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► To cite this version:

Maria M Martignoni, Miranda M Hart, Rebecca C Tyson, Jimmy Garnier. Diversity within mutualist guilds promotes coexistence and reduces the risk of invasion from an alien mutualist. *Proceedings of the Royal Society B: Biological Sciences*, 2020, 287 (1923), pp.20192312. 10.1098/rspb.2019.2312 . hal-03006649

HAL Id: hal-03006649

<https://hal.science/hal-03006649>

Submitted on 17 Nov 2020

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Diversity within mutualist guilds promotes coexistence and reduces the risk of invasion from an alien mutualist

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February 24, 2020

Abstract

Biodiversity is an important component of healthy ecosystems, and thus understanding the mechanisms behind species coexistence is critical in ecology and conservation biology. In particular, few studies have focused on the dynamics resulting from the co-occurrence of mutualistic and competitive interactions within a group of species. Here we build a mathematical model to study the dynamics of a guild of competitors who are also engaged in mutualistic interactions with a common partner. We show that coexistence as well as competitive exclusion can occur depending on the competition strength and on strength of the mutualistic interactions, and we formulate concrete criteria for predicting invasion success of an alien mutualist based on propagule pressure, alien traits (such as its resource exchange ability) and composition of the recipient community. We find that intra guild diversity promotes the coexistence of species that would otherwise competitively exclude each other, and makes a guild less vulnerable to invasion. Our results can serve as a useful framework to predict the consequences of species manipulation in mutualistic communities.

Keywords : Mutualist guilds, arbuscular mycorrhizal fungi (AMF), mathematical model, invasion, alien species, diversity, pollination.

1 Introduction

2 Recent decades have seen a drastic increase in biological invasion by alien organisms, for
3 instance due to climate change or to anthropogenic disturbance (Lockwood et al., 2013).
4 These invasions have led to significant ecological and economic damage throughout the world
5 (Cardinale et al., 2012), and it has thus become increasingly important to better understand
6 the mechanisms behind the invasion process, in order to identify the causal factors promoting
7 or hindering invasion success (Lowry et al., 2013; Vanbergen et al., 2018).

8 Invasion is a three stage process (Williamson and Griffiths, 1996), involving (1) the in-
9 troduction of an alien species, (2) its local establishment (which may cause different scales
10 of biodiversity loss within the recipient community), and eventually (3) its regional spread.
11 Factors making biological invasion more likely to occur have been identified in the recipient
12 ecosystem (Olyarnik et al., 2009; Lonsdale, 1999), in the introduced species (Kolar and Lodge,
13 2001; Fournier et al., 2019), and in the interaction between the two (Lowry et al., 2013; Shea
14 and Chesson, 2002). Studies agree that propagule pressure (i.e. the number of individuals in-
15 troduced in a potential invasion site) plays a decisive role in determining the establishment of
16 an alien species (Simberloff, 2009; Lockwood et al., 2005). Resource availability is also a main
17 factor contributing to successful establishment (Sher and Hyatt, 1999; Davis et al., 2000), as
18 well as the capacity of the alien species to make an effective use of the resources acquired
19 (Funk and Vitousek, 2007; Pyšek and Richardson, 2008). Resource availability is strongly
20 influenced by abiotic factors (Menke and Holway, 2006; Dethier and Hacker, 2005), by the
21 interactions of the organisms and the environment (Byers, 2002; Williamson and Harrison,
22 2002), or by the direct and indirect interactions between the alien species and the existing
23 community (Olyarnik et al., 2009; White et al., 2006). Additionally, the establishment of
24 the alien species can in turn have an impact on resource availability and affect the invasion
25 dynamics (Goldstein and Suding, 2014; Didham et al., 2007). Thus, biological invasion is
26 a complex process, and although individual ecological factors determining invasibility have
27 been identified, it remains challenging to understand how their interplay determines invasion
28 success (Gurevitch et al., 2011; Byun et al., 2015).

29 Ecological modeling can illuminate the investigation of mechanisms driving invasion, as
30 models can disentangle the roles played by different factors in the invasion process. Numerous
31 mathematical approaches and simulation model have been developed to analyse the processes
32 involved in biological invasions (Lewis et al., 2016). Many results focus on the spreading speed
33 of the invasion (Lewis et al., 2016) (step (3) of the invasion process), while establishment
34 success has received little attention. In particular, the invasibility of mutualistic communities
35 by an alien species has remained under-explored theoretically (Minoarivelo and Hui, 2016b,a;
36 Bray et al., 2019; Traveset and Richardson, 2014).

37 In nature, mutualistic interactions often involve multiple species of mutualists (the mutu-
38 alist guild) sharing a resource supplied by one or more partner (or host) species (Palmer et al.,
39 2003). A single plant, for example, can associate with dozens of species of beneficial mycor-
40 rhizal fungi that coexist in the plant roots and surrounding soil and compete between each
41 other for access to the plant resource (Verbruggen et al., 2012; Douds Jr and Millner, 1999).
42 Similarly, different competing animal pollinators can coexist on the same floral resources (But-
43 ton and Elle, 2014; Sardiñas and Kremen, 2015). Understanding of the mechanisms behind the
44 persistence of diversity among mutualists and the factors that can threaten this stability has
45 become crucial not only from an ecological point of view, but also for our socio-economical
46 wellbeing (Bronstein, 2015). Indeed pollination and below-ground mutualisms, two of the
47 most widespread earth-mutualisms, are essential drivers of agricultural productivity. Two
48 recent meta-analyses of experimental studies of plant-pollinator relationships (Morales and
49 Traveset, 2009; Charlebois and Sargent, 2017), underline how challenging it is to untangle

50 these relationships with experimental tools alone.

51 In this work, we will use an ordinary differential equation model to study the second stage
52 of the invasion process, i.e. alien species establishment, in a community of mutualists sharing
53 the same host. Additionally, we will explore the ability of the guild to prevent establishment
54 of the alien species. We are interested in the context wherein a native community is threat-
55 ened with invasion by a foreign species. We thus use the terms ‘mutualist guild’, ‘native
56 community’, and ‘established community’ to refer to the assemblage of species that was ini-
57 tially present (not necessarily at equilibrium). We use the terms ‘alien mutualist’, ‘introduced
58 species’, and ‘introduced mutualist’ to indicate an organism that can associate with the same
59 partner as the existing guild members. We assume that the alien species might differ in its
60 mutualist quality and/or competitive ability

61 More specifically, we study the relative effect on the growth dynamics of (i) invasor traits,
62 such as competition strength and resource exchange ability, (ii) propagule pressure, expressed
63 in terms of initial biomass of the introduced species, and (iii) composition of the recipient
64 community, in terms of diversity and initial biomass. Finally, we will discuss the impact
65 of the introduction of an alien species on the diversity of the native guild and on resource
66 availability, i.e. the biomass of the partner species, often associated with productivity in
67 mutualistic communities (for example in terms of crop yield) (Xu and Mage, 2001).

68 We show that the presence of multiple species in a guild promotes species coexistence and
69 reduces the risk of invasion by an alien mutualist. As our model is general, our conclusions
70 apply to a broad range of mutualisms. To simplify our presentation, however, my case study
71 will be the mutualistic interactions between arbuscular mycorrhizal (AM) fungi and their host
72 plant.

73 Model and Methods

74 Formulating a model for multi-species mutualisms

75 We formulate a model to study the dynamics of a guild of competing mutualists sharing a
76 resource supplied by the same partner. Mutualists compete for access to a common resource,
77 whose abundance in the model uniquely corresponds to the biomass of the partner species.
78 Resource availability is in turn affected by the benefit that the partner species receives from
79 its associated mutualists, and hence by the guild composition (Bever, 2002, 1999). The guild
80 and resource dynamics are therefore intrinsically coupled.

We focus on a system consisting of a plant and a guild of mutualist AM fungi. AM
fungi facilitate the plant’s absorption of nutrients (phosphorus in particular) that are limiting
to plant growth (Smith and Read, 2010). In exchange, the plant provides fixed carbon to
the fungi (Smith and Read, 2010). We use an existing model allowing for the coexistence
of multiple mutualists (Martignoni et al.) to model plant-fungi interactions, and consider
the effect of adding direct competition between fungi. This new model therefore includes
both mutualistic (plant to fungi) and competitive (fungi to fungi) interactions. The model
equations describe the evolution in time of the biomass of the plant (p) and the biomass of

the fungal species (m_j) as a function of the exchange of these critical nutrients. We write:

$$\frac{dp}{dt} = \overbrace{r_p(p)}^{\text{plant fitness}} + \sum_j \left[\overbrace{\alpha_j f_{hp}(p, m_j)}^{\text{phosphorus received}} - \overbrace{\beta_j f_{cp}(p, m_j) C(m_j, m_i)}^{\text{carbon supplied}} \right], \quad (1a)$$

$$\frac{dm_j}{dt} = \underbrace{r_{m_j}(m_j)}_{\text{fungal maintenance}} + \underbrace{\beta_j f_{cm_j}(p, m_j) C(m_j, m_i)}_{\text{carbon received}} - \underbrace{\alpha_j f_{hm_j}(p, m_j)}_{\text{phosphorus supplied}}. \quad (1b)$$

81 The components of the model are explained below.

82 **Mutualistic interactions between the plant and the AM fungi:** In the absence
 83 of AM fungi, plant fitness is given by the function $r_p(p)$, which takes into account the intrinsic
 84 growth of the plant as well as maintenance costs, such as respiration, or energy costs related to
 85 nutrient absorption. In the presence of fungi, the plant receives phosphorus from each fungal
 86 mutualist ($f_{hp}(p, m_j)$), and supplies carbon in return ($f_{cp}(p, m_j)$). Fungal biomass increases
 87 due to the carbon received by the plant ($f_{cm_j}(p, m_j)$), and decreases due to the phosphorus
 88 supplied to the plant ($f_{hm_j}(p, m_j)$), as well as due to costs related to the maintenance of the
 89 existing fungal biomass ($r_{m_j}(m_j)$). AM fungi are obligate mutualists and can not survive
 90 in the absence of a host plant, therefore no intrinsic growth term is present in the equation
 91 describing fungal growth. Parameters α_j and β_j represent the ability of fungal species j to
 92 exchange phosphorus and carbon respectively.

93 The choice of the functional forms of the $f(\cdot, \cdot)$ functions, describing nutrients transfer, is
 94 tied to the biology and fully explained in (Martignoni et al.). Here we present a brief summary.
 95 Phosphorus transfer is proportional to fungal and plant biomass, when plant biomass is small,
 96 and to fungal biomass only, when plant biomass is large enough, while carbon transfer is
 97 proportional to both, plant and fungal biomass. We write

$$98 \quad f_{hp}(p, m_j), f_{hm_j}(p, m_j) \propto m_j \frac{p}{d+p}, \quad \text{and} \quad f_{cm_j}(p, m_j), f_{cp}(p, m_j) \propto m_j p. \quad (2)$$

99 The complete forms of the $f(\cdot, \cdot)$ and $r(\cdot, \cdot)$ functions are given in the supplementary informa-
 100 tion (Eq. (6)).

101 **Competitive interactions between AM fungi:** Competition between fungal species
 102 reduces the amount of carbon received/supplied in a way that depends on the specific com-
 103 munity composition, where

$$104 \quad C(m_j, m_i) = 1 - \frac{\sum_{i \neq j} m_i}{a_j + \sum_{i \neq j} m_i}. \quad (3)$$

105 When only one fungal species is present, $C(m_j, m_i)$ is equal to 1 and Eq. (1) reduces to
 106 the original model of Martignoni et al.. When two or more species are present, competition
 107 between fungi reduces the carbon uptake capacity of each of the fungal species. The value of
 108 a_j determines how the presence of other fungal mutualists in the community influences the
 109 carbon uptake capacity, and therefore the growth, of species j .

110 The literature shows that competition between fungi, for example for access to plant
 111 roots, can limit fungal growth in a way that depends on both the species present and their
 112 abundance (Mummey et al., 2009; Hepper et al., 1988; Engelmoer et al., 2014). To determine
 113 a_j , we assume that each of the fungal species present has a direct negative effect on the growth

114 rate of other fungi that depends on its identity, determining the strength of the competitive
 115 interaction between those two species, and depending on the mass proportion occupied by the
 116 competitor. Hence, we define a_j as the mean competition strength experienced by species j ,
 117 where the competitive strength of each paired interaction is weighted by the proportion, in
 118 terms of biomass, that each species occupies within the competing community. We write

$$119 \quad a_j = \sum_{i \neq j} a_{ij} \frac{m_i}{\sum_{i \neq j} m_i}. \quad (4)$$

120 The a_{ij} parameter determines how much the biomass of species i affects the carbon uptake
 121 capacity of species j . Competition between species i and j constitutes two reciprocal interac-
 122 tions quantified by a_{ij} and a_{ji} .

123 We will study the system of Eq. (1) through linear analysis and numerical simulations
 124 (performed with the ODE solver ode45 of the software Matlab R2017a). We will consider
 125 multiple scenarios (see Fig. 1 for a summary), but we will discuss only the most ecologi-
 126 cally relevant cases. To understand the impact of alien species invasion on plant biomass we
 127 will simulate plant growth over time for different combinations of the initial biomass of the
 128 introduced species (propagule pressure) and of the existing community.

129 Results

130 The stability analysis of Eq. (1) is presented in detail in the supplementary information,
 131 and summarized in Fig. 1. Below, we present the key ecological insights emerging from the
 132 mathematical results.

133 **Mutualism promotes coexistence among competitors:** Coexistence of two mutu-
 134 alists (m_1 and m_2) is observed if competition between the two species is weak, while competi-
 135 tive exclusion occurs when competition is strong (Case A of Fig. 1). This outcome is similar
 136 to the output of classical competition models (Volterra, 1928), that predict coexistence of
 137 weak competitors and competitive exclusion of strong competitors.

138 The presence of a third species (m_3) that competes only weakly with the other two mu-
 139 tualists, can change the exclusion scenario to one of coexistence (Case B(iii) of Fig. 1). More
 140 specifically, indirect interactions are created that promote the coexistence of two strong com-
 141 petitors that would otherwise competitively exclude each other. The growth of the weak
 142 competitor (m_3) is not significantly reduced by the presence of the other mutualists in the
 143 guild, and m_3 improves the growth of the associated plant (p). An increase in plant biomass
 144 corresponds to an increase in resource availability for all mutualists present, with a consequent
 145 reduction in competition strength between m_1 and m_2 , allowing their coexistence (indeed a_1
 146 and a_2 in Eq. (7) increase in the presence of m_3). This scenario is illustrated in Fig. S4.

147 **Alien species introduction and invasion success:** The different possible outcomes,
 148 following the introduction of an alien mutualist in a guild, are summarized in Fig. 2. Four
 149 possible scenarios can be observed: (1) The alien species displaces the native community, (2)
 150 the alien species coexists with the native community, (3) either the alien or the native commu-
 151 nity is competitively excluded, depending on their initial biomasses, or (4) establishment of
 152 the alien species is prevented by the presence of a native community. Which scenario occurs
 153 depends on the competition strength between the alien mutualist and the native community,
 154 corresponding to the horizontal and vertical axes of Fig. 2 (parameters a_{wc} and a_{cw}). Small a
 155 parameters indicate strong competitive interactions, while large a parameters indicate weak

156 competition. The values a_{wc}^* and a_{cw}^* determine the thresholds above and below which the
 157 different scenarios (1)-(4) occur.

158 If a weak competitor is added to a guild (Fig. 2, right column), two outcomes are possible:
 159 Either the new species establishes and coexists with the community (scenario (2), top), or
 160 it is competitively excluded by the native community (scenario (4), bottom). Coexistence
 161 is achieved when competition between the alien mutualist and the community is weak (i.e.,
 162 $a_{cw} > a_{cw}^*$ and $a_{wc} > a_{wc}^*$). Exclusion is the outcome when the community competes strongly
 163 with the introduced mutualist (i.e., $a_{cw} > a_{cw}^*$ and $a_{wc} < a_{wc}^*$). If competition between
 164 the introduced species and the community is strong in both directions (i.e., $a_{cw} < a_{cw}^*$ and
 165 $a_{wc} < a_{wc}^*$), the existing community is displaced by the strong competitor or the community
 166 persists and the new species is driven to extinction (scenario (3)). The outcome depends
 167 strongly on the the initial biomass of the introduced species (propagule pressure) and of
 168 the biomass and diversity of the existing fungal community (see Fig. S5). Finally, if the
 169 introduced species is a strong competitor but the community competes only weakly against
 170 it (i.e., $a_{cw} < a_{cw}^*$ and $a_{wc} > a_{wc}^*$), the introduced mutualist will competitively exclude all of
 171 the other guild members (scenario (1) in Fig. 2), independent of its initial biomass.

172 The minimal competition strength needed in the community to overcome an invasion of
 173 the alien species, i.e., the value of a_{wc}^* determining whether scenario (1) or scenario (3) occurs,
 174 can be computed as

$$175 \quad a_{wc}^* = \frac{\rho_w \frac{\alpha_c}{\beta_c}}{1 - \rho_w \frac{\alpha_c}{\beta_c}} \sum_{j=1}^N m_{wj}^* . \quad (5)$$

176 where $\sum_j m_{wj}^*$ represents the total biomass of the native community, α_c/β_c is the ratio of
 177 phosphorus to carbon exchange capacity of the alien species and ρ_w is a constant that depends
 178 on the plant biomass and on the characteristics of the native community (explicitly stated
 179 in Eq. (33) of the supplementary information). As long as $a_{wc} < a_{wc}^*$, extinction of the
 180 native community is unlikely to happen (c.f. scenarios (3) and (4)). A large a_{wc}^* indicates,
 181 therefore, a more stable community. From Eq. (5) we can see that a_{wc}^* increases with increasing
 182 total biomass of the native community, and decreases for decreasing mutualist quality of the
 183 introduced species (i.e., for smaller α_c/β_c). Hence diversity increases the resilience of the guild
 184 against invasion (see Fig. S5), and cheaters are more likely to invade (see Fig. S6).

185 **The impact of invasion on resource availability (i.e. plant biomass):** To
 186 understand how plant biomass is affected by the introduction of an alien mutualist, we look
 187 at the evolution dynamics of an ecosystem composed of a plant, a native guild of two coexisting
 188 fungal species, and an introduced species, where competition between the introduced species
 189 and the native fungi is either strong (Fig. 2, scenario (2)) or weak (scenario (3)).

190 The introduction of a weak competitor in the guild results in the establishment of the
 191 introduced species and its coexistence with the rest of the community (Fig. 2, scenario (2)).
 192 In this case, the addition of a new species increases both plant growth rate and final plant
 193 biomass (see Fig. S2). If the introduced species is a strong competitor (scenario (3)), the
 194 consequences on plant growth (and therefore on resource availability) depend largely on the
 195 initial biomass of the introduced species and on the total biomass of the native community (see
 196 Fig. 3). If initially the biomass of the community is low, the addition of a new species initially
 197 speeds up plant growth, and at the same time reduces the growth rate of the community of
 198 mutualists (see Fig. 3, top two rows). When the initial biomass of the introduced species is
 199 not large enough to guarantee persistence, the community will displace the strong competitor,
 200 with no consequences on final plant and fungal biomass in the long term (top row). When
 201 the introduced species can persist, the native community will be displaced with negative

202 consequences on the plant final biomass (middle row). If initially the total biomass of the
203 community is large, the effect of the introduced species on the plant and fungal growth rates
204 is minimal (bottom row). In this case, the introduced species can not establish, therefore not
205 affecting the final biomass reached by the plant or by the fungal community.

206 Discussion

207 **Mutualism promotes coexistence among competitors:** We suggest that the pres-
208 ence of a weak competing mutualist within a guild can indirectly facilitate the coexistence of
209 species that would otherwise competitively exclude each other. If all guild members depend
210 on the resource provided by a single plant, the presence of a weak competitor increases plant
211 biomass and therefore resource availability. Increasing the amount of resource available leads
212 to a consequent reduction in competition among other mutualists present.

213 It has been acknowledged that the presence of particular species in a community can
214 enhance resource availability and provide habitat to the establishment of other organisms
215 that could not have otherwise survived (Floerl and Inglis, 2005; Schwindt and Iribarne, 2000).
216 More specifically, the role of mutualism in mediating competition and enhancing diversity
217 has also been noted experimentally (Schmitt and Holbrook, 2003; Aschehoug and Callaway,
218 2015; Siefert et al., 2019). However, very few models have dealt with this issue (Bever, 1999).
219 We find that the removal of a key species, such as a weak competitor from a community of
220 strongly competing mutualists (e.g., species m_3 in Fig. S4), may cause the extinction
221 of other species in the guild (e.g., species m_1 or species m_2 in Fig. S4).

222 **Predicting the invasion success of an alien mutualist:** In our results, we formulate
223 testable predictions on biological invasion in mutualist guilds. We disentangle the effect of
224 competition, propagule pressure and traits of the alien mutualist and the recipient community,
225 in determining the establishment of an introduced species. We found that if competition
226 between the introduced species and the existing community is weak, e.g. due to functional
227 complementarity among species, the alien species will establish and coexist with the rest of
228 the community (scenario (2) in Fig. 2). In agreement with our findings, niche opportunities
229 have already been identified as important drivers of invasion success (Shea and Chesson, 2002;
230 Vall-Ilosera et al., 2016).

231 We show that if competition between the alien species and the existing community is
232 strong, coexistence is not possible (scenario (3) in Fig. 2). The introduced species will either
233 competitively exclude the whole community, or fail to persist. Simulations show that when the
234 native community has a large biomass, establishment of the alien species is unlikely. However,
235 when the biomass of the native community is low, establishment of the alien species occurs
236 when its initial biomass is large enough. Hence, the biomass of the native community at the
237 time of introduction of the alien species and the propagule pressure of the alien species are key
238 factors determining invasion success. The literature shows that early arrivals can establish and
239 colonize available resources, and prevent their exploitation by late arrivals. This phenomenon
240 has been observed for competitors in general (Wainwright et al., 2012; Schantz et al., 2015),
241 as well as in the context of mutualistic communities (Kennedy and Bruns, 2005; Peay, 2018;
242 Werner and Kiers, 2015). Priority effects can therefore play a fundamental role in creating
243 invasion opportunities for competitors. Our model supports this finding, as early arrivals
244 have time to increase their biomass, and by doing so, to gain a competitive advantage over
245 an introduced species.

246 We found that the most worrisome scenario occurs when the competitive ability of the
247 introduced species is largely superior than that of the existing community (scenario (1) in

248 Fig. 2). In this case, the alien species invades and displaces the existing guild, independent of
249 its propagule pressure. The literature has reported cases where the introduction of a strong
250 competing alien pollinator, sharing nesting and floral resources with native species, causes
251 the decline or extinction of native pollinators (Morales et al., 2013; Ings et al., 2006). We
252 show that invasion is more likely to occur when the alien species has low mutualist quality,
253 and when diversity in the existing community is low. In the model, weak competitors, e.g.
254 species occupying different niches, do not significantly hinder each others' growth. Hence, the
255 biomass of a group of weak competitors increases much faster than the biomass of a single
256 species, even when the species in question is a strong competitor. A larger biomass provides
257 a competitive advantage to the coexisting community, by preventing access by the introduced
258 species to the common resource. The larger the number of weak competitors (e.g., functionally
259 different species), the faster the growth in terms of total biomass, and the easier it becomes
260 to outcompete a strong competitor. A large community can therefore prevent the invasion of
261 a strong competitor in cases where a smaller community would be competitively excluded.

262 Whether diversity promotes resilience of a community has been frequent matter of de-
263 bate in recent decades (McCann, 2000). Generally, similarly to our predictions, functional
264 complementary is reputed to lead to a better use of the resource available, what is directly
265 related to fitness of a community, and therefore to higher resistance to disturbance (Cardinale,
266 2011; Tilman, 2004). However, empirical observations have been inconsistent (Wiser et al.,
267 1998; Fargione and Tilman, 2005; Levine, 2000). In particular, the role of species identity
268 in promoting or opposing invasion is still under investigation (Zheng et al., 2018). Our work
269 adds further theoretical evidence in support of diversity promoting resilience, this time in
270 the specific context of a community of mutualists. We say that a diverse community can
271 efficiently monopolize the available resource, in a way that makes it more resilient to invasion
272 by a strong competitor.

273 **The impact of invasion on productivity:** Although the short term effect of the
274 introduction of an alien species on plant growth can be extremely positive, the situation
275 changes when looking at its long term consequences. The introduction of a mutualist that is
276 a weak competitor (e.g. a species whose function is complementary to the native community)
277 can result in an overall positive effect on both plant growth rate and final size. However, the
278 introduction of a highly competitive species and its permanent establishment may result in
279 an initial increase in the plant growth rate, but also in the subsequent displacement of native
280 species, with a consequent decrease in final plant size (see Fig. 3).

281 Experimental studies show that it is not clearly understood whether the short term positive
282 effects on productivity are related to diversity by itself, or are rather due to a general increase
283 in the abundance of mutualists (Pellegrino et al., 2011; Freeman et al., 2013). Our predictions
284 suggest that abundance, and not diversity, is positively related to plant growth rate on a short
285 time scale. Long term productivity and resilience are increased by diversity in the mutualist
286 community. In order to assess the impact of alien species introduction on productivity, field
287 studies should to take into account the long-term abundance and diversity of the existing
288 fungal community.

289 **Future work:** The model presented in this article sheds light on the mechanisms behind
290 the stability of mutualistic communities. Our results have direct implications for conservation
291 biology, by providing insights into the possible consequences of species manipulation among a
292 group of mutualists depending on the same resource, such as below-ground microbial commu-
293 nities or pollinators (Menz et al., 2011; Ings et al., 2010; Hanna et al., 2013). For example, our
294 model could be used to investigate the consequences for fungal diversity and plant produc-
295 tivity following the introduction of commercially grown AM fungi, commonly used as organic

296 fertilizers (Gianinazzi and Vosátka, 2004). The scientific community has raised important
297 concerns about the potential invasiveness of these commercial fungi, and their possible detri-
298 mental consequences on productivity (Schwartz et al., 2006; Hart et al., 2017; Ricciardi et al.,
299 2017; Thomsen and Hart, 2018). However, the invasion risk has never been fully assessed.
300 Because the model is based on a consumer-resource framework for mutualistic interactions
301 (Holland and DeAngelis, 2010), simulations predicting the output of competition within a
302 guild are easily testable in an experiment.

303 Fungal species or pollinators can often associate simultaneously with multiple different
304 plants. To better simulate this real world scenario, our model should be extended to multiple
305 possible partners. Considering associations with multiple different plants could, for example,
306 answer questions related to the impact of plant diversity on pollination services and produc-
307 tivity (Isbell et al., 2017), or give insights into community assemblage and invasion dynamics
308 in forests or agroecosystems (Horn et al., 2017; Potts et al., 2003).

309 Spatial factors may play an important role in invasion dynamics, or in creating hetero-
310 geneous patterns of guild and host persistence (Melbourne et al., 2007; Kerr et al., 2002; Yu
311 and Wilson, 2001; Westphal et al., 2006). Future modeling efforts should therefore focus on
312 the development of a spatially explicit version of the model.

313 Acknowledgment

314 JG acknowledges NONLOCAL project (ANR-14-CE25-0013), GLOBNETS project (ANR-16-
315 CE02-0009) and the European Research Council (ERC) under the European Unions Horizon
316 2020 research and innovation program (grant agreement No 639638, MesoProbio). MMH
317 acknowledges NSERC Discovery Grant RCT acknowledges NSERC Discovery Grant RGPIN-
318 2016-05277 and the ‘Make our planet great again (MOPGA)’ grant.

Figures

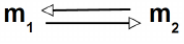
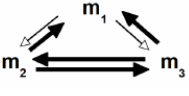

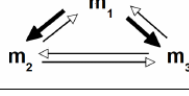
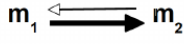
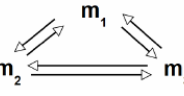
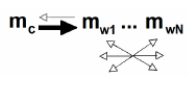
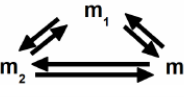
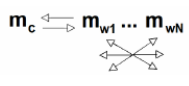
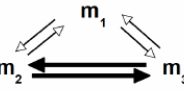
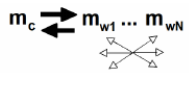
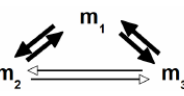
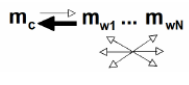
A (i)	 (m_1^*, m_2^*)	B (v)	 $(0, m_2^*, 0), (0, 0, m_3^*)$
(ii)	 $(m_1^*, 0), (0, m_2^*)$	(vi)	 $(m_1^*, 0)$
(iii)	 $(m_1^*, 0)$		
B (i)	 (m_1^*, m_2^*, m_3^*)	C (i)	 $(m_c^*, 0, \dots, 0)$
(ii)	 $(m_1^*, 0, 0), (0, m_2^*, 0), (0, 0, m_3^*)$	(ii)	 $(m_c^*, m_{w1}^*, \dots, m_{wN}^*)$
(iii)	 (m_1^*, m_2^*, m_3^*)	(iii)	 $(m_c^*, 0, \dots, 0), (0, m_{w1}^*, \dots, m_{wN}^*)$
(iv)	 $(m_1^*, 0, 0), (0, m_2^*, m_3^*)$	(iv)	 $(0, m_{w1}^*, \dots, m_{wN}^*)$

Fig. 1: Representation of the direct interactions between fungal species (m_i) sharing a resource supplied by the same host plant (not included in the figure), and corresponding steady state stability (presented in the supplementary information). Arrows indicate competition between mutualists where competition can be weak (thin arrows) or strong (thick arrows).

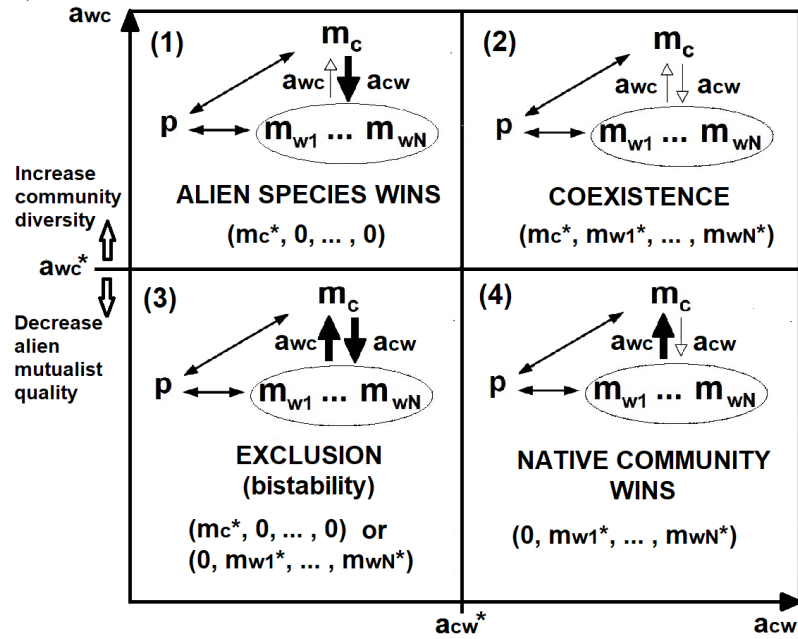


Fig. 2: Representation of the possible outcomes following the introduction of an alien species into a guild of coexisting mutualists. The diagrams represent the direct interactions between the plant (p), its mutualist guild (m_{w1}, \dots, m_{wN}), and the introduced mutualist (m_c), where plant-fungi interactions are mutualistic, while interactions among fungal species are competitive. Arrow thickness represents the strength of the interactions. In the figure, competition between the introduced mutualist and the guild (parameters a_{wc} and a_{cw}) is varied along a gradient of strong competition (a 's parameters are small) to weak competition (a 's parameters are large). The critical values a_{wc}^* and a_{cw}^* define the boundary between the occurrence of the different scenarios, and depend on diversity in the native community and on the mutualist quality of the introduced species.

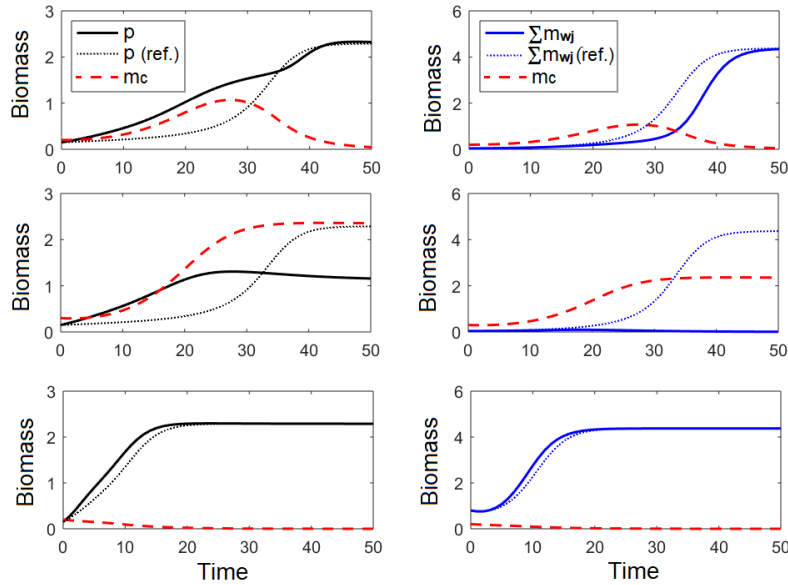


Fig. 3: Plant biomass (left panels, solid black lines) and fungal biomass over time (right panels, solid blue lines) in response to the addition of an alien species that is a strong competing mutualist (dashed red lines) to the native community, for the situation corresponding to scenario (3) of Fig. 2. The dotted lines show plant growth (left panels) and fungal growth (right panels) in the absence of the introduced species. Simulations were run with a guild of two native species (i.e., $N = 2$). In the top panels, the biomass of the introduced species is too low to guarantee persistence ($m_{c0} = 0.2$, $2m_{wj} = 0.04$). In the middle panels, the alien species establishes and displaces the native community ($m_c(0) = 0.3$, $2m_{wj}(0) = 0.04$). In the bottom panels, the initial biomass of native fungi is much larger than the alien propagule biomass, and species introduction has a very little effect on plant and fungal growth ($m_c(0) = 0.2$, $2m_{wj}(0) = 0.8$). The plant initial biomass used for the simulations is $p(0) = 0.15$, competition parameters are $a_{ww} = 2.2$, $a_{cw} = a_{wc} = 0.3$. Other parameters correspond to those for Fig. S6.

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Supplementary information

In this section we present the analytical criteria for stability of the mutualist guild. We analyse the model given in Eq. (1), to understand what are the conditions promoting coexistence or competitive exclusion among a community of mutualists. The whole model of Eq. (1) can be written as

$$\begin{aligned} \frac{dp}{dt} &= \underbrace{q_{hp}r_p p}_{\text{Intrinsic growth}} + q_{hp} \overbrace{\left(\sum_j \alpha_j m_j \right)}^{\text{phosphorus received}} \frac{p}{d+p} - q_{cp} \overbrace{\left(\sum_j \beta_j m_j \left[1 - \frac{\sum_{i \neq j} m_i}{a_j + \sum_{i \neq j} m_i} \right] \right)}^{\text{carbon supplied}} p - \underbrace{\mu_p p^2}_{\text{maintenance}}, \quad (6a) \\ \frac{dm_j}{dt} &= q_{cm_j} \beta_j p m_j \underbrace{\left[1 - \frac{\sum_{i \neq j} m_i}{a_j + \sum_{i \neq j} m_i} \right]}_{\substack{\text{Reduction in carbon uptake} \\ \text{due to competition}}} - q_{hm_j} \underbrace{\alpha_j \frac{p}{d+p} m_j}_{\text{phosphorus supplied}} - \underbrace{\mu_{m_j} m_j^2}_{\text{maintenance}}. \quad (6b) \\ &\quad \underbrace{\hspace{10em}}_{\text{carbon received}} \end{aligned}$$

Eq. (6) resembles the model developed by (Martignoni et al.), except for the term indicating the reduction in carbon uptake due to competition of a fungal species with the surrounding community. When only one fungal species is present, Eq. (1) reduces to the original model (Martignoni et al.). When two or more species are present, competition among fungi reduces the carbon uptake capacity of each of the fungal species.

Parameters α_j and β_j are respectively the phosphorus and carbon exchange ability of species j , μ_p and μ_{m_j} are the biomass dependent maintenance rates of the plant and of fungal species j , the q -parameters are conversion factors for the amount of resource (phosphorus h or carbon c) into plant biomass (p) or biomass of fungal species j (m_j), r_p is the intrinsic growth rate of the plant, and d is the half-saturation constant. The value of a_j is defined determines how the presence of other fungal mutualists in the community influences the carbon uptake capacity, and therefore the growth, of species j . It is defined as

$$a_j = \sum_{i \neq j} a_{ij} \frac{m_i}{\sum_{i \neq j} m_i}. \quad (7)$$

The a_{ij} parameter determines how much the biomass of species i affects the carbon uptake capacity of species j . If a_{ij} and a_{ji} are large, only a large quantity of species i influences the growth of species j (and viceversa), and competition between species i and j is minimal. This situation corresponds for example to the case where fungal species are functionally complementary, or have low niche overlap, and tend therefore to compete only weakly between each other. For small a_{ij} and a_{ji} , competition between species i and j is strong, and the two AM fungal species can be regarded as being functionally similar, or as having a large niche overlap. If a_{ij} is large and a_{ji} is small, species i has a strong negative influence on the growth of species j , but j has little influence on the growth of i . Species i is therefore a stronger competitor with respect to species j .

A linear analysis will be conducted on the 2 fungal species case ($j = 2$), on the 3 species case ($j = 3$) and on a $(N+1)$ -species case, where a new species of AM fungi is introduced in a community of N coexisting mutualists. These scenarios correspond to cases A-C of Table S1. We are interested in the situation in which the establishment of the plant-fungi mutualism is possible, and we will therefore discuss only the situation in which the extinction steady state

562 of the plant is unstable. The conditions for the establishment of the mutualism are given in
 563 the supplementary information of [Martignoni et al.](#)

564 In order to give more insights on the effect of the competition, I will explore numerically
 565 the impact of the competition parameters on different characteristic of the mutualist guild,
 566 such as total AMF biomass, productivity of the plant, and ratio of plant biomass and AMF
 567 biomass. Numerical computations have been performed with the built-in ode45 solver of the
 568 software Matlab R2017a.

569 Case A: One plant and 2 AM fungal species

570 When considering a system of a plant and 2 fungal mutualists m_1 and m_2 , Eq. (1) for $j = 2$
 571 can be rewritten as

$$\left\{ \begin{array}{l} \frac{dp}{dt} = q_{hp}r_p p + q_{hp} \left(\alpha_1 m_1 + \alpha_2 m_2 \right) \frac{p}{d+p} - q_{cp} \left(\beta_1 m_1 \left[1 - \frac{m_2}{a_{21} + m_2} \right] \right. \\ \left. + \beta_2 m_2 \left[1 - \frac{m_1}{a_{12} + m_1} \right] \right) p - \mu_p p^2, \end{array} \right. \quad (8a)$$

$$\frac{dm_1}{dt} = q_{cm_1} \beta_1 p m_1 \left[1 - \frac{m_2}{a_{21} + m_2} \right] - q_{hm_1} \alpha_1 \frac{p}{d+p} m_1 - \mu_{m_1} m_1^2, \quad (8b)$$

$$\frac{dm_2}{dt} = q_{cm_2} \beta_2 p m_2 \left[1 - \frac{m_1}{a_{12} + m_1} \right] - q_{hm_2} \alpha_2 \frac{p}{d+p} m_2 - \mu_{m_2} m_2^2. \quad (8c)$$

572 Note that when only two AM fungal species are present, the value of a_1 and a_2 (Eq. (7))
 573 reduce to the constants a_{21} and a_{12} respectively. These parameters are a measure for the
 574 amount of biomass of species 1 that limits the carbon absorption of species 2, and viceversa,
 575 and are expected to be large when competition between the two fungal species is weak, and
 576 small if competition between the two species is strong.

577 To facilitate computations we assume that the plant biomass has reached steady state
 578 (p^*). The value of the plant steady state may assume different values depending on the
 579 specific fungal community composition we are looking at. With no loss of generality, we will
 580 use the single symbol p^* to refer to all these values, without distinction. We further assume
 581 that the two fungal species have identical parameters α , β , q_{cm} , q_{hm} and μ_m . We can rewrite
 582 Eq. (8) as

$$\left\{ \begin{array}{l} \frac{dm_1}{dt} = q_{cm} \beta p^* m_1 \frac{a_{21}}{a_{21} + m_2} - q_{hm} \alpha \frac{p^*}{d+p^*} m_1 - \mu_m m_1^2, \end{array} \right. \quad (9a)$$

$$\left\{ \begin{array}{l} \frac{dm_2}{dt} = q_{cm} \beta p^* m_2 \frac{a_{12}}{a_{12} + m_1} - q_{hm} \alpha \frac{p^*}{d+p^*} m_2 - \mu_m m_2^2. \end{array} \right. \quad (9b)$$

583 We assess the dynamics of (9) through linear stability analysis and phase-plane portraits
 584 ([Case, 1999](#); [Edelstein-Keshet, 1988](#)). Nullclines can be found by setting Eqs. (9a) and (9b)
 585 to zero and solving for m_1 and m_2 . We obtain

$$\frac{dm_1}{dt} = 0 \iff m_1 = 0 \quad \text{or} \quad m_2 = f_1(m_1) = a_{21} \left(\frac{q_{cm} \beta p^*}{q_{hm} \alpha \frac{p^*}{d+p^*} + \mu_m m_1} - 1 \right), \quad (10a)$$

$$\frac{dm_2}{dt} = 0 \iff m_2 = 0 \quad \text{or} \quad m_1 = f_2(m_2) = \frac{1}{\mu_m} \left(q_{cm} \beta p^* \frac{a_{12}}{a_{12} + m_1} - q_{hm} \alpha \frac{p^*}{d+p^*} \right). \quad (10b)$$

586 A graphical representation of the nullclines is shown in Fig. S1. The first equations in (10a)
 587 and in (10b) correspond to the vertical and horizontal axes in the phase-plane. The nullclines
 588 $f_1(m_1)$ and $f_2(m_1)$ are hyperbolae, with vertical asymptote in the negative region of the
 589 phase-plane. As long as p is large enough, both curves intersect the positive horizontal and
 590 vertical axes at one point, and the competitive exclusion steady states $(m_1^*, 0)$ and $(0, m_2^*)$ do
 591 always exist (provided, as mentioned above, that the plant-fungi mutualism can establish).

In order for a coexistence steady state to exist, $f_1(m_1)$ and $f_2(m_1)$ must intersect. This condition is satisfied if $f_1(m_1)$ intersect the vertical axis at a larger value than $f_2(m_1)$ and the horizontal axis at a lower value (and viceversa). This condition translates into the equations

$$f_1(0) > f_2(0) \quad \& \quad a < b, \quad \text{where } f_1(m_1=a) = f_2(m_1=b) = 0, \quad \text{or} \quad (11a)$$

$$f_1(0) < f_2(0) \quad \& \quad a > b, \quad \text{where } f_1(m_1=a) = f_2(m_1=b) = 0. \quad (11b)$$

Conditions (11) simplify into

$$a_{12}, a_{21} > \frac{q_{hm} p^* \alpha}{(d + p^*) \mu_m} \quad \text{or} \quad (12a)$$

$$a_{12}, a_{21} < \frac{q_{hm} p^* \alpha}{(d + p^*) \mu_m}. \quad (12b)$$

592 Equations (12) indicate that in order for a coexistence steady state to exist, competition
 593 parameters a_{12} and a_{21} need to be either both small or both large. In the symmetric case
 594 $a_{12} = a_{21}$, one of the conditions in Eq. (12) is always satisfied and the steady state (m_1^*, m_2^*)
 595 does always exist. Note that mathematical equality in Eq. (12) corresponds to the case in
 596 which the two nullclines exactly overlap and each point on the nullcline is a stable equilibrium.
 597 When competition among two species is asymmetric and conditions (12) are not satisfied, only
 598 the competitive exclusion steady states $(m_1^*, 0)$ and $(0, m_2^*)$ exist.

599 **Stability of the exclusion steady states $(m_1^*, 0)$ and $(0, m_2^*)$:** To understand under
 600 which conditions the coexistence and competitive exclusion steady states are stable, we lin-
 601 earize the model around the steady states. We start by considering the competitive exclusion
 602 steady state $(m_1^*, 0)$. The Jacobian around the steady state $(m_1^*, 0)$ is given by

$$603 \quad J_{(m_1^*, 0)} = \begin{pmatrix} -\mu_m m_1^* & -\frac{q_{cm} \beta p^* m_1^*}{a_{21}} \\ 0 & q_{cm} \beta p^* \frac{a_{12}}{a_{12} + m_1^*} - q_{hm} \alpha \frac{p^*}{d + p^*} \end{pmatrix}, \quad (13)$$

with eigenvalues

$$\lambda_1 = -\mu_m m_1^*, \quad (14a)$$

$$\lambda_2 = q_{cm} \beta p^* \frac{a_{12}}{a_{12} + m_1^*} - q_{hm} \alpha \frac{p^*}{d + p^*}. \quad (14b)$$

604 In order for the $(m_1^*, 0)$ to be stable both eigenvalues should be negative. We can directly see
 605 that $\lambda_1 < 0$. The eigenvalue λ_2 is negative if

$$606 \quad \frac{a_{12}}{a_{12} + m_1^*} < \frac{q_{hm} \alpha}{q_{cm} \beta (d + p^*)}. \quad (15)$$

607 The values of the competitive exclusion steady state m_1^* and of p^* do not depend on a_{12} ,
 608 hence we can directly conclude that condition (15) is satisfied if a_{12} is small enough. That is,
 609 if m_1 is a strong competitor, the competitive exclusion steady state $(m_1^*, 0)$ is locally stable
 610 and species 1 and species 2 will not coexist. The same calculation can be applied to $(0, m_2^*)$ to

611 show that if m_2 is a strong competitor, m_1 can be driven to extinction. In sum, if a_{12} and a_{21}
612 are large enough, the competitive exclusion steady states are unstable, while if competition
613 between species 1 and 2 is strong, the most competitive species will competitively exclude
614 the other. If competition is asymmetric, e.g. a_{12} is small while a_{21} is large, then only the
615 steady state $(m_1^*, 0)$, corresponding to competitive exclusion of the weak competitor (in this
616 case species 2), is stable.

617 An important factor determining which species is competitively superior is initial biomass.
618 Fungal parameters can also shape the size of the basin of attraction of one species or the other.
619 For the analysis we assumed species 1 and 2 to have identical parameters. If fungal species
620 differ by other traits, such as phosphorus absorption capacity (α_i), carbon sink strength (β_i),
621 nutrient conversion efficiency (q_{cm_i} and q_{hm_i}) or maintenance cost (μ_m), the basin of attraction
622 of the species with the higher resource acquisition efficiency will increase in size, while the
623 basin of attraction of the less competitive species will decrease.

624 **Stability of coexistence steady state (m_1^*, m_2^*) :** We want to understand the con-
625 ditions leading to stability of the coexistence steady state (m_1^*, m_2^*) . For this purpose we
626 compute the Jacobian

$$627 \quad J_{(m_1^*, m_2^*)} = \begin{pmatrix} -\mu_m m_1^* & -\frac{q_{cm}\beta p^* a_{21} m_1^*}{(m_2^* + a_{21})^2} \\ -\frac{q_{cm}\beta p^* a_{12} m_2^*}{(m_1^* + a_{12})^2} & -\mu_m m_2^* \end{pmatrix}. \quad (16)$$

628 The steady state (m_1^*, m_2^*) is stable if $\text{Tr}(J) < 0$ and $\det(J) > 0$. The trace of the Jacobian
629 in (16) is always negative. The stability of the coexistence steady state depends therefore on
630 the sign of the determinant of the Jacobian in Eq. (16). By setting $\det(J) > 0$ and solving for
631 a_{12} and a_{21} we obtain the following condition for stability of the coexistence steady state:

$$632 \quad \frac{a_{12} a_{21}}{(a_{12} + m_1^*)^2 (a_{21} + m_2^*)^2} < \left(\frac{\mu_m}{q_{cm}\beta p^*} \right)^2. \quad (17)$$

633 The value of the steady states m_1^* , m_2^* and p^* depend on parameters a_{12} and a_{21} . There may
634 exist multiple coexistence steady states, however as long as the competitive exclusion steady
635 state is unstable, we can assume that coexistence should occur. As competition limits m_1
636 and m_2 growth, we expect the value of m_1^* and m_2^* to increase for decreasing competition,
637 i.e. for increasing a_{12} and a_{21} . For large a 's the dynamics approaches the zero competition
638 case discussed in [Martignoni et al.](#). We expect therefore the steady state to increase with
639 increasing competition parameter a , where the limit corresponds to the values of m_1^* , m_2^* and
640 p^* obtained in the absence of species 2 and 1 respectively. Fig. S2 shows a graphical repre-
641 sentation of the dependence of the plant and steady state on the competition parameter a .
642 As the value of the steady states are bounded, we can conclude that if a_{21} and a_{12} are large
643 enough, i.e. competitive interactions between m_1 and m_2 are weak, Eq. (17) is satisfied and
644 the coexistence steady state is stable.

645
646 In sum, coexistence of two mutualists sharing a resource supplied by the same plant is
647 observed if competition is weak, while competitive exclusion occurs when competition between
648 the two species is strong. When both species are strong competitors, either the one or the
649 other survives, depending on their competitive ability. When only one of the two species is
650 a strong competitor, the weak competitor is driven to extinction. Table S1 summarizes this
651 information. This scenario is similar to the output of the classic Lotka and Volterra model of
652 competition ([Volterra, 1928](#)), which predicts coexistence of weak competitors and competitive
653 exclusion of strong competitors.

Case B: One plant and 3 AM fungal species

We consider a system of a plant and 3 fungal mutualists m_1 , m_2 and m_3 . This system corresponds to the model given by Eq. (1) for $j = 3$. In order to capture the stability of the different steady states (coexistence or exclusion states), we assume parameters of all three species to be identical. We further assume that plant biomass has reached steady state, and is therefore constant. Eq. (1) can be rewritten as follow:

$$\left\{ \begin{array}{l} \frac{dm_1}{dt} = q_{cm}\beta p^* m_1 \underbrace{\left[\frac{a_{21}m_2 + a_{31}m_3}{a_{21}m_2 + a_{31}m_3 + (m_2 + m_3)^2} \right]}_{f(m_2, m_3)} - q_{hm}\alpha \frac{p^*}{d + p^*} m_1 - \mu_m m_1^2, \quad (18a) \\ \frac{dm_2}{dt} = q_{cm}\beta p^* m_2 \left[\frac{a_{12}m_1 + a_{32}m_3}{a_{12}m_1 + a_{32}m_3 + (m_1 + m_3)^2} \right] - q_{hm}\alpha \frac{p^*}{d + p^*} m_2 - \mu_m m_2^2, \quad (18b) \\ \frac{dm_3}{dt} = q_{cm}\beta p^* m_3 \left[\frac{a_{13}m_1 + a_{23}m_2}{a_{13}m_1 + a_{23}m_2 + (m_1 + m_2)^2} \right] - q_{hm}\alpha \frac{p^*}{d + p^*} m_3 - \mu_m m_3^2. \quad (18c) \end{array} \right.$$

655

Stability of the exclusion states: We investigate the stability of Eq. (18) by linearizing the model around the competitive exclusion steady state $(m_1^*, 0, 0)$. The Jacobian of the linearized model corresponds to the matrix

$$J_{(m_1^*, 0, 0)} = \begin{pmatrix} \mu_m m_1^* & q_{cm}\beta p^* m_1^* \frac{\partial f(m_2, m_3)}{\partial m_2} \Big|_{(0,0)} & q_{cm}\beta p^* m_1^* \frac{\partial f(m_2, m_3)}{\partial m_3} \Big|_{(0,0)} \\ 0 & q_{cm}\beta p^* \frac{a_{12}}{a_{12} + m_1^*} - q_{hm}\alpha \frac{p^*}{d + p^*} & 0 \\ 0 & 0 & q_{cm}\beta p^* \frac{a_{13}}{a_{13} + m_1^*} - q_{hm}\alpha \frac{p^*}{d + p^*} \end{pmatrix}. \quad (19)$$

Eigenvalues of (19) are

$$\lambda_1 = -\mu_m m_1^*, \quad (20a)$$

$$\lambda_2 = q_{cm}\beta p^* \frac{a_{12}}{a_{12} + m_1^*} - q_{hm}\alpha \frac{p^*}{d + p^*}, \quad (20b)$$

$$\lambda_3 = q_{cm}\beta p^* \frac{a_{13}}{a_{13} + m_1^*} - q_{hm}\alpha \frac{p^*}{d + p^*}. \quad (20c)$$

For stability, we require all eigenvalues to be negative. Clearly, $\lambda_1 < 0$. Eigenvalues λ_2 and λ_3 can assume positive or negative values, depending on the competition parameters a_{12} and a_{13} . By assuming $\lambda_2 < 0$ and $\lambda_3 < 0$ we find the following two conditions for stability:

$$\frac{a_{12}}{a_{12} + m_1^*} < \frac{q_{hm}\alpha}{q_{cm}\beta(p^* + d)} \quad \& \quad (21a)$$

$$\frac{a_{13}}{a_{13} + m_1^*} < \frac{q_{hm}\alpha}{q_{cm}\beta(p^* + d)}. \quad (21b)$$

Eq. (21) states that as long as m_1 is a strong competitor, i.e. a_{12} and a_{13} are small enough, the steady state $(m_1^*, 0, 0)$ is locally stable and competitive exclusion will occur. If a_{12} and a_{13} are large enough, the competitive exclusion steady state is unstable. The same calculation can be applied the steady states representing competitive exclusion of species 2 or 3, i.e. $(0, m_2^*, 0)$ and $(0, 0, m_3^*)$. If m_2 (or m_3) is a strong competitor, m_1 and m_3 (respectively m_1 and m_2) can be driven to extinction. We can conclude that if m_1 , m_2 and m_3 are all strong competitors, the species with higher biomass will competitively exclude the others. If only m_2 and m_3 are

666

667 strong competitors, while m_1 is a weak competitor, than m_2 or m_3 will competitively exclude
 668 the other. If fungal species have different fungal parameters α , β , q_{cm} , q_{hm} or μ_m , the basin of
 669 attraction of the most competitive species will increase in size, while the basin of attraction of
 670 the less competitive species will decrease. This situation correspond to cases B(ii) and B(v)
 671 of Table S1.

672 **Stability of the steady state including 2 AM fungal species:** If fungal m_1 ,
 673 m_2 and m_3 are weak competitors, the competitive exclusion steady states are unstable and
 674 coexistence can occur. To understand whether coexistence of all fungal species or of only two
 675 fungal species is observed, we investigate the stability of the steady state $(0, m_2^*, m_3^*)$. We
 676 linearize the model around $(0, m_2^*, m_3^*)$ and compute the corresponding Jacobian. We obtain

$$J_{(0, m_2^*, m_3^*)} = \begin{pmatrix} q_{cm}\beta p^* \frac{a_{21}m_2^* + a_{31}m_3^*}{a_{21}m_2^* + a_{31}m_3^* + (m_2^* + m_3^*)^2} - q_{hm}\alpha \frac{p^*}{d+p^*} & 0 & 0 \\ q_{cm}\beta p^* m_2^* \frac{a_{12} - 2a_{32}}{(a_{32} + m_3^*)^2} & -\mu_m m_2^* & -q_{cm}\beta p^* m_2^* \frac{m_3^*}{(a_{32} + m_3^*)^2} \\ q_{cm}\beta p^* m_3^* \frac{a_{13} - 2a_{23}}{(a_{23} + m_2^*)^2} & -q_{cm}\beta p^* m_3^* \frac{a_{23}}{(a_{23} + m_2^*)^2} & -\mu_m m_3^* \end{pmatrix}. \quad (22)$$

677

678 Eigenvalues of (22) are found by solving

$$\left(q_{cm}\beta p^* \frac{a_{21}m_2^* + a_{31}m_3^*}{a_{21}m_2^* + a_{31}m_3^* + (m_2^* + m_3^*)^2} - q_{hm}\alpha \frac{p^*}{d+p^*} - \lambda \right) \times \\ \left[(-\mu_m m_2^* - \lambda)(-\mu_m m_3^* - \lambda) - (q_{cm}\beta p^*)^2 m_2^* m_3^* \frac{a_{23} a_{32}}{(a_{23} + m_2^*)^2 (a_{32} + m_3^*)^2} \right] = 0. \quad (23)$$

679

680 For stability, we require λ_1 , λ_2 and λ_3 to be all negative. Looking at the first factor of Eq. (23),
 681 we obtain a first condition for $\lambda_1 < 0$, that is

$$\frac{a_{21}m_2^* + a_{31}m_3^*}{a_{21}m_2^* + a_{31}m_3^* + (m_2^* + m_3^*)^2} < \frac{q_{hm}\alpha}{q_{cm}\beta(d+p^*)}. \quad (24)$$

682

683 The values of m_2^* and m_3^* do not depend on parameters a_{21} and a_{31} , as the biomass of m_1 at
 684 steady state is zero. Therefore we can directly conclude that for a_{21} and a_{31} small enough,
 685 condition (24) is satisfied and $\lambda_1 < 0$. Hence, competition between m_1 and m_2 needs to be
 686 strong enough in order for the steady state $(0, m_2^*, m_3^*)$ to be locally stable.

687 To find eigenvalues λ_2 and λ_3 we consider the second factor of Eq. (23). We expand the
 688 bracket and obtain

$$\lambda^2 + \underbrace{(\mu_m m_2^* + \mu_m m_3^*)}_{:=B} \lambda + \underbrace{\mu_m^2 m_2^* m_3^* - \frac{(q_{cm}\beta p^*)^2 m_2^* m_3^* a_{23} a_{32}}{(a_{23} + m_2^*)^2 (a_{32} + m_3^*)^2}}_{:=C} = 0. \quad (25)$$

689

690 Eq. (25) is a quadratic with $B > 0$. As long as $C > 0$, the solutions to Eq. (25), corresponding
 691 to the eigenvalues λ_2 and λ_3 , have a negative real part. We find therefore the following
 692 condition for stability of the steady state $(0, m_2^*, m_3^*)$:

$$\frac{a_{23} a_{32}}{(a_{23} + m_2^*)^2 (a_{32} + m_3^*)^2} < \left(\frac{\mu_m}{q_{cm}\beta p^*} \right)^2. \quad (26)$$

693

694 Equation (26) resembles the condition of Eq. (17) derived for the 2 species case. As discussed
 695 above, when a gets large, i.e. competition among mutualists decreases, we expect the values

of m_2^* , m_3^* and p^* to tend to the steady states of the corresponding non-competitive model (Martignoni et al.). Because the values of p^* , m_2^* and m_3^* are bounded (see Fig. S2), and so is p^*/m^* (see Fig. S3), condition (26) is satisfied for a_{23} and a_{32} large enough, i.e. competition between m_2 and m_3 is weak.

We can conclude that in order for the steady state $(0, m_2^*, m_3^*)$ to be locally stable, both conditions (24) and (26) need to be satisfied. These conditions state that competition between m_1 and m_2 and between m_1 and m_3 needs to be strong, while competition between m_2 and m_3 needs to be weak.

In sum, the steady state $(m_1^*, 0, 0)$ is locally stable when m_1 is a strong competitor and the steady state $(0, m_2^*, m_3^*)$ is locally stable when competition between m_1 and both, m_2 and m_3 , is strong, while competition between m_2^* and m_3^* is weak. When m_1 competes strongly with m_2 and m_3 but m_2 and m_3 compete weakly with m_1 , only the steady state $(m_1^*, 0, 0)$ is stable and m_2 and m_3 will be driven to extinction by m_1 . These scenarios correspond to cases B(iii) and (vi) of Table S1. When neither the $(m_1^*, 0, 0)$ nor the $(0, m_2^*, m_3^*)$ steady states are stable (cases B(i) and B(iii)), the coexistence steady state (m_1^*, m_2^*, m_3^*) must be stable, as the extinction steady state is unstable and fungal growth is asymptotically bounded (Martignoni et al.).

Case C: one plant and multiple AM fungal species

To understand the impact of the introduction of a new fungal species into a coexisting community we consider Eq. (1) for $j = N + 1$. In the equations we use the variable m_c to indicate the introduced fungus and $m_{w1}, m_{w2}, \dots, m_{wN}$ to indicate the N fungal species present in the wild community. To simplify computations, we assume that the competition parameters a_{cw} and a_{wc} quantify the average competition strength between the introduced species and the existing community, are the same for each of the species present. Similarly we assume that competitive interactions among the existing community are on average determined by parameter a_{ww} . Like in the previous analyses, we further assume that all fungal species have identical parameters q_{cm} , q_{hm} and μ_m , and that plant biomass has reached steady state p^* . We denote α_w and β_w as the phosphorus and carbon exchange capacity of the wild community, and α_c and β_c as the phosphorus and carbon exchange capacity of the introduced species. With these adjustments, Eq. (1) can be rewritten as

$$\left\{ \begin{array}{l} \frac{dm_c}{dt} = q_{cm}\beta_c p^* m_c \left(\frac{a_{wc}}{a_{wc} + \sum_j^N m_{wj}} \right) - q_{hm}\alpha_c \frac{p^*}{d + p^*} m_c - \mu_m m_c^2, \\ \frac{dm_{wj}}{dt} = q_{cm}\beta_w p^* m_{wj} \left(\frac{a_{cw}m_c + a_{ww} \sum_{i \neq j}^N m_{wi}}{a_{cw}m_c + a_{ww} \sum_{i \neq j}^N m_{wi} + (m_c + \sum_{i \neq j}^N m_{wi})^2} \right) - q_{hm}\alpha_w \frac{p^*}{d + p^*} m_{wj} - \mu_m m_{wj}^2. \end{array} \right. \quad (27a)$$

727

Stability of the invasion state $(m_c^*, 0, \dots, 0)$: We first investigate the stability of the steady state $(m_c^*, 0, 0, \dots, 0)$, corresponding to the situation in which the introduced species drives the existing community to extinction. The $(N + 1) \times (N + 1)$ -Jacobian obtained by

731 linearising Eq. (27) around $(m_c^*, 0, 0, \dots, 0)$ is given by

$$732 \quad J_{(m_c^*, 0, \dots, 0)} = \begin{pmatrix} -\mu_m m_c^* & -\frac{q_{cm}\beta_c p^* m_c^*}{a_{wc}} & \dots & -\frac{q_{cm}\beta_c p^* m_c^*}{a_{wc}} \\ 0 & \frac{q_{cm}\beta_w p^* a_{cw}}{a_{cw} + m_c^*} - q_{hm}\alpha_w \frac{p^*}{d+p^*} & \dots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \dots & \frac{q_{cm}\beta_w p^* a_{cw}}{a_{cw} + m_c^*} - q_{hm}\alpha_w \frac{p^*}{d+p^*} \end{pmatrix}, \quad (28)$$

with eigenvalues

$$\lambda_1 = -\mu_m m_c^*, \quad (29a)$$

$$\lambda_2 = \frac{q_{cm}\beta_w p^* a_{cw}}{a_{cw} + m_c^*} - q_{hm}\alpha_w \frac{p^*}{d+p^*}, \quad (29b)$$

733 where λ_2 has multiplicity N . Because λ_1 is always negative, the steady state $(m_c^*, 0, 0, \dots, 0)$
734 is locally stable as long as the unique condition

$$735 \quad \frac{a_{cw}}{a_{cw} + m_c^*} < \frac{q_{hm}\alpha_w}{q_{cm}\beta_w(d+p^*)}. \quad (30)$$

736 is satisfied. That is, as long as a_{cw} is small enough, i.e. the introduced species m_c competes
737 strongly with the existing community, Eq. (30) holds true and competitive exclusion can occur.

738 **Stability of the native community:** To understand whether the existing community
739 can as well competitively exclude the introduced species, we investigate under which conditions
740 the steady state $(0, m_{w1}^*, m_{w2}^*, \dots, m_{wN}^*)$ is locally stable. The analysis will give us information
741 on whether the existing community can defend itself from invasion by a strong competitor
742 (in this case, the introduced species). We linearize Eq. (27) around $(0, m_{w1}^*, m_{w2}^*, \dots, m_{wN}^*)$,
743 and obtain the Jacobian

$$744 \quad J_{(0, m_{w1}^*, \dots, m_{wN}^*)} = \begin{pmatrix} \frac{q_{cm}\beta_c p^* a_{wc}}{\sum_j^N m_{wj}^* + a_{wc}} - q_{hm}\alpha_c \frac{p^*}{d+p^*} & 0 & \dots & 0 \\ \frac{q_{cm}\beta_w p^* (a_{cw} - 2a_{ww}) m_{w1}^*}{(a_{ww} + \sum_{i \neq 1}^N m_{wi}^*)^2} & -\mu_m m_{w1}^* & \dots & -\frac{q_{cm}\beta_w p^* a_{ww} m_{w1}^*}{(a_{ww} + \sum_{i \neq 1}^N m_{wi}^*)^2} \\ \vdots & \vdots & \ddots & \vdots \\ \frac{q_{cm}\beta_w p^* (a_{cw} - 2a_{ww}) m_{wN}^*}{(a_{ww} + \sum_{i \neq N}^N m_{wi}^*)^2} & -\frac{q_{cm}\beta_w p^* a_{ww} m_{wN}^*}{(a_{ww} + \sum_{i \neq N}^N m_{wi}^*)^2} & \dots & -\mu_m m_{wN}^* \end{pmatrix}. \quad (31)$$

745 Eigenvalues of (31) are given by the solutions to

$$746 \quad \left(\frac{q_{cm}\beta_c p^* a_{wc}}{\sum_j^N m_{wj}^* + a_{wc}} - q_{hm}\alpha_c \frac{p^*}{d+p^*} - \lambda \right) \times \begin{vmatrix} -\mu_m m_{w1}^* - \lambda & -\frac{q_{cm}\beta_w p^* a_{ww} m_{w1}^*}{(a_{ww} + \sum_{i \neq 1}^N m_{wi}^*)^2} & \dots & -\frac{q_{cm}\beta_w p^* a_{ww} m_{w1}^*}{(a_{ww} + \sum_{i \neq 1}^N m_{wi}^*)^2} \\ -\frac{q_{cm}\beta_w p^* a_{ww} m_{w2}^*}{(a_{ww} + \sum_{i \neq 2}^N m_{wi}^*)^2} & -\mu_m m_{w2}^* - \lambda & \dots & -\frac{q_{cm}\beta_w p^* a_{ww} m_{w2}^*}{(a_{ww} + \sum_{i \neq 2}^N m_{wi}^*)^2} \\ \vdots & \vdots & \ddots & \vdots \\ -\frac{q_{cm}\beta_w p^* a_{ww} m_{wN}^*}{(a_{ww} + \sum_{i \neq N}^N m_{wi}^*)^2} & -\frac{q_{cm}\beta_w p^* a_{ww} m_{wN}^*}{(a_{ww} + \sum_{i \neq N}^N m_{wi}^*)^2} & \dots & -\mu_m m_{wN}^* - \lambda \end{vmatrix} = 0. \quad (32)$$

747
748

From Eq. (32) we can directly derive the first condition for stability, that is

$$749 \quad \frac{a_{wc}}{a_{wc} + \sum_j^N m_{wj}^*} < \frac{q_{hm}\alpha_c}{q_{cm}\beta_c(d + p^*)}. \quad (33)$$

750 Eq. (33) is a generalisation of Eqs. (17) and (24). Because the values of the plant and fungal
751 steady states are bounded (Fig. S2), we can conclude that in order for the existing community
752 to outcompete the introduced species m_c , a_{wc} needs to be small enough, i.e. the existing
753 community should compete strongly enough with the introduced species.

754 If the existing community is large enough, stability can be achieved for weaker competition
755 between the community and the introduced species, i.e. for larger a_{wc} . This means, that
756 the basin of attraction of $(0, m_{w1}^*, \dots, m_{wN}^*)$ increases with increasing N , while the basin of
757 attraction of $(m_c^*, 0, \dots, 0)$ decreases. Hence, for the same competition strength, a more diverse
758 community can outcompete an introduced species there where a less diverse community would
759 be driven to extinction. From the analysis, it emerges therefore that a community composed
760 of multiple species is less vulnerable to invasion by a strong competitor. This outcome is
761 investigated numerically in Fig. S5.

762 If the ratio α_c/β_c is small (i.e. if the introduced species provides low phosphorus to the
763 plant and takes a large amount of carbon), than stability is achieved for smaller values of a_{wc} ,
764 hence for larger competition strength between the community and the introduced species.
765 The basin of attraction of $(0, m_{w1}^*, \dots, m_{wN}^*)$ decreases therefore when the mutualist quality
766 of the introduced species is low. These results are illustrated in Fig. S6.

767

768 To derive the second condition for stability of the steady state $(0, m_{w1}^*, \dots, m_{wN}^*)$ we look
769 at the second factor of Eq. (32). We assume that all fungal species in the community are
770 identical, and therefore $m_{w1}^* = \dots = m_{wN}^* = m_w^*$, and $\sum_{i \neq j}^N m_{wi}^* = (N - 1)m_w^*$. We set

$$771 \quad b = -\frac{q_{cm}\beta_w p^* a_{ww} m_w^*}{(a_{ww} + (N - 1)m_w^*)^2} \quad (34)$$

772 and we rewrite the determinant of Eq. (32) as

$$773 \quad M = \begin{pmatrix} -\mu_m m_w^* - \lambda & b & \dots & b \\ b & -\mu_m m_w^* - \lambda & \dots & b \\ \vdots & \vdots & \ddots & \vdots \\ b & b & \dots & -\mu_m m_w^* - \lambda \end{pmatrix}. \quad (35)$$

774 Let us define the diagonal matrix

$$775 \quad D = \text{diag}(M) - bI, \quad (36)$$

776 where I is the $(N \times N)$ -identity matrix. We can rewrite

$$777 \quad M = D + b e e^T, \quad (37)$$

778 where e is a all-one $(N \times 1)$ -vector. According to the matrix determinant lemma (Ding and
779 Zhou, 2007), we obtain

$$780 \quad \det(M) = \det(D + b e e^T) = \det(D)(1 + b e^T D^{-1} e), \quad (38)$$

781 We know that

$$782 \det(D) = (-\mu_m m_w^* - \lambda - b)^N, \quad (39)$$

783 and

$$784 e^T D^{-1} e = \frac{N}{-\mu_m m_w^* - \lambda - b}. \quad (40)$$

785 Hence, by using Eq. (38), the determinant of M can be computed as

$$786 \det(M) = (-\mu_m m_w^* - b - \lambda)^{N-1} (-\mu_m m_w^* + b(N-1) - \lambda). \quad (41)$$

The additional eigenvalues of Eq. (31) can be found by setting Eq. (41) equal to zero and solving for λ . By substituting the expression for b (Eq. (34)), we obtain

$$\lambda_2 = -\mu_m m_w^* - (N-1) \frac{q_{cm} \beta_w p^* a_{ww} m_w^*}{(a_{ww} + (N-1)m_w^*)^2}, \quad (42a)$$

$$\lambda_3 = -\mu_m m_w^* + \frac{q_{cm} \beta_w p^* a_{ww} m_w^*}{(a_{ww} + (N-1)m_w^*)^2}, \quad (42b)$$

787 where λ_3 has multiplicity $(N-1)$.

788 The eigenvalue λ_2 is always negative. As long as λ_3 is negative as well, the steady state
789 $(0, m_{w1}^*, \dots, m_{wN}^*)$ is locally stable. Hence, for stability we require

$$790 \frac{a_{ww}}{(a_{ww} + (N-1)m_w^*)^2} < \frac{\mu_m}{q_{cm} \beta_w p^*}. \quad (43)$$

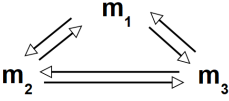
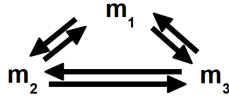
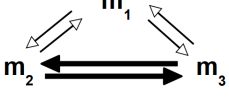

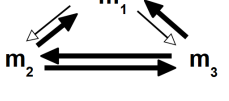
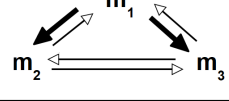
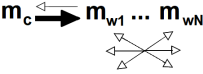
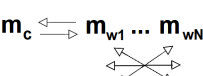
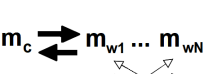
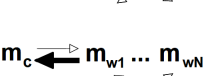
791 Eq. (43) is a generalisation of Eqs. (17) and (26). Because the values of p^* , m_w^* and of the quo-
792 tient p^*/m_w^* are bounded (see Figs. S2 and S3), condition (43) holds as long as a_{ww} is large
793 enough. This means, if competitive interactions among the existing community are weak,
794 coexistence is observed. For large N , coexistence is observed even for stronger competitive
795 interactions among mutualists (i.e., for a smaller a_{ww}). Hence, the presence of higher diversity
796 promotes the coexistence of species that would otherwise competitively exclude each others.

797
798 These findings are summarized in Table S1 and in Fig. 2. We conclude that if the in-
799 troduced species is a weak competitor (Cases C(ii) and C(iv) of Table S1 and scenarios (2)
800 and (4) of Fig. 2), neither condition (30) nor condition (33) are satisfied, and the competitive
801 exclusion steady state $(m_c^*, 0, \dots, 0)$ is therefore unstable. If the native community competes
802 weakly against the introduced species (Case C(ii) and scenario (2)), the coexistence steady
803 state $(m_c^*, m_{w1}^*, \dots, m_{wN}^*)$ is stable, meaning that in this case the introduced species can estab-
804 lish and coexist with the existing community. If the introduced species is a strong competitor
805 (Cases C(i) and C(iii) of Table S1 and scenarios (1) and (3) of Table 2), a_{cw} is small enough
806 to satisfy condition (30), and the introduced species can competitively exclude the mutualist
807 community. However if the existing community competes strong enough with the introduced
808 species (i.e., a_{wc} is small enough to satisfy condition (33)), and competitive interactions among
809 the existing community are weak (i.e. a_{ww} is large enough and condition (43)) holds), then
810 either the introduced species or the existing community survives (Case (iv) and scenario (4)).
811 This phenomenon is a consequences of the bistability of the steady states $(m_c^*, 0, \dots, 0)$ and
812 $(0, m_{w1}^*, \dots, m_{wN}^*)$. Thus the invasion of the commercial AMF or the survival of the estab-
813 lished community will strongly depends on the initial amount of m_c compared to the one of
814 the community. The size of the basin of attraction of the steady state $(0, m_{w1}^*, \dots, m_{wN}^*)$ is
815 directly related to a larger total fungal biomass of the community, achieved when a larger
816 number of weak competing species are present. Higher resource acquisition efficiency (ex-
817 pressed in terms of fungal parameters) can lead to a competitive advantage. These results are
818 explored numerically in Figs. S5 and S6. If the community competes only weakly with the

819 introduced species, i.e. a_{wc} is large and condition (33) is not satisfied, then only the steady
820 state indicating competitive exclusion of the community by the strong competitor is stable
821 (Case C(i) and scenario (1)). In this case, the introduced species m_c will possibly invade and
822 displace the wild community.

Tables and Figures

Table S1: Representation of the direct interactions between fungal species (m_i) sharing a resource supplied by the same host plant (not included in the figure). Arrows indicate competition between mutualists, for space or access to plant roots, where competition can be weak (thin arrows) or strong (thick arrows). The last column summarizes the steady states stability resulting from the linear analysis presented in the supplementary information.

SCENARIOS			Stable steady states
Case A	(i)	$m_1 \rightleftharpoons m_2$	(m_1^*, m_2^*)
	(ii)	$m_1 \rightleftarrows m_2$	$(m_1^*, 0)$ and $(0, m_2^*)$
	(iii)	$m_1 \leftleftarrows m_2$	$(m_1^*, 0)$
Case B	(i)		(m_1^*, m_2^*, m_3^*)
	(ii)		$(m_1^*, 0, 0)$, $(0, m_2^*, 0)$ and $(0, 0, m_3^*)$
	(iii)		(m_1^*, m_2^*, m_3^*)
	(iv)		$(m_1^*, 0, 0)$ and $(0, m_2^*, m_3^*)$
	(v)		$(0, m_2^*, 0)$ and $(0, 0, m_3^*)$
	(vi)		$(m_1^*, 0)$
Case C	(i)		$(m_c^*, 0, \dots, 0)$
	(ii)		$(m_c^*, m_{w1}^*, \dots, m_{wN}^*)$
	(iii)		$(m_c^*, 0, \dots, 0)$ and $(0, m_{w1}^*, \dots, m_{wN}^*)$
	(iv)		$(0, m_{w1}^*, \dots, m_{wN}^*)$

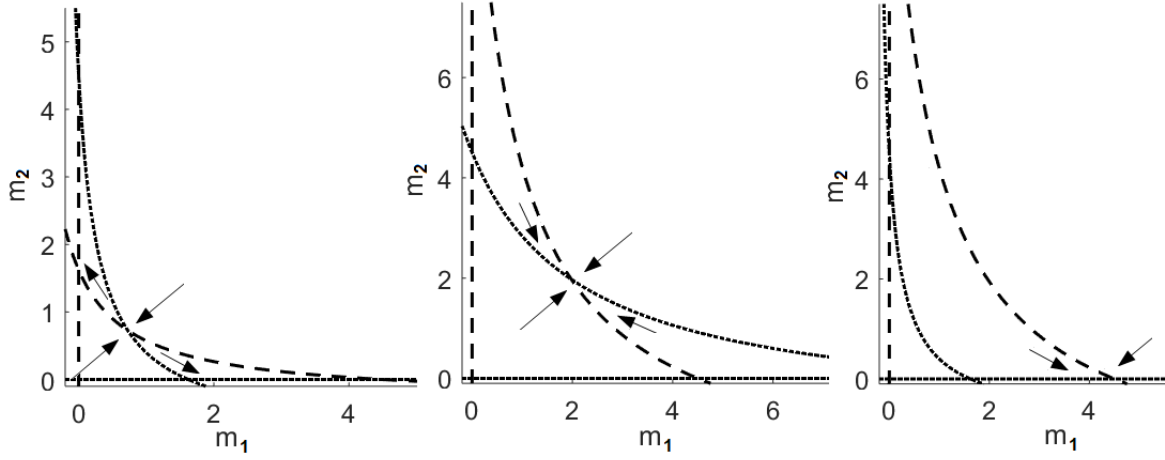


Fig. S1: Phase-plane portrait of the model of Eq. (9). The horizontal and vertical axes represent the biomass of fungal species 1 and 2 respectively. Plant biomass is assumed to be at steady state. Left panel: Competition between species 1 and 2 is strong ($a_{12} = a_{21} = 0.3$). In this case the coexistence steady state is unstable while the competitive exclusion steady states $(m_1^*, 0)$ and $(0, m_2^*)$ are both stable. Central panel: Competition between species 1 and 2 is weak ($a_{12} = a_{21} = 2.2$) and the coexistence steady state (m_1^*, m_2^*) is stable. Right panel: Species 1 is a strong competitor while species 2 is a weak competitor. In this case, only the competitive exclusion steady state $(m_1^*, 0)$ is stable. Model parameters are $q_{hp} = 3$, $q_{cm} = 2$, $q_{hm} = q_{cp} = 1$, $\beta = \alpha = 0.4$, $\mu_m = \mu_p = 0.3$, $r_p = 0.02$, $d = 1.2$.

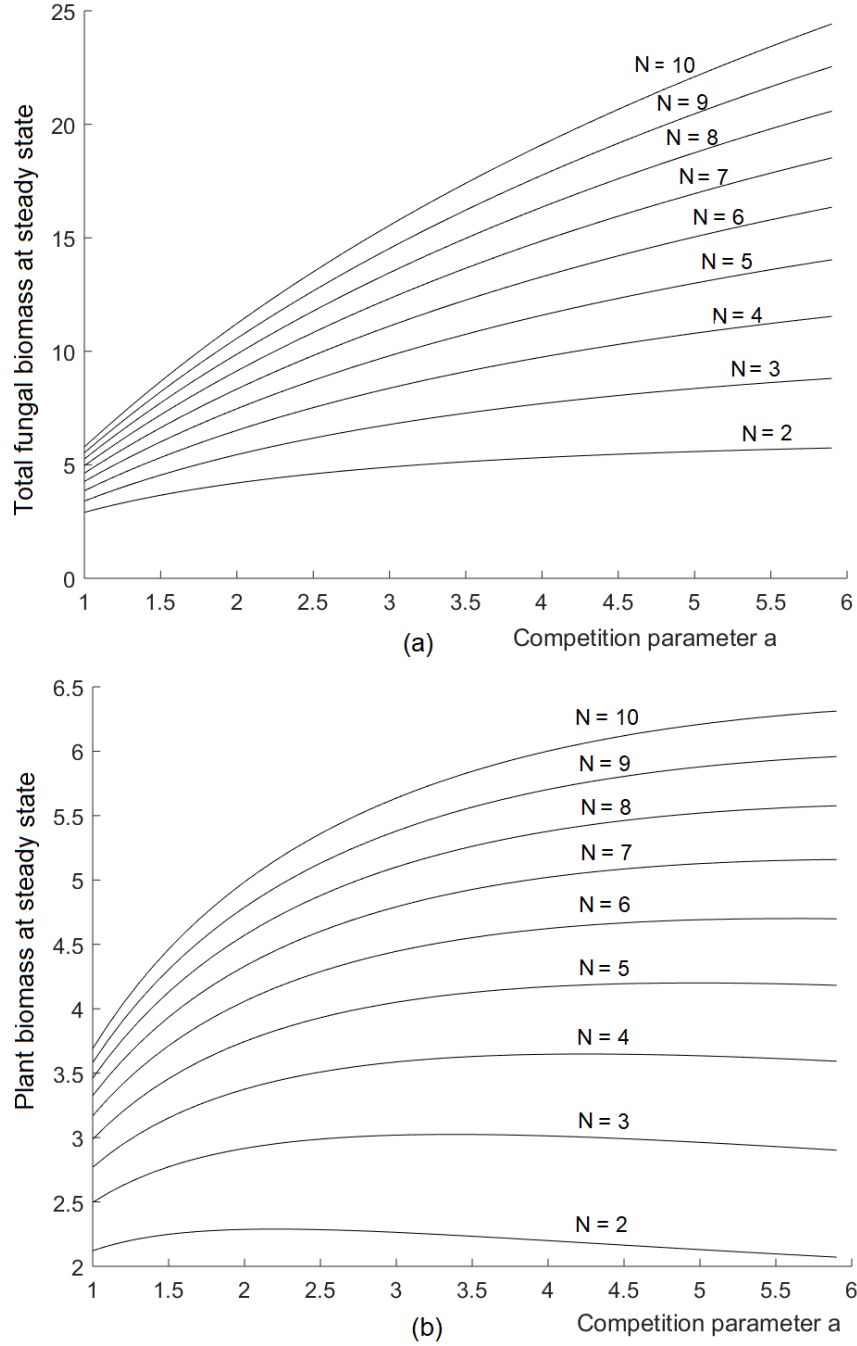


Fig. S2: Dependence of (a) total fungal biomass at steady state and (b) plant biomass at steady state on the competition parameter a , when a plant is associating with a community of N -coexisting mutualists. Different curves indicates the value of the steady states for a different number of mutualists present in the community ($N = 2 \dots 10$). To simplify computations, I assume that all model parameters are equal for the two fungal species and that $a_{ij} = a_{ji} = a$. I thus have the result that $m_j^* = m^*$ and $\sum_j^N m_j^* = Nm^*$. The parameters used for the simulations correspond to those for Fig. S1.

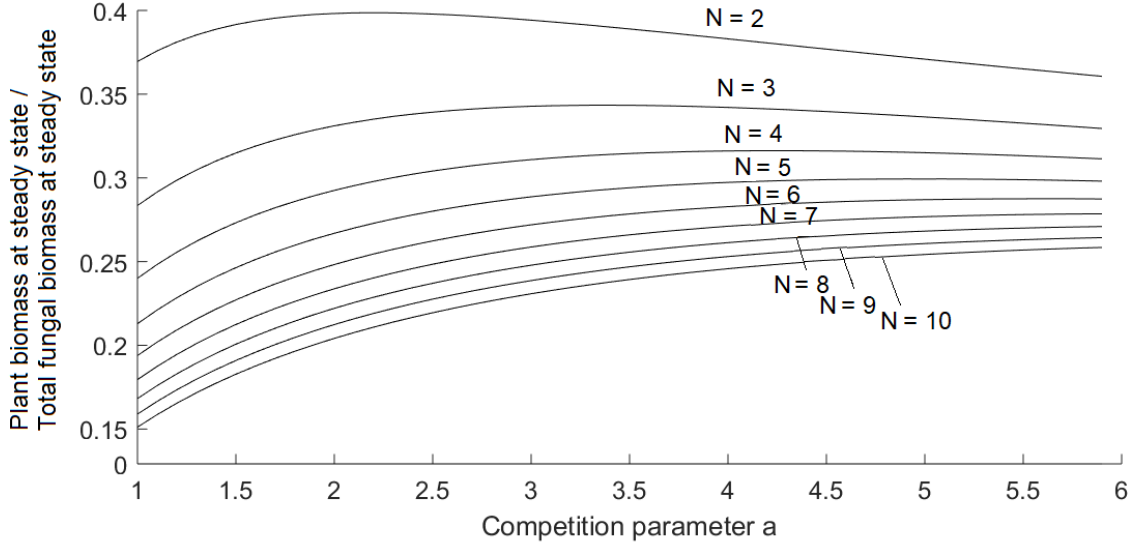


Fig. S3: Ratio of plant biomass at steady state (p^*) to total the fungal biomass at steady state of a community of N -coexisting mutualists ($\sum_j m_j^*$), as a function of the competition parameter a . Different curves corresponds to a different number of mutualists present in the community ($N = 2 \dots 10$). Similarly to Fig. S2, to simplify computations, we assume that all model parameters are equal for the two fungal species and that $a_{ij} = a_{ji} = a$, and therefore that $m_j^* = m^*$ and $\sum_j^N m_j^* = Nm^*$. The parameters used for the simulations correspond to those for Fig. S1.

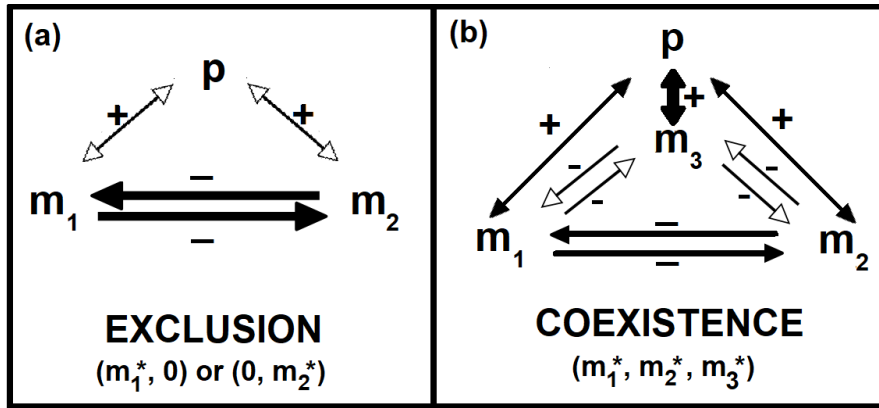


Fig. S4: Diagram representing the direct interactions of a plant (p) in association with two or three mutualists (m_1 , m_2 and m_3), corresponding to case B(iii) of Fig. 1 and Table S1. Interactions can be mutualistic ('+') or competitive ('-'). Arrow thickness represents the strength of the interactions. (a) When only two strongly competing mutualists (m_1 and m_2) are in association with the plant, coexistence is not possible and one of the two species will drive the other to extinction. (b) When a third weakly competing mutualist is present, coexistence is achieved. The presence of m_3 increases plant biomass (i.e. resource availability), reduces competition between m_1 and m_2 and promotes their mutualistic interactions with the plant.

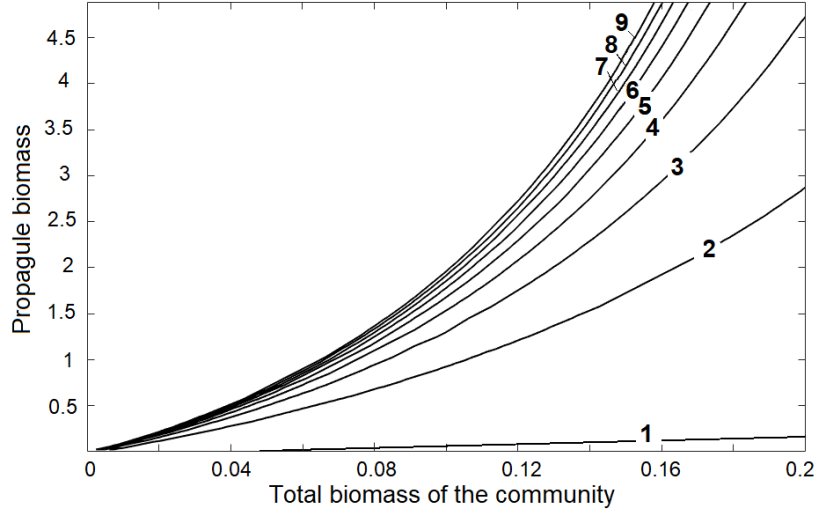


Fig. S5: Outcome of competition between a strong competitor (the alien species m_c) and a native community of mutualists (m_{w_j}), for different initial biomasses. The solid curves represent the boundaries between establishment of the alien species (area above each line) and establishment of the community (area below each line) for the situation illustrated in scenario (3) of Fig. 2. The horizontal axis represents the total initial biomass of the community, while the vertical axis represents the initial biomass of the alien species (or propagule biomass). Different curves correspond to a different number of species present in the community, ranging from 1 to 9. Increasing the number of species in the community increases resilience of the community against invasion, in the sense that for the same total biomass of the community, a higher propagule biomass is needed in order to displace the community. Competition parameters used for the simulations are $a_{wc} = a_{cw} = 0.3$, $a_{ww} = 2.2$. Other model parameters are $q_{hp} = 3$, $q_{cm_j} = 2$, $q_{hm_j} = q_{cp} = 1$, $\beta_j = \alpha_j = 0.4$, $\mu_p = \mu_{m_j} = 0.3$, $r_p = 0.02$, $d = 1.2$, $\alpha_c = \alpha_w = \beta_c = \beta_w = 0.4$.

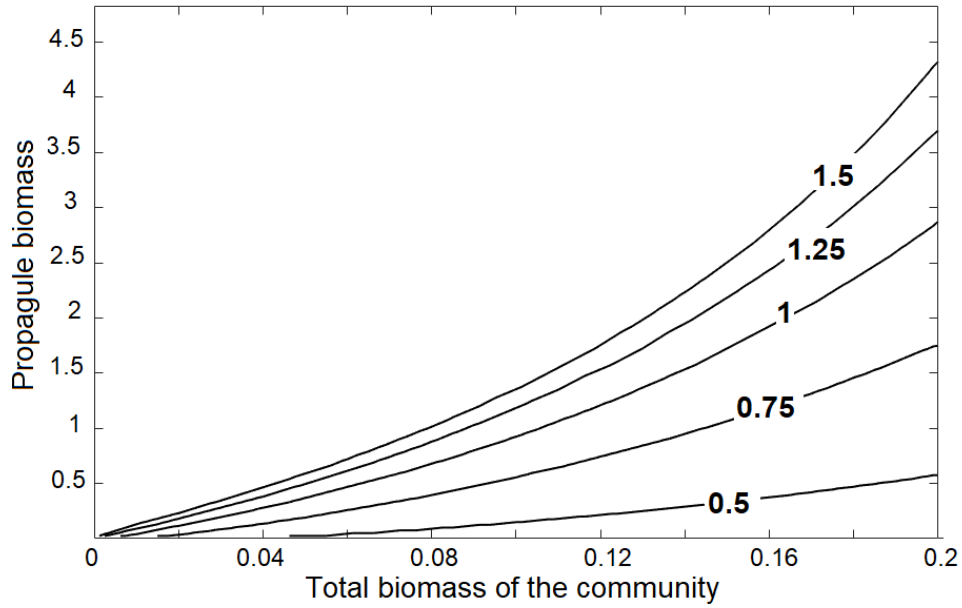


Fig. S6: Outcome of competition between a strong competitor (m_c) and a community of weak competing mutualists (m_{w_j}), corresponding to case C(ii) in Fig. 1 and Table S1, for different ratios of the phosphorus and carbon exchange ability of the alien species (parameters α_c and β_c respectively). The solid curves represent the boundaries between establishment of the alien species (area above each line) and establishment of the community (area below each line). The curve labeled with a ‘1’ corresponds to the case in which the native community and the alien species have the same resource exchange ability (i.e. $\alpha_c/\beta_c = \alpha_w/\beta_w$). Other curves correspond to situations where the alien species has a higher/lower resource exchange ability with respect to the native community (i.e. $\alpha_c/\beta_c = x \alpha_w/\beta_w$, where $x = 0.5, 0.75, 1.25, 1.5$). The plot shows that establishment of an alien is more likely if the introduced species has lower mutualist quality. Exact values are chosen for the resource exchange parameters are: $\alpha_w = \beta_w = 0.4$ for all curves, while $\alpha_c = 0.3, 0.35, 0.4, 0.45, 0.5$ and $\beta_c = 0.6, 0.467, 0.4, 0.36, 0.333$ respectively. $N = 2$, while other parameters correspond to those of Fig. S5.