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.

The confusion over complementarity

Global biodiversity is declining at unprecedented rates [1,2]. Yet, biodiversity is crucial

for maintaining **ecosystem functioning** (see glossary) and ecosystems' ability to deliver goods

and services (reviewed by [3,4]). Complementarity is often invoked to explain this enhanced

ecosystem functioning in diverse plant communities [5,6]. The intuitive idea behind this concept

is that plant species are complementary if they fit together like puzzle pieces. Each species

(puzzle piece) adds, at least partially, to total community functioning.

Yet, complementarity is currently used as both a cause of enhanced ecosystem

functioning in diverse communities and a consequence of some community process (Figure

1,[7]). For example, in biodiversity–ecosystem functioning research, it is common to calculate

measures of overproduction such as the '**complementarity effect'**. These measures of

overproduction are statistical measures that demonstrate whether the performance of plant

species mixtures exceeds their expected performance based on the monocultures of their

component species [8]. These measures (Figure 1, right side) answer the question: do mixtures

perform better than monocultures? The complementarity effect and other measures of

overproduction of mixtures document the consequence (i.e enhanced ecosystem functioning) but

not the underlying mechanistic cause [7]. Yet, these measures of overproduction in mixture are

often interpreted as evidence for complementarity in the colloquial sense as a cause or more

specifically for **resource partitioning**. In a review of 137 studies that calculated a

complementarity effect (see Table 1 for search terms and methods), we found that 63% of studies

conflated the complementarity effect (consequence) with complementarity (cause) already in the

abstracts of the papers. Often, this interpretation is further misconstrued as evidence that species

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

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]).

References

1 (2006) *Millenium Ecosystem Assessment Ecosystem and human well-being: synthesis*,

2 Ceballos, G. *et al.* (2015) Accelerated modern human–induced species losses: Entering the sixth mass extinction. *Sci. Adv.* 1, e1400253

3 Weisser, W.W. *et al.* (2017) Biodiversity effects on ecosystem functioning in a 15-year grassland experiment: Patterns, mechanisms, and open questions. *Basic Appl. Ecol.* 23, 1–73

4 Isbell, F. *et al.* (2017) Linking the influence and dependence of people on biodiversity across scales. *Nature* 546, 65

5 Hooper, D.U. *et al.* (2005) Effects of Biodiversity on Ecosystem Functioning: A Consensus of Current Knowledge. *Ecol. Monogr.* 75, 3–35

6 Cardinale, B.J. *et al.* (2007) Impacts of plant diversity on biomass production increase through time because of species complementarity. *Proc. Natl. Acad. Sci.* 104, 18123–18128

7 Petchey, O.L. (2003) Integrating methods that investigate how complementarity influences ecosystem functioning. *Oikos* 101, 323–330

8 Loreau, M. and Hector, A. (2001) Partitioning selection and complementarity in biodiversity experiments. *Nature* 412, 72–76

9 Hooper, D.U. and Dukes, J.S. (2004) Overyielding among plant functional groups in a long-term experiment. *Ecol. Lett.* 7, 95–105

10 Tilman, D. *et al.* (1997) The influence of functional diversity and composition on ecosystem processes. *Science* 277, 1300–1302

11 Mamolos, A.P. *et al.* (1995) Depth of root activity of coexisting grassland species in relation to N and P additions, measured using nonradioactive tracers. *J. Ecol.*

451   12 Kahmen, A. *et al.* (2006) Niche complementarity for nitrogen: an explanation for the

452   biodiversity and ecosystem functioning relationship? *Ecology* 87, 1244–1255

453   13 Ashton, I.W. *et al.* (2010) Niche complementarity due to plasticity in resource use: plant

454   partitioning of chemical N forms. *Ecology* 91, 3252–3260

455   14 McKane, R.B. *et al.* (2002) Resource-based niches provide a basis for plant species diversity

456   and dominance in arctic tundra. *Nature* 415, 68–71

457   15 Spehn, E.M. *et al.* (2002) The role of legumes as a component of biodiversity in a cross-

458   European study of grassland biomass nitrogen. *Oikos* 98, 205–218

459   16 Lorentzen, S. *et al.* (2008) Species richness and identity affect the use of aboveground space

460   in experimental grasslands. *Perspect. Plant Ecol. Evol. Syst.* 10, 73–87

461   17 Isbell, F.I. and Wilsey, B.J. (2011) Rapid biodiversity declines in both ungrazed and

462   intensely grazed exotic grasslands. *Plant Ecol.* 212, 1663–1674

463   18 Jucker, T. *et al.* (2015) Crown plasticity enables trees to optimize canopy packing in mixed-

464   species forests. *Funct. Ecol.* 29, 1078–1086

465   19 Niklaus, P.A. *et al.* (2017) Can niche plasticity promote biodiversity–productivity

466   relationships through increased complementarity? *Ecology* 98, 1104–1116

467   20 Williams, L.J. *et al.* (2017) Spatial complementarity in tree crowns explains overyielding in

468   species mixtures. *Nat. Ecol. Evol.* 1, 0063

469   21 Mueller, K.E. *et al.* (2013) Root depth distribution and the diversity–productivity

470   relationship in a long-term grassland experiment. *Ecology* 94, 787–793

471   22 Oram, N.J. *et al.* (2018) Below-ground complementarity effects in a grassland biodiversity

472   experiment are related to deep-rooting species. *J. Ecol.* 106, 265–277

473 23 Ravenek, J.M. *et al.* (2014) Long-term study of root biomass in a biodiversity experiment

474   reveals shifts in diversity effects over time. *Oikos* 123, 1528–1536

475 24 Mommer, L. *et al.* (2010) Unveiling below-ground species abundance in a biodiversity

476   experiment: a test of vertical niche differentiation among grassland species. *J. Ecol.* 98,

477   1117–1127

478 25 von Felten, S. *et al.* (2009) Belowground nitrogen partitioning in experimental grassland

479   plant communities of varying species richness. *Ecology* 90, 1389–1399

480 26 Wardle, D.A. and Peltzer, D.A. (2003) Interspecific interactions and biomass allocation

481   among grassland plant species. *Oikos* 100, 497–506

482 27 Bachmann, D. *et al.* (2015) No evidence of complementary water use along a plant species

483   richness gradient in temperate experimental grasslands. *PloS One* 10, e0116367

484 28 Jesch, A. *et al.* (2018) Below-ground resource partitioning alone cannot explain the

485   biodiversity–ecosystem function relationship: A field test using multiple tracers. *J. Ecol.*

486   106, 2002–2018

487 29 Guderle, M. *et al.* (2018) Dynamic niche partitioning in root water uptake facilitates efficient

488   water use in more diverse grassland plant communities. *Funct. Ecol.* 32, 214–227

489 30 Verheyen, K. *et al.* (2008) Can complementarity in water use help to explain diversity–

490   productivity relationships in experimental grassland plots? *Oecologia* 156, 351–361

491 31 Brooker, R.W. *et al.* (2008) Facilitation in plant communities: the past, the present, and the

492   future. *J. Ecol.* 96, 18–34

493 32 Wright, A.J. *et al.* (2017) The Overlooked Role of Facilitation in Biodiversity Experiments.

494   *Trends Ecol. Evol.* 32, 383–390

495 33 Michalet, R. and Pugnaire, F.I. (2016) Facilitation in communities: underlying mechanisms,

496   community and ecosystem implications. *Funct. Ecol.* 30, 3–9

497 34 Li, M. *et al.* (2014) A Review of Remote Sensing Image Classification Techniques: the Role

498   of Spatio-contextual Information. *Eur. J. Remote Sens.* 47, 389–411

499 35 Hacker, N. *et al.* (2015) Plant diversity shapes microbe-rhizosphere effects on P mobilisation

500   from organic matter in soil. *Ecol. Lett.* 18, 1356–1365

501 36 Li, L. *et al.* (2007) Diversity enhances agricultural productivity via rhizosphere phosphorus

502   facilitation on phosphorus-deficient soils. *Proc. Natl. Acad. Sci.* 104, 11192–11196

503 37 Emerman, S.H. and Dawson, T.E. (1996) Hydraulic lift and its influence on the water

504   content of the rhizosphere: an example from sugar maple, Acer saccharum. *Oecologia* 108,

505   273–278

506 38 Dawson, T.E. (1993) Hydraulic lift and water use by plants: implications for water balance,

507   performance and plant-plant interactions. *Oecologia* 95, 565–574

508 39 Sekiya, N. and Yano, K. (2004) Do pigeon pea and sesbania supply groundwater to

509   intercropped maize through hydraulic lift?—Hydrogen stable isotope investigation of xylem

510   waters. *Field Crops Res.* 86, 167–173

511 40 Ludwig, F. *et al.* (2004) Below-ground competition between trees and grasses may

512   overwhelm the facilitative effects of hydraulic lift. *Ecol. Lett.* 7, 623–631

513 41 Steudel, B. *et al.* (2012) Biodiversity effects on ecosystem functioning change along

514   environmental stress gradients. *Ecol. Lett.* 15, 1397–1405

515 42 Milcu, A. *et al.* (2016) Plant functional diversity increases grassland productivity-related

516   water vapor fluxes: an Ecotron and modeling approach. *Ecology* 97, 2044–2054

517   43 Klaus, V.H. *et al.* (2016) Plant diversity moderates drought stress in grasslands: Implications

518   from a large real-world study on 13C natural abundances. *Sci. Total Environ.* 566–567, 215–

519   222

520   44 Pugnaire, F.I. *et al.* (1996) Facilitation between Higher Plant Species in a Semiarid

521   Environment. *Ecology* 77, 1420–1426

522   45 Mulder, C.P.H. *et al.* (2001) Physical stress and diversity-productivity relationships: The role

523   of positive interactions. *Proc. Natl. Acad. Sci.* 98, 6704–6708

524   46 Eisenhauer, N. (2012) Aboveground–belowground interactions as a source of

525   complementarity effects in biodiversity experiments. *Plant Soil* 351, 1–22

526   47 Rottstock, T. *et al.* (2014) Higher plant diversity promotes higher diversity of fungal

527   pathogens, while it decreases pathogen infection per plant. *Ecology* 95, 1907–1917

528   48 Janzen, D.H. (1970) Herbivores and the number of tree species in tropical forests. *Am. Nat.*

529   49 Connell, J.H. (1971) On the role of natural enemies in preventing competitive exclusion in

530   some marine animals and in rain forest trees. *Dyn. Popul.* 298, 312

531   50 Jactel, H. and Brockerhoff, E.G. (2007) Tree diversity reduces herbivory by forest insects.

532   *Ecol. Lett.* 10, 835–848

533   51 Duffy, J.E. *et al.* (2007) The functional role of biodiversity in ecosystems: incorporating

534   trophic complexity. *Ecol. Lett.* 10, 522–538

535   52 Bever, J.D. (2003) Soil community feedback and the coexistence of competitors: conceptual

536   frameworks and empirical tests. *New Phytol.* 157, 465–473

537   53 Kulmatiski, A. *et al.* (2008) Plant-soil feedbacks: a meta-analytical review. *Ecol. Lett.* 11,

538   980–992

539 54 Petermann, J.S. *et al.* (2008) Janzen-Connell effects are widespread and strong enough to

540   maintain diversity in grasslands. *Ecology* 89, 2399–2406

541 55 Schnitzer, S.A. *et al.* (2011) Soil microbes drive the classic plant diversity-productivity

542   pattern. *Ecology* 92, 296–303

543 56 Maron, J.L. *et al.* (2011) Soil fungal pathogens and the relationship between plant diversity

544   and productivity. *Ecol. Lett.* 14, 36–41

545 57 Hendriks, M. *et al.* (2013) Independent variations of plant and soil mixtures reveal soil

546   feedback effects on plant community overyielding. *J. Ecol.* 101, 287–297

547 58 Seabloom, E.W. *et al.* (2017) Food webs obscure the strength of plant diversity effects on

548   primary productivity. *Ecol. Lett.* 20, 505–512

549 59 Morris, W.F. *et al.* (2007) Direct and Interactive Effects of Enemies and Mutualists on Plant

550   Performance: A Meta-Analysis. *Ecology* 88, 1021–1029

551 60 Ebeling, A. *et al.* (2008) How does plant richness affect pollinator richness and temporal

552   stability of flower visits? *Oikos* 117, 1808–1815

553 61 Gross, K. and Cardinale, B.J. (2005) The functional consequences of random vs. ordered

554   species extinctions. *Ecol. Lett.* 8, 409–418

555 62 Dimitrakopoulos, P.G. and Schmid, B. (2004) Biodiversity effects increase linearly with

556   biotope space. *Ecol. Lett.* 7, 574–583

557 63 Iii, F.S.C. *et al.* 11-May-(2000) , Consequences of changing biodiversity. , *Nature.*

558 64 Duffy, J.E. (2003) Biodiversity loss, trophic skew and ecosystem functioning. *Ecol. Lett.* 6,

559   680–687

560 65 Smith, M.D. and Knapp, A.K. (2003) Dominant species maintain ecosystem function with

561   non-random species loss. *Ecol. Lett.* 6, 509–517

562   66   Kaiser-Bunbury, C.N. *et al.* (2010) The robustness of pollination networks to the loss of
563   species and interactions: a quantitative approach incorporating pollinator behaviour. *Ecol.*
564   *Lett.* 13, 442–452

565   67   Guerrero-Ramírez, N.R. *et al.* (2017) Diversity-dependent temporal divergence of ecosystem
566   functioning in experimental ecosystems. *Nat. Ecol. Evol.* 1, 1639–1642

567   68   Ratcliffe, S. and et al. (2017) Biodiversity and ecosystem function relations in European
568   forests depend on environmental context. *Ecol. Lett.*

569   69   Harpole, W.S. *et al.* (2016) Addition of multiple limiting resources reduces grassland
570   diversity. *Nature* 537, 93–96

571   70   Bertness, M.D. and Callaway, R. (1994) Positive interactions in communities. *Trends Ecol.*
572   *Evol.* 9, 191–193

573   71   Callaway, R.M. *et al.* (2002) Positive interactions among alpine plants increase with stress.
574   *Nature* 417, 844–848

575   72   Wright, A.J. *et al.* (2017) Plants are less negatively affected by flooding when growing in
576   species-rich plant communities. *New Phytol.* 213, 645–656

577   73   Fernandes, I. *et al.* (2011) Intraspecific traits change biodiversity effects on ecosystem
578   functioning under metal stress. *Oecologia* 166, 1019–1028

579   74   Schemske, D.W. *et al.* (2009) Is There a Latitudinal Gradient in the Importance of Biotic
580   Interactions? *Annu. Rev. Ecol. Evol. Syst.* 40, 245–269

581   75   Paquette, A. and Messier, C. (2011) The effect of biodiversity on tree productivity: from
582   temperate to boreal forests. *Glob. Ecol. Biogeogr.* 20, 170–180

583   76   Liang, J. *et al.* (2016) Positive biodiversity-productivity relationship predominant in global
584   forests. *Science* 354, aaf8957

585 77 Tilman, D. *et al.* (1997) Plant diversity and ecosystem productivity: theoretical

586   considerations. *Proc. Natl. Acad. Sci.* 94, 1857–1861

587 78 Michalet, R. *et al.* (2006) Do biotic interactions shape both sides of the humped-back model

588   of species richness in plant communities? *Ecol. Lett.* 9, 767–773

589 79 Chase, J.M. and Leibold, M.A. (2003) *Ecological Niches: Linking classical and*

590   *contemporary approaches*, University of Chicago Press.

591 80 Isbell, F. *et al.* (2015) Biodiversity increases the resistance of ecosystem productivity to

592   climate extremes. *Nature*.

593 81 Lange, M. *et al.* (2015) Plant diversity increases soil microbial activity and soil carbon

594   storage. *Nat. Commun.* 6, 6707

595 82 Schoener, T.W. (1974) Resource Partitioning in Ecological Communities. *Science* 185, 27–

596   39

597 83 Finke, D.L. and Snyder, W.E. (2008) Niche partitioning increases resource exploitation by

598   diverse communities. *Science* 321, 1488–1490

599 84 Wagg, C. *et al.* (2015) Complementarity in both plant and mycorrhizal fungal communities

600   are not necessarily increased by diversity in the other. *J. Ecol.* 103, 1233–1244

601 85 Craven, D. *et al.* (2016) Plant diversity effects on grassland productivity are robust to both

602   nutrient enrichment and drought. *Philos. Trans. R. Soc. B* 371,

603 86 Marquard, E. *et al.* (2009) Plant species richness and functional composition drive

604   overyielding in a six-year grassland experiment. *Ecology* 90, 3290–3302

605 87 Roscher, C. *et al.* (2007) Detecting the role of individual species for overyielding in

606   experimental grassland communities composed of potentially dominant species. *Oecologia*

607   154, 535–549

608 88 Fargione, J. *et al.* (2007) From selection to complementarity: shifts in the causes of

609   biodiversity–productivity relationships in a long-term biodiversity experiment. *Proc. R. Soc.*

610   *Lond. B Biol. Sci.* 274, 871–876

611 89 Temperton, V.M. *et al.* (2007) Positive interactions between nitrogen-fixing legumes and

612   four different neighbouring species in a biodiversity experiment. *Oecologia* 151, 190–205

613 90 Gubsch, M. *et al.* (2011) Foliar and soil δ15N values reveal increased nitrogen partitioning

614   among species in diverse grassland communities. *Plant Cell Environ.* 34, 895–908

615 91 Tilman, D. (2001) Diversity and Productivity in a Long-Term Grassland Experiment.

616   *Science* 294, 843

617 92 Roscher, C. *et al.* (2011) N2 fixation and performance of 12 legume species in a 6-year

618   grassland biodiversity experiment. *Plant Soil* 341, 333–348

619 93 Van der Heijden, M.G. *et al.* (1998) Mycorrhizal fungal diversity determines plant

620   biodiversity, ecosystem variability and productivity. *Nature* 396, 69–72

621 94 Wagg, C. *et al.* (2011) Belowground biodiversity effects of plant symbionts support

622   aboveground productivity. *Ecol. Lett.* 14, 1001–1009

623 95 Walder, F. *et al.* (2012) Mycorrhizal Networks: Common Goods of Plants Shared under

624   Unequal Terms of Trade. *Plant Physiol.* 159, 789–797

625 96 Hättenschwiler, S. and Gasser, P. (2005) Soil animals alter plant litter diversity effects on

626   decomposition. *Proc. Natl. Acad. Sci.* 102, 1519–1524

627 97 Chen, H. *et al.* (2017) Plant species richness negatively affects root decomposition in

628   grasslands. *J. Ecol.* 105, 209–218

629 98 Chen, H. *et al.* (2017) Root chemistry and soil fauna, but not soil abiotic conditions explain

630   the effects of plant diversity on root decomposition. *Oecologia* 185, 499–511

631   99 Eisenhauer, N. *et al.* (2010) Plant diversity effects on soil microorganisms support the

632   singular hypothesis. *Ecology* 91, 485–496
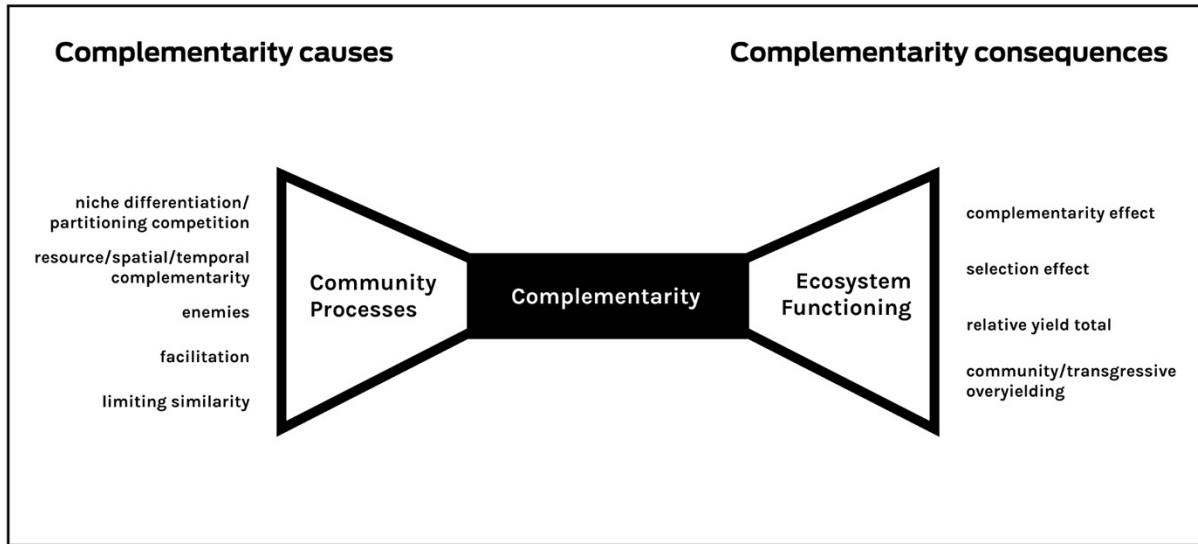
633   100   Cong, W.-F. *et al.* (2014) Plant species richness promotes soil carbon and nitrogen stocks

634   in grasslands without legumes. *J. Ecol.* 102, 1163–1170

635   101   Fox, J.W. (2005) Interpreting the 'selection effect' of biodiversity on ecosystem function.

636   *Ecol. Lett.* 8, 846–856

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

Complementarity causes

niche differentiation/
partitioning competition

resource/spatial/temporal
complementarity

enemies

facilitation

limiting similarity

Community Processes

Complementarity

Complementarity consequences

complementarity effect

selection effect

relative yield total

community/transgressive
overyielding

Ecosystem Functioning

652

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.
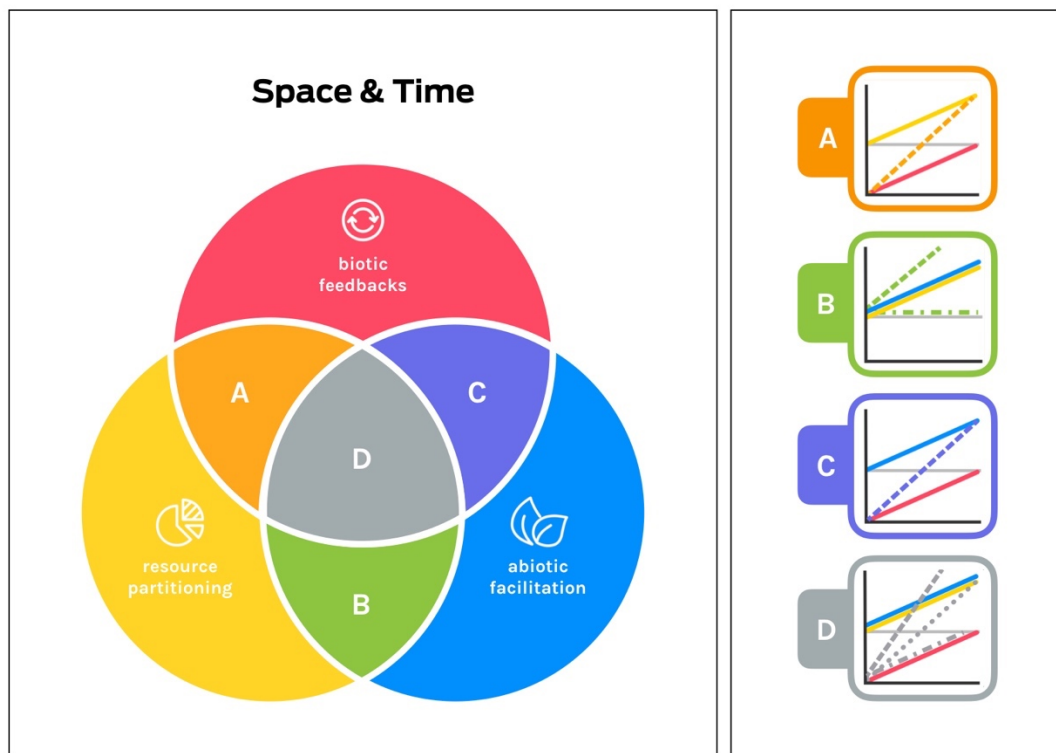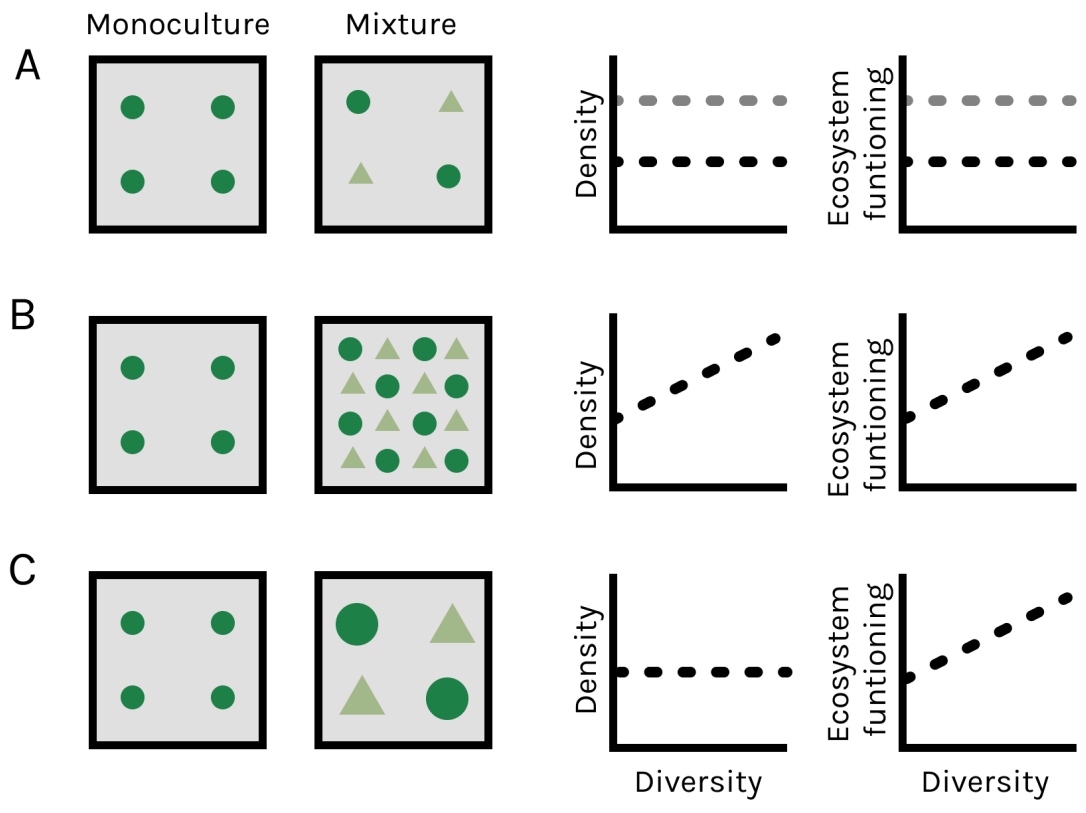

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710

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.

Monoculture Mixture

A

Density

Ecosystem funtioning

B

Density

Ecosystem funtioning

C

Density

Ecosystem funtioning

Diversity

Diversity

728

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

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

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

In addition to crucial mutualists, plants also harbor a diverse community of non-mutualist 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.
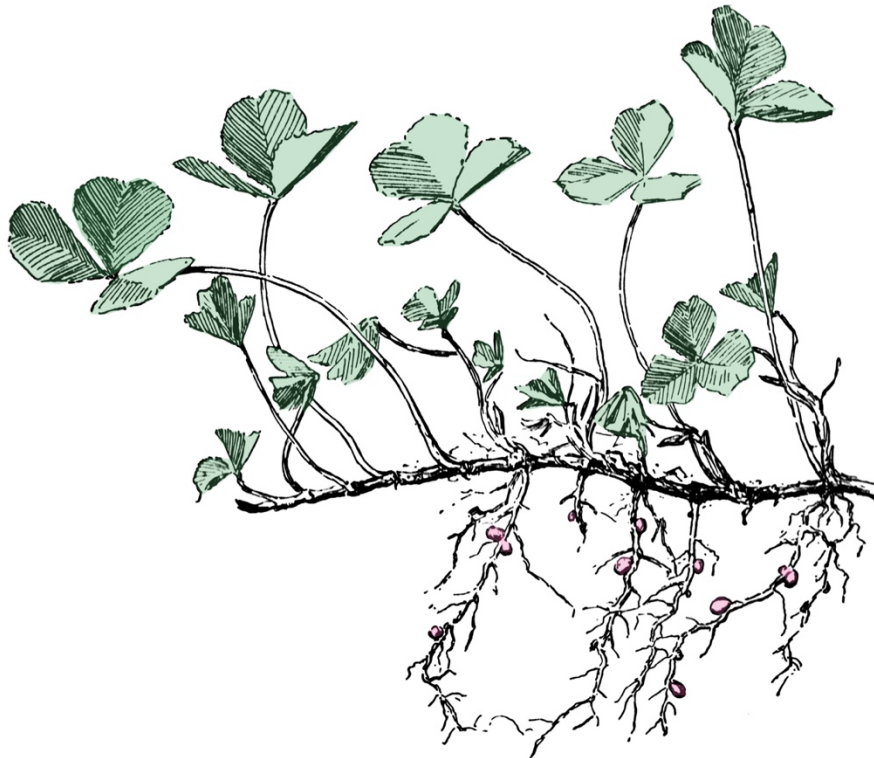
759

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

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