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Parasitism within mutualist guilds explains the maintenance of diversity in multi-species mutualisms

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Abstract

We consider here mutualisms where there are multiple species sharing a resource supplied by the same partner. If, as commonly assumed, there is competition between the species, then only the superior competitor should persist. Nevertheless, coexistence of multiple species sharing the same mutualistic partner is a widespread phenomenon. Regulation of nutrient exchange, where each species receives resources from the partner in proportion to the strength of the mutualism between the two, has been proposed as the main mechanism for coexistence in multi-species mutualisms involving the transfer of nutrients. Significant arguments, however, challenge the importance of partner selection processes. We present a mathematical model, applied to the arbuscular mycorrhizal symbiosis, to propose an alternative explanation for this coexistence. We show that asymmetric resource exchange between the plant and its fungal guild can lead to indirect parasitic interactions between guild members. In our model, the amount of carbon supplied by the plant to the fungi depends on both plant and fungal biomass, while the amount of phosphorus supplied by the fungi to the plant depends on both plant and fungal biomass when the plant is small, and effectively on fungal biomass only when the plant is large. As a consequence of these functional responses, more beneficial mutualists increase resource availability, and are indirectly exploited by less beneficial species that consume the resource and grow larger than they would in the absence of the better mutualists. As guild mutualists are not competing, competitive exclusion does not occur. Hence, the interaction structure can explain the maintenance of diversity within guilds in the absence of spatial structure and niche-related processes.

Keywords : Mutualism, mutualist guilds, coexistence, arbuscular mycorrhizal fungi, indirect interactions, mathematical model, ordinary differential equations, functional response, density-dependent resource exchange.

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1 Introduction

2 Within mutualist guilds, the principle of competitive exclusion seems not to apply. Indeed,
3 within a guild, mutualists occupying closely related niches coexist on the same partner (Palmer
4 et al., 2003). This fact presents a paradox: According to the principle of competitive exclusion
5 one would expect less beneficial mutualists, i.e., species that provide a lower amount of nutrient
6 in return for the benefit received, to dominate and outcompete more beneficial mutualists
7 (Palmer et al., 2003; Hardin, 1960). Yet, mutualisms involving only two interacting species
8 are relatively rare (Hoeksema and Bruna, 2000; Herre et al., 1999). New evidence has revealed
9 that even mutualisms previously thought to be species-specific, such as for example the fig
10 tree-fig wasp mutualism, are now recognised to involve a guild of mutualists with very similar
11 habits and morphology (Molbo et al., 2003; Pellmyr, 1999; Knowlton and Rohwer, 2003; Herre
12 et al., 1999; Hoeksema and Bruna, 2000).

13 The arbuscular mycorrhizal (AM) mutualism is another example that is particularly chal-
14 lenging to explain. AM fungi exist in the roots of most terrestrial plants (Smith and Read,
15 2010). The hyphae of the fungi grow from the plant roots into the soil, where they are able to
16 efficiently increase the absorption of nutrients that are limiting to plant growth (e.g., phospho-
17 rus). In return for these nutrients, the host plant provides carbon to the fungi. In nature, a
18 single host plant often associates with dozens of AM fungal species, many of them functionally
19 indistinguishable (Herre et al., 1999; Hoeksema and Bruna, 2000; Öpik et al., 2006). Guild
20 members coexist tightly in space within the roots and in the soil (Bennett and Bever, 2009;
21 Aldrich-Wolfe, 2007), rarely displaying the patchy distribution typically associated with niche
22 differentiation or aggregation (Powell and Bennett, 2016).

23 There has been some investigation as to the mechanism for this coexistence. Niche differ-
24 ences (Batstone et al., 2018), colonization-competition trade-offs (Smith et al., 2018), spatial
25 structure (Wilson et al., 2003), or physio-evolutionary feedbacks (Bever, 2015), can facilitate
26 coexistence in trophic communities as well as in multi-species mutualisms. None of these
27 mechanisms, however, can explain coexistence of species with a high degree of niche overlap
28 in the absence of spatial structure.

29 One of the most popular explanations for coexistence of multiple fungal species has been
30 regulation of resource exchange (Palmer et al., 2003). This mechanism requires that the
31 host favours guild members with more beneficial traits, thereby explaining the persistence of
32 good mutualists. Such preferential allocation of resources has been documented in the AM
33 symbiosis (Kiers et al., 2011; Hammer et al., 2011; Bever et al., 2009; Ji and Bever, 2016)
34 and has theoretical support (Bachelot and Lee, 2018; Bever, 2015; Moeller and Neubert,
35 2016; Hoeksema and Kummel, 2003; Christian and Bever, 2018; Krivan and Revilla, 2019;
36 Valdovinos et al., 2013). However, experimental studies have yielded inconsistent results
37 (Fitter, 2006; Kiers and Van Der Heijden, 2006; Walder and van der Heijden, 2015) and no
38 physiological basis for host discrimination has been identified. In addition, those experiments
39 showing preferential allocation by the plant (allocation of plant carbon to fungi in proportion
40 to the benefit received from each fungus) relied on an artificial spatial structure where the
41 fungi were spatially segregated (Kiers et al., 2011; Bever et al., 2009; Walder et al., 2012).

42 We propose an alternative mechanism that stabilises coexistence of multiple AM fungi
43 sharing a single host. We develop a mathematical model to show that asymmetric biomass-
44 dependent resource exchange can lead to stable coexistence of multiple AM fungal species,
45 without appealing to niche-based mechanisms, spatial segregation, or preferential allocation.
46 In our model, carbon transfer depends on plant and fungal biomass, while phosphorus transfer
47 depends on both plant and fungal biomass when the plant is small, and effectively on fungal
48 biomass only when the plant is large. We show that this asymmetry in nutrient exchange
49 results in indirect parasitism between fungal mutualists, where less mutualistic members indi-

50 rectly parasitise more mutualistic members. These results provide a new perspective on how
 51 diversity within a guild of mutualists could be maintained.

52 Model and Methods

53 Formulating a model for a multi-species mutualism

To investigate the dynamics of multi-species mutualisms we develop a model for the inter-
 actions between a host plant and its associated fungal mutualists. Resources exchanged are
 phosphorus (fungi to plant) and carbon (plant to fungi). Here, the changes in plant and fungal
 biomass are related to the amount of resource received, to the amount of resource given, and
 to maintenance costs. All of the mutualists coexist on a single plant, i.e., the carbon provided
 by the single plant supports the growth of all of the mutualists. The amount of resource
 exchanged depends on the plant and fungal biomass. We use ‘plant biomass’ to indicate the
 individual below- and above-ground parts. As it is not feasible to define fungal biomass at
 an individual scale, we use the term ‘fungal biomass’ to refer to the population biomass of a
 fungal species. In our model therefore, this scenario can be represented by a series of differ-
 ential equations describing the change over time of plant biomass (p) and of the biomass (m_i)
 of each of the N species of AM fungi (m_1, m_2, \dots, m_N):

$$\underbrace{\frac{dp}{dt}}_{\text{change in plant biomass}} = q_{hp} \underbrace{\sum_i (\alpha_i m_i)}_{\text{phosphorus from AM fungi}} \frac{p}{d+p} - q_{cp} \underbrace{\sum_i (\beta_i m_i)}_{\text{carbon to AM fungi}} p + \underbrace{r_p p}_{\text{intrinsic growth}} - \underbrace{\mu_p p^n}_{\text{maintenance cost}}, \quad (1a)$$

$$\underbrace{\frac{dm_i}{dt}}_{\text{change in fungal biomass}} = q_{cm_i} \underbrace{\beta_i p m_i}_{\text{carbon from plant}} - q_{hm_i} \underbrace{\alpha_i \frac{p}{d+p} m_i}_{\text{phosphorus to plant}} - \underbrace{\mu_{m_i} m_i^s}_{\text{maintenance cost}}, \quad i = 1 \dots N. \quad (1b)$$

54 A brief description of the parameters used in the model is given in Table 1. Here, we present
 55 an overview of the main features of the model.

56 The first terms on the right sides of Eqs. (1a) and (1b) describe the gain in plant and fungal
 57 biomass per unit time due to the resource received. The second terms represent the loss in
 58 biomass per unit time due to resource given. The relationship between the specific functional
 59 forms chosen for these terms is tied to the biology, and discussed in detail in the following
 60 section. The last terms for both equations describes the resource required for maintaining the
 61 existing biomass. The additional term in Eq. (1a), the intrinsic growth term, represents plant
 62 growth per unit time in the absence of the fungi (Smith et al., 2003). AM fungi are obligate
 63 mutualists with no saprobic ability and cannot survive in the absence of the host plant, so no
 64 intrinsic growth term appears in Eq. (1b).

65 Fungal species can be differentiated according to four specific traits: the efficiency with
 66 which carbon and phosphorus are converted into biomass (q_{cm_i} and q_{hm_i}) (van Aarle and
 67 Olsson, 2003), the ability to provide phosphorus to the plant (α_i) (Ravnskov and Jakobsen,
 68 1995; Drew et al., 2003), the access to host carbon (β_i) (Pearson and Jakobsen, 1993; Zhu and
 69 Miller, 2003) or the maintenance cost (μ_{m_i}) (Sylvia and Williams, 1992). Consistent with the
 70 literature, fungal species in the model can be distinguished accordingly to these four traits.

71 The literature provides little evidence about how the maintenance costs of plant and
 72 fungi depend on their respective biomasses (last term in Eqs. (1a) and (1b)). As density
 73 dependent and non-density dependent population growth are found in nature (Hassell, 1975),
 74 we investigate the effect of both linear (i.e. $n = 1$ and $s = 1$) and nonlinear forms of the
 75 maintenance cost term (i.e. $n > 1$ and $s > 1$).

76 Quantification of resource exchange

77 Nutrient exchange between the host plant and the fungal mutualists occurs inside the plant
78 root cells, where the AM fungi build nutrient exchange zones called ‘arbuscules’ (Peterson
79 and Guinel, 2000; Wang et al., 2017). It is reasonable to assume that the amount of phospho-
80 rus transferred increases with increasing root colonization and with increasing hyphal length
81 (Douds et al., 2000; Treseder, 2013; Sawers et al., 2017); More arbuscules means more contact
82 locations where nutrients can be exchanged, and longer hyphae in the soil mean greater fungal
83 access to soil phosphorus. In the model, we thus assume a linear relationship between fungal
84 biomass and phosphorus transfer.

85 The percentage of root colonization by a fungal species is typically between 20% and 50%
86 of plant roots, reaching 80% at most (Hart and Reader, 2002; Klironomos and Hart, 2002).
87 That is, space availability in the roots seems not to be a factor limiting the presence of AM
88 fungi. Thus, we assume that the plant limits phosphorus transfer only when plant biomass is
89 small, i.e., when less plant availability implies less habitat for the fungus and therefore less
90 phosphorus transfer, but not when the plant is big.

91 Mathematically, these assumptions lead to the phosphorus transfer term

$$92 \text{ Phosphorus transfer} \propto m_i \frac{p}{d+p}. \quad (2)$$

93 where d is the half-saturation constant. When $p \ll d$, phosphorus transfer depends linearly on
94 fungal and plant biomass, while when $p \gg d$, phosphorus transfer depends on fungal biomass
95 only. Eq. (2) corresponds to the second term of Eq. (1a) and to the first term of Eq. (1b).
96 Eq. (2) implies that in the presence of multiple mutualists, each of the mutualists supplies
97 to the plant a quantity of phosphorus per unit time that is proportional to its own biomass.
98 Note that, in our model, the non-linearity in the phosphorus transfer term (Eq. (2)) is due
99 to a limitation that the fungus experiences at low plant biomass, and not a limitation in the
100 benefit of mutualism set by the plant (i.e., the benefit is not saturating at large biomass of
101 the species giving the benefit, as seen in previous models of mutualistic interactions (Holland
102 and DeAngelis, 2010)). Thus, phosphorus transfer is limited by low plant biomass, but is
103 independent of plant biomass (i.e., depends only on fungal biomass) when plant biomass is
104 large.

105 The literature shows that the plant supplies its associated mutualists with a proportion of
106 the carbon it synthesizes (Douds et al., 2000; Treseder and Cross, 2006; Graham, 2000). It has
107 been shown that carbon transfer from the plant to the AM fungi depends on photosynthetic
108 capacity and on the extent of root colonization by AM fungi (Thomson et al., 1990; Vierheilig
109 et al., 2002). In the model, we assume a linear relationship between plant biomass and carbon
110 fixation. We further assume a linear relationship between carbon fixation and carbon transfer.
111 Finally, we assume linear dependence of carbon transfer and fungal biomass. In sum

$$112 \text{ Carbon transfer} \propto m_i p, \quad (3)$$

113 as indicated by the first and second terms of Eqs. (1a) and (1b). The choice of the term
114 for carbon transfer in Eq. (3) implies that when multiple mutualists are associated with the
115 same host, each species is supplied with an amount of host carbon per unit time that is
116 proportional to its individual fungal biomass and to the existing plant biomass. The fungi
117 do not directly compete for carbon, but each accesses a different proportion of host carbon
118 depending on each fungus’ biomass.

119 One can directly observe that the phosphorus and carbon transfer terms (Eqs. (2) and
120 (3)) show a different dependence on the biomass of the supplying and receiving species. These
121 differences are tied to the biology of the system, as explained above. Resource exchange is

122 therefore asymmetric, where carbon transfer depends on both plant and fungal biomass, while
123 phosphorus transfer depends on fungal biomass only, once the plant is large enough.

124 Although the dependence of the nutrient transfer terms (Eqs. (2) and (3)) on plant and
125 fungal biomass is the same for all fungi, the exact amount of phosphorus and carbon trans-
126 ferred varies with the parameters α_i and β_i respectively, and can vary among species. Fungi
127 characterised by a larger α_i and lower β_i parameters have a higher ability to transfer phos-
128 phorus to the plant and take less carbon in return, and therefore can be said to be more
129 mutualistic than species having a smaller α_i and larger β_i . Thus, where a fungus lies on the
130 mutualism-parasitism continuum depends on the context provided by the other fungi present
131 (Lekberg and Koide, 2014).

132 Model analysis and the impact on growth of differences in the 133 resource exchange ability of the fungi

134 We will analyse the model of Eq. (1) using both linear stability analysis and numerical sim-
135 ulations. Numerical simulations have been performed using the built-in ode45 solver in Mat-
136 labR2017a. First, we will determine the conditions under which a stable mutualism can be
137 established. Second, we will investigate how differences in the resource exchange ability of the
138 fungi affects plant growth and the growth of other guild members. For this purpose, we will
139 study the system dynamics when all model parameters are held at a constant value (given in
140 the caption of Fig. 3) except those that quantify the exchange of nutrients between plant and
141 fungi, i.e., α_i and β_i . These parameters represent, respectively, the ability of fungal species
142 i to provide phosphorus to the plant and the access of fungal species i to plant carbon. We
143 will determine analytically how the plant and fungal steady states depend on the resource
144 exchange capacity of the whole guild. We will then validate the analytical results numerically.

145 Because host discrimination has been one of the most popular explanations for coexistence
146 in multi-species mutualisms (Fitter, 2006; Kiers and Van Der Heijden, 2006; Walder and
147 van der Heijden, 2015), we are interested in seeing how it affects the system dynamics. We
148 will consider the following two cases:

- 149 (a) No host discrimination: Access to host carbon is the same for all fungi, regardless of the
150 amount of phosphorus they provide (i.e., parameter β_i is held constant for all species
151 while α_i varies). Since all of the species are characterised by the same carbon transfer
152 rate parameter, cheaters are those that provide little phosphorus (low α_i).
- 153 (b) Host discrimination: More beneficial fungi (high phosphorus transfer) have access to
154 more host carbon, while fungi that are less beneficial (low phosphorus transfer), have
155 a reduced access to host carbon (i.e., species with large/low parameter α_i also have
156 large/low β_i).

157 Results

158 Mutualism establishment and coexistence

159 **One plant - one fungus mutualism:** The establishment of a mutualistic relationship
160 between a plant and one fungal species can occur as long as (i) the plant receives enough
161 nutrients to support its growth (i.e., $\alpha > (q_{cp}\beta d)/q_{hp}$), (ii) plant and AM fungi are able to
162 make effective use of the resource received (i.e., $(q_{cm}q_{hp})/(q_{cp}q_{hm}) > 1$), and (iii) maintenance
163 costs are kept low (i.e., $\mu_p\mu_m < \beta^2(q_{cm}q_{hp} - q_{hm}q_{cp})/(4q_{hm}q_{hp})$). As long as these three

164 conditions are satisfied, the two nullclines in the phase plane of Fig. 1 intersect and coexistence
 165 is observed (see SI, section 1 for details).

166 From the phase plane in Fig. 1 we can also notice that when fungal biomass is large
 167 compared to plant biomass, fungal biomass will decrease and plant biomass will increase. The
 168 plant will therefore be exploiting the fungi, till its biomass is large enough to allow fungal
 169 growth. Similarly, when fungal biomass is low compared to plant biomass, the fungi will not
 170 be able to support plant growth. In this case, before showing mutual growth, plant biomass
 171 will decrease (suggesting parasitic fungi) and fungal biomass will increase.

172 **Graphical insights into the establishment of mutualistic interactions:** Plant
 173 growth saturates at the point where there is a balance between the benefit and cost of the
 174 mutualism. This balance is reached as a consequence of the asymmetry in phosphorus and
 175 carbon transfer (Eqs. (2) and (3)). Fig. 2 demonstrates how the benefits and costs of the
 176 mutualism are distributed across the plant and fungus, as a function of plant or fungal biomass.
 177 The figure shows plots of the three key functional responses of the mutualism: the gross benefit
 178 (GB), cost (C), and net effect (NE), where $NE = GB - C$. These functions are given in Table 2.
 179 In the right panel of Fig. 2, one can see that when plant biomass is small, the gross benefit
 180 functional response of the plant is larger than the cost functional response. This situation
 181 results in a positive net effect on plant growth, and therefore in an increase in plant biomass.
 182 When plant biomass is large, however, the gross benefit functional response decreases, while
 183 the cost functional response remains constant, eventually leading to a negative effect on plant
 184 growth. Plant biomass is therefore expected to stabilise around a certain value for which the
 185 plant gross benefit and cost functional responses are equal to each other. That is, the plant
 186 stops growing when the net effect (see Table 2) is zero. Consequently, plant growth is limited
 187 by its interaction with the fungal mutualists.

188 Fungal growth is not limited by its interaction with the host plant. As long as plant
 189 biomass is large enough, the net effect of mutualism for the fungi remains positive (see left
 190 panel of Fig. 2). Without any kind of self-limitation ($s = 1$) fungal growth is unlimited (see last
 191 term in Eq. (1b)). Fungal growth is limited for $s > 1$. In either case, the model predicts plant-
 192 fungi coexistence (see Fig. S6). Plant-fungus coexistence is observed whether the maintenance
 193 cost per unit time of the plant (see last term in Eq. (1a)) is linearly proportional to plant
 194 biomass ($n = 1$) or increases non-linearly ($n > 1$) with plant biomass (see Fig. S5), and for a
 195 positive intrinsic growth rate $r_p > 0$ (see Fig. S4).

One plant - multiple fungi case: When considering a plant associating with N fungal
 species, either coexistence or extinction of all mutualists is observed. And as long as (i) at
 least one of the fungal species provides enough nutrients to the plant (i.e., the inequality
 $\alpha_i > (q_{cp}\beta_i d)/q_{hp}$ is satisfied for at least one species), and as long as (ii) plant and fungi are
 able to make effective use of the resource received (i.e., $(q_{cm}q_{hp})/(q_{cp}q_{hm}) > 1$), the mutualism
 can establish and coexistence is observed. Additionally, for mutualism establishment, it must
 hold

$$\begin{aligned}
 \text{(iii)} \quad & (1 + Q)^2 \left(1 + \frac{Cov(\boldsymbol{\alpha}/\sqrt{\boldsymbol{\mu}_m}, \boldsymbol{\beta}/\sqrt{\boldsymbol{\mu}_m})}{(\boldsymbol{\alpha}/\sqrt{\boldsymbol{\mu}_m})(\boldsymbol{\beta}/\sqrt{\boldsymbol{\mu}_m})} \right)^2 \\
 & - 4Q \left(1 + \frac{Var(\boldsymbol{\alpha}/\sqrt{\boldsymbol{\mu}_m})}{(\boldsymbol{\alpha}/\sqrt{\boldsymbol{\mu}_m})^2} \right) \left(1 + \frac{\mu_p}{Nq_{cm}q_{cp}(\boldsymbol{\beta}/\sqrt{\boldsymbol{\mu}_m})^2} + \frac{Var(\boldsymbol{\beta}/\sqrt{\boldsymbol{\mu}_m})}{(\boldsymbol{\beta}/\sqrt{\boldsymbol{\mu}_m})^2} \right) > 0, \quad (4)
 \end{aligned}$$

196 where $\boldsymbol{\alpha} = (\alpha_1, \dots, \alpha_N)$ and $\boldsymbol{\beta} = (\beta_1, \dots, \beta_N)$ represent respectively the ability of the whole
 197 guild to transfer phosphorus and get carbon from the plant, $\boldsymbol{\mu}_m = (\mu_1, \dots, \mu_N)$ represents

198 the maintenance cost of the guild, $Cov(\cdot)$ is the covariance, $Var(\cdot)$ is the variance, and $\overline{\alpha/\mu_m}$
 199 and $\overline{\beta/\mu_m}$ represent the mean of the individual resource exchange capacities divided by the
 200 maintenance cost of each of the fungi present. Condition (iii) is more likely to be satisfied
 201 when the covariance between α and β and the mean $\bar{\alpha}$ are large, and when the variances
 202 $Var(\alpha)$ and $Var(\beta)$ are small. Additionally, the condition is less likely to be satisfied when
 203 the maintenance cost μ_m of the fungi is large (see SI, section 2 for details). Altogether, con-
 204 ditions (i)-(iii) tell us that it is the overall exchange capacity of all mutualists that determines
 205 whether coexistence or extinction of the whole guild will be observed. Plant association with
 206 a sufficiently beneficial mutualist can compensate for the presence of a minimally beneficial
 207 species, or even for a species that does not provide any nutrients to the plant (i.e. $\alpha_i = 0$), as
 208 long as the plant receives on average enough nutrients to support its growth, and as long as
 209 guild members are similar enough in their ability to transfer phosphorus and get host carbon.

210 Fig. 3 shows typical results of simulation experiments where the carbon supplied by a single
 211 plant is shared among fungi characterized by different resource exchange capacities. In the first
 212 two subfigures we investigate the two cases described in the methods: No host discrimination
 213 (Fig. 3a) and host discrimination (Fig. 3b). As expected from the model analysis, coexistence
 214 is observed whether or not the plant rewards more mutualistic fungi with more carbon. The
 215 growth dynamics, however, differ. When all fungi have access to the same amount of carbon
 216 independent of the phosphorus supplied, less mutualistic fungi reach a higher abundance than
 217 more mutualistic ones (Fig. 3a). Mutualists supplying more phosphorus and accessing more
 218 carbon reach a higher biomass than less mutualistic fungi (Fig. 3b). The presence of more
 219 mutualistic fungi increases plant biomass, and therefore resource availability. If the plant is
 220 supported by enough high quality mutualists, then less mutualistic species can exploit the
 221 plant's resource and, indirectly, the more beneficial species. If the guild does not provide
 222 enough phosphorus to the host plant (i.e., the conditions for coexistence mentioned above are
 223 not satisfied), extinction of the whole guild is observed (see Fig. 3c).

224 Indirect parasitism among guild members

225 Fig. 4 compares plant and fungal growth when the plant is associated with a more mutualistic
 226 fungus (species 1), a less mutualistic fungus (species 2), or a combination of the two species.
 227 When a less mutualistic fungus (species 2) is considered in pairwise association with the plant,
 228 the growth rates and final sizes of the plant and the fungus are lowest. When the plant is
 229 considered in pairwise association with the more mutualistic fungus (species 1), growth rates
 230 and final sizes are highest. If species 1 and 2 are both present, the growth rate and final
 231 size of the plant and species 1 are lowered, while the growth rate of species 2 is increased.
 232 The presence of species 2 negatively affects the growth of species 1, while the presence of
 233 species 1 positively affects the growth of species 2. Indirect interactions between species 1
 234 and 2 are therefore parasitic, with the less mutualistic fungus (species 2) exploiting the more
 235 mutualistic one (species 1). The larger the difference in net benefit provided by guild members,
 236 the stronger the indirect parasitic interactions. The analysis presented in the SI (section 3)
 237 shows that our numerical findings hold for any value of the ability of the fungi to transfer
 238 phosphorus (parameter α_i).

239 These indirect relationships are shown schematically in Fig. 5. The diagram qualitatively
 240 represents the interactions of a plant and three fungal species differing in their resource ex-
 241 change capacities. Species 1 is assumed to be a better mutualist than species 2 and 3, and
 242 species 2 is a better mutualist than species 3. Pairwise direct interactions of the plant with
 243 each of the three AM fungal species are mutualistic, where the plant provides equal access
 244 to the resource to all three fungi, and receives resource from each species according to its re-
 245 source exchange ability. Consequently, pairwise indirect interactions among fungal species are

246 parasitic, since the less mutualistic species takes advantage of the plant growth resulting from
247 the benefit provided by the more mutualistic species. In other words, species 1 is exploited
248 by 2 and 3, and species 2 is exploited by 3.

249 The model predicts none of the interactions between the fungi to be competitive, i.e.,
250 disadvantageous for both parties. In the absence of competitive interactions, competitive
251 exclusion is not expected to occur. Instead, in the pairwise indirect interactions between
252 fungal mutualists, one of the two always benefits. In terms of Fig. 5, each parallel set of arrows
253 between fungi represents interactions that are parasitic, i.e. positive for the less mutualistic
254 species and negative for the more mutualistic one.

255 Discussion

256 Modelling of mutualistic interactions

257 I present a model that allows for stable coexistence of multiple mutualists sharing a resource
258 supplied by a single partner, in the absence of niche-based mechanisms, spatial structure, or
259 preferential allocation. In the model, multi-species mutualism establishment depends on the
260 overall net benefit provided by the guild to the partner. As long as the plant receives enough
261 nutrients to support its growth, coexistence of all mutualists is observed. Similarly, in public
262 goods games, coexistence of more and less beneficial mutualists has been shown to occur
263 as long as there are enough good mutualists to produce the public good (Archetti and
264 Scheuring, 2011, 2013). In our model, we obtain the additional requirement that establishment
265 is more likely if the variance across guild members is small, i.e., that the guild members are
266 similar in mutualistic quality.

267 Previous ordinary differential equation models of mutualistic interactions have shown that
268 stable coexistence in mutualisms involving only two interacting species can be obtained by
269 setting an upper limit to the benefit that each species can provide to the other (i.e., the gross
270 benefit (GB) and cost (C) curves in Fig. 2 level off for sufficiently large biomass) (Wright,
271 1989; Ingvarsson and Lundberg, 1995; Kot, 2001; May, 1976; Addicott, 1981; Holland et al.,
272 2002; Holland and DeAngelis, 2006; Holland et al., 2004; Holland and DeAngelis, 2009, 2010).
273 However, saturation in the benefit makes stable coexistence of multiple mutualists impossible,
274 in the absence of secondary mechanisms. Inevitably, one of the mutualists will be better than
275 the others at obtaining resource from the partner species. Consequently, the biomass of this
276 species will increase, leading to the consumption of an increasing proportion of the available
277 resource, eventually driving the other mutualists to extinction. On the other hand, symmetric
278 non-saturating resource exchange (corresponding to linear gross benefit (GB) functional
279 responses) results in unlimited growth of both, the mutualists and the partner species (Gause
280 and Witt, 1935; Vandermeer and Boucher, 1978). In our model, the benefit increases linearly
281 with the biomass of the species providing the benefit, and does not saturate at high biomass
282 of the species giving the benefit. Hence, coexistence is possible. At the same time, asymmetry
283 in the benefit and cost of mutualism (Eqs. (2) and (3)) sets a limit to plant growth, which is
284 reached when, for the plant, the benefit and cost of the mutualism equalize.

285 Mutualism-parasitism continuum

286 Experimental work has shown that symbiotic associations are not always necessarily beneficial,
287 but can, under certain circumstances, become parasitic or commensalistic. For example,
288 the nature of the symbiosis may depend on the genotypes of the interacting species or on
289 environmental conditions (Johnson et al., 1997; Lekberg and Koide, 2014). Here, we present

290 a mechanism that causes interactions to change from mutualistic to parasitic when there is a
291 disproportion in plant and fungal biomass, where the more abundant species is exploited by
292 the less abundant one before mutual growth can be observed. It has already been hypothesized
293 that depletion in plant growth may be observed when the carbon cost set by the fungi is not
294 sufficiently compensated by phosphorus transfer (Lekberg and Koide, 2014; Smith and Smith,
295 2012). This mechanism could explain a depletion in plant growth when abundance of AM
296 fungi is low, as observed by Smith and Smith (2012).

297 Indirect parasitism between guild members

298 In this article, we show that the main form of interaction between guild members is indirect
299 parasitism, and as guild members are not competing, competitive exclusion is not expected
300 to occur. The presence of a more mutualistic species increases plant biomass, and therefore
301 resource availability, for other guild members. Each fungal mutualist exploits all of the other
302 species that are more mutualistic fungi than itself, and at the same time is itself exploited by
303 each of the species that are less mutualistic. The most mutualistic species is exploited by all
304 other species, and the least mutualistic one is not exploited by any. The more similar the net
305 benefit provided by the guild members, the more negligible the indirect parasitism and the
306 effect that the mutualist species have on each other's biomass.

307 Previous work has proposed that stable coexistence of multiple species sharing a limiting
308 resource can emerge as a consequence of indirect interactions in multitrophic communities
309 (Stanton, 2003; McCann, 2000). The presence of a third species may affect the population
310 size of a superior competitor through an interaction chain, e.g., by predation (May, 1972;
311 Caswell, 1978; Allesina and Levine, 2011; Kerr et al., 2002), or it can alter the effect that
312 one species has on another through higher-order interactions, e.g., by varying the amount of
313 resource available (Schoener, 1974; Abrams, 1983; Mayfield and Stouffer, 2017; Levine et al.,
314 2017). In the model presented here, the amount of shared resource available (i.e., plant
315 biomass) is determined by its interaction with the associated mutualists. The fungal species
316 are not directly competing for the resource they are sharing, because the amount of resource
317 available increases with increasing fungal abundance.

318 Experimental work

319 While there is a great deal of work looking at fungal diversity in the microbiome of plants
320 (Husband et al., 2002; Sugiyama et al., 2014) the results are largely focussed on diversity,
321 rather than fungal biomass over time. Only a few studies show the progression of fungal
322 biomass and plant biomass over time when two or more fungal species are present (for example
323 producing data like that shown in plots in Fig. 4).

324 Hart et al. (2013) found that the abundance of a less mutualistic fungal species is increased
325 by the addition of a better mutualist colonizing the same host plant, and Argüello et al. (2016)
326 showed that a plant receives more phosphorus from a less mutualistic species in the presence
327 of a better mutualist. Jansa et al. (2008) showed that plant and fungal growth in the presence
328 of multiple mutualists were mostly within the range of what was observed when the plant
329 was grown separately with the most and less mutualistic species. All of these results are in
330 agreement with model predictions.

331 Other observations, however, show that plant growth is higher in the presence of multiple
332 species of AM fungi than in the presence of any of the species separately (Jansa et al., 2008;
333 Alkan et al., 2006; Maherali and Klironomos, 2007; Van der Heijden et al., 1998; Gianinazzi
334 et al., 2010). This fact presents a contradiction with model predictions, as plant biomass is
335 expected to be maximized by the presence of a single, most beneficial species (e.g., species 1

336 in Fig. 4). The contradiction could be explained by the fact that in the model we assume
337 phosphorus supply to be the only benefit provided to the plant by the fungi. Root colonization
338 with AM fungi has also been shown to increase plant resistance to diseases (Jung et al., 2012),
339 protection against parasites (Parniske, 2008), and plant tolerance to abiotic stress (Latef et al.,
340 2016). The presence of fungal species providing complementary benefits can therefore help to
341 maximize plant growth (Afkhani et al., 2014). Further monitoring of plant and fungal growth
342 over time in monocultures of AM fungi and in cultures containing different fungal species is
343 needed for experimental verification of the hypotheses presented here.

344 Future directions

345 Asymmetric nutrient exchange is an important part of the dynamics observed in the model.
346 The veracity of this assumption remains to be tested; very few studies have attempted to
347 bridge theory and empiricism by experimentally testing different mathematical forms of ben-
348 efit and cost functional responses of mutualisms (Morris et al., 2010; Morales, 2011; Kang
349 et al., 2011; Geib and Galen, 2012). Further empirical work is needed to determine whether
350 mutualistic interactions can effectively be characterised by the asymmetric resource exchange
351 rates assumed in the model.

352 Additionally, while much can be learned from the model presented here, there are certain
353 features of the system that may be important to include in future modelling efforts. In
354 particular, we do not distinguish between plant structure above or below ground, although
355 plants are known to differentially allocate carbon depending on plant size, environmental
356 conditions or AM fungal abundance (Andersen and Rygielwicz, 1991; Rygielwicz and Andersen,
357 1994). Also, AM fungi have been shown to contribute to nutrient uptake only after having
358 built a fungal network inside the plant root cells (Dickson et al., 1999). There should therefore
359 exist a threshold of fungal biomass below which the fungi do not contribute to plant growth.
360 Future models may regard plant and fungal biomass as a system of multiple coupled differential
361 equations, to distinguish plant biomass above- and below- ground and intra- and extraradical
362 fungal biomass.

363 In our work, we also do not consider plant-soil feedback (Van der Putten et al., 2013;
364 Miki, 2012). These types of feedback can indeed influence coexistence patterns (Johnson and
365 Bronstein, 2019). A simple study of the dynamics of these feedbacks could be carried out with
366 the model presented here by considering variations in the intrinsic growth rate of the plant
367 (characterised by parameters r_p and μ_p), as a function of different soils. Our model could
368 also be used as a building block in larger community models which are at present conceptual
369 (Van der Putten et al., 2013) or based on very simple mass action kinetics (Miki, 2012).

370 Additionally, our model could be used to investigate how different plant-mutualist guild
371 combinations can be more or less evolutionary successful, where the total mutualist quality of
372 the guild depends on the resource exchange capacities of each mutualist in the guild. Such a
373 study would therefore offer an opportunity to couple the physiological qualities of the fungal
374 species present (i.e., their resource exchange capacities) with evolutionary processes (Lekberg
375 and Koide, 2014).

376 It is important to note that the model presented here is not spatially explicit, and allows
377 for an indefinite number of mutualists to be associated with the same host plant. Space should
378 become a limiting factor, however, at large fungal density (Hepper et al., 1988; Mummey et al.,
379 2009; Koch et al., 2011; Engelman et al., 2014). An extension of this model to explicitly
380 considering competition between fungal species is studied by Martignoni et al. (2020).

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Table 1: Brief description of the parameters of the model of Eq. (1).

Parameter	Description
α_i	Phosphorus exchange ability of fungal species i
β_i	Access to host carbon of fungal species i
μ_p	Maintenance rate of the plant
μ_{m_i}	Maintenance rate of fungal species i
q_{hp}	Conversion factor of phosphorus into plant biomass
q_{cp}	Conversion factor of carbon into plant biomass
q_{hm_i}	Conversion factor of phosphorus into fungal biomass of species i
q_{cm_i}	Conversion factor of carbon into fungal biomass of species i
r_p	Intrinsic growth rate of the plant
d	Half-saturation constant
n	Biomass dependence of the plant maintenance rate
s	Biomass dependence of the fungal maintenance rate

387 **Tables and Figures**

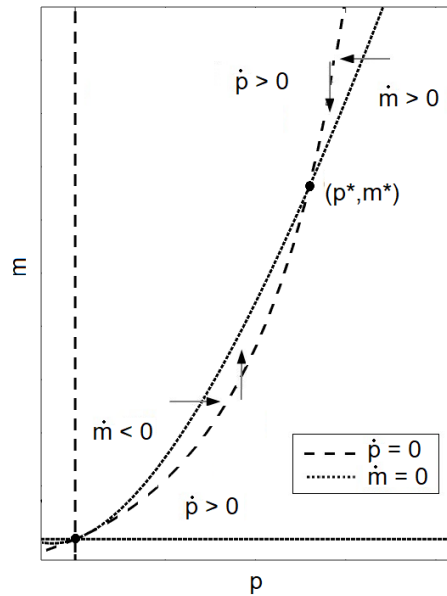


Fig. 1: Nullclines $\dot{p} = 0$ (dashed line) and $\dot{m} = 0$ (dotted line) of the system of differential equations given in (1) for $N = 1$. Arrows represent qualitatively the direction of the flow nearby the stable steady state (p^*, m^*) .

Table 2: Biomass-dependence of the gross benefit (GB), cost (C) and net effect (NE) functional responses of plant (p) and a species of AM fungi (m_i), characterizing the model described in Eq. (1). The GB and C functional responses of plant and fungi are obtained by dividing Eqs. (2) and (3), representing the biomass-dependence of phosphorus/carbon transfer per unit time, by the biomass of the species receiving (GB) or providing (C) the nutrient. The net effect functional response is calculated as the difference between the gross benefit and cost functional responses ($NE = GB - C$).

	GB	C	NE
Plant (p)	$\frac{m_i}{d+p}$	m_i	$m_i \left(\frac{1}{d+p} - 1 \right)$
AM fungi (m_i)	p	$\frac{p}{d+p}$	$p \left(1 - \frac{1}{d+p} \right)$

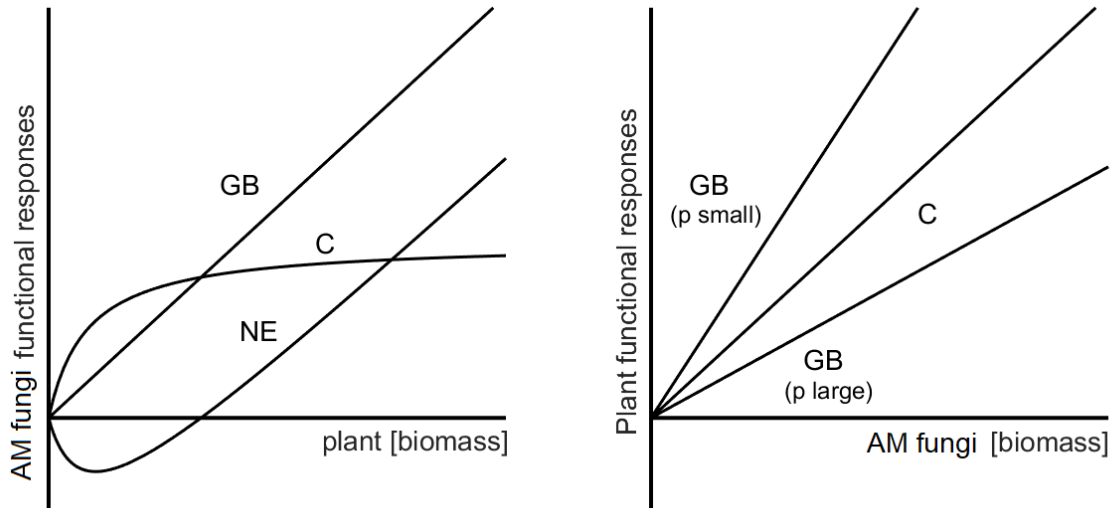


Fig. 2: Qualitative graphical representation of the functional responses of plant and AM fungi given in Table 2. Functional response curves of gross benefit (GB), cost (C) and net effect ($NE = GB - C$) of a species of AM fungi (left panel) and plant (right panel) are plotted as a function of plant, respectively fungal, biomass. Note that the GB functional response of the plant depends on both, fungal and plant biomass, making the NE functional response of the plant negative at large plant biomass and positive when plant biomass is small. Plant growth will therefore stabilise about a certain value of p for which plant GB and C functional responses are equal to each other.

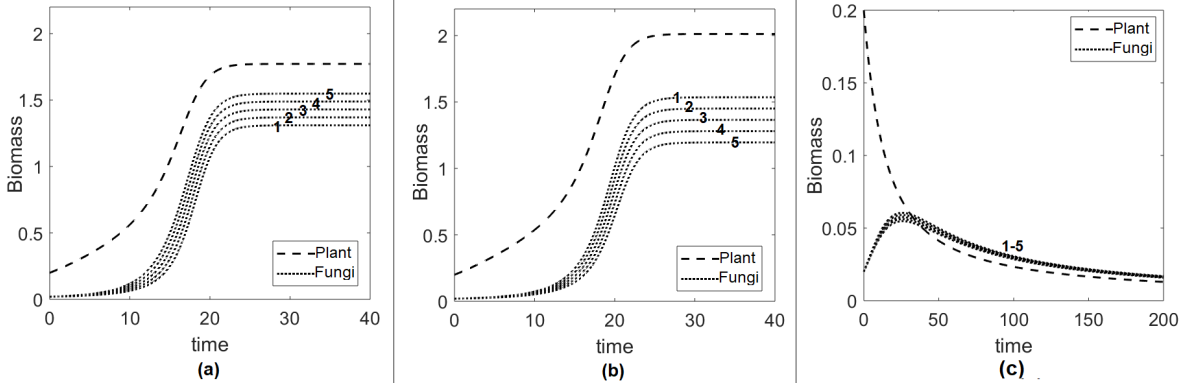


Fig. 3: Plant and fungal growth over time where (a) fungi differ only in their phosphorus supply to the plant and access to host carbon is the same for all species, (b) fungi supplying the plant with a large/small amount of phosphorus (α_i) have high/low access to host carbon (β_i), and (c) fungi provide a very low amount of phosphorus to the plant. Species 1 provides the greatest net benefit to the plant, and species 5 provides the lowest. The plant p is represented as a dashed line, while different fungal species m_i are dotted lines, with the numbers close to each curve indicating the species number. Numerical solutions are obtained by solving Eq. (1) for $i = 1..5$ where (a) α_i decreases from 0.62 to 0.38 in steps of size 0.08, while $\beta_i = 0.4$ for all species. (b) α_i increases from 0.40 to 0.48 in steps of size 0.02, for $i = 1..5$ and β_i decreases from 0.38 to 0.30 in steps of size 0.02. (c) α_i decreases from 0.2 to 0.12 in steps of size 0.02, while $\beta_i = 0.4$ for all species. Other parameters are $q_{hp} = 3$, $q_{cm_i} = 2$, $q_{cp} = q_{hm_i} = 1$, $r_p = 0.04$, $\mu_p = 0.3$, $\mu_m = 0.8$, $n = s = 2$ and $d = 1.2$, for all species. Initial abundances are $p(0) = 0.2$, $m_i(0) = 0.02$.

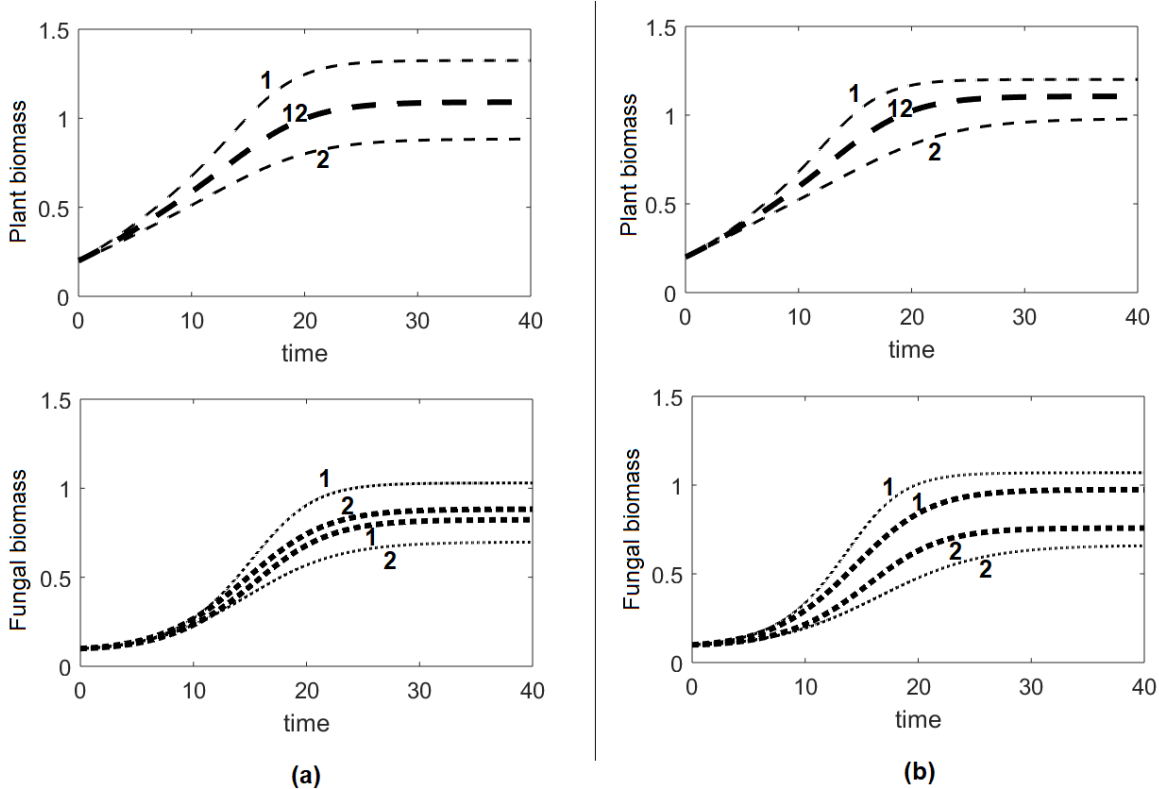


Fig. 4: Growth over time of a single plant associating with two species of AM fungi. Species 1 is more mutualistic and provides the plant with more phosphorus than species 2 ($\alpha_1 > \alpha_2$). (a) Access to host carbon is the same for both species ($\beta_1 = \beta_2$) or (b) Species 1 have access to more host carbon than species 2 ($\beta_1 > \beta_2$). In both cases, the upper figures represent plant biomass over time when the mycorrhizal association is between a plant and two individuals of the more mutualistic species (thin dashed curves, number 1), of the less mutualistic species (thin dashed curves, number 2) or a combination of species 1 and species 2 (thick dashed curves, 12). The bottom figures represent fungal biomass over time when the fungal species are considered in separate association with the plant (thin dotted curves) or grown simultaneously on the same plant (thick dotted curves). Parameters are: $\alpha_1 = 0.45$ and $\alpha_2 = 0.35$, (a) $\beta_1 = 0.45$ and $\beta_2 = 0.35$, (b) $\beta_1 = \beta_2 = 0.4$. Other parameters correspond to those for Fig. 3. Note that we are using parameter values for which plant growth is always enhanced in the presence of AM fungi.

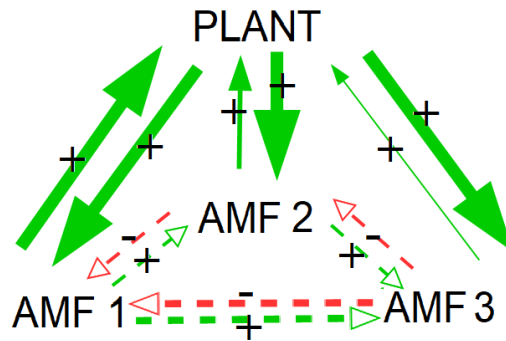


Fig. 5: Diagram representation of direct (solid arrows) and indirect (dotted arrows) interactions between a plant and its associated mutualist guild. Species 1 is more mutualistic than species 2, and species 2 is more mutualistic than species 3. Arrows indicate the direction of each interaction, with the sender at the tail of the arrow and the receiver at the head. Green arrows represent positive effects ('+') , while red arrows represent negative effects on growth ('-'). Arrows thickness qualitatively represents the interaction strength. A '+'/'-' indicates that the sender has a positive/negative effect on the growth of the receiver. A mutualistic interaction is one in which the two parallel interactions are denoted as ('+', '+'), while a parasitic interaction is one in which one of the parallel interactions is positive and the other is negative ('+', '-'). A competitive interaction is one in which each species negatively impacts the other one, and so it would be labeled ('-', '-'). Interactions between guild members are not competitive ('-', '-'), but parasitic ('+', '-').

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Supplementary information

1 Analysis of the one plant - one fungus system

Conditions for the existence of coexistence steady states: We are interested in deriving conditions for the existence of steady states for which plant and AM fungi coexistence is observed. To facilitate computations, we reduce the number of model parameters in Eq. (1) and non-dimensionalise the equations by carrying out the substitutions given in Table S2. We consider a version of the model for which $r_p = 0$ and maintenance costs are non-linear (i.e., $n = 2$ and $s = 2$). Insights on the cases $r_p > 0$ and $n, s \neq 2$ will be given below (see Figs. S4, S5 and S6). We obtain the non-dimensional model

$$\frac{dP}{d\tau} = Q \frac{M}{D+P} P - M P - \eta_P P^2, \quad (5a)$$

$$\frac{dM}{d\tau} = P M - \frac{P}{D+P} M - \eta_M M^2. \quad (5b)$$

Nullclines of Eq. (5) can be found by setting $dP/d\tau$ and $dM/d\tau$ to zero and solving for P and M . We obtain

$$\frac{dP}{d\tau} = 0 \iff P = 0 \quad or \quad M = \frac{\eta_P P(D+P)}{Q-D-P}, \quad (6a)$$

$$\frac{dM}{d\tau} = 0 \iff M = 0 \quad or \quad M = \frac{P(P+D-1)}{\eta_M(D+P)}. \quad (6b)$$

The first nullcline in Eq. (6a) and in Eq. (6b) correspond to the absence of AM fungi and plant biomass respectively, and to the horizontal and vertical axes in the phase plane. The origin is therefore always a steady state.

The second nullcline of Eq. (6a) is an hyperbola with vertical asymptote at $P = Q - D$ (Fig. S1). In order for Eq. (6a) to allow positive values for M and P the asymptote must be in the positive quadrant, i.e. we require $Q - D > 0$. This requirement yields us the first condition for the existence of a steady state, which can be expressed in terms of the original parameters as

$$\alpha > \frac{q_{cp}}{q_{hp}} \beta d. \quad (7)$$

Expression (7) essentially states that for a coexistence steady state to occur, the ability of the fungi to supply phosphorus to the plant (α) must be sufficiently large. At the same time, the ratio between the conversion factors of nutrients given to received into plant biomass (q_{hp}/q_{cp}) and the carbon sink strength (β) must be small enough. Moreover d must be small, i.e., the threshold of plant biomass that determines when the benefit of the mutualism for the plant is limited by the plant or by the fungal biomass must be relatively low.

The second nullcline of Eq. (6b) is also an hyperbola with asymptote at $-D$. Intersections of the hyperbola with the horizontal axis occur at $P = 0$ and $P = 1 - D$. If $D > 1$, the

Table S1: Variables and parameters of the model given in Eq. (1), with respective measurement units.

p	plant biomass	α	$\frac{\text{phosphorus}}{(\text{unit time}) \times (\text{unit fungal biomass})}$	q_{hp}	$\frac{\text{plant biomass}}{\text{phosphorus}}$
m	fungal biomass	β	$\frac{\text{carbon}}{(\text{unit time}) \times (\text{unit fungal biomass}) \times (\text{unit plant biomass})}$	q_{cm}	$\frac{\text{fungal biomass}}{\text{carbon}}$
d	plant biomass	μ_p	$\frac{1}{(\text{unit time}) \times (\text{unit plant biomass})}$	q_{cp}	$\frac{\text{plant biomass}}{\text{carbon}}$
r_p	intrinsic growth rate	μ_m	$\frac{1}{(\text{unit time}) \times (\text{unit fungal biomass})}$	q_{hm}	$\frac{\text{fungal biomass}}{\text{phosphorus}}$

Table S2: Description of the non-dimensional parameters used to translate Eq. (1) into Eq. (5) .

$P = \frac{q_{cm}\beta}{q_{hm}\alpha} p$	$M = \frac{q_{cp}\beta}{q_{hm}\alpha} m$	$\tau = q_{hm}\alpha t$	
$D = \frac{q_{cm}\beta}{q_{hm}\alpha} d$	$Q = \frac{q_{cm}q_{hp}}{q_{cp}q_{hm}}$	$\eta_P = \frac{\mu_p}{q_{cm}\beta}$	$\eta_M = \frac{\mu_m}{q_{cp}\beta}$

656 hyperbola assumes values in the positive quadrant for $P > 0$, while if $D < 1$ the hyperbola
657 assumes values in the first quadrant for $P > 1 - D$ (Fig. S1). In order for the nullclines
658 in Eqs. (6a) and (6b) to intersect, the asymptote at $P = Q - D$ in (6a) must occur at
659 $P > 1 - D$. This condition gives a second requirement for the existence of a steady state, that
660 is $Q - D > 1 - D \Leftrightarrow Q > 1$. In term of the original parameters, this condition translates to

$$661 \quad \frac{q_{cm}q_{hp}}{q_{cp}q_{hm}} > 1. \quad (8)$$

662 Eq. (8) states that the product of the conversion factors of the nutrients received, i.e., carbon
663 for the fungi and phosphorus for the plant, must be larger than the conversion factors of the
664 nutrients given.

665 An expression for the values of P^* at steady state can be derived by setting Eqs. (6a) and
666 (6b) equal to each other and finding the roots of the polynomial

$$667 \quad \eta_P \eta_M (P^* + D)^2 - (Q - D - P^*)(P^* + D - 1) = 0. \quad (9)$$

668 Steady states occur at

$$669 \quad P_{1,2}^* = \frac{Q + 1 \pm \sqrt{(Q - 1)^2 - 4Q\eta_P\eta_M}}{2(1 + \eta_P\eta_M)} - D. \quad (10)$$

670 The steady states P^* assume real values only if the expression under the square root is
671 greater than zero. This requirement translates into a third condition for coexistence, i.e.,
672 $\eta_P\eta_M < (Q - 1)^2/4Q$. In term of the original parameters this condition can be written as

$$673 \quad \mu_p\mu_m < \beta^2 \frac{q_{cm}q_{hp} - q_{hm}q_{cp}}{4q_{hm}q_{hp}}. \quad (11)$$

674 Expression (11) essentially states that to allow stable coexistence of plant and AM fungi the
675 maintenance rates for plant and AMF (μ_p and μ_m) can not be too large.

676 Eq. (10) can have zero, one or two positive solutions depending on the choice of the
677 parameters. The stability analysis conducted below and the graphical stability analysis of
678 Fig. S1 show that when only one coexistence steady state exists (i.e., $P_1^* < 0$ and $P_2^* > 0$), it
679 is always an attractor and the origin is a saddle. When two coexistence steady states exist the
680 origin and P_2^* are attractors and P_1^* is a saddle, where $P_1^* < P_2^*$. In this case there are two
681 distinct basins of attraction, one for the origin and one for the P_2^* steady state . The biological
682 interpretation of this case is that below certain thresholds of plant and fungal biomass, mutual
683 growth can not be observed.

684 The steady state value of the plant (the positive root in Eq. (10)) corresponds to the non-
685 dimensionalised version of the upper bound to plant growth, and determines the maximal
686 plant biomass at which plant growth saturates. This value increases with Q , and decreases
687 with D , η_P or η_M . Eq. (10) can be rewritten in terms of the original parameters as

$$688 \quad p_{1,2}^* = \frac{\frac{q_{hp}\alpha}{q_{cp}} + \frac{\alpha q_{hm}}{q_{cm}} \pm \frac{\alpha q_{hm}}{q_{cm}} \sqrt{\left(\frac{q_{hp}q_{cm}}{q_{cp}q_{hm}} - 1\right)^2 - 4\frac{q_{hp}\mu_p\mu_m}{q_{hm}q_{cp}^2\beta^2}}}{2\left(\beta + \frac{\mu_p\mu_m}{q_{cm}q_{cp}\beta}\right)} - d. \quad (12)$$

689 We are interested in determining how variations in all of the model parameters affect the value
690 of the stable steady states p_2^* and m_2^* , representing the final biomass of the plant and of the
691 AM fungi respectively (the stability analysis will be given in the following section). Plots in
692 Fig. S2 shows variations of p_2^* as a function of each parameter. From Eq. (6) one can derive
693 an expression for the non-dimensional steady state M_2^* , that is

$$694 \quad M_2^* = \frac{\eta_P P_2^* (D + P_2^*)}{Q - D - P_2^*}. \quad (13)$$

695 Or, in terms of the original parameters

$$696 \quad m_2^* = \frac{\mu_p}{\alpha q_{hm}} \frac{p_2^* (d + p_2^*)}{\left(\frac{q_{cp} \alpha}{q_{hp} \beta} - d - p_2^*\right)}. \quad (14)$$

697 The plots in Fig. S3 show how m_2^* varies as a function of the model parameters.

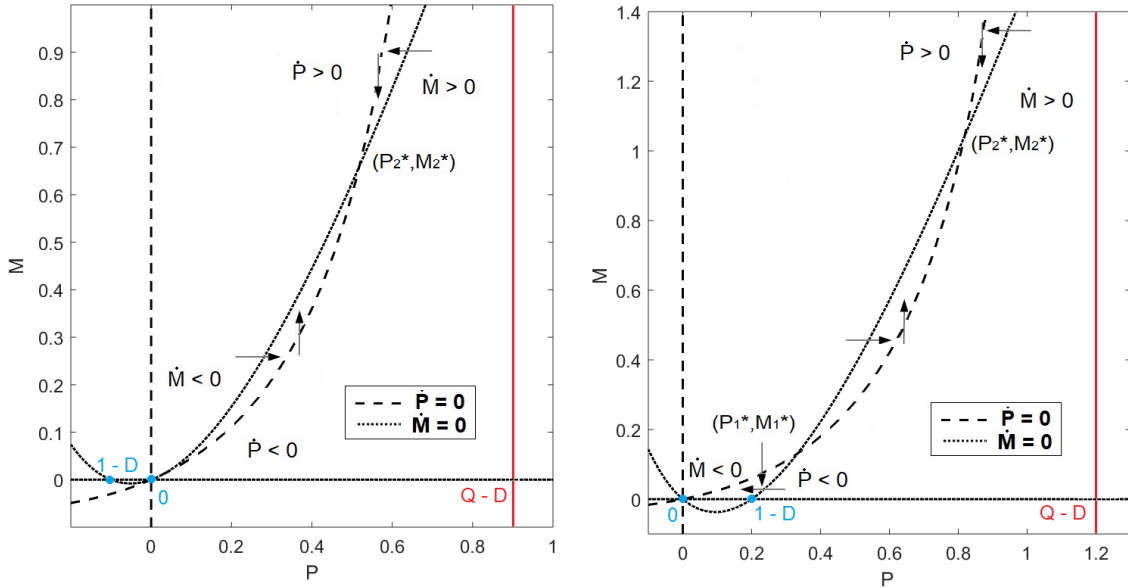


Fig. S1: Nullclines $\dot{P} = 0$ (dashed line) and $\dot{M} = 0$ (dotted line) of Eq. (1), where $Q = 2$, $\eta_P = \eta_M = 0.3$, $N = 1$ and $D = 1.1$ (left panel) or $D = 0.8$ (right panel). Blue dots represent the intersections of the nullcline $\dot{M} = 0$ with the horizontal axis. When $D < 1$ the non-zero interception occurs for $P > 0$. When $D < 1$ the non-zero interception occurs for $P < 0$. Arrows represent qualitatively the direction of the flow on the nullclines and nearby the steady states. The steady states at (P^*, M^*) (left panel) and (P_2^*, M_2^*) (right panel) are always stable. The left panel represents the situation for which only one positive steady state exists, and the steady state at the origin is a saddle. The right panel corresponds to the case where two steady states occur. The steady state at (P_1^*, M_1^*) is a saddle and the origin an attractor. The asymptote of the nullcline $\dot{P} = 0$ occurring at $P = Q - D$ is shown in red.

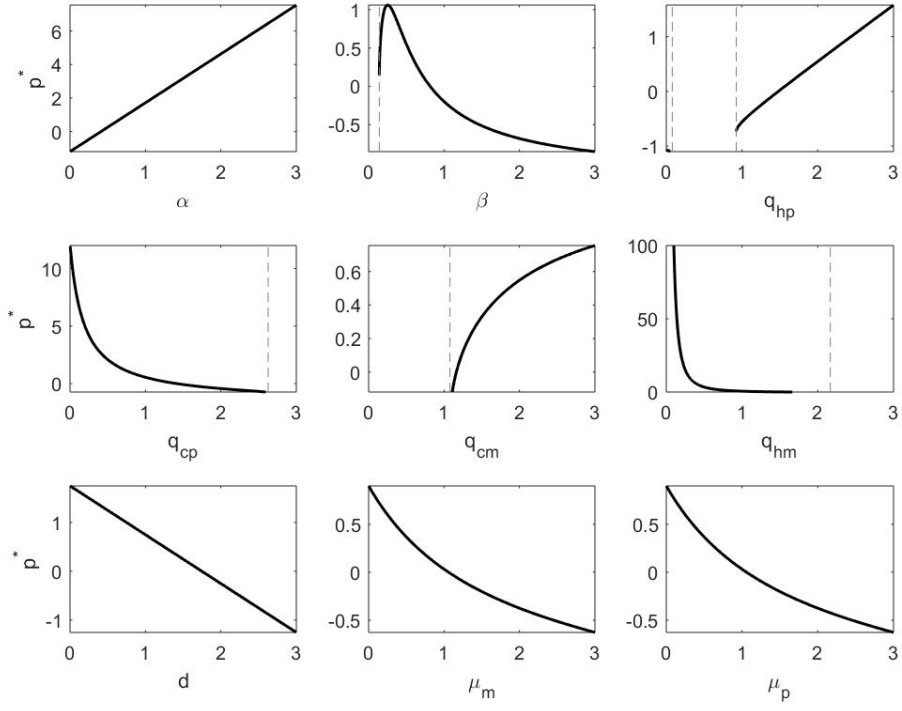


Fig. S2: Steady state value p_2^* (or plant final biomass) as a function of the model parameters. Default parameter values are $q_{hp} = q_{cm} = 2$, $q_{hm} = q_{cp} = 1$, $\alpha = 0.6$, $\beta = 0.5$, $\mu_m = \mu_p = 0.3$, $d = 1.2$.

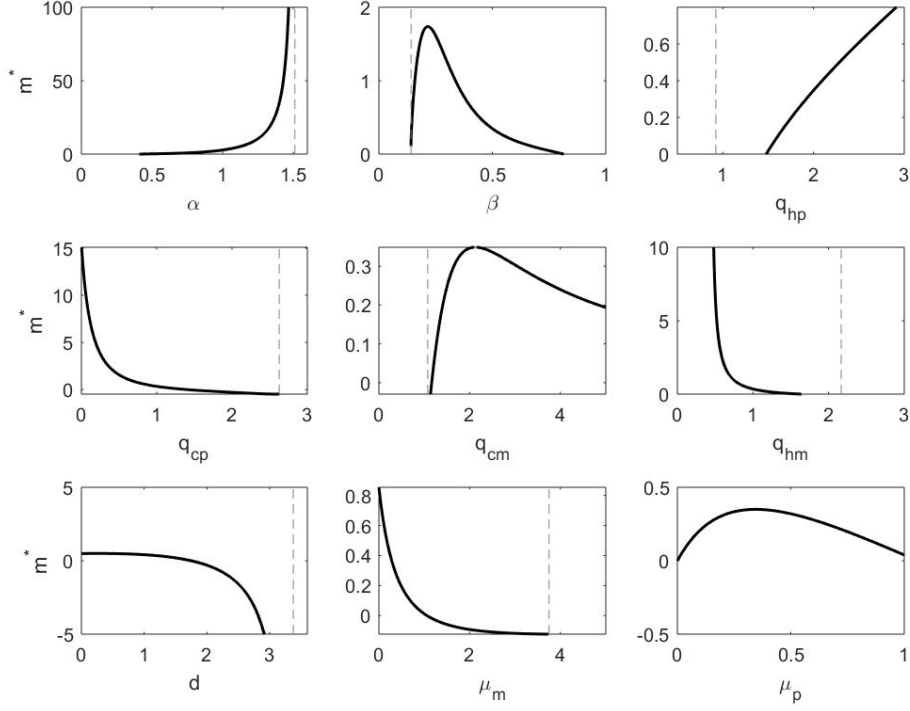


Fig. S3: Steady state value m_2^* (or fungal final biomass) as a function of the model parameters. Default parameter values correspond to those in Fig. S2.

Stability of the coexistence steady states: I consider Eq. (5), describing variation in plant and fungal biomass over time, when the plant is associating with a single species of AM fungi. As shown in the previous section, as long as conditions (7), (8) and (11) are satisfied this system presents a minimum of one and a maximum of two coexistence steady states $(P_{1,2}^*, M_{1,2}^*)$. We are interested in determining the stability of these coexistence steady states. For practicality, we will initially refer to both steady states as (P^*, M^*) and distinguish the two different cases toward the end of the analysis. At steady state, it holds that

$$P^* \left(\frac{Q}{P^* + D} - 1 \right) = \frac{\eta_P (P^*)^2}{M^*}, \quad (15a)$$

$$M^* \left(1 - \frac{1}{P^* + D} \right) = \frac{\eta_M (M^*)^2}{P^*}. \quad (15b)$$

698 Hence the Jacobian of Eq. (5) at steady state can be written as

$$\begin{aligned}
 J_{(P^*, M^*)} &= \begin{pmatrix} -\left(\frac{QM^*}{(P^* + D)^2} + \eta_P \right) P^* & P^* \left(\frac{Q}{P^* + D} - 1 \right) \\ M^* \left(1 - \frac{1}{P^* + D} \right) + \frac{P^* M^*}{(P^* + D)^2} & -\eta_M M^* \end{pmatrix} \\
 &= \begin{pmatrix} -\left(\frac{QM^*}{(P^* + D)^2} + \eta_P \right) P^* & \frac{\eta_P (P^*)^2}{M^*} \\ \frac{\eta_M (M^*)^2}{P^*} + \frac{P^* M^*}{(P^* + D)^2} & -\eta_M M^* \end{pmatrix}
 \end{aligned} \quad (16)$$

700 One can first observe that the trace of J is always negative. The determinant of J can be
 701 computed by using the relationships found in Eq. (15)

$$\begin{aligned}
 \det(J) &= \left(\frac{QM^*}{(P^*+D)^2} + \eta_P \right) P^* \eta_M M^* - \frac{\eta_P (P^*)^2}{M^*} \left(\frac{\eta_M (M^*)^2}{P^*} + \frac{P^* M^*}{(P^*+D)^2} \right) \\
 &= \frac{P^*}{(P^*+D)^2} (\eta_M (M^*)^2 Q - \eta_P (P^*)^2) \\
 &= \frac{P^*}{(P^*+D)^2} \left(P^* M^* \left(1 - \frac{1}{P^*+D} \right) Q - P^* M^* \left(\frac{Q}{P^*+D} - 1 \right) \right) \\
 &= \frac{(P^*)^2 M^*}{(P^*+D)^3} ((1+Q)(P^*+D) - 2Q).
 \end{aligned} \tag{17}$$

703 The sign of $\det(J)$ depends therefore on the sign of $(1+Q)(P^*+D) - 2Q$, where the coexistence
 704 steady state (P^*, M^*) is stable if $P^* + D \geq 2Q/(1+Q)$, and it is a saddle point otherwise.

705 From the analysis conducted above, we know that $X = (P^*+D)$ are roots of the polynomial
 706 $T(X) = \eta_P \eta_M X^2 - (Q - X)(X - 1)$ (see Eq. (9)). I use X^+ and X^- to denote the positive
 707 and negative root of $T(X)$, where

$$X^\pm = \frac{1+Q \pm \sqrt{(1-Q)^2 - 4Q\eta_P\eta_M}}{2(1+\eta_M\eta_P)}. \tag{18}$$

709 To determine the stability of the steady states it is sufficient to show that

$$X^- \leq 2Q/(1+Q) \leq X^+. \tag{19}$$

711 To prove Eq. (19), we want to understand the location of $2Q/(1+Q)$ with respect to the roots
 712 of the polynomial $T(X)$. For this purpose, we need to determine the sign of $T(2Q/1+Q)$.

713 We obtain

$$\begin{aligned}
 T(2Q/(1+Q)) &= \eta_P \eta_M \frac{4Q^2}{(1+Q)^2} - \left(Q - \frac{2Q}{1+Q} \right) \left(\frac{2Q}{1+Q} - 1 \right) \\
 &= \eta_P \eta_M \frac{4Q^2}{(1+Q)^2} - \frac{Q(Q-1)(Q-1)}{(1+Q)(1+Q)} \\
 &= (4\eta_P \eta_M Q - (Q-1)^2) \frac{Q}{(1+Q)^2} \\
 &= -\Delta \frac{Q}{(1+Q)^2} \leq 0.
 \end{aligned} \tag{20}$$

715 Because $T(X)$ is an upward parabola, Eq. (20) implies that Eq. (19) holds true. One can
 716 conclude that the coexistence steady state (P_2^*, M_2^*) associated to X^+ is stable (as $\text{Tr}(J) < 0$
 717 and $\det(J) > 0$), and the steady state (P_1^*, M_1^*) associated to X^- is a saddle point (as
 718 $\text{Tr}(J) < 0$ and $\det(J) < 0$).

719 **Facultative mutualism for the plant ($r_p > 0$) and variation in** 720 **the maintenance costs ($n, s \neq 2$)**

The analysis conducted above considered the case where the intrinsic growth rate of the plant
 is zero ($r_p = 0$), and maintenance costs increase non-linearly with plant and fungal biomass
 ($s, n = 2$). Here we investigate the behaviour of systems where $r_p > 0$ and $n, s \neq 2$. We
 consider the model

$$\frac{dp}{dt} = q_{hp} \alpha m \frac{p}{d+p} - q_{cp} \beta m p + r_p p - \mu_p p^n, \tag{21a}$$

$$\frac{dm}{dt} = q_{cm} \beta p m - q_{hm_i} \alpha \frac{p}{d+p} m - \mu_m m^s. \tag{21b}$$

Nullclines of Eq. (21) for $s > 1$ are given by:

$$\dot{p} = 0 \leftrightarrow m = \frac{\mu_p p^{n-1} - r_p}{\left(q_{hp} \frac{\alpha}{d+p} - q_{cp} \beta\right)}, \quad (22a)$$

$$\dot{m} = 0 \leftrightarrow m = \sqrt[s-1]{\frac{1}{\mu_m} \left(q_{cm} \beta p - q_{hm} \alpha \frac{p}{d+p}\right)}. \quad (22b)$$

721 A graphical representation of the nullclines of Eq. (22) is given in Fig. S4, for the case where
 722 $r_p > 0$, and in Figs. S5, for the cases $n = 1$ and $s = 2$ (left figure), $n = 3$ and $s = 2$ (middle
 723 figure) and $n = 2$ and $s = 3$ (right figure). We can see that for all these cases a stable steady
 724 state exists, where the phase planes qualitatively resemble Fig. S1 (considered in the analysis).

725 When $s = 1$, the nullcline of Eq. (22b) corresponds to a vertical axis at

$$726 \quad p = -q_{cm} \beta d + q_{hm} \alpha + \mu_m + \sqrt{(q_{cm} \beta d - q_{hm} \alpha - \mu_m)^2 + 4q_{cm} \beta \mu_m d} \quad (23)$$

727 For d large enough, the nullclines do not intersect (see Fig. S6, left panel), what causes fungal
 728 biomass growth unbounded, while plant growth is limited. For d small enough, intersection of
 729 the nullclines results into an unstable steady state (see Fig. S6). This situation corresponds
 730 to the right panel of Fig. S1.

731 Therefore, graphically we can observe that plant-fungus coexistence is observed whether
 732 the plant maintenance cost increases linearly ($n > 1$) or non-linearly with plant biomass
 733 ($n = 1$), and for $r_p > 0$. Without any kind of self-limitation ($s = 1$) fungal growth is
 734 unlimited, however also in this case plant-fungus coexistence is observed. Further analytical
 735 work should provide the exact parameter range for which nullclines intersection (and thus
 736 mutualism establishment) is observed when $r_p > 0$ and $n, s \neq 2$. Conditions for mutualism
 737 establishment for the case $r_p = 0$ and $n, s = 2$ are derived in the analysis above (see Eq. (7),
 738 (8), and (11)).

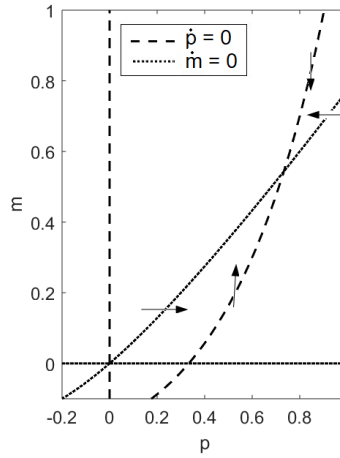


Fig. S4: Nullclines $\dot{p} = 0$ (dashed line) and $\dot{m} = 0$ (dotted line) of the system of differential equations given in Eq. (22) for $r_p > 0$. Arrows represent qualitatively the direction of the flow nearby the stable steady state (p^*, m^*) . Parameter values are $r_p = 0.1$, $q_{hp} = 3$, $q_{cm} = 2$, $q_{cp} = q_{hm} = 1$, $\alpha = \beta = 0.4$, $\mu_m = \mu_p = 0.3$, $d = 1.2$, $s = n = 2$.

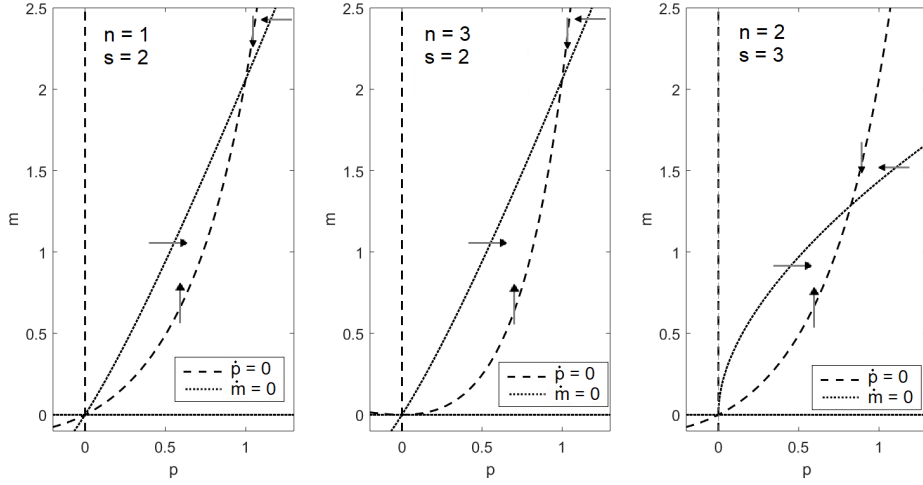


Fig. S5: Nullclines $\dot{p} = 0$ (dashed line) and $\dot{m} = 0$ (dotted line) of the system of differential equations given in Eq. (22) for different biomass dependence of the maintenance costs of the plant (parameter n) and the fungus (parameter s). Arrows represent qualitatively the direction of the flow nearby the stable steady state (p^*, m^*) . Parameter values are $n = 1$ and $s = 2$ (left figure), $n = 3$ and $s = 2$ (middle figure), and $n = 2$ and $s = 3$ (right figure). Other parameters corresponds to those of Fig. S4, except for $r_p = 0$.

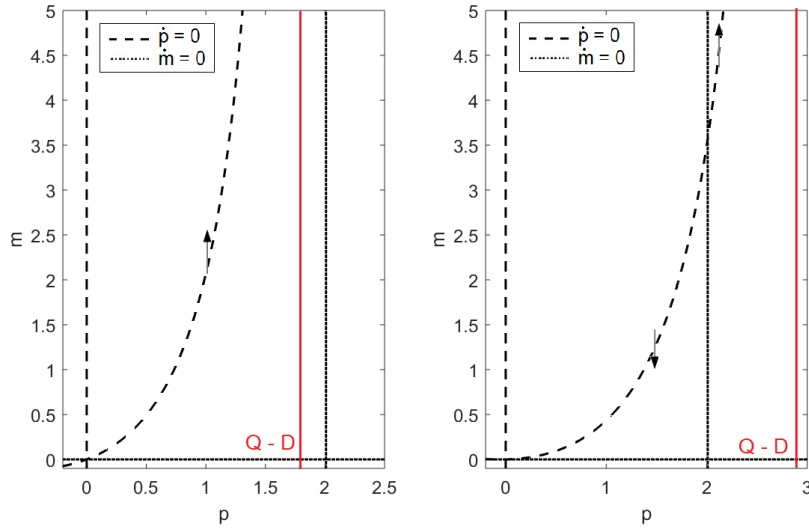


Fig. S6: Nullclines $\dot{p} = 0$ (dashed line) and $\dot{m} = 0$ (dotted line) of the system of differential equations given in Eq. (22) for linear maintenance cost of the fungus (parameter $s = 1$). When d is large enough, no coexistence steady state is observed (left figure) and fungal biomass increases unbounded. When d is small enough, nullclines intersection results into an unstable steady state. Arrows represent qualitatively the direction of the flow nearby the stable steady state (p^*, m^*) . Parameter values are $n = 2$ and $r_p = 0$. Other parameters corresponds to those of Fig. S6.

739

2 Analysis of the one plant - multiple fungi system

Plant and fungal biomass as a function of the number of fungal species N : Let us consider a system consisting of a plant (p) and N fungi (m_i). I assume that all AM fungi have identical parameters. Then the non-dimensionalised model of Eq. (5) can be rewritten

as

$$\frac{dP}{d\tau} = \left[\left(\frac{Q}{D+P} - 1 \right) \sum_{i=1}^N M_i - \eta_P P \right] P, \quad (24a)$$

$$\frac{dM_i}{d\tau} = \left[\left(1 - \frac{1}{D+P} \right) P - \eta_{M_i} M_i \right] M_i. \quad (24b)$$

The coexistence steady state are solutions to

$$M_i^* = \frac{1}{\eta_{M_i}} P^* \frac{(D + P^* - 1)}{D + P^*}, \quad (25a)$$

$$\sum_{i=1}^N M_i^* = \eta_P P^* \frac{(D + P^*)}{Q - D + P^*}. \quad (25b)$$

Since all M_i are identical, Eq. (25) becomes

$$M_i^* = \frac{1}{\eta_{M_i}} P^* \frac{(D + P^* - 1)}{D + P^*}, \quad (26a)$$

$$M_i^* = \frac{\eta_P}{N} P^* \frac{(D + P^*)}{Q - D + P^*}. \quad (26b)$$

740 Combining those two equation one obtains an expression for the plant steady state

$$741 \quad P^* = \frac{Q + 1 \pm \sqrt{(Q - 1)^2 - \frac{4Q\eta_P\eta_{M_i}}{N}}}{2(1 + \frac{\eta_P\eta_{M_i}}{N})} - D. \quad (27)$$

742 One can observe from Eq. (27) that P^* is an increasing function of N , where the value of P^*
743 is bounded and approaches the asymptote $Q - D$ (see Fig. S1) as N tends to infinity, i.e.,

$$744 \quad P^*(N \rightarrow \infty) \rightarrow Q - D. \quad (28)$$

745 The value of the steady state M_i^* is also increasing in N , where

$$746 \quad M_i^* = \frac{1}{\eta_{M_i}} P^*(N) \left(1 - \frac{1}{D + P^*(N)} \right) \quad (29)$$

747 and

$$748 \quad M_i^*(N \rightarrow \infty) \rightarrow \frac{Q - D}{\eta_{M_i}} \frac{Q - 1}{Q}. \quad (30)$$

749 Hence, the total fungal biomass tends to infinity for large N , i.e.,

$$750 \quad \sum_{i=1}^N M_i^*(N) \sim N \frac{Q - D}{\eta_{M_i}} \frac{Q - 1}{Q} \rightarrow \infty \text{ as } N \rightarrow \infty. \quad (31)$$

751 The results of Eq. (31) can be explained by the fact that the model presented here does not
752 take competition between fungi into account. Indeed competition should set a limit to fungal
753 biomass at large fungal density. Extended versions of this model should consider this issue.

Table S3: Description of the non-dimensional parameters used to translate Eq. (32a) into Eq. (37). These parameters correspond to the ones defined in Table 5, where the quantities α and β have been substituted by $\bar{\alpha}$ and $\bar{\beta}$ (see Eq. (34)).

$P = \frac{q_{cm}\bar{\beta}}{q_{hm}\bar{\alpha}} p$	$M_i = \frac{q_{cp}\beta_i}{q_{hm}\alpha_i} m_i$	$\tau = q_{hm}\bar{\alpha} t$
$D = \frac{q_{cm}\bar{\beta}}{q_{hm}\bar{\alpha}} d$	$Q = \frac{q_{cm}q_{hp}}{q_{cp}q_{hm}}$	$\eta_P = \frac{\mu_p}{q_{cm}\bar{\beta}}$
		$\eta_{M_i} = \frac{\mu_{m_i}}{q_{cp}\beta_i}$

Conditions for the existence of coexistence steady state: In this section, we will derive conditions for the existence of coexistence steady states in a system consisting of one plant (p) and multiple AM fungi (m_i , where $i = 1 \dots N$). Similarly to the previous section, for simplicity, we consider the case where the intrinsic growth rate of the plant is zero (i.e. $r_p = 0$) and plant and fungi have non-linear maintenance costs ($n, s = 2$). We assume that different AM fungi have different resource exchange capacities α_i and β_i , and different maintenance rate μ_{m_i} . The system of ordinary differential equations representing this situation is given by

$$\frac{dp}{dt} = q_{hp} \sum_i (\alpha_i m_i) \frac{p}{d+p} - q_{cp} \sum_i (\beta_i m_i) p - \mu_p p^2, \quad (32a)$$

$$\frac{dm_i}{dt} = q_{cm_i} \beta_i p m_i - q_{hm_i} \alpha_i \frac{p}{d+p} m_i - \mu_{m_i} m_i^2, \quad i = 1 \dots N. \quad (32b)$$

754 We are interested at looking at the steady state where there is coexistence of all species,
755 $(p^*, m_1^*, \dots, m_N^*)$, where the m_i are solutions to

$$756 \quad m_i^* = \frac{p^*}{\mu_{m_i}} \left(q_{cm_i} \beta_i - \frac{q_{hm_i} \alpha_i}{d+p^*} \right). \quad (33)$$

I non-dimensionalise Eq. (33) by using the same substitutions given in Table 5 for m_i and μ_{m_i} . However, the non-dimensionalisation of p and d are expected to include the parameters of all fungi present. Hence we define

$$\bar{\alpha} = \frac{1}{N} \sum_{i=1}^N \alpha_i, \quad (34a)$$

$$\bar{\beta} = \frac{1}{N} \sum_{i=1}^N \beta_i. \quad (34b)$$

757 The quantities $\bar{\alpha}$ and $\bar{\beta}$ correspond to the arithmetic mean of the resource exchange capacities
758 α_i and β_i of all AM fungi present. Eq. (34) can be used to non-dimensionalise Eq. (32a) by
759 carrying on the substitutions illustrated in Table S3.

760 Eq. (33) can therefore be rewritten as

$$761 \quad M_i^* = \frac{1}{\eta_{M_i}} P^* \left(\frac{b_i}{a_i} - \frac{1}{P^* + D} \right), \quad (35)$$

762 where $a_i = \alpha_i / \bar{\alpha}$ and $b_i = \beta_i / \bar{\beta}$.

763 From Eq. (35) one can see that in order for the steady state M_i^* to be in the first quadrant,
764 $b_i/a_i - 1/(P^* + D)$ needs to be positive. One can therefore derive a first condition for the
765 existence of a coexistence steady state, that is

$$766 \quad P^* + D > \frac{a_i}{b_i}. \quad (36)$$

767 By substituting Eq. (35) and the parameters of Table S3 into Eq. (32a), we obtain that
 768 the value of the steady state P^* is a solution to

$$769 \quad \sum_{i=1}^N \left(Q \frac{a_i}{b_i} - (P^* + D) \right) \left(\frac{b_i}{a_i} (P^* + D) - 1 \right) \frac{a_i}{\eta_{M_i}} - \eta_P (P^* + D)^2 = 0. \quad (37)$$

770 There must therefore exist $i_0 \in 1, \dots, N$ such that $Q a_{i_0}/b_{i_0} - D > 0$, otherwise the polynomial
 771 of Eq. (37) is always negative for $P^* > 0$. Hence a second condition for the existence of a
 772 coexistence steady state is that there must exist an i_0 such that

$$773 \quad \alpha_{i_0} > \frac{q_{cp}}{q_{hp}} d \beta_{i_0}. \quad (38)$$

774 This condition corresponds to Eq. (7) of the one plant - one fungus case. One can see that
 775 when multiple AM fungi are present, it is sufficient that one of the fungi satisfies Eq. (7).
 776 Combining the conditions given in Eqs. (36) and (38) one obtain

$$777 \quad Q \frac{a_{i_0}}{b_{i_0}} - (P^* + D) > Q \frac{a_{i_0}}{b_{i_0}} - \frac{a_{i_0}}{b_{i_0}} = \frac{a_{i_0}}{b_{i_0}} (Q - 1) > 0. \quad (39)$$

778 Hence we obtain the unique condition $Q > 1$, or, in terms of the original parameters

$$779 \quad \frac{q_{cm} q_{hp}}{q_{hm} q_{cp}} > 1, \quad (40)$$

780 which corresponds to condition (8), stated for the one plant - one fungus case.

781 By solving Eq. (37) we obtain an expression for the steady state P^* , that is

$$782 \quad P^* = \frac{(1 + Q) \sum_{i=1}^N \frac{a_i}{\eta_{M_i}} \pm \sqrt{\Delta}}{2 \left(\sum_{i=1}^N \frac{b_i}{\eta_{M_i}} + \eta_P \right)} - D, \quad (41)$$

783 with

$$784 \quad \Delta = (1 + Q)^2 \left(\sum_{i=1}^N \frac{a_i}{\eta_{M_i}} \right)^2 - 4Q \left(\sum_{i=1}^N \frac{a_i^2}{b_i \eta_{M_i}} \right) \left(\sum_{i=1}^N \frac{b_i}{\eta_{M_i}} + \eta_P \right) \quad (42)$$

785 We obtain therefore a third condition for the existence of a coexistence steady state, i.e.,

$$786 \quad \left(1 + \frac{q_{cm} q_{hp}}{q_{cp} q_{hm}} \right)^2 \left(\sum_{i=1}^N \frac{q_{cp} \alpha_i \beta_i}{\mu_{m_i}} \right)^2 - 4 \frac{q_{cm} q_{hp}}{q_{cp} q_{hm}} \left(\sum_{i=1}^N \frac{q_{cp} \alpha_i^2}{\mu_{m_i}} \right) \left(\sum_{i=1}^N \frac{q_{cp} \beta_i^2}{\mu_{m_i}} + \frac{\mu_p}{q_{cm}} \right) > 0. \quad (43)$$

787 The expression of Eq. (43) involves the product and sum of the resource exchange capac-
 788 ities α_i and β_i . If we set $\mathbf{a} = \boldsymbol{\alpha}/\sqrt{\boldsymbol{\mu}_m} = (\alpha_1/\sqrt{\mu_1}, \dots, \alpha_n/\sqrt{\mu_n})$ and $\mathbf{b} = \boldsymbol{\beta}/\sqrt{\boldsymbol{\mu}} =$
 789 $(\beta_1/\sqrt{\mu_1}, \dots, \beta_n/\sqrt{\mu_n})$, then we can rewrite condition (43) as follows:

$$790 \quad (1 + Q)^2 \left(1 + \frac{Cov(\mathbf{a}, \mathbf{b})}{\bar{a}\bar{b}} \right)^2 - 4Q \left(1 + \frac{Var(\mathbf{a})}{\bar{a}^2} \right) \left(1 + \frac{\mu_p}{N q_{cm} q_{cp} \bar{b}^2} + \frac{Var(\mathbf{b})}{\bar{b}^2} \right) > 0. \quad (44)$$

791 We can observe that condition (44) is more likely to be satisfied when the covariance between
 792 \mathbf{a} and \mathbf{b} and the means of \mathbf{a} and \mathbf{b} are large, and when the variances of \mathbf{a} and \mathbf{b} are small.
 793 Additionally, the condition is less likely to be satisfied when the maintenance cost of the fungi
 794 is large.

795 In sum, we can see that conditions for the existence of a coexistence steady state depend
 796 therefore on the resource exchange ability of the whole guild. Altogether, conditions (38),

797 (40), and (44) suggest that as long as a good mutualist is present and the average mutualist
 798 quality of all species is large enough, a coexistence steady state exists.

799 Let us assume now that all fungi have the same resource exchange capacities α and β and
 800 the same maintenance cost μ_m , condition (44) reduces to

$$801 \quad \frac{\eta_F \eta_{M_i}}{N} < \frac{(1-Q)^2}{4Q}, \quad (45)$$

802 what corresponds to condition (11) for the case where multiple AM fungi are present. This
 803 condition tells us that in the presence of multiple species, guild survival can be guaranteed
 804 even when maintenance costs are higher than what could be tolerated when only one fungal
 805 species is present.

Conditions for stability of the coexistence steady state: Let us consider a system
 consisting of one plant (p) and two AM fungal species (m_1 and m_2), differing only in their
 resource exchange capacities α_i and β_i . We write

$$\frac{dp}{dt} = q_{hp}(\alpha_1 m_1 + \alpha_2 m_2) \frac{p}{d+p} - q_{cp}(\beta_1 m_1 + \beta_2 m_2)p - \mu_p p^2, \quad (46a)$$

$$\frac{dm_1}{dt} = q_{cm}\beta_1 p m_1 - q_{hm}\alpha_1 \frac{p}{d+p} m_1 - \mu_{m_i} m_1^2, \quad (46b)$$

$$\frac{dm_2}{dt} = q_{cm}\beta_2 p m_2 - q_{hm}\alpha_2 \frac{p}{d+p} m_2 - \mu_{m_i} m_2^2. \quad (46c)$$

806 We are interested at looking at the steady state (p^*, m_1^*, m_2^*) . The Jacobian of Eq. (46) at
 807 steady state is given by

$$J_{(p^*, m_1^*, m_2^*)} = \begin{pmatrix} \underbrace{-q_{hp}(\alpha_1 m_1^* + \alpha_2 m_2^*) \frac{p^*}{(d+p^*)^2} - \mu_p p^*}_{:= -A} & \underbrace{q_{hp}\alpha_1 \frac{p^*}{d+p^*} - q_{cp}\beta_1 p^*}_{:= C_1} & \underbrace{q_{hp}\alpha_2 \frac{p^*}{d+p^*} - q_{cp}\beta_2 p^*}_{:= C_2} \\ m_1^* \left(\underbrace{q_{cm}\beta_1 - \frac{q_{hm}\alpha_1}{d+p^*} + q_{hm}\alpha_1 \frac{p^*}{(d+p^*)^2}}_{:= B_1} \right) & -\mu_m m_1^* & 0 \\ m_2^* \left(\underbrace{q_{cm}\beta_2 - \frac{q_{hm}\alpha_2}{d+p^*} + q_{hm}\alpha_2 \frac{p^*}{(d+p^*)^2}}_{:= B_2} \right) & 0 & -\mu_m m_2^* \end{pmatrix}. \quad (47)$$

808 We know that $A > 0$, $B_1 > 0$, and $B_2 > 0$ (see Eq. (33)). The sign of C_1 and C_2 is
 809 unknown, however we can notice that these terms increase for increasing α_i and decrease for
 810 increasing β_i . We can therefore say that C_i (where $i = 1, 2$) increase for increasing resource
 811 exchange capacity of the fungal species. The characteristic polynomial of Eq. (47) is given by
 812
 813

$$814 \quad P(\lambda) = \lambda^3 + \lambda^2 \underbrace{\mu_m(m_1^* + m_2^*) + A}_{:= a_1} + \lambda \underbrace{(\mu_m^2 m_1^* m_2^* + \mu_m(m_1^* + m_2^*) - B_1 C_1 - B_2 C_2)}_{:= a_2} \\ + \underbrace{A \mu_m^2 m_1^* m_2^* - \mu_m m_1^* B_2 C_2 - \mu_m m_2^* B_1 C_1}_{:= a_3} = 0. \quad (48)$$

815 According to the Routh-Hurwitz conditions for stability (Murray, 2007), in order for $\text{Re}(\lambda) > 0$
 816 the following three conditions need to be satisfied

$$817 \quad (i) a_1 > 0, \quad (ii) a_3 > 0, \quad \text{and} \quad (iii) a_1 a_2 - a_3 > 0. \quad (49)$$

818 One can directly see that $a_1 > 0$, i.e., (i) is always satisfied. Hence we obtain the following
819 two conditions for stability of the coexistence steady state

$$(ii) A\mu_m m_1^* m_2^* - m_1^* B_2 C_2 - m_2^* B_1 C_1 > 0, \quad (50a)$$

$$(iii) \mu_m (m_1^* + m_2^*) (\mu_m^2 m_1^* m_2^* + \mu_m (m_1^* + m_2^*) + A) - B_1 C_1 (A + \mu_m m_1^*) - B_2 C_2 (A + \mu_m m_2^*) > 0. \quad (50b)$$

820

821 We want now to show that condition (ii) is always satisfied as well. We first reformulate
822 the expression for a_3 as follows:

$$a_3 = \mu_m^2 m_1^* m_2^* \left(\mu_p p^* - \sum_i \frac{m_i^* C_i}{p^*} \right) + \frac{\mu_m^2 m_1^* m_2^* p^*}{p^* + d} \left(q_{hp} (\alpha_1 m_1^* + \alpha_2 m_2^*) - q_{hm} \left(\frac{\alpha_1 C_1}{\mu_m} + \frac{\alpha_2 C_2}{\mu_m} \right) \right). \quad (51)$$

823

824 The first term is equal to 0, as from the one plant - one fungus model we know that

$$P^* \left(M^* \left(\frac{Q}{P^* + D} - 1 \right) - \eta_p P^* \right) = 0 \leftrightarrow P^* \left(\frac{Q}{P^* + D} - 1 \right) = \frac{\eta_p (P^*)^2}{M^*}. \quad (52)$$

826 To do so we look at the eigenvalues of the linearized problem around this steady state. Additionally
827 from

$$M^* \left(P^* \left(1 - \frac{1}{P^* + D} \right) - \eta_m M^* \right) = 0 \leftrightarrow M^* \left(1 - \frac{1}{P^* + D} \right) = \frac{\eta_m (M^*)^2}{P^*} \quad (53)$$

829 and using the definition of C_i we get

$$\begin{aligned} a_3 &= \frac{\mu_m^2 m_1^* m_2^* p^*}{p^* + d} \left(q_{hp} \left(q_{cm} (\alpha_1 \beta_1 + \alpha_2 \beta_2) - q_{hm} \frac{\alpha_1^2 + \alpha_2^2}{(p^* + d)} \right) \right. \\ &\quad \left. - q_{hm} \left(q_{hp} \frac{\alpha_1^2 + \alpha_2^2}{(p^* + d)} - q_{cp} (\alpha_1 \beta_1 + \alpha_2 \beta_2) \right) \right) \\ &= \frac{\mu_m^2 m_1^* m_2^* p^*}{p^* + d} \left((q_{hp} q_{cm} + q_{cp} q_{hm}) (\alpha_1 \beta_1 + \alpha_2 \beta_2) - 2q_{hm} q_{hp} \frac{\alpha_1^2 + \alpha_2^2}{(p^* + d)} \right). \end{aligned} \quad (54)$$

831 Thus we can see that $a_3 > 0$ if and only if $p^* + d \geq \frac{2q_{hp} \sum_i \alpha_i^2}{(1+Q) \sum_i \alpha_i \beta_i}$ where $Q = \frac{q_{cm} q_{hp}}{q_{hm} q_{cp}}$. Then
832 in the adimensional variable it means that

$$P^* + D \geq X_0 = \frac{2Q \sum_i \frac{\alpha_i^2}{\alpha^2}}{(1+Q) \sum_i \frac{\alpha_i \beta_i}{\alpha \beta}} = \frac{2Q \sum_i a_i^2}{(1+Q) \sum_i a_i b_i}. \quad (55)$$

834 To prove that we only need to evaluate the polynomial T at X_0 . Since $P^* + D$ is a root of
835 polynomial $T(X)$ defined in Eq. (37), we only need to compute the value $T(X_0)$. We can
836 show that

$$T(X_0) = \frac{\Delta Q \sum_i a_i^2}{(1+Q)^2 (\sum_i a_i b_i)^2} > 0. \quad (56)$$

838 Thus we can conclude that $P^* + D > X_0$ and the coefficient a_3 is positive.

839 Hence, conditions (i) and (ii) are always satisfied. As long as condition (iii), together with
840 the conditions for existence of the coexistence steady state derived previously in (38), (40)
841 and (44), a stable steady state of multi-species coexistence exists. Numerically, we observe
842 that the conditions for stability are always satisfied for the range of parameters for which a
843 coexistence steady state exists.

3 The effect of differences in the resource exchange capacities of the fungi

Analytical insights: I want to investigate how differences in the phosphorus exchange ability of the mutualists impact plant growth and the growth of other guild members. I will consider a guild of mutualists having different phosphorus exchange abilities (parameter α_i), while all other parameters are held constant across all fungi.

Impact on plant biomass: I want to investigate how the value of the plant at steady state (p^*) depends on the phosphorus exchange ability of all species present (i.e., how p^* depends on $\boldsymbol{\alpha} = (\alpha_1, \alpha_2, \dots, \alpha_N)$). For this purpose, we consider a plant (p) associating with multiple fungal species (m_i), differing in their ability to transfer phosphorus (α_i), and I compare the biomass of the plant at steady state (p^*) when the plant is associating with N identical fungi (i.e., $\alpha_i = \alpha$), to the biomass of the plant at steady state when the plant is associating with N fungi differing in their resource exchange capacities. When multiple species are present, we know from Eq. (41) that the plant steady state corresponds to

$$p^*(\boldsymbol{\alpha}) = \frac{q_{hm}\bar{\alpha}}{q_{cm}\beta} P^*(\boldsymbol{\alpha}) - d$$

$$\text{with } P^*(\boldsymbol{\alpha}) = \frac{1 + Q + \sqrt{(1 + Q)^2 - 4Q \frac{1}{N} \sum_{i=1}^N a_i^2 \left(1 + \frac{\eta_P \eta_M}{N}\right)}}{2 \left(1 + \frac{\eta_P \eta_M}{N}\right)}. \quad (57)$$

Considering that $\sum_i \alpha_i = N\bar{\alpha}$ and $\sum_i a_i = N$, the term $\sum_i a_i^2$ can be written as

$$\frac{1}{N} \sum_{i=1}^N a_i^2 = \frac{1}{N} \sum_{i=1}^N \left(a_i - \frac{1}{N} \sum_i a_i \right)^2 + \left(\frac{1}{N} \sum_i a_i \right)^2 = \frac{Var(\boldsymbol{\alpha})}{\bar{\alpha}^2} + 1, \quad (58)$$

where $Var(\boldsymbol{\alpha})$ is the variance of $\boldsymbol{\alpha}$, defined by

$$Var(\boldsymbol{\alpha}) = \frac{1}{N} \sum_{i=1}^N (\alpha_i - \bar{\alpha})^2 \quad \text{with } \bar{\alpha} = \frac{1}{N} \sum_{i=1}^N \alpha_i. \quad (59)$$

The value of the plant at steady state can be rewritten as

$$p^*(\boldsymbol{\alpha}) = \frac{q_{hm}\bar{\alpha}}{q_{cm}\beta} P^*(\boldsymbol{\alpha}) - d$$

$$\text{with } P^*(\boldsymbol{\alpha}) = \frac{1 + Q + \sqrt{(1 + Q)^2 - 4Q \left(1 + \frac{Var(\boldsymbol{\alpha})}{\bar{\alpha}^2}\right) \left(1 + \frac{\eta_P \eta_M}{N}\right)}}{2 \left(1 + \frac{\eta_P \eta_M}{N}\right)}. \quad (60)$$

Hence the final size of the plant $p^*(\boldsymbol{\alpha})$ depends on the mean as well as the variance of the phosphorus exchange capacities of all mutualists present. One can directly observe that $p^*(\boldsymbol{\alpha})$ decreases with respect to the variance. Additionally, if the AM fungi are identical (i.e., $Var(\boldsymbol{\alpha}) = 0$), p^* increases linearly with the value of $\bar{\alpha}$, and

$$p^*(\boldsymbol{\alpha}) \leq p^*((\bar{\alpha}, \dots, \bar{\alpha})) \leq p^*((\max(\alpha_i), \dots, \max(\alpha_i))) \quad \text{for any } \boldsymbol{\alpha} \in (0, \infty)^N. \quad (61)$$

To give more insights into the analysis, we consider the case $N = 2$, where a plant is associating with two AM fungi. We want to compare the biomass of the plant and the total fungal biomass

872 at steady state when the plant is associating with two individuals that are good mutualists
873 (species 1), with two individuals that are less beneficial mutualists (species 2), or with a
874 combination of species 1 and species 2. I assume that species 1 is a better mutualist with
875 respect to species 2, with $\alpha_1 > \alpha_2$. We define $\alpha_1 = \alpha + \epsilon$ and $\alpha_2 = \alpha$, where $\epsilon \in (0, \infty)$. In
876 this case the variance and mean of the resource exchange capacities can be computed as

$$877 \quad \bar{\alpha} = \alpha + \frac{\epsilon}{2} \quad \text{and} \quad \text{Var}(\boldsymbol{\alpha}) = \frac{\epsilon^2}{4}, \quad (62)$$

878 and the plant biomass at steady state is given by

$$879 \quad p^*(\alpha, \alpha + \epsilon) = \frac{q_{hm}(\alpha + \epsilon/2)}{q_{cm}\beta} P^*(\epsilon) - d$$

$$1 + Q + \sqrt{(1 + Q)^2 - 4Q \left(1 + \left(\frac{\epsilon/2}{\alpha + \epsilon/2}\right)^2\right) \left(1 + \frac{\eta_P \eta_M}{2}\right)} \quad (63)$$

$$\text{with } P^*(\epsilon) = \frac{2 \left(1 + \frac{\eta_P \eta_M}{2}\right)}{2 \left(1 + \frac{\eta_P \eta_M}{2}\right)}.$$

880 From Eq. (61) we already know that

$$881 \quad p^*(\alpha, \alpha + \epsilon) < p^*(\alpha + \epsilon/2, \alpha + \epsilon/2) < p^*(\alpha + \epsilon, \alpha + \epsilon). \quad (64)$$

882 Eq. (64) tells us that plant biomass at steady state is larger when the plant is associating with
883 two individuals of species 1, then when the plant is associating with a combination of species
884 1 and species 2.

885 I want now to determine whether $p^*(\alpha, \alpha)$ is larger or smaller than $p^*(\alpha, \alpha + \epsilon)$, i.e., we
886 want to understand if plant biomass at steady state is larger when the plant is associating
887 with two individuals that are less beneficial mutualists (species 2), or with a combination of
888 species 1 and species 2. I first consider the case where ϵ is large. For $\epsilon \rightarrow \infty$ we have,

$$889 \quad P^*(\epsilon) \sim \frac{1 + Q + \sqrt{(1 + Q)^2 - 4Q(1 + \eta_P \eta_M) - 4Q}}{2 \left(1 + \frac{\eta_P \eta_M}{2}\right)} = P_\infty^* > 0, \quad (65)$$

$$\text{and } p^*(\alpha, \alpha + \epsilon) \sim \frac{q_{hm}(\alpha + \epsilon/2)}{q_{cm}\beta} P_\infty^* - d.$$

890 Thus for ϵ large enough P^* has a lower bound, however p^* increases with increasing ϵ . We
891 can conclude that Eq. (67) holds true for ϵ large enough.

892 Let us consider now the case where ϵ is small. By using a Taylor expansion, we have the
893 following estimates for plant biomass at steady state

$$894 \quad p^*(\alpha, \alpha + \epsilon) = p^*(\alpha, \alpha) + \frac{q_{hm}}{2q_{cm}\beta} P^*(0)\epsilon + \mathcal{O}(\epsilon) \quad (66)$$

895 One can conclude that also for small ϵ it holds

$$896 \quad p^*(\alpha, \alpha) < p^*(\alpha, \alpha + \epsilon). \quad (67)$$

897 Therefore

$$898 \quad p^*(\alpha, \alpha) < p^*(\alpha, \alpha + \epsilon) < p^*(\alpha + \epsilon, \alpha + \epsilon) \quad \text{for any } \epsilon > 0. \quad (68)$$

899 Eq. (68) states that the biomass of the plant at steady state is at highest when the plant is
900 associating with a good mutualist (species 1), is at lowest when the plant is associating with
901 a less beneficial mutualist (species 2) and it is between these two values when the plant is
902 associating with a combination of good and less beneficial mutualists (species 1 and 2).

903

904 *Impact on fungal biomass:* I consider now how differences in the phosphorus exchange ability
 905 of the fungi in a guild affect fungal biomass. The fungal biomass of each species at steady
 906 state is a function of the phosphorus exchange ability α and of plant biomass at steady state,
 907 and it is given by

$$908 \quad m_{(\alpha_i, p^*(\alpha))}^* = \frac{p^*(\alpha)}{\mu_m} \left(q_{cm}\beta - \frac{q_{hm}\alpha_i}{d + p^*(\alpha)} \right), \quad (69)$$

909 I want to understand if fungal biomass at steady state is increased or decreased in the
 910 presence of a species that has different phosphorus exchange ability. I assume that fungal
 911 species 1 has a higher phosphorus exchange ability than fungal species 2, with $\alpha_1 = \alpha + \epsilon$ and
 912 $\alpha_2 = \alpha$. Let us first consider the fungal biomass of the more beneficial species (species 1)
 913 when the plant is associating with two good mutualists:

$$914 \quad \begin{aligned} m_{(\alpha+\epsilon, p^*(\alpha+\epsilon, \alpha+\epsilon))}^* &= \frac{p^*(\alpha + \epsilon, \alpha + \epsilon)}{\mu_m} \left(q_{cm}\beta - \frac{q_{hm}(\alpha + \epsilon)}{d + p^*(\alpha + \epsilon, \alpha + \epsilon)} \right) \\ &= \frac{p^*(\alpha + \epsilon, \alpha + \epsilon)}{\mu_m} \left(\frac{q_{cm}\beta(d + p^*(\alpha + \epsilon, \alpha + \epsilon)) - q_{hm}(\alpha + \epsilon)}{d + p^*(\alpha + \epsilon, \alpha + \epsilon)} \right) \\ &= \frac{p^*(\alpha + \epsilon, \alpha + \epsilon)}{\mu_m} \left(\frac{q_{hm}(\alpha + \epsilon)(P^* - 1)}{d + p^*(\alpha + \epsilon, \alpha + \epsilon)} \right). \end{aligned} \quad (70)$$

915 where P^* has been defined in Eq. (60) and does not depend on α if the fungal species are
 916 identical, as in this case $Var(\alpha) = 0$. Similarly, the biomass of species 1 when the plant is
 917 associating with a combination of a good (species 1) and a less beneficial mutualist (species
 918 2) can be expressed as

$$919 \quad m_{(\alpha+\epsilon, p^*(\alpha, \alpha+\epsilon))}^* = \frac{p^*(\alpha, \alpha + \epsilon)}{\mu_m} \left(\frac{q_{hm}(\alpha + \epsilon)(P^*(\epsilon) - 1) - q_{hm}\frac{\epsilon}{2}P^*(\epsilon)}{d + p^*(\alpha, \alpha + \epsilon)} \right). \quad (71)$$

920 where $P^*(\epsilon)$ is given in Eq. (63). As $P^*(\epsilon) < P^*$, and $p^*(\alpha, \alpha + \epsilon) < p^*(\alpha + \epsilon, \alpha + \epsilon)$ (see
 921 Eq. 68), one can directly say that

$$922 \quad m_{(\alpha+\epsilon, p^*(\alpha, \alpha+\epsilon))}^* < m_{(\alpha+\epsilon, p^*(\alpha+\epsilon, \alpha+\epsilon))}^*, \quad (72)$$

923 i.e., the fungal biomass of a good mutualist is decreased by the presence of a less beneficial
 924 mutualist.

925 Let us first consider the fungal biomass of the less beneficial species (species 2) when the
 926 plant is associating with two individuals of species 2:

$$927 \quad m_{(\alpha, p^*(\alpha, \alpha))}^* = \frac{p^*(\alpha, \alpha)}{\mu_m} \left(\frac{q_{hm}\alpha(P^* - 1)}{d + p^*(\alpha, \alpha)} \right). \quad (73)$$

928 The fungal biomass of species 2 when the plant is associating with a combination of a good
 929 (species 1) and a less beneficial mutualist (species 2) is given by

$$930 \quad m_{(\alpha, p^*(\alpha, \alpha+\epsilon))}^* = \frac{p^*(\alpha, \alpha + \epsilon)}{\mu_m} \left(\frac{q_{hm}\alpha(P^*(\epsilon) - 1) + q_{hm}\frac{\epsilon}{2}P^*(\epsilon)}{d + p^*(\alpha, \alpha + \epsilon)} \right). \quad (74)$$

931 I want to show that

$$932 \quad m_{(\alpha, p^*(\alpha, \alpha))}^* < m_{(\alpha, p^*(\alpha, \alpha+\epsilon))}^*, \quad (75)$$

933 i.e., the fungal biomass of the less beneficial mutualist is increased by the presence of a good
 934 mutualist. We know that $P^*(\epsilon) \rightarrow P_\infty^*$ for ϵ large enough (Eq. (65)). Hence the value of $P^*(\epsilon)$

935 has a lower bound, however $p^*(\alpha, \alpha + \epsilon)$ increases with increasing ϵ . We can conclude that
 936 Eq. (75) holds true for ϵ large enough. If ϵ is small, $P^*(\epsilon)$ can be expressed as

$$937 \quad P^*(\epsilon) = P^*(0) - \frac{Q}{2\alpha^2\sqrt{(1+Q)^2 - 4Q(1 + \frac{\eta P \eta M}{2})}} \epsilon^2 + \mathcal{O}(\epsilon), \quad (76)$$

938 where $P^*(0) = P^*$. Hence, for ϵ small, Eq. (74) can be rewritten as

$$\begin{aligned} m_{(\alpha, p^*(\alpha, \alpha + \epsilon))}^* &\simeq \frac{p^*(\alpha, \alpha + \epsilon)}{\mu_m} \left(\frac{q_{hm}\alpha(P^* - 1)}{d + p^*(\alpha, \alpha + \epsilon)} \right) \\ &+ \frac{p^*(\alpha, \alpha + \epsilon)}{\mu_m(d + p^*(\alpha, \alpha + \epsilon))} \left(-\frac{Q}{2\alpha^2\sqrt{(1+Q)^2 - 4Q(1 + \frac{\eta P \eta M}{2})}} \epsilon^2 + q_{hm} \frac{\epsilon}{2} P^*(\epsilon) \right). \end{aligned} \quad (77)$$

939 Because $p^*(\alpha, \alpha) < p^*(\alpha, \alpha + \epsilon)$ (see Eq. (67)), we can conclude that also for ϵ small enough
 940 it holds

$$942 \quad m_{(\alpha, p^*(\alpha, \alpha))}^* < m_{(\alpha, p^*(\alpha, \alpha + \epsilon))}^*, \quad (78)$$

943 i.e., fungal biomass of a less beneficial fungus increases in the presence of a more beneficial
 944 species. Hence, in sum, the biomass of a fungus decreases in the presence of a less beneficial
 945 mutualist (Eq. (78)), and increases in the presence of a more beneficial mutualist (Eq. (72)).