the amplifying (positive feedback) or
394 dampening (negative feedback) effect on the performance of a plant species or
395 community caused by another trophic level in response to changes in plant diversity.

396 **Competition** — occurs when an increase in the performance of one species decreases the
397 performance of a different species.

398 **Complementarity effect** — the performance of mixtures relative to the performance of
399 the component monocultures [8].

400 **Density dependence** — a process that increases in strength when a species becomes
401 more abundant in a given area. For example, negative density dependent effects occur
402 when the relative performance of a species is reduced with increasing abundance.

403 **Ecosystem functioning** — sizes of pools of materials or energy (pools of carbon,
404 nitrogen or biomass) and rates of processes (fluxes of materials or energy among pools).
405 High or low values are not inherently good or bad [5].

406 **Ecological gradient** — a gradient across which a specific environmental factor or
407 ecological context varies (*e.g.*, a gradient of abiotic stress, a gradient of pathogen
408 specificity).

409 **Net response** — the combined effect of two or more complementarity causes (does not
410 refer to the statistical “net biodiversity effect” used by the additive partitioning method).

411 **Pattern** — a set of circumstances created by a process (*i.e.* the effect in a cause–effect
412 relationship).

413 **Resources** — limiting factors that decrease in availability as the total abundance of
414 species in a community increases (*e.g.*, nitrogen,[79])

415 **Resource complementarity** — the theory that posits that the addition of species to a
416 community increases average relative performance of species because each species
417 specializes on different resources and thus the whole community more thoroughly utilizes
418 the available resources [77].

419 **Resource partition** – multidimensional measure of the share of the total resource pool
420 that a species uses [82,83] (roughly synonymous to a resource niche)

421 **Fundamental resource partition** — Species' resource partition when growing
422 alone (similar to the fundamental resource niche).

423 **Realized resource partition** – Species' resource partition when growing with
424 other species (similar to the realized resource niche).

425 **Resource partitioning** — occurs when species use different portions of the available
426 resource pool (cause). The result of resource partitioning is that the existing resource pool
427 is more completely used in higher-diversity communities compared to monocultures

428 **Stress** — limiting factors that are abundance independent (*e.g.*, temperature, [79]).

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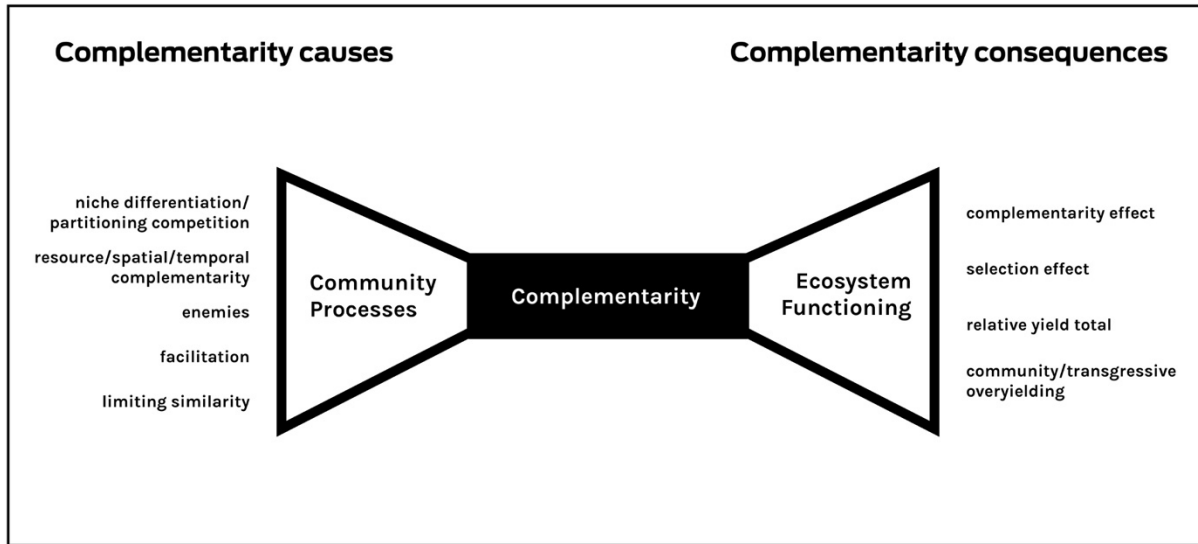
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637

638 **Figure 1. Looking inside the black box of complementarity.** We found that in the
639 biodiversity–ecosystem functioning literature, uses for the term complementarity generally fall
640 into two categories: complementarity causes (see left), and complementarity consequences (see
641 right) of the coupling between diversity and ecosystem functioning. On the left, we list potential
642 causes that, historically, are credited with driving complementarity. On the right, we list
643 consequences that have historically been derived from species being complementary in some
644 fashion. Some studies use complementarity as both a cause and a consequence. When
645 complementarity is used by itself, which is common, it is often unclear whether the intended
646 definition falls under a specific usage (on either the causes or consequences side) or rather as the
647 center portrays. We believe that the multitude of uses of complementarity on both sides of this
648 model and in the center, without explicitly stating which perspective is taken, often leads to
649 misinterpretation and confusion in communicating.
650



653 **Figure 2. Proposed framework for ‘complementarity’ in the biodiversity-ecosystem**
654 **functioning literature with predictions for enhanced ecosystem functioning.**

655 Resource partitioning (yellow), biotic feedbacks (red), and abiotic facilitation (blue) can
656 each lead to enhanced ecosystem functioning. In many ecosystems, these three will occur at the
657 same time. Thus, enhanced ecosystem functioning, when it occurs, is the net response of these
658 different causes in this system. Here, we assume that when two or more processes are present,
659 they are roughly the same magnitude. Inlaid plots (A-D) are our predictions for each
660 complementarity cause and their combined effects on any generic ecosystem function
661 (consequence, y-axis) with increasing diversity (x-axis). These predictions are general
662 predictions for the slope and the intercept relative to the average ecosystem functioning (grey
663 midline) when biodiversity enhances ecosystem functioning. These three causes can enhance
664 ecosystem functioning via reduced performance in monoculture or via enhanced performance in
665 mixture or both as indicated here by the intercept. That is, if the intercept is below the midline it
666 indicates that performance is reduced in monoculture. The slope describes the strength of the
667 increase in functioning. We do not intend to predict the magnitude of the differences between the
668 intercepts of different causes. Furthermore, we depict these relationships as linear for simplicity
669 though they take a variety of forms depending on the function measured. Finally, we combine
670 positive feedbacks and abiotic facilitation via nutrient addition for the purposes of these plots.

671 If enemies are species-specific then negative biotic feedbacks reduce performance of
672 species in monoculture (A, C, and D - pink lines,[57]). In contrast, resource partitioning (A, B,
673 and D - yellow lines, [25]) and abiotic facilitation via resource addition or positive feedback
674 from biota (B, C, and D – blue lines, [32], [84]) will enhance ecosystem functioning when
675 diversity is high.

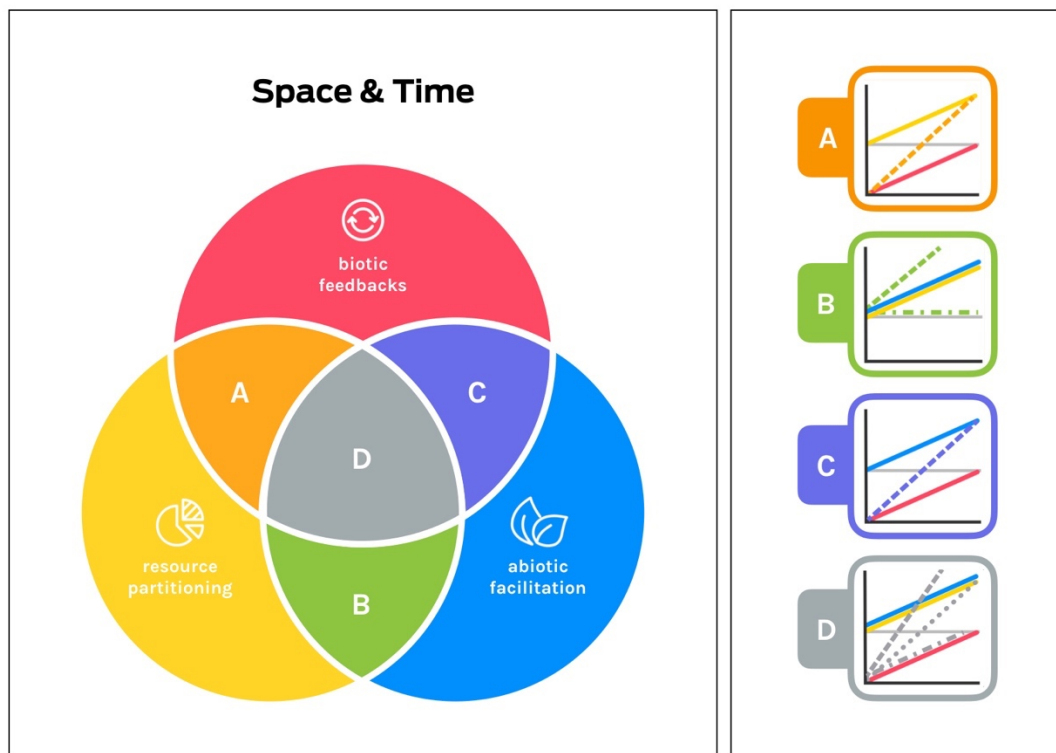
676 We expect that when negative biotic feedbacks and resource partitioning act
677 simultaneously, the slope of the biodiversity–ecosystem functioning relationship will increase as
678 enemies suppress functioning in monoculture and resource partitioning enhances functioning in
679 mixture (A – orange line, see [58] for general increase in biodiversity–ecosystem functioning
680 relationship with multiple potential causes likely).

681 We expect that resource partitioning and abiotic facilitation both enhance function at high
682 diversity if they occur for different limiting resources. Thus, the slope of the biodiversity–
683 ecosystem functioning relationship may increase (B, dashed green line) relative to either process
684 alone (B, blue or yellow line). Alternatively, if both resource partitioning and abiotic facilitation
685 via nutrient addition or positive feedback from biota occur simultaneously for the same limiting
686 resource and in the same amount, then that resource is no longer limiting and only abiotic
687 facilitation or positive feedback will enhance ecosystem function (C – blue line, [85]).
688 Alternatively, if the resource that plants are able to partition and provide is non-limiting, we
689 expect a non-significant relationship between ecosystem functioning and biodiversity (C – green
690 dashed-dotted line [85]).

691 Resource limitation is also an important concern for predicting the net result of
692 combining resource partitioning, biotic feedback, and abiotic facilitation (D). Resource
693 partitioning and abiotic facilitation both will enhance function at high diversity when they occur
694 for different resources. Negative biotic feedback will suppress monoculture function [55]. We
695 predict that this combination will increase the slope of the biodiversity–ecosystem functioning
696 relationship (D, dashed grey line). Similarly, abiotic facilitation may enhance ecosystem
697 functioning at high diversity while biotic feedback suppresses monoculture function (D, dotted
698 line). If resource partitioning and abiotic facilitation both occur for the same limiting resource,

699 then the net result is likely the same as the result for biotic feedback and abiotic facilitation
700 combined (D, dotted line). Alternatively, if the resource that plants can partition and provide via
701 abiotic facilitation is non-limiting then only the signal of biotic feedbacks may be present (D –
702 dashed-dotted line).

703 We expect that the slope of the biodiversity–ecosystem functioning relationship increases
704 for many interactions between processes relative to a single process alone. That is — each
705 species likely adds more to ecosystem functioning when causes that reduce monoculture
706 performance (such as negative feedback from species specific enemies) and causes that enhance
707 mixture performance (such as resource partitioning) occur together.



708

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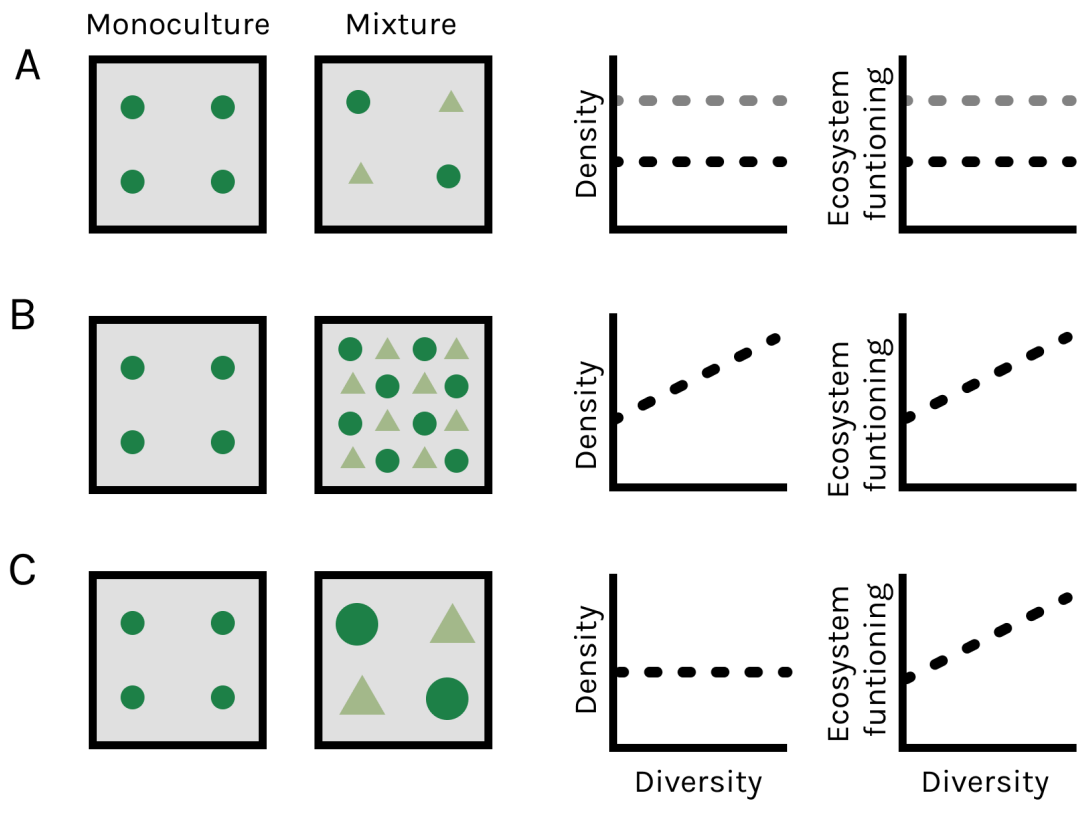
710

711 **Box 1. Abundance, plasticity, and biodiversity–ecosystem functioning relationships.**

712 We define enhanced ecosystem functioning as the increase in the community performance of
713 mixtures relative to monoculture. Plant populations may have altered performance in mixture
714 relative to monoculture in two general ways: 1. via plastic changes to their individual
715 performance (*e.g.* through growing larger or having deeper roots), or 2) via changed numbers of
716 individuals that perform at the same level (*i.e.*, changed abundance) [86,87].

717

718 **Figure I. Illustration of how changes to density and performance both together and alone**
719 **can drive enhanced ecosystem functioning in more diverse mixtures.** If the abundance or
720 individual performance relative to monoculture does not change, then ecosystem functioning is
721 not enhanced relative to monocultures (Figure I, **A**). The black line represents a community with
722 low abundance/small size while the grey line represents high abundance/large size).
723 Alternatively, if the abundance of individuals increases (Figure I,**B**), individuals perform better
724 (Figure I, **C**), or both in mixture, then the ecosystem functioning of mixtures will increase
725 relative to average monocultures. It should be noted that only scenario C or the combination of C
726 and B are the result of plastic responses on the part of the plant to being in mixture. Yet,
727 enhanced ecosystem functioning can be achieved by scenario B as well.



729 **Box 2: Nitrogen fixation, mycorrhizal colonization, and root interaction partners**

730 Plant roots harbor a diverse community of mutualists and interaction partners that
731 influence the capacity of plants to take up resources and transfer those resources to their
732 neighbors. We consider many of these interactions including nitrogen fixation and increased
733 nutrient availability from colonization by mycorrhiza to be positive biotic feedbacks from a
734 member of a different trophic level. These positive biotic feedbacks, however, result in both the
735 ability of a species to potentially partition resources (one species specializes on nitrogen fixation
736 while another must forage to find nitrogen) and the ability to confer resources to the surrounding
737 community. The presence of nitrogen fixing plants increases the overall availability of nitrogen
738 [88–90]. Furthermore, there is significant evidence that legumes provide a generally positive
739 effect on the biodiversity-ecosystem function relationship [91]. This nitrogen fixation also
740 enables facilitation and the proportion of N derived from legumes relative to non-legume sources
741 increases with increasing plant diversity [90,92].

742 Similarly, mycorrhizae enable plants to take up additional resources. Thus, if resource
743 partitioning occurs it may be enabled by mycorrhizal colonization. Alternatively, mycorrhizae
744 may also transfer nitrogen that has been fixed by rhizobia to plants that don't harbor rhizobia
745 thus enabling facilitation [46]. There is limited evidence that a higher diversity of mycorrhizal
746 fungi may increase plant productivity [93,94]. Additionally, Walder *et al.* [95] suggest that plant
747 communities that harbor different mycorrhiza perform better in mixture. However, Schnitzer *et*
748 *al.* [55] found that removing the beneficial portion of soil fungi from a diversity experiment had
749 negligible effects on the relationship between biodiversity and productivity.

750 In addition to crucial mutualists, plants also harbor a diverse community of non-mutualist
751 soil biota in and around their roots. There is strong evidence that plants increase soil microbial

752 activity [81]. Furthermore, plant diversity alters decomposition [96–99]. These alterations to the
753 soil community positively influence many ecosystem functions including soil carbon storage
754 [81]. Further, this impact on the soil community also influences resource availability and thereby
755 provides a feedback on the plant community via resource partitioning and/or abiotic facilitation
756 [100].

757 **Figure I Illustration of a legume.** Root nodules containing nitrogen fixing rhizobia are
758 highlighted in red.



759

760 **Table 1: Quantifying complementarity uses and complementarity causes in the biodiversity**
 761 **ecosystem functioning literature.**

762 In order to quantify the use of the term complementarity in the biodiversity-ecosystem
 763 functioning literature, we performed a Web of Science search of study topics using the search
 764 terms: literature citing Loreau and Hector 2001 Nature AND ecosystem function* (* indicates
 765 Web of Science search function that allows Web of Science to search for terms including
 766 function in addition to function itself, e.g. functioning or functions). This search returned 400
 767 results as of August 2018. We read the abstracts of these 400 studies and determined which ones
 768 calculated a “complementarity effect” *sensu* Loreau and Hector [8] or Fox [101](137 studies).
 769 We then determined which of these 137 studies explicitly used complementarity in the colloquial
 770 sense as a mechanism driving the complementarity effect in the abstract alone (86 studies). We
 771 also determined which of these studies further conflated the “complementarity effect” with what
 772 we refer to as resource partitioning (25 out of 86 studies, ‘resource use complementarity’,
 773 ‘resource partitioning’, ‘niche complementarity’, or ‘niche differentiation’) in the abstract alone.

774 In order to quantify the prevalence of each of our complementarity causes in the
 775 biodiversity-ecosystem functioning literature, we performed a number of Web of Science
 776 searches of study topics. As of August 2018, resource partitioning was more prevalent in the
 777 biodiversity-ecosystem functioning literature than both abiotic facilitation and biotic feedbacks.
 778 Similarly, abiotic facilitation was more commonly invoked than biotic feedbacks. Only two
 779 studies met all of our search criteria simultaneously.

780

Search number	Cause	Search terms	Number of studies
1		literature citing Loreau and Hector 2001 Nature AND ecosystem function*	400

2	Resource partitioning	("resource complementarity" OR "resource partitioning" OR "niche partitioning" OR "niche differentiation") AND biodiversity AND ecosystem function* AND plant* AND complementarity	71
3	Abiotic facilitation	("facilitation" OR "stress amelioration") AND biodiversity AND ecosystem function* AND plant* AND complementarity	57
4	Biotic feedbacks	("plant-soil feedback" OR "mutualist" OR "rhizobia" OR "pathogen" OR "enemies" OR "herbivore") AND biodiversity AND ecosystem function* AND plant* AND complementarity	43
2 AND 3	Resource partitioning and abiotic facilitation		14
2 AND 4	Resource partitioning and biotic feedbacks		10
3 AND 4	Abiotic facilitation and biotic feedbacks		3
2 AND 3 AND 4	All three inclusive		2