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Mechanistic approaches to investigate soil microbe-mediated plant competition

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1   **TITLE**

2   *Mechanistic approaches to investigate soil microbe-mediated plant competition*

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18   **ABSTRACT**

19   1. Interactions between plants and soil microbes can influence plant population dynamics and diversity

20   in plant communities. Traditional theoretical paradigms view the microbial community as a black box

21   with net effects described by phenomenological models.

22   2. This approach struggles to quantify the importance of plant-microbe interactions relative to other

23   competition and coexistence mechanisms and to explain context dependence in microbe effects.

24   3. We argue that a mechanistic framework focused on microbial functional groups will lead to

25   conceptual and empirical advances, as demonstrated by extending resource ratio theory to plant-

26   microbe interactions.

27   4. We review the diverse pathways by which different microbial functional groups can influence plant

28   resource competition. Finally, we suggest approaches to link theory with observations to measure the

29   key parameters of our framework.

30   5. *Synthesis.* Our review highlights recent experimental advancements for uncovering microbial

31   mechanisms that alter plant host resource competition and coexistence. We synthesize these

32   mechanisms into a conceptual model that provides a framework for future experiments to investigate

33   the importance of plant-microbe interactions in structuring plant populations and communities.

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39   *Soil microbes mediate plant competition*

40   Plant-soil microbe interactions are ubiquitous, and recognition of their role in mediating plant

41   competition has advanced our understanding of plant coexistence (Bever 2003, Wagg et al. 2011, Chung

42   and Rudgers 2016). In the past few decades, negative feedbacks between plant hosts and soil microbes

43   (negative plant-soil feedbacks, negative PSFs) have become the dominant paradigm for understanding

44   the role of soil microbes in maintaining plant diversity (Ke and Miki 2015, Crawford et al. 2019). This

45   paradigm holds that plant species cultivate soil legacies via species-specific microbial assemblages that

46   are more detrimental to themselves than co-occurring species; this self-limitation promotes coexistence.

47   Classic theory for PSFs is an extension of phenomenological models in which coexistence

48   depends on the relative strength of intraspecific and interspecific interactions, without explicit reference

49   to the mechanisms underlying those interactions (Bever et al. 1997, Revilla et al. 2013). This approach is

50   experimentally tractable. The soil community can be treated as a single entity and evaluated based on

51   its net effects on plant hosts. However, this tractability comes at the expense of mechanistic

52   understanding. Recent reviews of PSFs have emphasized their importance (Gundale and Kardol 2021),

53   but warned of high context-dependence and low predictability (Smith-Ramesh and Reynolds 2017,

54   Bennett and Klironomos 2019, De Long et al. 2019). For example, PSF magnitude and direction can

55   change depending on plant age and development stage, resource availability, abiotic environmental

56   gradients, and host competitive context (Beals et al. 2020, Chung 2023). We should not be satisfied with

57   demonstrations that PSFs occur, but should strive to quantify their contribution to the maintenance of

58   diversity in nature.

59   To understand and predict the role of plant-soil microbe interactions in plant competition and

60   coexistence, we must go beyond phenomenological description and consider the underlying plant-soil

61   microbe interactions that drive the feedback. A mechanistic framework that explicitly considers

62   microbial functions will help us predict microbial effects on plant coexistence in changing biotic and

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63   abiotic contexts, and determine their importance relative to other coexistence mechanisms (van der

64   Putten et al. 2016, Abbott et al. 2021, Semchenko et al. 2022). While microbial functions are

65   hyperdiverse, they interact with plants primarily as mutualists, pathogens, or decomposers. Within the

66   context of plant coexistence, PSF research has focused primarily on pathogens due to the emphasis on

67   negative density (or frequency) dependence. However, strong evidence exists that coexistence-

68   promoting feedbacks can also be facilitated by mutualists, such as nitrogen-fixing bacteria and

69   mycorrhizal fungi, and decomposers (e.g. Bever 2002, Bennett et al. 2017, Whitaker et al. 2017, Siefert

70   et al. 2018, Veen et al. 2019). Mechanistic approaches that open up the soil microbial black box may

71   require more measurements than traditional phenomenological approaches (see *Future directions*), but

72   are essential for predicting the consequences of rapid environmental change without the need to repeat

73   experiments in new environments. We aim to synthesize recent evidence for microbial mechanisms that

74   mediate resource competition between plants, and propose a resource-based mechanistic framework

75   for understanding and predicting the role of soil microbes in plant competition and coexistence (Fig. 1).

76

77   *Applying resource ratio theory to understand microbe-mediated plant competition*

78   One of the most important alternative mechanisms for plant coexistence is soil resource

79   partitioning. However, surprisingly few studies have investigated both the effects of resource addition

80   and soil microbes on plant competition, and results have been equivocal due partly to a lack of clear

81   theory (reviewed in Beals et al. 2020). Resource ratio theory (Tilman 1982) provides a way to directly

82   link plant-soil microbe interactions to the key components of resource competition, namely the system's

83   resource supply, the species' resource consumption, and the species' resource requirements (Box 1).

84   These three components are inextricably linked with soil microbes (summarized in Table 1 and reviewed

85   below). Since different microbial functional groups operate simultaneously and are linked by their

86   impacts on resource flow (Fig. 1), a clear understanding of microbial function should help us to predict

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87   how microbial effects vary with environmental context. Below, we highlight recent evidence for each of

88   these mechanistic pathways and empirical approaches to quantify their effects.

89

90   *Plant-soil microbe interactions and resource supply*

91   One key component of the resource ratio theory is the resource supply (black point in Figure I in

92   Box 1), defined as the resource availability for plants in the absence of plant consumption. Microbe-

93   mediated decomposition alters resource supply for plants, sometimes in species-specific ways. Changes

94   in resource supply caused by plant-soil microbe interactions could move competitors in and out of

95   regions of coexistence (grey region of Figure I in Box 1). Studies in "home field advantage" in litter

96   decomposition show that litter can decompose faster in its "home" location compared to other

97   locations due to local adaptation of decomposers to the prevailing litter chemistry (Veen et al. 2015).

98   This phenomenon can also operate at the scale of different plants within a community, where positive

99   host-decomposer feedbacks favor competitive exclusion by moving resource supply points out of the

100   coexistence region. For example, two Mediterranean oaks (*Quercus suber* and *Q. canariensis*) differed in

101   their foliar nutrient content and associated saprotroph communities, generating soil conditions that

102   favor the establishment of their own seedlings, which causes local aggregation (Aponte et al. 2013).

103   Among co-occurring European grassland species, grasses with more exploitative sulfur acquisition

104   strategies also increased microbial arylsulphatase activities in their rhizospheres, thus promoting their

105   own growth in a positive feedback loop (Legay et al. 2014).

106   Microbes can also alter resource availability by mediating nutrient losses. Theoretical models

107   that include decomposition and nutrient recycling have demonstrated that coexistence is promoted

108   when each plant species associates with microbes that accelerate loss of the nutrient that more limits its

109   own growth compared to that of its competitor (Daufresne and Hedin 2005). On the contrary, host-

110   specific decomposers that accelerate loss of nutrients that more limits its competitor's growth should

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111   promote exclusion. In an example that promotes exclusion and leads to monodominance, some pines

112   and poplars thrive in N-poor environments where their litter chemistry and decomposer associations

113   continue to promote N losses. This maintains a favorable environment for these taxa, who are better

114   competitors for N in such systems (Northup et al. 1995, Fierer et al. 2001).

115   Mutualistic plant growth promoting bacteria (PGPB) can also increase nutrient availability in the

116   soil via specialized metabolic pathways (Ramakrishna et al. 2019). While the host-specificity of these

117   taxa are less well known, plants likely differ in their ability to attract PGPB consortia, which could result

118   in feedbacks. Finally, interactions between microbial groups could also moderate resource supply. For

119   example, the Gadgil effect suggests that competition between ectomycorrhizal fungi and saprotrophs in

120   forest ecosystems can reduce decomposition rates (Gadgil and Gadgil 1971, Fernandez and Kennedy

121   2016). However, whether these effects impact host coexistence may depend on host resource

122   requirements and the N mining abilities of their respective ectomycorrhizal and saprotroph associates.

123

124   *Plant-soil microbe interactions and resource consumption*

125   The second component determining species coexistence is their *resource consumption*

126   (consumption vectors in Figure I in Box 1), theoretically defined as the relative rates at which plants

127   deplete resources. Differentiation in species' consumption vector stabilizes coexistence via self-limiting

128   negative feedbacks (Letten et al. 2017). As long as each competitor consumes more of the resource

129   most limiting its growth, then the greater the difference in their consumption vector, the wider the

130   resource supply state-space available for coexistence. A species' consumption vector depends on its

131   resource-specific consumption rates and its stoichiometry, which can be modified by resource

132   mutualisms. For example, mycorrhizal associations increase concentrations of macro- and

133   micronutrients in host tissues, implying increased consumption rates and altered stoichiometry (Smith

134   and Smith 2011, Lehmann and Rillig 2015, Verzeaux et al. 2017, but see Nazeri et al. 2014). Rhizobia are

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135   known to increase tissue N for legume hosts, and some hosts reap benefits when co-infected with

136   rhizobia and mycorrhizal fungi (Primieri et al. 2022). Pathogens can also indirectly alter host

137   consumption and stoichiometry via effects on host physiology. For example, the bacteria *Candidatus*

138   Liberibacter spp. causes huanglongbing in citrus by disrupting phloem transport and feeder root

139   development. This results in plant hosts with imbalanced photosynthate distribution and decreased

140   micronutrient consumption (Mattos-Jr et al. 2020).

141   Evidence that plant-soil microbe interactions alter the host resource consumption is clear, but

142   there is less consensus about whether such changes increase or decrease opportunities for host

143   coexistence. Among hosts with similar mutualists, the evidence is mixed. For example, several studies

144   have failed to find support for AMF-mediated partitioning of plant access to diverse phosphorus forms

145   (Vogelsang et al. 2006, Reynolds et al. 2006, Ceulemans et al. 2017). However, hosts that associate with

146   different mutualists (e.g. arbuscular mycorrhizal fungi (AMF), ectomycorrhizal (ECM) fungi, or rhizobia)

147   may have access to different subsets of resources, thus altering their consumption vectors in a way that

148   promotes coexistence (Steidinger and Bever 2014, Tedersoo et al. 2020). Furthermore, different

149   resource mutualists respond in predictable ways to changing abiotic conditions. For example, plants

150   benefit most from AMF association when phosphorus is limited (high tissue N:P) (Hoeksema et al. 2010).

151   Thus, we can experimentally test the prediction that an increase in P supply will also decrease AMF

152   effects on host resource consumption vectors (see *Future directions*).

153

154   *Plant-soil microbe interactions and resource requirement*

155   The final determinant of species coexistence in resource ratio theory is the species' resource

156   requirement, reflected by the species' R* for resources. A species' R* is the minimum amount of a

157   resource required to maintain zero population growth (i.e., where growth balances mortality at the

158   population level). Thus, any effects of soil microbes on a host's mortality rate will alter the host's R*

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159   values, as long as the effects of the microbes are independent of resource-supply rates. For example,

160   when pathogens increase host mortality, the host's R* will also increase (Fig. IA). On the other hand,

161   many belowground microbial mutualists benefit host survival, either via increased tolerance to

162   environmental stress or protection from pathogens (Olanrewaju et al. 2017, Kumar and Verma 2018).

163   There is also evidence of host-specific root endophytes decreasing the P requirement of legume

164   *Ornithopus* species relative to *Trifolium*, potentially due to reduced C demand and P availability

165   compared to the alternative treatment which was an AMF inoculation (Jeffery et al. 2018).

166   Microbe-mediated changes in R* for a given resource are empirically measurable (see *Future*

167   *directions*), and could lead to changes in coexistence outcomes. For example, protective mycorrhizae

168   interacting with an inferior competitor could decrease its R* due to lowered mortality rate, potentially

169   shifting the outcome from exclusion to coexistence. How much a protective mutualism decreases

170   mortality also depends on abiotic context, leading to testable hypotheses. For example, survival benefits

171   of symbiosis with an *Epichloë* fungal endophyte for a native grass host was highest in locations with

172   lowest precipitation (Afkhami et al. 2014). This interaction suggests that the relative decrease in R* for

173   this native grass would be the strongest in contexts of low water supply.

174

175   *Future directions to link theory and observation*

176   Our synthesis identifies new research directions to understand the role of microbial functions in

177   plant competition. First, how can we measure the components of resource ratio theory for plants?

178   Second, how can we isolate microbial contributions to those components? Past work has approximated

179   R* by allowing plant monocultures to draw down a major resource until its concentration in the soil is

180   constant (at R*) (Dybzinski and Tilman 2007). Supply rates, however, are more challenging to measure in

181   a plant-soil system, and are often approximated by nutrient availability at the beginning of the

182   experiment (Dybzinski and Tilman 2007), or more directly by measuring mineralization rates (Menge et

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183   al. 2009). Finally, total resource consumption can be approximated by multiplying plant biomass and

184   tissue resource concentration (Dybzinski and Tilman 2007). Or, it could be possible to use change in

185   tissue stoichiometry to monitor the change in consumption vector angle. Given the number of moving

186   parts, a good starting point for empiricists could be the single resource scenario, where dynamics are

187   controlled by only R* and other components can be ignored (Fig. IA). This provides an entry point for

188   experiments to verify model predictions before moving on to consider plants' consumption and

189   requirements for other limiting resources

190   Empirical approaches exist to manipulate and quantify the influence of plant-soil microbe

191   interactions on components of the resource ratio theory, with the ultimate goal of parameterizing a

192   mechanistic model. For example, inoculation and exclusion experiments could isolate microbe effects on

193   resource ratio components. While there is no perfect method to manipulate the presence or absence of

194   microbial mutualists vs. pathogens vs. decomposers, established size-based and biocide methods can

195   come close. To target the presence of AMF, researchers can inoculate whole AMF communities using

196   spore extraction from field soils and pair it with a background microbial wash of a smaller size fraction as

197   a control (Schnitzer et al. 2011). A gradient of increasingly small cell size restrictions can create a series

198   of subset communities which can be mapped to known microbial traits (Zanne et al. 2020, Wagg et al.

199   2021). Size-based exclusion can be used in the greenhouse or field as colonization barriers using

200   different-sized mesh (Chung et al. 2019). In addition to inoculating with specific microbial cultures,

201   selective biocides are also available to remove target specific pathogen groups, such as fungal vs.

202   oomycete pathogens, in competition and feedback experiments (Domínguez-Begines et al. 2021, Liu et

203   al. 2022). While not as naturalistic, recent developments in "EcoFAB" flow-through root chambers allow

204   potential for mechanistic experiments where plant-soil microbe interactions can be studied in close to

205   chemostat conditions with constant resource supply (Gao et al. 2018). Finally, 'omics-based correlative

206   approaches have potential, but rely on future improvements in quantitative microbiome profiling and

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207   functional annotation. As annotations in microbial metagenomics and metatranscriptomics become

208   more robust, it may be possible to link snapshots of microbiome composition to resource function

209   (Knight et al. 2018, Shakya et al. 2019, Taş et al. 2021).

210   We have highlighted just a few ways that soil microbes affect plant coexistence, but future work

211   should consider the full diversity of microbe-mediated impacts on plant niches. Microbes can modify

212   niche elements for plant resource competition (Peay 2016), microbes can be limiting factors themselves

213   (Koffel et al. 2021), or they can function as competitors of plants for nutrients (Orwin et al. 2011).

214   Furthermore, one microbial functional group could simultaneously modify many elements of

215   coexistence (Table 1). For example, pathogens can affect coexistence by changing host resource

216   consumption, yet the literature has primarily focused on pathogen-mediated host coexistence via

217   effects on mortality. A logical extension of our framework would consider how altered abiotic contexts,

218   such as temperature or soil moisture, could change how multiple microbes alter not just one, but all

219   components of the resource ratio theory. Finally, recognizing roles of specific microbial functional

220   groups also makes it possible to study their interactions which, in theory, can lead to a wider range of

221   possible dynamics than previously appreciated (Jiang et al. 2020).

222

223   *Conclusions*

224   The microbial black box has served us well. However, we now have the theory and technology to

225   open it up using mechanistic approaches. Our framework generates specific, testable hypotheses that

226   can guide future theory and experiments in a tractable way. Characterizing specific mechanisms by

227   which microbial mutualists, decomposers, and pathogens affect plants is the critical next step in

228   understanding how plant-soil microbe interactions mediate coexistence. Here, we used resource ratio

229   theory as an example to demonstrate how a clear understanding of microbial function can help us

230   predict microbial effects on plant communities under varying environmental contexts. Combining plant

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231   and microbial ecology with plant physiological ecology and ecological stoichiometry could advance our

232   empirical understanding of mechanisms that underlie microbe-mediated plant competition and

233   coexistence. Ultimately, a shift away from phenomenological indices will promote better understanding

234   of plant-soil microbe interactions in the context of other coexistence mechanisms and environmental

235   change.

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242   *Author contributions*

243   All authors worked together to conceive and develop the ideas. Anny Chung took the lead in writing the

244   manuscript. All authors contributed critically to the drafts and gave final approval for publication.

245

246   *Data availability*

247   No novel data are associated with this manuscript

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249   Figure 1: This conceptual diagram incorporates different plant-soil microbe interactions into a traditional

250   resource partitioning framework with two plant competitors and two resources. Arrows represent the

251   flow of energy and matter, not effects. The width of arrows indicates the strength of flow, which reflect

252   hypothetical interaction specificity between plants, microbes, and resources (e.g. here each plant is

253   attacked more by its specific enemy, and its specific decomposer processes more host litter). The

254   dashed box represents the plant-enemy system, which contributes to litter via enemy-induced plant

255   mortality. Blue arrows show external supply of resources. When microbes lack host specificity, this

256   figure can be simplified by merging the microbial A and B components for each functional group.
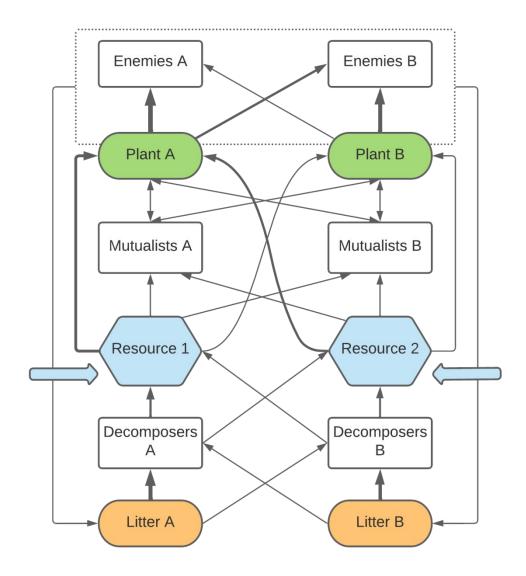

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258   Table 1: Examples of ways different microbial functional groups can affect coexistence through key

259   components of resource ratio theory. Reference cited follow the specific examples discussed in the main

260   text. Empty cells indicate knowledge gaps where the impact of the microbial functional group on the

261   theoretical component requires further research.

262

	Resource supply	Resource consumption	Resource requirement (R*)
Decomposers	Plant litter stimulates specific decomposer community to alter resource supply rates and ratios. Related to home field advantage effects (Veen et al. 2019)		
Mutualists	The Gadgil effect suggests that competition between ECM and saprotrophs results in reduced litter decomposition rates in ECM forests (Gadgil and Gadgil 1971)

Some plant growth promoting bacteria can solubilize phosphorus, calcium, iron, and increase their plant availability (Olanrewaju et al. 2017) | Resource mutualists such as mycorrhizal fungi and rhizobia are known to alter host consumption rates and stoichiometry (Smith and Smith 2011, Primieri et al. 2022) | Resource mutualists can lower R* for hosts by reducing mortality via stress tolerance or protection from antagonists (Kumar and Verma 2018)

Other changes to R* are also possible via changes to host stoichiometry (Jeffery et al. 2018) |
| Pathogens | Indirectly contribute to litter availability for decomposers via the increased production of senesced host tissues. | Pathogens can indirectly alter the host's consumption vector by changing its stoichiometry (Verzeaux et al. 2017) | Pathogens directly increase host R* by increasing mortality. |

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264   **BOX 1: Overview of resource ratio theory**

265   The resource ratio theory (Tilman 1982), and its later generalization as contemporary niche

266   theory (Chase and Leibold 2003, Koffel et al. 2021), provides a framework to study how different soil

267   microbes affect plant-plant resource competition. We summarize the key components of the framework

268   and the criteria for plant coexistence using a graphical approach.

269   When two hypothetical plants (green and gold colors in Fig. IA) compete for a single resource

270   (e.g., nitrogen), the amount of resource where per capita growth rate equals zero (i.e., where growth

271   balances mortality and the colored lines intercept the x-axis in Fig. IA) is their resource requirement, R*.

272   In this scenario, the species with the lower R* (gold) will outcompete the other species (green) as it

273   depletes resource to a level where the inferior species experiences negative growth.

274   When plants are competing for two resources, one needs to consider how the availability of the

275   two resources jointly determine plant population growth and how plants differentially consume

276   different resources. We consider two hypothetical plants competing for two essential resources that co-

277   limit plant growth according to Liebig's law of minimum, such as nitrogen and phosphorus (Fig. IB; but

278   see Tilman 1982 for other types of resource pairs). We now need to take into account the resource

279   supply point of the environment, which represents the resource availability of the two resources in the

280   absence of plant consumption (black point in Fig. IB). Plant species are characterized by the relative

281   rates at which they deplete the two resources (depicted as consumption vectors; dashed arrows in Fig.

282   IB), and their resource requirement, the resource combinations at which growth balances mortality

283   (depicted as zero net growth isoclines, ZNGIs; solid lines in Fig. IB). For purposes of simplicity, we

284   consider essential resources, a plant's ZNGI is a right-angle corner positioned based on its R* values for

285   the two resources, defined as the amount of a resource that causes growth to balance mortality when

286   the other resource is not limiting. A plant is most limited by the resource with a higher R* value. This

287   graphical framework can be extended to substitutable resources.

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288   When the two plants compete for the two essential resources, coexistence is possible when the

289   following three conditions are met. First, their ZNGIs must intersect, indicating a tradeoff where each

290   plant is most limited by a different resource. Second, each plant must consume more of the resource it

291   finds more limiting. In Fig. IB, these two conditions are fulfilled as the green plant has a higher R* for

292   nitrogen and consumes more nitrogen relative to phosphorus, and vice versa for the gold plant. A final

293   condition for coexistence is that the supply of the two resources must not disproportionately favor any

294   particular plant; specifically, the supply point must be encompassed by the inverse of the consumption

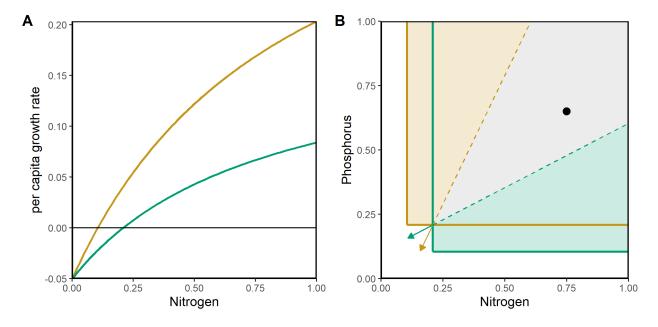295   vectors (dotted lines in Fig. IB).

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297   Figure I. (A) State-space diagram of two hypothetical plant species (colored as green and gold)

298   competing for one resource. The colored lines represent a species' per capita growth rate under

299   different resource level. (B) State-space diagram of two hypothetical plant species competing for two

300   essential resources. Here, we depict the coexistence criteria in terms of the elements of niche theory,

301   i.e., the resource requirements (solid lines), the resource consumptions (solid arrows as consumption

302   vectors), and the resource supply (black point). See box text for more details.

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303   **References cited**

304   Abbott, K. C., M. B. Eppinga, J. Umbanhowar, M. Baudena, and J. D. Bever. 2021. Microbiome

305   influence on host community dynamics: Conceptual integration of microbiome feedback

306   with classical host–microbe theory. Ecology Letters 24:2796–2811.

307   Afkhami, M. E., P. J. McIntyre, and S. Y. Strauss. 2014. Mutualist-mediated effects on species'

308   range limits across large geographic scales. Ecology Letters 17:1265–1273.

309   Aponte, C., L. V. García, and T. Marañón. 2013. Tree species effects on nutrient cycling and

310   soil biota: A feedback mechanism favouring species coexistence. Forest Ecology and

311   Management 309:36–46.

312   Beals, K. K., J. A. M. Moore, S. N. Kivlin, S. L. J. Bayliss, C. Y. Lumibao, L. C. Moorhead, M.

313   Patel, J. L. Summers, I. M. Ware, J. K. Bailey, and J. A. Schweitzer. 2020. Predicting

314   Plant-Soil Feedback in the Field: Meta-Analysis Reveals That Competition and

315   Environmental Stress Differentially Influence PSF. Frontiers in Ecology and Evolution

316   8:191.

317   Bennett, J. A., and J. Klironomos. 2019. Mechanisms of plant–soil feedback: interactions among

318   biotic and abiotic drivers. New Phytologist 222:91–96.

319   Bennett, J. A., H. Maherali, K. O. Reinhart, Y. Lekberg, M. M. Hart, and J. Klironomos. 2017.

320   Plant-soil feedbacks and mycorrhizal type influence temperate forest population

321   dynamics. Science 355:181–184.

322   Bever, J. D. 2002. Host-specificity of AM fungal population growth rates can generate feedback

323   on plant growth. Plant and Soil 244:281–290.

324   Bever, J. D. 2003. Soil community feedback and the coexistence of competitors: conceptual

325   frameworks and empirical tests. New Phytologist 157:465–473.

326   Bever, J. D., K. M. Westover, and J. Antonovics. 1997. Incorporating the soil community into

327   plant population dynamics: The utility of the feedback approach. Journal of Ecology

328   85:561–573.

16

329   Ceulemans, T., S. Bodé, J. Bollyn, S. Harpole, K. Coorevits, G. Peeters, K. Van Acker, E.

330   Smolders, P. Boeckx, and O. Honnay. 2017. Phosphorus resource partitioning shapes

331   phosphorus acquisition and plant species abundance in grasslands. Nature Plants 3:1–

332   7.

333   Chase, J. M., and M. A. Leibold. 2003. Ecological Niches: Linking Classical and Contemporary

334   Approaches. University of Chicago Press, Chicago, IL.

335   Chung, Y. A. 2023. The temporal and spatial dimensions of plant–soil feedbacks. New

336   Phytologist 237:2012–2019.

337   Chung, Y. A., S. L. Collins, and J. A. Rudgers. 2019. Connecting plant–soil feedbacks to long-

338   term stability in a desert grassland. Ecology 100:e02756.

339   Chung, Y. A., and J. A. Rudgers. 2016. Plant–soil feedbacks promote negative frequency

340   dependence in the coexistence of two aridland grasses. Proc. R. Soc. B 283:20160608.

341   Crawford, K. M., J. T. Bauer, L. S. Comita, M. B. Eppinga, D. J. Johnson, S. A. Mangan, S. A.

342   Queenborough, A. E. Strand, K. N. Suding, J. Umbanhowar, and J. D. Bever. 2019.

343   When and where plant-soil feedback may promote plant coexistence: a meta-analysis.

344   Ecology Letters 22:1274–1284.

345   Daufresne, T., and L. O. Hedin. 2005. Plant coexistence depends on ecosystem nutrient cycles:

346   Extension of the resource-ratio theory. Proceedings of the National Academy of

347   Sciences 102:9212–9217.

348   De Long, J. R., E. L. Fry, G. F. Veen, and P. Kardol. 2019. Why are plant–soil feedbacks so

349   unpredictable, and what to do about it? Functional Ecology 33:118–128.

350   Domínguez-Begines, J., J. M. Ávila, L. V. García, and L. Gómez-Aparicio. 2021. Disentangling

351   the role of oomycete soil pathogens as drivers of plant–soil feedbacks. Ecology

352   102:e03430.

353   Dybzinski, R., and D. Tilman. 2007. Resource Use Patterns Predict Long-Term Outcomes of

354   Plant Competition for Nutrients and Light. The American Naturalist 170:305–318.

17

355 Fernandez, C. W., and P. G. Kennedy. 2016. Revisiting the 'Gadgil effect': do interguild fungal

356   interactions control carbon cycling in forest soils? New Phytologist 209:1382–1394.

357 Fierer, N., J. P. Schimel, R. G. Cates, and J. Zou. 2001. Influence of balsam poplar tannin

358   fractions on carbon and nitrogen dynamics in Alaskan taiga floodplain soils. Soil

359   Biology:13.

360 Gadgil, R. L., and P. D. Gadgil. 1971. Mycorrhiza and Litter Decomposition. Nature 233:133–

361   133.

362 Gao, J., J. Sasse, K. M. Lewald, K. Zhalnina, L. T. Cornmesser, T. A. Duncombe, Y. Yoshikuni,

363   J. P. Vogel, M. K. Firestone, and T. R. Northen. 2018. Ecosystem Fabrication (EcoFAB)

364   Protocols for The Construction of Laboratory Ecosystems Designed to Study Plant-

365   microbe Interactions. JoVE (Journal of Visualized Experiments):e57170.

366 Gundale, M. J., and P. Kardol. 2021. Multi-dimensionality as a path forward in plant-soil

367   feedback research. Journal of Ecology 109:3446–3465.

368 Hoeksema, J. D., V. B. Chaudhary, C. A. Gehring, N. C. Johnson, J. Karst, R. T. Koide, A.

369   Pringle, C. Zabinski, J. D. Bever, J. C. Moore, G. W. T. Wilson, J. N. Klironomos, and J.

370   Umbanhowar. 2010. A meta-analysis of context-dependency in plant response to

371   inoculation with mycorrhizal fungi. Ecology Letters 13:394–407.

372 Jeffery, R. P., R. J. Simpson, H. Lambers, S. Orchard, D. R. Kidd, R. E. Haling, and M. H. Ryan.

373   2018. Contrasting communities of arbuscule-forming root symbionts change external

374   critical phosphorus requirements of some annual pasture legumes. Applied Soil Ecology

375   126:88–97.

376 Jiang, J., K. C. Abbott, M. Baudena, M. B. Eppinga, J. A. Umbanhowar, and J. D. Bever. 2020.

377   Pathogens and Mutualists as Joint Drivers of Host Species Coexistence and Turnover:

378   Implications for Plant Competition and Succession. The American Naturalist 195:591–

379   602.

18

380   Ke, P.-J., and T. Miki. 2015. Incorporating the soil environment and microbial community into

381   plant competition theory. Frontiers in Microbiology 6.

382   Knight, R., A. Vrbanac, B. C. Taylor, A. Aksenov, C. Callewaert, J. Debelius, A. Gonzalez, T.

383   Kosciolek, L.-I. McCall, D. McDonald, A. V. Melnik, J. T. Morton, J. Navas, R. A. Quinn,

384   J. G. Sanders, A. D. Swafford, L. R. Thompson, A. Tripathi, Z. Z. Xu, J. R. Zaneveld, Q.

385   Zhu, J. G. Caporaso, and P. C. Dorrestein. 2018. Best practices for analysing

386   microbiomes. Nature Reviews Microbiology 16:410–422.

387   Koffel, T., T. Daufresne, and C. A. Klausmeier. 2021. From competition to facilitation and

388   mutualism: a general theory of the niche. Ecological Monographs 91:e01458.

389   Kumar, A., and J. P. Verma. 2018. Does plant—Microbe interaction confer stress tolerance in

390   plants: A review? Microbiological Research 207:41–52.

391   Legay, N., E. Personeni, S. Slezack-Deschaumes, S. Piutti, and J.-B. Cliquet. 2014. Grassland

392   species show similar strategies for sulphur and nitrogen acquisition. Plant and Soil

393   375:113–126.

394   Lehmann, A., and M. C. Rillig. 2015. Arbuscular mycorrhizal contribution to copper, manganese

395   and iron nutrient concentrations in crops – A meta-analysis. Soil Biology and

396   Biochemistry 81:147–158.

397   Letten, A. D., P.-J. Ke, and T. Fukami. 2017. Linking modern coexistence theory and

398   contemporary niche theory. Ecological Monographs 87:161–177.

399   Liu, X., I. M. Parker, G. S. Gilbert, Y. Lu, Y. Xiao, L. Zhang, M. Huang, Y. Cheng, Z. Zhang, and

400   S. Zhou. 2022. Coexistence is stabilized by conspecific negative density dependence via

401   fungal pathogens more than oomycete pathogens. Ecology 103:e3841.

402   Mattos-Jr, D., D. M. Kadyampakeni, J. R. da Silva, T. Vashisth, and R. M. Boaretto. 2020.

403   Reciprocal effects of huanglongbing infection and nutritional status of citrus trees: a

404   review. Tropical Plant Pathology 45:586–596.

19

405   Menge, D. N. L., S. W. Pacala, and L. O. Hedin. 2009. Emergence and Maintenance of Nutrient

406   Limitation over Multiple Timescales in Terrestrial Ecosystems. The American Naturalist

407   173:164–175.

408   Nazeri, N. K., H. Lambers, M. Tibbett, and M. H. Ryan. 2014. Moderating mycorrhizas:

409   arbuscular mycorrhizas modify rhizosphere chemistry and maintain plant phosphorus

410   status within narrow boundaries. Plant, Cell & Environment 37:911–921.

411   Northup, R. R., Z. Yu, R. A. Dahlgren, and K. A. Vogt. 1995. Polyphenol control of nitrogen

412   release from pine litter. Nature 377:227–229.

413   Olanrewaju, O. S., B. R. Glick, and O. O. Babalola. 2017. Mechanisms of action of plant growth

414   promoting bacteria. World Journal of Microbiology and Biotechnology 33:197.

415   Orwin, K. H., M. U. F. Kirschbaum, M. G. St John, and I. A. Dickie. 2011. Organic nutrient

416   uptake by mycorrhizal fungi enhances ecosystem carbon storage: a model-based

417   assessment. Ecology Letters 14:493–502.

418   Peay, K. G. 2016. The Mutualistic Niche: Mycorrhizal Symbiosis and Community Dynamics.

419   Annual Review of Ecology, Evolution, and Systematics 47:143–164.

420   Primieri, S., S. M. Magnoli, T. Koffel, S. L. Stürmer, and J. D. Bever. 2022. Perennial, but not

421   annual legumes synergistically benefit from infection with arbuscular mycorrhizal fungi

422   and rhizobia: a meta-analysis. New Phytologist 233:505–514.

423   van der Putten, W. H., M. A. Bradford, E. Pernilla Brinkman, T. F. J. van de Voorde, and G. F.

424   Veen. 2016. Where, when and how plant–soil feedback matters in a changing world.

425   Functional Ecology 30:1109–1121.

426   Ramakrishna, W., R. Yadav, and K. Li. 2019. Plant growth promoting bacteria in agriculture:

427   Two sides of a coin. Applied Soil Ecology 138:10–18.

428   Revilla, T. A., G. F. (Ciska) Veen, M. B. Eppinga, and F. J. Weissing. 2013. Plant–soil

429   feedbacks and the coexistence of competing plants. Theoretical Ecology 6:99–113.

20

430 Reynolds, H. L., K. M. Vogelsang, A. E. Hartley, J. D. Bever, and P. A. Schultz. 2006. Variable

431 responses of old-field perennials to arbuscular mycorrhizal fungi and phosphorus

432 source. Oecologia 147:348–358.

433 Schnitzer, S. A., J. N. Klironomos, J. HilleRisLambers, L. L. Kinkel, P. B. Reich, K. Xiao, M. C.

434 Rillig, B. A. Sikes, R. M. Callaway, S. A. Mangan, E. H. van Nes, and M. Scheffer. 2011.

435 Soil microbes drive the classic plant diversity–productivity pattern. Ecology 92:296–303.

436 Semchenko, M., K. E. Barry, F. T. de Vries, L. Mommer, M. Moora, and J. G. Maciá-Vicente.

437 2022. Deciphering the role of specialist and generalist plant-microbial interactions as

438 drivers of plant-soil feedback. New Phytologist in press.

439 Shakya, M., C.-C. Lo, and P. S. G. Chain. 2019. Advances and Challenges in

440 Metatranscriptomic Analysis. Frontiers in Genetics 10.

441 Siefert, A., K. W. Zillig, M. L. Friesen, and S. Y. Strauss. 2018. Mutualists stabilize the

442 coexistence of congeneric legumes. The American Naturalist 193.

443 Smith, S. E., and F. A. Smith. 2011. Roles of arbuscular mycorrhizas in plant nutrition and

444 growth: New paradigms from cellular to ecosystem scales. Annual Review of Plant

445 Biology 62:227–250.

446 Smith-Ramesh, L. M., and H. L. Reynolds. 2017. The next frontier of plant–soil feedback

447 research: unraveling context dependence across biotic and abiotic gradients. Journal of

448 Vegetation Science 28:484–494.

449 Steidinger, B. S., and J. D. Bever. 2014. The Coexistence of Hosts with Different Abilities to

450 Discriminate against Cheater Partners: An Evolutionary Game-Theory Approach. The

451 American Naturalist 183:762–770.

452 Taş, N., A. E. de Jong, Y. Li, G. Trubl, Y. Xue, and N. C. Dove. 2021. Metagenomic tools in

453 microbial ecology research. Current Opinion in Biotechnology 67:184–191.

454 Tedersoo, L., M. Bahram, and M. Zobel. 2020. How mycorrhizal associations drive plant

455 population and community biology. Science 367:eaba1223.

21

456   Tilman, D. 1982. Resource Competition and Community Structure. Princeton University Press.

457   Veen, G. F. (Ciska), G. T. Freschet, A. Ordonez, and D. A. Wardle. 2015. Litter quality and

458   environmental controls of home-field advantage effects on litter decomposition. Oikos

459   124:187–195.

460   Veen, G. F. (Ciska), E. L. Fry, F. C. ten Hooven, P. Kardol, E. Morriën, and J. R. De Long. 2019.

461   The role of plant litter in driving plant-soil feedbacks. Frontiers in Environmental Science

462   7:168.

463   Verzeaux, J., B. Hirel, F. Dubois, P. J. Lea, and T. Tétu. 2017. Agricultural practices to improve

464   nitrogen use efficiency through the use of arbuscular mycorrhizae: Basic and agronomic

465   aspects. Plant Science 264:48–56.

466   Vogelsang, K. M., H. L. Reynolds, and J. D. Bever. 2006. Mycorrhizal fungal identity and

467   richness determine the diversity and productivity of a tallgrass prairie system. New

468   Phytologist 172:554–562.

469   Wagg, C., Y. Hautier, S. Pellkofer, S. Banerjee, B. Schmid, and M. G. van der Heijden. 2021.

470   Diversity and asynchrony in soil microbial communities stabilizes ecosystem functioning.

471   eLife 10:e62813.

472   Wagg, C., J. Jansa, M. Stadler, B. Schmid, and M. G. A. van der Heijden. 2011. Mycorrhizal

473   fungal identity and diversity relaxes plant-plant competition. Ecology 92:1303–1313.

474   Whitaker, B. K., J. T. Bauer, J. D. Bever, and K. Clay. 2017. Negative plant-phyllosphere

475   feedbacks in native Asteraceae hosts - a novel extension of the plant-soil feedback

476   framework. Ecology Letters 20:1064–1073.

477   Zanne, A. E., K. Abarenkov, M. E. Afkhami, C. A. Aguilar-Trigueros, S. Bates, J. M. Bhatnagar,

478   P. E. Busby, N. Christian, W. K. Cornwell, T. W. Crowther, H. Flores-Moreno, D.

479   Floudas, R. Gazis, D. Hibbett, P. Kennedy, D. L. Lindner, D. S. Maynard, A. M. Milo, R.

480   H. Nilsson, J. Powell, M. Schildhauer, J. Schilling, and K. K. Treseder. 2020. Fungal

22

481   functional ecology: bringing a trait-based approach to plant-associated fungi. Biological

482   Reviews 95:409–433.

483

23