



HAL
open science

Investigating the impact of the mycorrhizal inoculum on the resident fungal community and on plant growth

Maria Martignoni, Jimmy Garnier, Miranda Hart, Rebecca Tyson

► To cite this version:

Maria Martignoni, Jimmy Garnier, Miranda Hart, Rebecca Tyson. Investigating the impact of the mycorrhizal inoculum on the resident fungal community and on plant growth. *Ecological Modelling*, 2020, pp.109321. 10.1016/j.ecolmodel.2020.109321 . hal-03006657

HAL Id: hal-03006657

<https://hal.science/hal-03006657>

Submitted on 17 Nov 2020

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Investigating the impact of the mycorrhizal inoculum on the resident fungal community and on plant growth

Maria M. Martignoni¹, Jimmy Garnier², Miranda M. Hart³, and Rebecca C. Tyson⁴

¹Department of Mathematics, University of British Columbia, maria.martignonimseya@ubc.ca

²Laboratoire de Mathématiques (LAMA), Université de Savoie, jimmy.garnier@univ-smb.fr

³Department of Biology, University of British Columbia, miranda.hart@ubc.ca

⁴Department of Mathematics, University of British Columbia, rebecca.tyson@ubc.ca

November 16, 2020

Abstract

In the last few decades, microbial inoculants have been used as organic fertilizers worldwide. Among the most widely used commercial products are arbuscular mycorrhizal (AM) fungi, as these fungi can associate with a variety of crops. Despite the potential benefits for soil quality and crop yield associated with AM fungal colonization, experiments assessing the persistence of the fungi in the field have yielded inconsistent results. Additionally, it is not yet clear whether or not the introduction of commercial inoculants could lead to changes to the resident fungal community, and eventually to invasion of the commercial products with a possible displacement of resident species. Here we use a partial differential equation model to assess the potential biodiversity risks and productivity benefits deriving from inoculation. We study the impact of AM fungal inoculation on the resident fungal community and on plant growth at a landscape scale. We determine how inoculant persistence and spread is affected by its competition with resident fungal species, by its mutualist quality, and by fungal dispersal. **Our findings suggest that the increase in fungal abundance due to inoculation always leads to a short-term increase in host productivity, regardless of inoculant identity. However, the use of strongly competing inoculants constitutes a biodiversity risk, and may result in the invasion of low quality mutualists.**

Keywords : Arbuscular mycorrhizal fungi (AMF), inoculum, inoculants, model, invasion, spread, persistence, establishment, agriculture, productivity, diversity, traveling waves, mutualism, competition

1 Introduction

Arbuscular mycorrhizal (AM) fungi are beneficial fungi living in association with the roots of the vast majority of plants and facilitating plant access to nutrients in the soil (Smith and Read, 2010; Jeffries et al., 2003). Additional benefits provided to the plant by AM fungi are pathogen protection (Poza and Azcón-Aguilar, 2007) and resistance against abiotic stress, such as drought or salinity (Latef et al., 2016). The plant, in exchange, provides the fungi with fixed carbon (Smith and Read, 2010). Because of their positive influence on plant fitness, AM fungi have been commercialised, and are widely used as organic fertilizers for a large variety of crops, such as maize, wheat, soybeans, tomatoes, or strawberries (Gianinazzi and Vosátka, 2004).

Despite the potential benefits of field inoculation with commercial AM fungi, studies investigating the effective establishment of mycorrhizal inoculants have contradictory results (Berruti et al., 2016; Baum et al., 2015; Verbruggen et al., 2013). Some observations show field establishment and improved crop yield (Bender et al., 2019; Köhl et al., 2016; Buysens et al., 2016), while other studies show poor establishment of the inoculated species (Emam, 2016; Loján et al., 2017; Ryan and Graham, 2002). Moreover, it is still unclear how resident fungal communities respond to the introduction of a new fungal species (Thomsen and Hart, 2018; Hart et al., 2018). In some studies, inoculation caused little or no impact on the resident fungal community (Loján et al., 2017; Šýkorová et al., 2012), while other observations show that resident species were displaced by the introduction of inoculants (Koch et al., 2011; Pellegrino et al., 2012; Symanczik et al., 2015; Bender et al., 2019). These last results in particular raise concerns over whether inoculated fungi could possibly spread to non-target areas causing a loss in soil biodiversity and, ultimately, negative effects on plant productivity (Schwartz et al., 2006; Hart et al., 2017; Ricciardi et al., 2017). It is therefore important to assess the conditions under which the use of commercial inoculants is beneficial or harmful, at short or large time scale.

Due to the challenges presented by large scale application and monitoring of inoculants, the current understanding of the impact of inoculation is largely based on short-term greenhouse experiments, comparing plant performance before and after inoculation (Berruti et al., 2016), while fewer studies have considered the long term persistence of inoculants in field conditions (Pellegrino et al., 2012; Farmer et al., 2007; Pellegrino et al., 2011; Šýkorová et al., 2012; Kokkoris et al., 2019a). Additionally, less is known about the spread of non-pathogenic microbes in general (Litchman, 2010; Peay and Bruns, 2014; Peay et al., 2012; Davison et al., 2012; Thiet and Boerner, 2007). While some empirical work has been conducted on the dispersal of ectomycorrhizal fungi (Thiet and Boerner, 2007; Vellinga et al., 2009) no existing empirical or theoretical studies focus on the spread of AM inoculants in the field.

Mathematical modeling and computer simulations have proven to be useful tools for generating long-term predictions at a landscape scale when field trials are logistically not feasible (Jørgensen, 1994; Odenbaugh, 2005; Haller, 2014). Here we use a theoretical approach to determine the potential biodiversity risks and productivity benefits associated with inoculation. In particular, we aim to provide useful information for the selection of inoculants that are likely to promote plant growth while helping with the persistence or restoration of the resident fungal community. To undertake this task, we develop a partial differential equation model to investigate conditions for the establishment, persistence and spread of AM inoculants, and the resulting consequences on the resident fungal community and on plant growth.

Although many theoretical approaches have been used to study the spread of pathogenic fungi (Soubeyrand et al., 2008; Burie et al., 2008), the mechanisms driving the spread of AM fungi are substantially different, as these fungi are obligate symbionts, and their growth strictly depends on their mutualistic relationship with a host plant. Plant growth, in turn, is enhanced

50 by fungal mutualists, where the degree of benefit depends on the specific fungal community
51 composition and on the strength of the competitive interactions among the different fungal
52 mutualists present (Smith and Read, 2010; Bever, 2002). Our model can be used to investigate
53 how the spatio-temporal distribution of plant and fungal biomass is affected by mutualistic
54 interactions between the plant and the fungi, and by competitive interactions between fungal
55 species, what will give us information about the impact of the mycorrhizal inoculum on plant
56 and fungal growth on a landscape scale. We will also investigate how the mutualistic quality
57 of the inoculated fungus and its dispersal ability can affect the dynamics of the resident
58 community. As our model is general, our results are not limited to a specific inoculant, nor
59 to specific crops, but apply to any inoculants and crops.

60 2 Model and Methods

61 We consider the scenario in which an inoculant (whose biomass density is represented by the
62 variable m_c) is introduced in a crop field inhabited by a resident community consisting of N
63 fungal species (with biomass density m_{w_j} , where $j = 1..N$). We assume that the plant is
64 present across the landscape (with continuous biomass density p). With the term ‘resident
65 community’ we indicate the assemblage of AM fungal species that were present before the
66 introduction of the inoculant (not necessarily at equilibrium). With the term ‘inoculant’ we
67 indicate a fungal species that is introduced to the resident community and can associate with
68 the same plant as the resident fungi present.

69 AM fungi can spread in the soil through hyphae (Friese and Allen, 1991), or through short
70 or long range dispersal of spores by different agents (Warner et al., 1987). To model fungal
71 spread, we will consider only short range dispersal of fungal biomass, either through hyphae or
72 spores (not distinguishable in the model). We assume therefore that fungi disperse by random
73 diffusion, and quantify the dispersal ability of each fungal species by its diffusion coefficient
74 (D_c for the inoculant and D_{w_j} for each of the resident fungal species).

75 All fungi are in a mutualistic relationship with the plants, where nutrients exchanged are
76 phosphorus (fungi to plant) and carbon (plant to fungi). Competition between fungal species
77 can reduce the amount of carbon received by both competitors. Mathematically, we write

$$\begin{aligned}
\partial_t p(x, t) &= f_p(p, m_c, m_{w_j}), \\
\partial_t m_c(x, t) &= D_c \partial_x^2 m_c + f_{m_c}(p, m_c, m_{w_j}), \\
\partial_t m_{w_j}(x, t) &= D_{w_j} \partial_x^2 m_{w_j} + f_{m_{w_j}}(p, m_c, m_{w_j}), \quad \text{with } j = 1..N,
\end{aligned} \tag{1}$$

79 where the growth functions f_p , f_{m_c} and $f_{m_{w_j}}$ describe the interactions between the plant and
80 the AM fungi and were introduced in Martignoni et al. (2020b). More precisely, the form of
81 the growing functions is the following:

$$\begin{aligned}
f_p &= \underbrace{\alpha_c f_{hp}(p, m_c)}_{\text{phosphorus received}} + \underbrace{\sum_{j=1}^N \alpha_{w_j} f_{hp}(p, m_{w_j})}_{\text{phosphorus received}} - \underbrace{\beta_c f_{cp}(p, m_c) C_{m_c}}_{\text{carbon supplied}} - \underbrace{\sum_{j=1}^N \beta_{w_j} f_{cp}(p, m_{w_j}) C_{m_{w_j}}}_{\text{carbon supplied}} + \underbrace{r_p(p)}_{\text{plant fitness}}, \\
f_{m_c} &= \underbrace{\beta_c f_{cm}(p, m_c)}_{\text{carbon received}} C_{m_c} - \underbrace{\alpha_c f_{hm}(p, m_c)}_{\text{phosphorus supplied}} - \underbrace{\mu_{m_c} m_c^2}_{\text{fungal maintenance}}, \\
f_{m_{w_j}} &= \underbrace{\beta_{w_j} f_{cm}(p, m_{w_j})}_{\text{carbon received}} C_{m_{w_j}} - \underbrace{\alpha_{w_j} f_{hm}(p, m_{w_j})}_{\text{phosphorus supplied}} - \underbrace{\mu_{m_{w_j}} m_{w_j}^2}_{\text{fungal maintenance}}, \quad \text{with } j = 1..N.
\end{aligned} \tag{2}$$

82

83 A description of the model parameters is given in Table 1. Below we explain the key com-
 84 ponents of the model. The complete version of the model is provided in the supplementary
 85 information, Eq. (6).

86 Nutrient exchange with the plant is determined by the functions f_{cp} and f_{cm} (carbon
 87 transfer), and f_{hp} and f_{hm} (phosphorus transfer). Carbon transfer depends linearly on plant
 88 and fungal biomass densities (i.e., $\propto pm_s$, where $s = w_j, c$), while phosphorus transfer depends
 89 on fungal biomass density only, when the plant is large enough, while plant biomass limits
 90 phosphorus transfer at low density (i.e., $\propto \frac{p}{d+p}m_s$, where $s = w_j, c$) (Martignoni et al., 2020a).
 91 Fungal species may differ in their ability to transfer phosphorus to the plant (α_s parameters)
 92 and in their access to plant carbon (β_s parameters), where the α_s/β_s ratio will be used
 93 throughout the manuscript to characterise the mutualist quality of a fungal species. Plant
 94 growth in the absence of the fungi is logistic, and expressed by the function $r_p(p)$. AM fungi
 95 can not survive in the absence of the host plant, therefore no intrinsic growth terms appear
 96 in $f_{m_{w_j}}$ and f_{m_c} .

97 The functions C_{m_c} and $C_{m_{w_j}}$ quantify the reduction in access to host carbon by fungal
 98 species, either the inoculant (m_c) or a resident fungal species (m_{w_j}), due to competition with
 99 other fungi in the community. The competitive effect exerted by a fungal species on another
 100 depends on its competitive ability (a_{s_1, s_2} -parameters) and on the proportion, in terms of
 101 biomass, that this species occupies within the competing community. We write

$$\begin{aligned}
 C_{m_c} &= \frac{\sum_j a_{w_j c} m_{w_j}}{\sum_j a_{w_j c} m_{w_j} + (\sum_j m_{w_j})^2}, \\
 C_{m_{w_j}} &= \frac{a_{c w_j} m_c + \sum_{i \neq j} a_{w_i w_j} m_{w_i}}{a_{c w_j} m_c + \sum_{i \neq j} a_{w_i w_j} m_{w_i} + (m_c + \sum_{i \neq j} m_{w_j})^2},
 \end{aligned}
 \tag{3}$$

103 where large a_{s_1, s_2} parameters result in weak competition, and small a_{s_1, s_2} parameters result
 104 in strong competition, as the carbon uptake capacity of a species is significantly reduced for
 105 small a_{s_1, s_2} but not for large a_{s_1, s_2} (i.e., the terms C_{m_c} and $C_{m_{w_j}}$ tend to 1 for large a_{s_1, s_2}
 106 and tend to zero for small a_{s_1, s_2}). Note that when only one species is present, Eq. (3) tends
 107 to 1 as no competition is observed. To ensure coexistence of resident species, we assume $a_{w_j w_i}$
 108 parameters to be large (i.e., competition between resident fungal species is small) (Martignoni
 109 et al., 2020b), while we vary parameters $a_{c w_j}$ and $a_{w_j c}$, quantifying the competitive interactions
 110 between the inoculant and resident fungal species.

111 We will first study the model dynamics analytically (see section 2.1) to quantify the fun-
 112 gal dispersal patterns that can be observed, with respect to the entire parameter space, and
 113 identify which factors can accelerate the invasion process or prevent an invasion. Through
 114 numerical simulations, we will then use the model to provide useful practical insights into
 115 agroecosystem management (see section 2.2), e.g., evaluating the impact of inoculation on
 116 productivity and assessing the risk of dispersal of low quality mutualists between neighbour-
 117 ing fields. Numerical simulations will be computed in Matlab R2017a using a semi-implicit
 118 scheme (Tyson et al., 2000), where the reaction term is solved explicitly and the diffusion term
 119 is solved implicitly. The discretization used for the space is $dx = 0.05$, and the discretion used
 120 for the time is $dt = 0.05$.

121 2.1 Investigating inoculum persistence and spread

122 To simplify the analysis, we assume that resident fungal species have the same competitive
 123 effect on each other (i.e., $a_{w_i w_j} = a_{w w}$ for all i, j), that each of the resident fungal species
 124 present has the same competitive effect on the inoculated species (i.e., $a_{w_j c} = a_{w c}$ for all j),
 125 and that the inoculant has the same competitive effect on each resident fungal species (i.e.,

126 $a_{cw_j} = a_{cw}$ for all j). Additionally, we assume that resident fungal species have identical
127 fungal parameters, while resident and inoculated fungal species differ only in their diffusive
128 ability (D_c and D_w parameters), and mutualist quality (i.e., α_s and β_s parameters).

129 We investigate four different scenarios which differ by the intensity of competition be-
130 tween the inoculum and resident fungal species, as described in Table 2. These scenarios are
131 representative for the whole parameter space for which mutualism establishment can occur
132 (Martignoni et al., 2020a,b). In case (A) competition between resident fungal species and
133 the inoculated species is weak (i.e., parameters a_{wc} and a_{cw} are large), e.g., due to functional
134 complementarity between the inoculant and the resident species present. In cases (B) and (C)
135 competition between resident fungal species and the inoculated species is asymmetric, where
136 the superior competitor is either the resident fungal species (if $a_{wc} < a_{cw}$) or the inoculated
137 species (if $a_{cw} < a_{wc}$). In case (D) competition between resident fungal species and the
138 inoculated species is strong (a_{cw} and a_{wc} are small), e.g., due to functional overlap between
139 the inoculant and any of the resident species present. Quantitative criteria and steady sta-
140 bility for these four cases in the non-spatial case are given in Table 2. Since the output of
141 case (D) depends on the initial distribution of inoculant, we distinguish between case (Da),
142 where the inoculant is introduced over a small proportion of the field, and case (Db), where
143 the inoculant is introduced over a large proportion of the field.

144 Analytical criteria to determine a lower bound for the spreading speed of resident fungi
145 and of the inoculant will be provided for cases (A)-(C), while the sign of the spreading speed
146 will be determined for cases (Da). Analytical spreading speed will be compared with numerical
147 solutions. Case (Db) will be investigated numerically.

148 2.2 Agroecosystem management issues

149 To investigating the spread of inoculants between neighboring fields, we consider a landscape
150 consisting of two fields next to each other. We assume that the field on the left comprises only
151 the fungal inoculant, while the field on the right is inhabited by an established resident fungal
152 community. We use numerical simulations to look at the spread of the inoculant from the
153 left to the right field, when competition between the inoculant and resident fungal species is
154 weak or strong. As it has been proposed that commercial inoculants invest more in their own
155 reproduction at the expenses of their mutualistic relationship with the plant (Kokkoris et al.,
156 2019b), we assume that the inoculant has lower resource exchange capacity than resident
157 species (i.e., lower α_c/β_c ratio). We consider the situation in which the resident community
158 consists of two fungal species, and the situation in which only one resident fungal species is
159 present.

160 Finally, to evaluate productivity in response to inoculation, we assume that inoculation
161 occurs at the left edge of the landscape and we simulate plant and fungal growth and spread
162 over time, when the inoculant can be a weak or a strong competitor. We focus on the effect of
163 inoculation in depleted soils (i.e., when density of resident fungi is low), as the model predicts
164 that the introduction of inoculants has little or no effect on plant growth in the presence of a
165 well-established resident fungal community (Martignoni et al., 2020b).

166 3 Results

167 3.1 Investigating inoculant persistence and spread

168 When varying the strength of competition between the community and the inoculated species
169 we encounter four possible combinations (cases (A)-(D)), summarised in Table 2. Case (D)

170 can lead to two possible outcomes depending on the initial distribution of inoculants, cases
 171 (Da) and (Db), shown in Fig. 1. These scenarios cover the whole parameter space for which
 172 mutualism establishment can occur (Martignoni et al., 2020a,b), and quantitative bounds on
 173 the parameters corresponding to each of the cases discussed are given in Table 2. We find that
 174 the inoculant can either not persist in the soil (cases (B) and (Da)), coexist with the resident
 175 fungal community (case (A)), or competitively exclude resident fungal species (cases (C) and
 176 (Db)). A complete mathematical analysis is presented in the supplementary information.
 177 Below we discuss the key results and ecological insights emerging from the analysis.

178 **The inoculant does not persist (cases (B) and (Da)):** If resident fungi are strong
 179 (initially localised) competitors, the community prevents the persistence of the inoculant,
 180 regardless of whether the inoculant is a weak (case (B)) or strong competitor (case (Da)). In
 181 case (B), a weakly competing inoculant is displaced by resident fungal species at a speed with
 182 lower bound given by

$$183 \quad c_w = 2\sqrt{D_w p_c^* \left(\frac{q_{cm} \beta_w a_{cw}}{a_{cw} + m_c^*} - \frac{q_{hm} \alpha_w}{p_c^* + d} \right)}, \quad (4)$$

184 where D_w is the dispersal ability of resident fungal species, α_w and β_w are respectively the
 185 phosphorus and carbon exchange abilities of resident fungal species, a_{cw} indicates the competi-
 186 tive effect of the inoculant toward resident fungal species, and q_{cm} , q_{hm} , and d are other model
 187 parameters defined in Table 1. Parameters m_c^* and p_c^* are respectively the biomass density of
 188 the inoculant and plant at equilibrium in the absence of resident fungi. From the restrictions
 189 imposed on the parameters in cases (B) and (D) (see Table 2), we know that $c_w^* > 0$. From
 190 the analytical expression in Eq. (4) and from the numerical simulations shown in Fig. 2 (case
 191 (B)) we can see that resident fungal species displace the inoculant at a speed that increases
 192 with increasing mutualist quality of the inoculant (as higher values of p_c^* and m_c^* are observed
 193 when the α_c/β_c ratio is high) and with decreasing competitive ability of the inoculant (i.e.,
 194 with larger a_{cw}). In contrast, the displacement speed is independent of the dispersal ability
 195 of the inoculant and on the number of resident fungal species in the community (i.e., D_c and
 196 N do not appear in Eq. (4)).

197 For a combination of low resident fungal density and high (initially localised) propagule
 198 pressure (case (Da)), the inoculant can temporarily establish and spread (see Fig. 1, case
 199 (Da), $T = 0, 20$). The initial spread of the inoculant accelerates plant growth, but prevents
 200 the growth of resident fungi in areas where inoculant density is high. Beyond the dispersal
 201 range of the inoculant, the density of resident fungi increases and so does plant productivity,
 202 eventually reaching a higher density than in the region where only the inoculant is present
 203 (Fig. 1, case (Da), $T = 30, 40$). A higher plant biomass density determines higher resource
 204 availability, and gives a competitive advantage to resident fungal species with respect to the
 205 inoculant. Eventually, the resident community is able to stop the spread of the inoculant and
 206 recolonize the field (see Fig. 1, case (Da), $T = 60, 100$). Numerical simulations show that
 207 when recolonization is possible, resident fungal species displace the inoculant at a speed that
 208 increases with increasing mutualist quality, and with increasing diversity of resident fungal
 209 species, but that decreases with increasing dispersal ability of the inoculant (see Fig. 2, case
 210 (Da)).

211 **Inoculant and resident community coexistence (case (A)):** When competition
 212 between the inoculant and the existing community is low (e.g., the inoculated species is func-
 213 tionally complementary to resident fungal species), coexistence is possible and the inoculant
 214 can establish and spread in the field. In this case, inoculation has a positive effect on plant
 215 growth, due to an increase in diversity in the fungal community and therefore to a better use

216 of the resource available (i.e., plant carbon) (Martignoni et al., 2020b). On the other hand,
 217 the persistence of the inoculant leads to a reduction in the total density of resident fungi.
 218 This reduction, however, does not threaten community survival.

219 The spreading speed of the inoculant c_c can be expressed as

$$220 \quad c_c = 2\sqrt{D_c p_w^* \left(\frac{q_{cm}\beta_c a_{wc}}{a_{wc} + Nm_{wj}^*} - \frac{q_{hm}\alpha_c}{p_w^* + d} \right)}, \quad (5)$$

221 where D_c is the dispersal ability of the inoculant, α_c and β_c are respectively the phosphorus
 222 and carbon exchange abilities of the inoculant, a_{wc} is a parameter indicating the competition
 223 strength of the resident fungal species towards the inoculant, and q_{cm} , q_{hm} , and d are other
 224 model parameters defined in Table 1. Parameters p_w^* and Nm_{wj}^* are respectively the plant
 225 biomass density and total biomass density of resident fungal species at equilibrium in the
 226 absence of the inoculant. From the restrictions imposed on the parameters (see Table 2), we
 227 know that $c_c^* > 0$. From the analytical expression in Eq. (5) and from numerical simulations
 228 shown in Fig. 2 (case (A)) we can see that the spreading speed of the inoculant increases with
 229 increasing dispersal ability and with decreasing mutualist quality of the inoculant (i.e., for
 230 small α_c/β_c). Additionally, the spreading speed is lower in the presence of a diverse resident
 231 community (i.e., for high N).

232 **Invasion of the inoculant and displacement of the resident community (cases**
 233 **(C) and (Db)):** If the inoculant is competitively superior to the resident fungal species,
 234 the inoculant will establish, displace resident fungi and spread, causing regional biodiversity
 235 loss (case (C)). Diversity of resident fungal species increases community resilience to invasion
 236 (Martignoni et al., 2020b). That is, the introduction of a strongly competing inoculant leads
 237 to invasion of the inoculant if diversity in the resident community is low, but constitutes a
 238 lower risk if diversity in the resident community is high. Additionally, inoculants with low
 239 mutualist quality (i.e., low α_c/β_c) are most likely to invade (Martignoni et al., 2020b), as
 240 the quantitative criteria of case (C) provided in Table 2 are more likely to be satisfied for
 241 small α_c/β_c ratio. Abundant inoculation over a large proportion of field, combined with low
 242 abundance of resident fungi, can also lead to invasion (Fig. 1, case (Db)).

243 The analytical expression for the speed of invasion of the inoculant in case (C) is equivalent
 244 to the speed derived for case (A) (see Eq. (5)), despite the fact that case (A) implies coexistence
 245 of the inoculant with resident fungal species, while in case (C) resident fungal species are
 246 displaced by the inoculant. Diversity in the resident community contributes to a reduction
 247 of the invasion speed, while low mutualist quality and high dispersal ability of the inoculant
 248 contribute to an increase (see Fig. 2, case (C)).

249 3.2 Agroecosystem management issues

250 **Neighboring fields:** The spread of a weakly competing inoculant in a field causes a decline
 251 in the biomass density of resident fungi (without, however, causing the extinction of resident
 252 species), and an increase in plant biomass density (case (A), discussed above). The decline
 253 in resident fungi and the increase in plant productivity are more pronounced when diversity
 254 in the resident fungal community is low (see Fig. 3). A strongly competing inoculant can not
 255 spread into a field inhabited by two or more strongly competing resident species (Fig. 3(a)).
 256 When only one resident fungal species is present however, a strongly competing inoculant
 257 with low mutualist quality is able to invade the field, displace the resident fungi and cause a
 258 reduction in plant productivity (see Fig. 3(b)).

259 **Inoculation and productivity:** Generally, an increase in fungal abundance automat-
260 ically corresponds to an increase in plant growth rate, independent of the identity of the
261 inoculant and its persistence in the long term (see the first two subfigures of Fig. 1, case (Da)
262 and Fig. 4). In Fig. 4 we simulate plant and fungal growth over a landscape, following inoc-
263 ulation with a weakly competing inoculant in a community consisting of strongly competing
264 resident fungi (case (B)). Despite the fact that the inoculant does not persist in the field (see
265 Fig. 4, $T = 40$), inoculation significantly enhances the plant growth rate and the growth rate
266 of resident fungal species (Fig. 4, $T = 20, 40$). Inoculation with strongly competing species
267 can also lead to an initial enhancement in plant growth (see the first two subfigures of Fig. 1,
268 case (Da)), but subsequently lead to a displacement of resident fungi, and to negative long
269 term consequences for plant productivity (see case (C), Table 2).

270 4 Discussion

271 4.1 Investigating inoculum persistence and spread

272 **The inoculant does not persist (cases (B) and (Da)):** We found that if resident
273 fungal species compete strongly with the inoculant (e.g., if no niche space is available in the
274 soil), persistence of the inoculant will not occur. Experiments have reported that competition
275 can have a strong effect on inoculants establishment (Bender et al., 2019; Niwa et al., 2018;
276 Thomsen and Hart, 2018), where high species richness in the resident community may act as a
277 competitive advantage through a better exploitation of the resources available (Mallon et al.,
278 2015). In the model, the displacement of the inoculant by resident fungi may occur through
279 two mechanisms: either resident fungi are superior competitors, and displace the weakly
280 competing inoculant through direct competition between fungi for resources (case (B)), or
281 through an improved mutualistic relationship with the plant (case (Da)). Indeed, in case
282 (Da), high diversity in the resident fungal species allows for maximum resource exchange with
283 the plant. Increased resource exchange contributes to higher plant density and thus higher
284 resource availability (i.e., plant carbon), constituting an indirect competitive advantage of
285 resident fungi with respect to the inoculant, once plant density has increased sufficiently.

286 The model predicts that, when the biomass density of the resident community is low, high
287 propagule pressure can lead to the local establishment of the inoculant even if resident species
288 are strong competitors (Verbruggen et al., 2013; Streeter, 1994; Bender et al., 2019; Niwa
289 et al., 2018; Sýkorová et al., 2012). However, we found that if the inoculant is introduced only
290 over a small proportion of field, persistence may not occur, as resident fungi will eventually
291 outcompete the inoculant and recolonize the field (see Fig. 1, case (Da)).

292 **Inoculant and resident community coexistence (case (A)):** Our results suggest
293 that if competition between the introduced inoculant and resident fungal species is weak,
294 e.g., due to small niche overlap between resident fungi present and the inoculated species, the
295 inoculant will coexist with the rest of the community (case (A), Table 2). For example, if
296 the introduced species comes to occupy an empty niche space available in the soil (Herbold
297 and Moyle, 1986; Lekevičius, 2009; MacArthur and Levins, 1967), the inoculant will establish,
298 persist, and spread in the field. Experiments agree with these predictions, showing that
299 inoculum establishment in the presence of a resident fungal community is possible, and niche
300 availability is one of the factors determining inoculation success (Verbruggen et al., 2013;
301 del Mar Alguacil et al., 2011; Sýkorová et al., 2012; Farmer et al., 2007; Mummey et al.,
302 2009). Mummey et al. (2009) showed that the identity of the fungal species present before
303 inoculation is a strong determinant of inoculant establishment, and Farmer et al. (2007) found

304 that establishment was more successful when the inoculant had a functionality different from
305 that of the indigeneous fungal species present in the field.

306 **Invasion of the inoculant and displacement of the resident community (cases**
307 **(C) and (Db)):** We find that highly competitive fungi are likely to become invaders and
308 cause a biodiversity loss in the resident fungal community. Concerns about the invasiveness of
309 commercial inoculants and the possible detrimental consequences on ecosystem functionality
310 have been raised by the scientific community (Schwartz et al., 2006; Hart et al., 2017; Ricciardi
311 et al., 2017; Thomsen and Hart, 2018), and a decline in resident AM fungi following inoculation
312 success has been experimentally observed (Koch et al., 2011; Pellegrino et al., 2012; Symanczik
313 et al., 2015; Bender et al., 2019). Commercial fungi are subjected to intense breeding pressure
314 (Gianinazzi and Vosátka, 2004), which leads to the selection of highly competitive traits
315 such high sporulation and a propensity to invest in their own reproduction rather than in
316 the mutualistic relationship with the plant (Kokkoris et al., 2019b; Calvet et al., 2013; Jin
317 et al., 2013). Our analysis indicates that there is a risk of invasion from inoculants, and that
318 competitive inoculants with lower mutualist quality are more likely to become invasive.

319 The presence of a diverse resident community can mitigate the invasion risk by reducing the
320 invasion speed (see Eq. (5)), or by making establishment of the invader less likely (see Fig. 3).
321 Additionally, when resident species abundance is low, the introduction of strongly competing
322 inoculants can result in invasion if inoculants are introduced over a large portion of field
323 (Fig. 1, case (Db)). Hence, our results underscore the presence of an increased invasion risk
324 when competitive inoculants are used in conjunction with agricultural management practices
325 that reduce the abundance and diversity of resident fungi, such as tillage, chemical fertilization
326 strategies, or fallow periods (Karasawa and Takebe, 2012; Schnoor et al., 2011; Curaqueo et al.,
327 2011; Säle et al., 2015).

328 4.2 Speed of invasion

329 We obtain concrete analytical criteria for the speed of invasion of inoculants in a field inhab-
330 ited by a resident fungal community. The replacement of resident species by an invasive species
331 has already been investigated using Lotka-Volterra competition models (Hosono, 1998; Okubo
332 et al., 1989). However, an analytical expression for the spreading speed has been obtained only
333 recently (Holzer and Scheel, 2012; Girardin, 2017), and only in a homogeneous environment.
334 Other studies have described the spread of competitors in spatially heterogeneous (Goldstein
335 et al., 2019; Real and Biek, 2007) or periodic environments (Kinezaki et al., 2003). In our
336 model the resource (i.e., the plant) is involved in a mutualistic interaction with the species in
337 competition (i.e., the fungi), and so the local plant density depends on the local fungal com-
338 munity composition and density. Thus, since we are investigating invasion scenarios where
339 the fungi are not uniformly distributed through space, the environment for the competitors
340 is heterogeneous, and the heterogeneity evolves with the spread of the competing species.
341 In this heterogeneous context, we obtain analytical expressions for the speed of invasion of
342 competitors (i.e., resident and inoculated fungal species).

343 Previous studies investigating traveling wave solutions in competitive systems have found
344 that the speed of propagation can be linear or non-linear (Okubo et al., 1989; Lewis et al., 2002;
345 Huang, 2010; Girardin, 2017), depending for example on interspecific competition (Roques
346 et al., 2015; Huang and Han, 2011), or on the dispersal ability of the invader (Holzer and
347 Scheel, 2012). Our analysis shows that the linear speed appears to be a valid approximation
348 in two of the monostable cases (Fig. 2, cases (A) and (C)). However, for high mutualist qual-
349 ity and high competitive ability of the inoculant (Fig. 2, case (B)), the speed appears to be

350 non-linear. Similarly, [Roques et al. \(2015\)](#) found non-linearity when interspecific competition
351 is high, and linearity when interspecific competition is low.

352 In the bistable case, we are able to show that a strong competitor is displaced by a resident
353 community consisting of two or more species that compete weakly between each other, but
354 we are unable to obtain an analytic expression for the speed of spread. [Guo et al. \(2019\)](#) also
355 investigated a bistable system and found that two weaker competitors can displace a stronger
356 competitor, under certain parametric conditions. As the competition system studied by [Guo](#)
357 [et al. \(2019\)](#) is similar to the one discussed here, we could expect to gain more analytical
358 insights into the bistable case by adapting the [Guo et al. \(2019\)](#) analysis to our specific case.
359 This task, however, is beyond the scope of the current paper, and is left to future work.

360 4.3 Agroecosystem management issues

361 Competitiveness has been seen as a desirable trait in fungal inoculants, as it increases es-
362 tablishment success ([Verbruggen et al., 2013](#); [Farmer et al., 2007](#)). However, we find that
363 the spread of competitive and less mutualistic inoculants leads to the displacement of the
364 resident fungi and a decrease in plant productivity ([Koch et al., 2011](#); [Pellegrino et al., 2012](#);
365 [Symanczik et al., 2015](#); [Bender et al., 2019](#)). Invasion is more likely to happen if strongly
366 competing inoculants are abundantly distributed over a large proportion of the field.

367 We show that the use of weakly competing inoculants is desirable, as their spread can
368 boost plant growth and the growth of resident fungi, even when inoculants do not persist in
369 the field. This result is in agreement with the observations of [del Mar Alguacil et al. \(2011\)](#).
370 Therefore, we suggest that weakly competing inoculants are a better choice in agricultural
371 contexts, as strongly competing fungi may lead to reduced soil biodiversity and, ultimately,
372 reduce ecosystem functioning.

373 We show that inoculant abundance, and not necessarily the type of inoculant itself, can
374 contribute to a short-term increase in plant productivity in depleted soils (i.e., when fungal
375 biomass is low) (see the first two subfigures of Fig. 1, case (Da) and Fig. 4), while the increase
376 is less significant when fungal abundance in the resident community is high ([Martignoni et al.,](#)
377 [2020b](#)). Experiments investigating variation in crop yield following field inoculation with AM
378 fungi agree with these results, by showing that the immediate consequences of inoculation
379 can range from positive ([Zhang et al., 2019](#); [Ceballos et al., 2013](#); [Hijri, 2016](#); [Omirou et al.,](#)
380 [2016](#)) to no significant effect ([Hamel and Smith, 1991](#); [Loján et al., 2017](#); [Ryan and Graham,](#)
381 [2002](#); [Emam, 2016](#)). Our observations support the view that short term positive impact on
382 plant growth can be related to an increase in fungal abundance, rather than to fungal identity
383 ([Wagg et al., 2015](#); [Gosling et al., 2016](#); [Lekberg and Koide, 2005](#); [Pellegrino et al., 2011](#); [del](#)
384 [Mar Alguacil et al., 2011](#)).

385 5 Conclusion

386 We show that the use of weakly competing inoculants can lead to improved crop yield and
387 soil quality, but the use of strongly competing fungi constitutes a biodiversity risk. Our model
388 provides concrete criteria to assess the risks and benefits of inoculation and to determine the
389 spreading speed of inoculants in the field. We show that invasion of the inoculated species,
390 and the subsequent displacement of resident fungi, is unlikely to occur in the presence of an
391 established resident community. However, the invasion risk increases if strongly competing
392 inoculants with low mutualistic quality are introduced in fields presenting low abundance and
393 diversity of resident fungi.

394 Our framework shows that monitoring plant growth is not sufficient to properly evaluate

395 the long-term impact of inoculation, as the presence of a resident fungal community plays a
396 critical role in determining inoculum establishment success and productivity. To confirm our
397 hypotheses, there is an urgent need for empirical studies considering the effect of inoculation
398 on the resident community over space and time. We hope that the theoretical findings exposed
399 in this manuscript will help to focus future experimental efforts in productive directions. Our
400 model is based on the consumer-resource framework of mutualism (Holland and DeAngelis,
401 2010), where growth rates can be directly associated with nutrient exchange, making an in-
402 terplay between theory and experiments feasible. Indeed important model parameters (such
403 as α , the fungal ability to transfer phosphorus to the plant) can be estimated by monitoring
404 phosphorus or carbon transfer between the plant and the fungus over time.

405 Finally, we also see further benefits of our work outside the context of mycorrhizal inoc-
406 ulants. As our model is general, the framework presented here can be used to improve our
407 understanding of mechanisms behind the invasion of other symbiotic fungi (Dickie et al., 2016;
408 Litchman, 2010), or animal pollinators (Acosta et al., 2016).

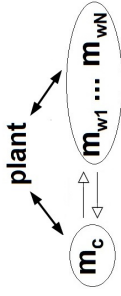
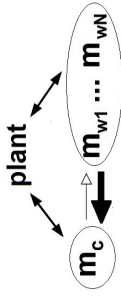
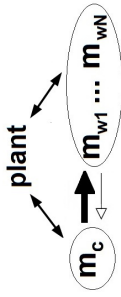
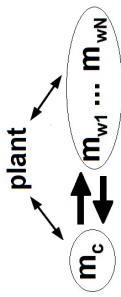
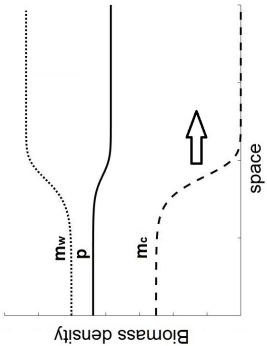
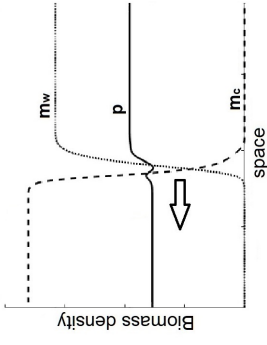
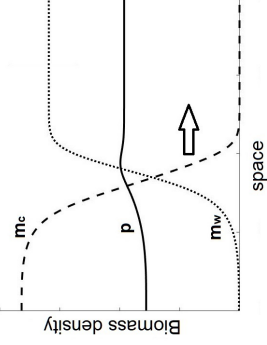
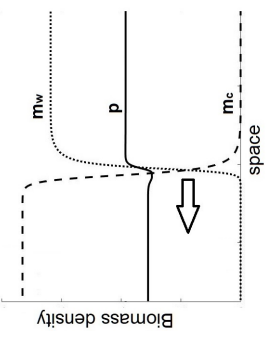
409 Acknowledgment

410 JG acknowledges NONLOCAL project (ANR-14-CE25-0013), GLOBNETS project (ANR-16-
411 CE02-0009) and the European Research Council (ERC) under the European Unions Horizon
412 2020 research and innovation program (grant agreement No 639638, MesoProbio). MMH
413 acknowledges NSERC Discovery Grant RGPIN-2018-237774. RCT acknowledges NSERC
414 Discovery Grant RGPIN-2016-05277 and the ‘Make our planet great again (MOPGA)’ grant.

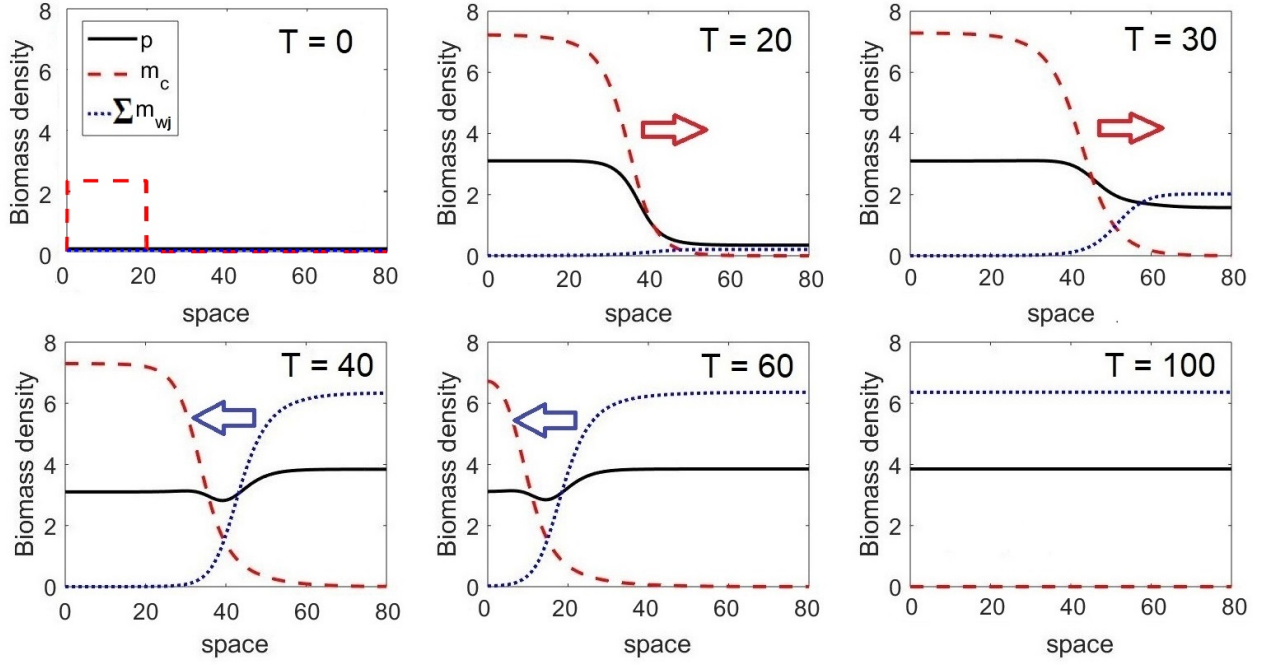
Table 1: Description of variables and parameters of the model.

Symbol	Description
p	Plant biomass density
m_{w_j}	Biomass density of resident fungal species
m_c	Biomass density of fungal inoculant
D_{w_j} and D_c	Fungal dispersal ability
α_{w_j} and α_c	Fungal ability to transfer phosphorus to the plant
β_{w_j} and β_c	Fungal ability to uptake carbon from the plant
$a_{w_j c}$	Competitive effect of m_{w_j} toward m_c
$a_{c w_j}$	Competitive effect of m_c toward m_{w_j}
$a_{w_i w_j}$	Competitive effect of m_{w_i} on m_{w_j}
$\mu_{m_{w_j}}$ and μ_{m_c}	Fungal maintenance rates
μ_p	Plant maintenance rate
d	Half-saturation constant
q_{hm}	Conversion factor (phosphorus to fungal biomass density)
q_{cm}	Conversion factor (carbon to fungal biomass density)
q_{hp}	Conversion factor (phosphorus to plant biomass density)
q_{cp}	Conversion factor (carbon to plant biomass density)
Note: m_c^* , m_w^* and p^* represent the values of fungal and plant biomass at equilibrium.	

Table 2: Cases A-D indicate the four possible scenarios occurring when varying the competition strength between the introduced fungal inoculant (m_c) and resident fungal species (m_{w_j} , $j = 1 \dots N$), with respective quantitative criteria (Martignoni et al., 2020b). Interactions between the fungi and the plant are mutualistic, while interactions between fungal species are competitive. In the top row, arrow thickness represents the strength of the interactions. The second row summarises and predictions on inoculum establishment discussed in Martignoni et al. (2020b). The third and four rows illustrate the predictions on inoculum spread in each of the four cases. The big arrows in the bottom row indicate the spread direction and on the left of each arrow are the plant, inoculant and resident community densities expected after inoculation. The output of case (D) depends on the initial density of the inoculant, as shown in Fig. 1. The outcome shown for case (D) here corresponds to case (Da).

Case	(A)	(B)	(C)	(D)
Interactions	$\frac{a_{c,w}}{a_{c,w}+m_c^*} > \frac{q_{hm}\alpha_w}{q_{cm}\beta_w(d+p^*)}$ $\& \frac{a_{w,c}}{a_{w,c}+Nm_{w_j}^*} > \frac{q_{hm}\alpha_c}{q_{cm}\beta_c(d+p^*)}$ 	$\frac{a_{c,w}}{a_{c,w}+m_c^*} > \frac{q_{hm}\alpha_w}{q_{cm}\beta_w(d+p^*)}$ $\& \frac{a_{w,c}}{a_{w,c}+Nm_{w_j}^*} < \frac{q_{hm}\alpha_c}{q_{cm}\beta_c(d+p^*)}$ 	$\frac{a_{c,w}}{a_{c,w}+m_c^*} < \frac{q_{hm}\alpha_w}{q_{cm}\beta_w(d+p^*)}$ $\& \frac{a_{w,c}}{a_{w,c}+Nm_{w_j}^*} > \frac{q_{hm}\alpha_c}{q_{cm}\beta_c(d+p^*)}$ 	$\frac{a_{c,w}}{a_{c,w}+m_c^*} < \frac{q_{hm}\alpha_w}{q_{cm}\beta_w(d+p^*)}$ $\& \frac{a_{w,c}}{a_{w,c}+Nm_{w_j}^*} < \frac{q_{hm}\alpha_c}{q_{cm}\beta_c(d+p^*)}$ 
Steady states stability (no diffusion)	Coexistence Stable: $(\tilde{p}^*, \tilde{m}_c^*, \tilde{m}_{w1}^*, \dots, \tilde{m}_{wN}^*)$ Unstable: $(p^*, 0, m_{w1}^*, \dots, m_{wN}^*)$	Community only Stable: $(p^*, 0, m_{w1}^*, \dots, m_{wN}^*)$ Unstable: $(\tilde{p}^*, m_c^*, 0, \dots, 0)$	Inoculant only Stable: $(\tilde{p}^*, m_c^*, 0, \dots, 0)$ Unstable: $(p^*, 0, m_{w1}^*, \dots, m_{wN}^*)$	Bistability Stable: $(\tilde{p}^*, m_c^*, 0, \dots, 0)$ and $(p^*, 0, m_{w1}^*, \dots, m_{wN}^*)$
Spread	from $(p^*, 0, m_{w1}^*, \dots, m_{wN}^*)$ to $(\tilde{p}^*, \tilde{m}_c^*, \tilde{m}_{w1}^*, \dots, \tilde{m}_{wN}^*)$	from $(\tilde{p}^*, m_c^*, 0, \dots, 0)$ to $(p^*, 0, m_{w1}^*, \dots, m_{wN}^*)$	from $(p^*, 0, m_{w1}^*, \dots, m_{wN}^*)$ to $(\tilde{p}^*, m_c^*, 0, \dots, 0)$	from $(\tilde{p}^*, m_c^*, 0, \dots, 0)$ to $(p^*, 0, m_{w1}^*, \dots, m_{wN}^*)$
Sketch of the spread				

Case (Da) : The inoculant does not persist



Case (Db): Invasion of the inoculant

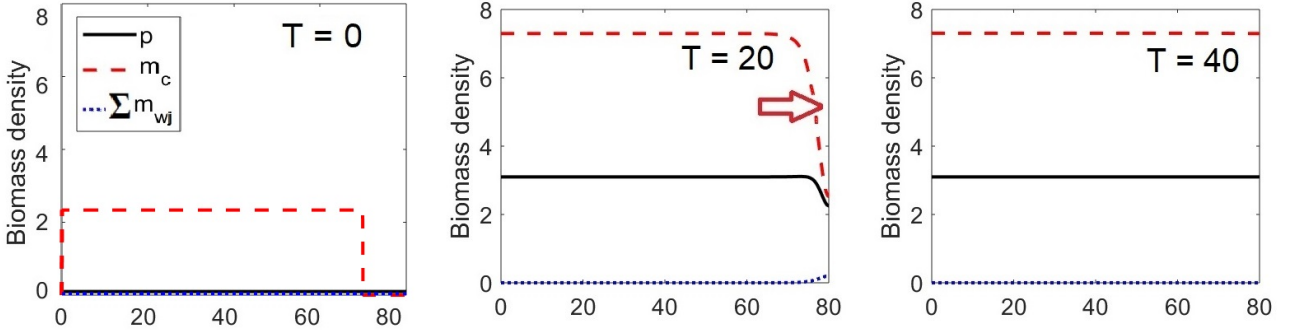


Fig. 1: Spatio-temporal dynamics observed when propagule pressure is high, the density of resident fungi is small, and competition between the inoculant (m_c) and the resident fungal community ($\sum m_{wj}$, $j = 1, 2$) is strong (Case (D)). In case (Da), the inoculant initially occupies a small proportion of the whole field, while in (Db) the inoculant initially covers a large part of the field. Competition parameters are $a_{ww} = 2.2$, $a_{wc} = a_{cw} = 0.3$. Other model parameters are $q_{hp} = 3$, $q_{cm} = 2$, $q_{hm} = q_{cp} = 1$, $\alpha_w = \beta_w = \alpha_c = \beta_c = 0.4$, $\mu_p = \mu_m = 0.3$, $d = 1.2$, $r_p = 0.02$, $D_c = D_{w_j} = 0.3$, $N = 2$.

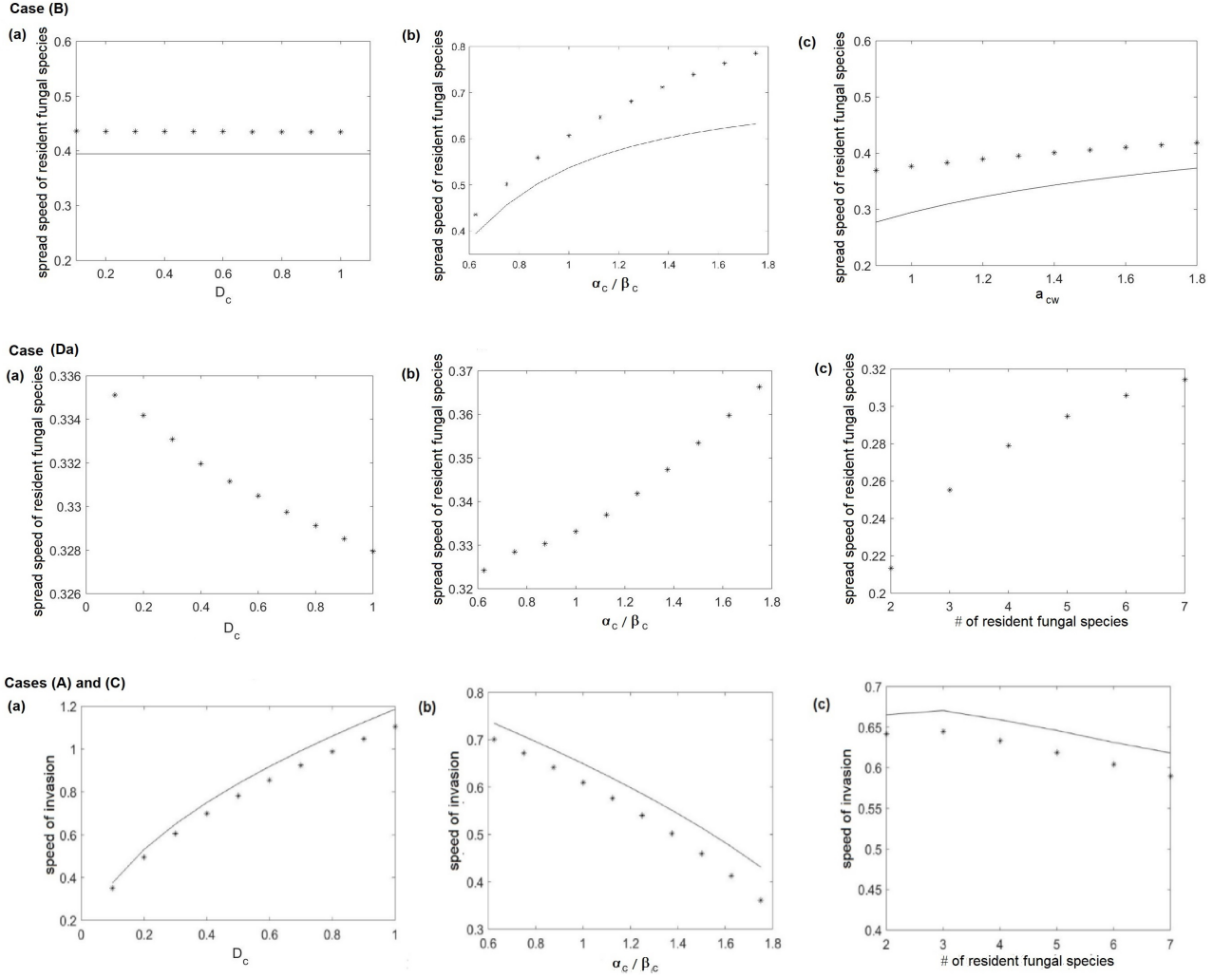


Fig. 2: Speed at which the inoculant is displaced by resident fungal species (cases (B) and (Da)) and speed of invasion of the inoculant (cases (A) and (C)) as a function of the diffusive ability and mutualist quality of the inoculant, of the competitive ability of the inoculant towards resident fungal species, and of the number of species present in the resident fungal community. Solid lines are the theoretically predicted lower bounds (see Eq. (5) for case (B), and Eq. (4) for cases (A) and (C)). The scattered plots are the results of the numerical simulations. Note that the speed obtained in cases (A) and (C) is identical, i.e., the speed of invasion does not depend on whether the inoculant coexist with the resident community (case (A)) or displace the resident community (case (C)). Standard parameter values correspond to those of Fig. 1. Competition parameters are $a_{ww} = a_{wc} = a_{cw} = 2.2$, for case (A). $a_{ww} = a_{cw} = 2.2$, $a_{wc} = 0.3$ for case (B). $a_{ww} = a_{wc} = 2.2$ and $a_{cw} = 0.3$ for case (C), plots (a) and (b). $a_{ww} = a_{wc} = 3.0$, $a_{cw} = 0.1$, $\alpha_w = 0.7$ and $\beta_w = 0.3$ for case (C), plot (c). $a_{ww} = 2.2$, $a_{wc} = a_{cw} = 0.3$ for case (Da), plots (a) and (b). $a_{ww} = 3$, $a_{wc} = a_{cw} = 0.1$, for case (Da), plot (c).

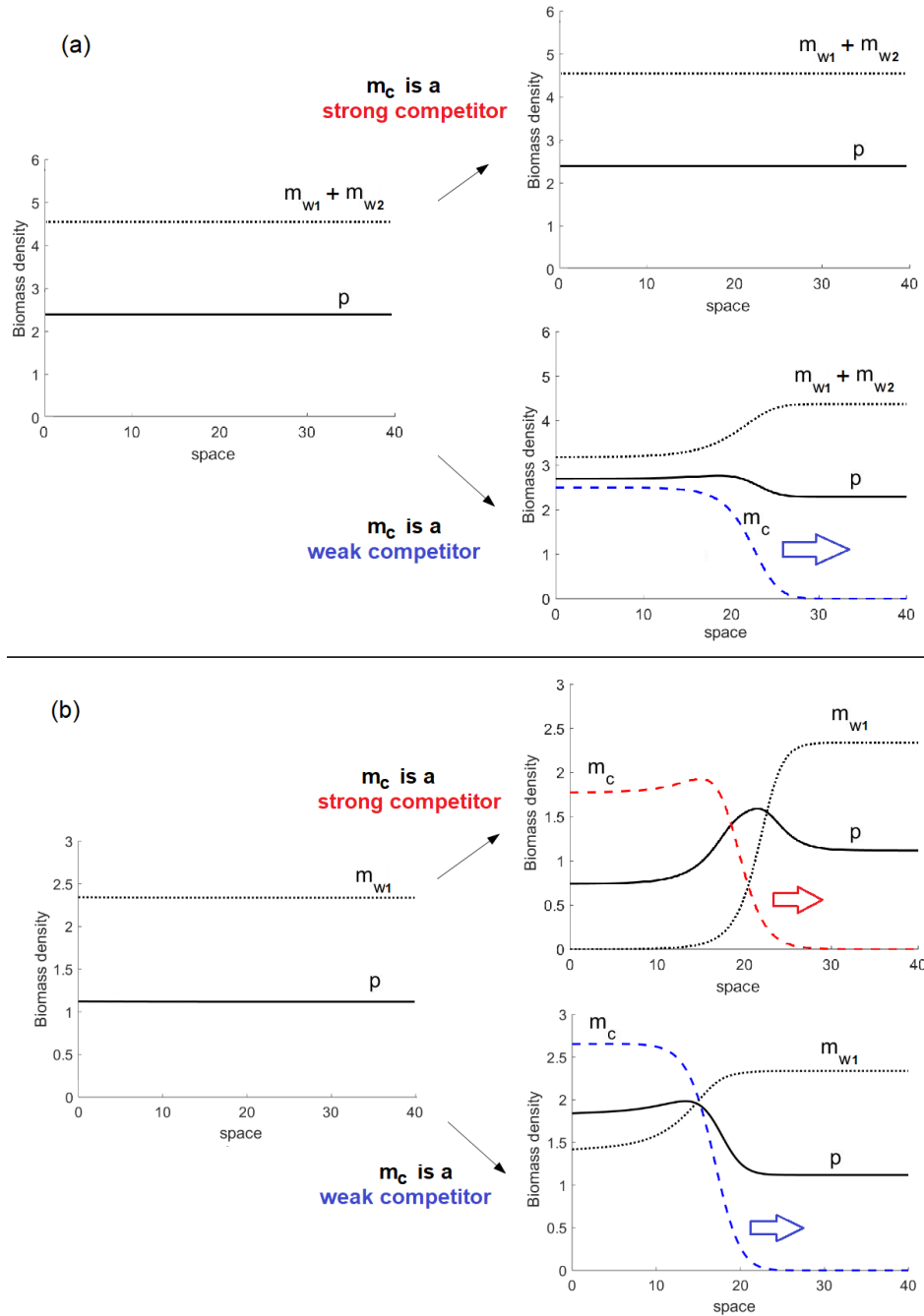


Fig. 3: Simulation showing the dispersal of the inoculant in a field consisting of (a) two or (b) one resident fungal species. We assume that a field inhabited by one or more resident fungi (see figures on the left) is next to a field containing only the inoculant. The figures on the right show how the inoculant will disperse in the field if the inoculant is a strong competitor and a bad mutualist ((a) and (b), top right figures) or a weak competitor ((a) and (b), bottom right figures). In case (a), the resident fungal community is at high density and consists of two fungi. (Note that we show the two-fungi case for simplicity; the result would be qualitatively the same if there were more than two species, i.e., $N > 2$). In case (b), the resident fungal community is at low density and consists of just one fungus. The biomass density of the strongly competing inoculant is indicated by the dashed red line, while the biomass density of the weakly competing inoculant is shown by the dashed blue line. Competition parameters are $a_{wc} = a_{cw} = 0.3$ for the strongly competing inoculant, and $a_{wc} = a_{cw} = 2.2$ for the weakly competing inoculant. The mutualist quality of the inoculant is assumed to be lower than the mutualist quality of resident fungal species, where $\alpha_c = 0.35$ and $\beta_c = 0.45$, while $\alpha_w = 0.4$ and $\beta_w = 0.4$. Other parameters correspond to those of Fig. 1.

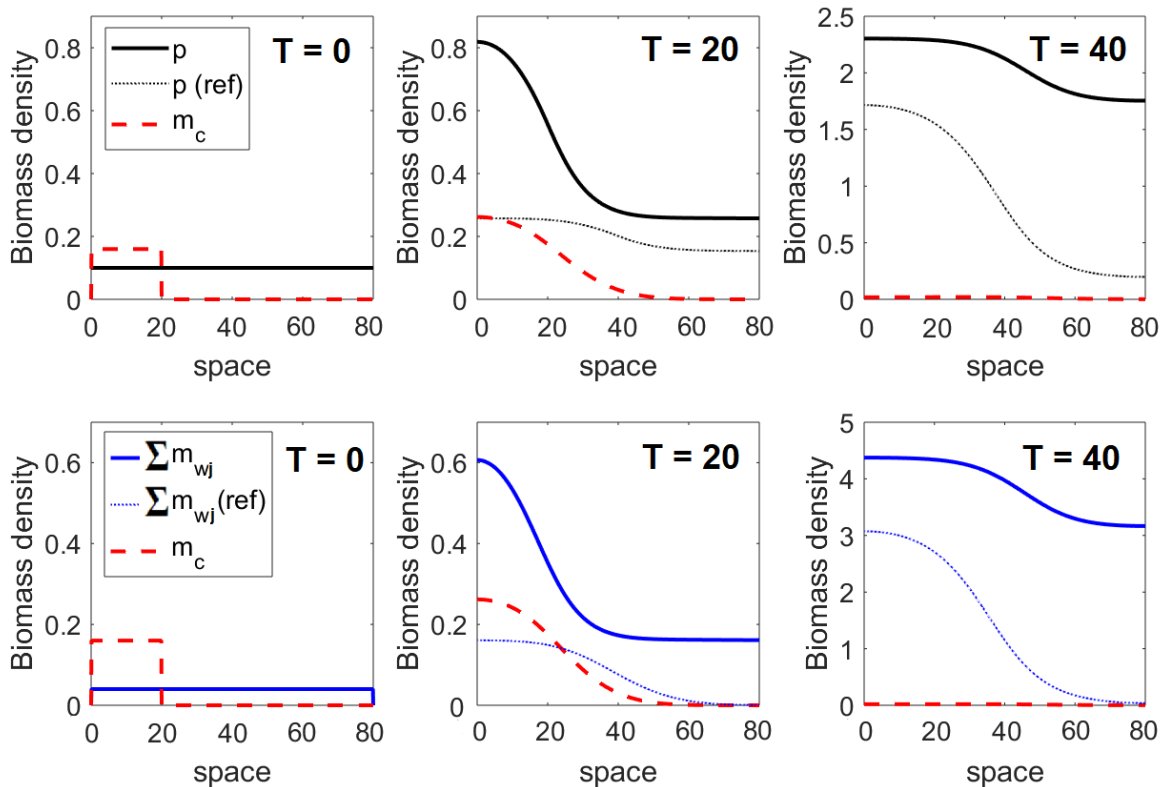


Fig. 4: Spatio-temporal dynamics observed when the inoculant (m_c) is a weak competitor and is eventually displaced by the resident community ($\sum m_{wj}$, $j = 1, 2$) (Case (B)). The dashed red line represents the biomass density of the inoculant. The top row represents plant growth in the presence (solid black line) or absence (dotted black line) of the inoculant. The bottom row represents resident fungal density in the presence (solid blue line) or absence (dotted blue line) of the inoculant. Model parameters used for the simulation correspond to those for Fig. 1, except for the competition parameters that are $a_{ww} = a_{cw} = 2.2$, $a_{wc} = 0.3$.

References

- Acosta, A. L., Giannini, T. C., Imperatriz-Fonseca, V. L., and Saraiva, A. M. (2016). World-wide alien invasion: A methodological approach to forecast the potential spread of a highly invasive pollinator. *PLoS one*, 11(2):e0148295.
- Baum, C., El-Tohamy, W., and Gruda, N. (2015). Increasing the productivity and product quality of vegetable crops using arbuscular mycorrhizal fungi: A review. *Scientia Horticulturae*, 187:131–141.
- Bender, S. F., Schlaeppli, K., Held, A., and Van der Heijden, M. G. (2019). Establishment success and crop growth effects of an arbuscular mycorrhizal fungus inoculated into swiss corn fields. *Agriculture, Ecosystems & Environment*, 273:13–24.
- Berruti, A., Lumini, E., Balestrini, R., and Bianciotto, V. (2016). Arbuscular mycorrhizal fungi as natural biofertilizers: let’s benefit from past successes. *Frontiers in Microbiology*, 6:1559.
- Bever, J. D. (2002). Host-specificity of am fungal population growth rates can generate feedback on plant growth. *Plant and Soil*, 244(1-2):281–290.

- 430 Burie, J.-B., Calonnec, A., and Langlais, M. (2008). Modeling of the invasion of a fungal
431 disease over a vineyard. In *Mathematical Modeling of Biological Systems, Volume II*, pages
432 11–21. Springer.
- 433 Buysens, C., César, V., Ferrais, F., de Boulois, H. D., and Declerck, S. (2016). Inoculation
434 of medicago sativa cover crop with rhizophagus irregularis and trichoderma harzianum
435 increases the yield of subsequently-grown potato under low nutrient conditions. *Applied*
436 *Soil Ecology*, 105:137–143.
- 437 Calvet, C., Camprubi, A., Pérez-Hernández, A., and Lovato, P. E. (2013). Plant growth
438 stimulation and root colonization potential of in vivo versus in vitro arbuscular mycorrhizal
439 inocula. *HortScience*, 48(7):897–901.
- 440 Ceballos, I., Ruiz, M., Fernández, C., Peña, R., Rodríguez, A., and Sanders, I. R. (2013).
441 The in vitro mass-produced model mycorrhizal fungus, rhizophagus irregularis, significantly
442 increases yields of the globally important food security crop cassava. *PLoS One*, 8(8):e70633.
- 443 Curaqueo, G., Barea, J. M., Acevedo, E., Rubio, R., Cornejo, P., and Borie, F. (2011).
444 Effects of different tillage system on arbuscular mycorrhizal fungal propagules and physical
445 properties in a mediterranean agroecosystem in central chile. *Soil and Tillage Research*,
446 113(1):11–18.
- 447 Davison, J., Öpik, M., Zobel, M., Vasar, M., Metsis, M., and Moora, M. (2012). Communities
448 of arbuscular mycorrhizal fungi detected in forest soil are spatially heterogeneous but do
449 not vary throughout the growing season. *PloS One*, 7(8).
- 450 del Mar Alguacil, M., Torrecillas, E., Kohler, J., and Roldán, A. (2011). A molecular approach
451 to ascertain the success of “in situ” am fungi inoculation in the revegetation of a semiarid,
452 degraded land. *Science of the Total Environment*, 409(15):2874–2880.
- 453 Dickie, I. A., Nuñez, M. A., Pringle, A., Lebel, T., Tourtellot, S. G., and Johnston, P. R.
454 (2016). Towards management of invasive ectomycorrhizal fungi. *Biological Invasions*,
455 18(12):3383–3395.
- 456 Emam, T. (2016). Local soil, but not commercial amf inoculum, increases native and non-
457 native grass growth at a mine restoration site. *Restoration Ecology*, 24(1):35–44.
- 458 Farmer, M., Li, X., Feng, G., Zhao, B., Chatagnier, O., Gianinazzi, S., Gianinazzi-Pearson,
459 V., and Van Tuinen, D. (2007). Molecular monitoring of field-inoculated amf to evaluate
460 persistence in sweet potato crops in china. *Applied Soil Ecology*, 35(3):599–609.
- 461 Friese, C. F. and Allen, M. F. (1991). The spread of va mycorrhizal fungal hyphae in the soil:
462 inoculum types and external hyphal architecture. *Mycologia*, 83(4):409–418.
- 463 Gianinazzi, S. and Vosátka, M. (2004). Inoculum of arbuscular mycorrhizal fungi for produc-
464 tion systems: science meets business. *Canadian Journal of Botany*, 82(8):1264–1271.
- 465 Girardin, L. (2017). Non-cooperative fisher–kpp systems: traveling waves and long-time be-
466 havior. *Nonlinearity*, 31(1):108.
- 467 Goldstein, J., Park, J., Haran, M., Liebhold, A., and Bjørnstad, O. N. (2019). Quanti-
468 fying spatio-temporal variation of invasion spread. *Proceedings of the Royal Society B*,
469 286(1894):20182294.

- 470 Gosling, P., Jones, J., and Bending, G. D. (2016). Evidence for functional redundancy in
471 arbuscular mycorrhizal fungi and implications for agroecosystem management. *Mycorrhiza*,
472 26(1):77–83.
- 473 Guo, J.-S., Nakamura, K.-I., Ogiwara, T., and Wu, C.-H. (2019). The sign of traveling wave
474 speed in bistable dynamics. *Discrete & Continuous Dynamical Systems-A*.
- 475 Haller, B. C. (2014). Theoretical and empirical perspectives in ecology and evolution: a
476 survey. *Bioscience*, 64(10):907–916.
- 477 Hamel, C. and Smith, D. L. (1991). Plant development in a mycorrhizal field-grown mixture.
478 *Soil Biology and Biochemistry*, 23(7):661–665.
- 479 Hart, M. M., Antunes, P. M., and Abbott, L. K. (2017). Unknown risks to soil biodiversity
480 from commercial fungal inoculants. *Nature Ecology & Evolution*, 1(4):0115.
- 481 Hart, M. M., Antunes, P. M., Chaudhary, V. B., and Abbott, L. K. (2018). Fungal inoculants
482 in the field: Is the reward greater than the risk? *Functional Ecology*, 32(1):126–135.
- 483 Herbold, B. and Moyle, P. B. (1986). Introduced species and vacant niches. *The American*
484 *Naturalist*, 128(5):751–760.
- 485 Hijri, M. (2016). Analysis of a large dataset of mycorrhiza inoculation field trials on potato
486 shows highly significant increases in yield. *Mycorrhiza*, 26(3):209–214.
- 487 Holland, J. N. and DeAngelis, D. L. (2010). A consumer–resource approach to the density-
488 dependent population dynamics of mutualism. *Ecology*, 91(5):1286–1295.
- 489 Holzer, M. and Scheel, A. (2012). A slow pushed front in a lotka–volterra competition model.
490 *Nonlinearity*, 25(7):2151.
- 491 Hosono, Y. (1998). The minimal speed of traveling fronts for a diffusive lotka-volterra com-
492 petition model. *Bulletin of Mathematical Biology*, 60(3):435–448.
- 493 Huang, W. (2010). Problem on minimum wave speed for a lotka–volterra reaction–diffusion
494 competition model. *Journal of Dynamics and Differential Equations*, 22(2):285–297.
- 495 Huang, W. and Han, M. (2011). Non-linear determinacy of minimum wave speed for a lotka–
496 volterra competition model. *Journal of Differential Equations*, 251(6):1549–1561.
- 497 Jeffries, P., Gianinazzi, S., Perotto, S., Turnau, K., and Barea, J.-M. (2003). The contribution
498 of arbuscular mycorrhizal fungi in sustainable maintenance of plant health and soil fertility.
499 *Biology and Fertility of Soils*, 37(1):1–16.
- 500 Jin, H., G., J. J., and Walley, F. L. (2013). Impact of arbuscular mycorrhizal fungal inoculants
501 on subsequent arbuscular mycorrhizal fungi colonization in pot-cultured field pea (*pisum*
502 *sativum* l.). *Mycorrhiza*, 23(1):45–59.
- 503 Jørgensen, S. (1994). Models as instruments for combination of ecological theory and envi-
504 ronmental practice. *Ecological Modelling*, 75:5–20.
- 505 Karasawa, T. and Takebe, M. (2012). Temporal or spatial arrangements of cover crops to
506 promote arbuscular mycorrhizal colonization and p uptake of upland crops grown after
507 nonmycorrhizal crops. *Plant and Soil*, 353(1-2):355–366.

- 508 Kinezaki, N., Kawasaki, K., Takasu, F., and Shigesada, N. (2003). Modeling biological inva-
509 sions into periodically fragmented environments. *Theoretical Population Biology*, 64(3):291–
510 302.
- 511 Koch, A. M., Antunes, P. M., Barto, E. K., Cipollini, D., Mummey, D. L., and Klironomos,
512 J. N. (2011). The effects of arbuscular mycorrhizal (am) fungal and garlic mustard intro-
513 ductions on native am fungal diversity. *Biological Invasions*, 13(7):1627–1639.
- 514 Köhl, L., Lukasiewicz, C. E., and Van der Heijden, M. G. (2016). Establishment and ef-
515 fectiveness of inoculated arbuscular mycorrhizal fungi in agricultural soils. *Plant, Cell &*
516 *Environment*, 39(1):136–146.
- 517 Kokkoris, V., Li, Y., Hamel, C., Hanson, K., and Hart, M. (2019a). Site specificity in estab-
518 lishment of a commercial arbuscular mycorrhizal fungal inoculant. *Science of The Total*
519 *Environment*, 660:1135–1143.
- 520 Kokkoris, V., Miles, T., and Hart, M. M. (2019b). The role of in vitro cultivation on asym-
521 biotic trait variation in a single species of arbuscular mycorrhizal fungus. *Fungal Biology*,
522 123(4):307–317.
- 523 Latef, A. A. H. A., Hashem, A., Rasool, S., Abd-Allah, E. F., Alqarawi, A., Egamberdieva,
524 D., Jan, S., Anjum, N. A., and Ahmad, P. (2016). Arbuscular mycorrhizal symbiosis and
525 abiotic stress in plants: A review. *Journal of Plant Biology*, 59(5):407–426.
- 526 Lekberg, Y. and Koide, R. (2005). Is plant performance limited by abundance of arbuscular
527 mycorrhizal fungi? a meta-analysis of studies published between 1988 and 2003. *New*
528 *Phytologist*, 168(1):189–204.
- 529 Lekevičius, E. (2009). Vacant niches in nature, ecology, and evolutionary theory: a mini-
530 review. *Ekologija*, 55(3-4):165–74.
- 531 Lewis, M. A., Li, B., and Weinberger, H. F. (2002). Spreading speed and linear determinacy
532 for two-species competition models. *Journal of Mathematical Biology*, 45(3):219–233.
- 533 Li, B., Weinberger, H. F., and Lewis, M. A. (2005). Spreading speeds as slowest wave speeds
534 for cooperative systems. *Mathematical biosciences*, 196(1):82–98.
- 535 Litchman, E. (2010). Invisible invaders: non-pathogenic invasive microbes in aquatic and
536 terrestrial ecosystems. *Ecology Letters*, 13(12):1560–1572.
- 537 Loján, P., Senés-Guerrero, C., Suárez, J. P., Kromann, P., Schüßler, A., and Declerck, S.
538 (2017). Potato field-inoculation in ecuador with rhizophagus irregularis: no impact on
539 growth performance and associated arbuscular mycorrhizal fungal communities. *Symbiosis*,
540 73(1):45–56.
- 541 MacArthur, R. and Levins, R. (1967). The limiting similarity, convergence, and divergence of
542 coexisting species. *The American Naturalist*, 101(921):377–385.
- 543 Mallon, C. A., Van Elsas, J. D., and Salles, J. F. (2015). Microbial invasions: the process,
544 patterns, and mechanisms. *Trends in microbiology*, 23(11):719–729.
- 545 Martignoni, M. M., Hart, M. M., Garnier, J., and Tyson, R. C. (2020a). Parasitism within mu-
546 tualist guilds explains the maintenance of diversity in multi-species mutualisms. *Theoretical*
547 *Ecology*, pages 1–13.

- 548 Martignoni, M. M., Hart, M. M., Tyson, R. C., and Garnier, J. (2020b). Diversity within mu-
549 tualist guilds promotes coexistence and reduces the risk of invasion from an alien mutualist.
550 *Proceedings of the Royal Society B*, 287(1923):20192312.
- 551 Mumme, D. L., Antunes, P. M., and Rillig, M. C. (2009). Arbuscular mycorrhizal fungi
552 pre-inoculant identity determines community composition in roots. *Soil Biology and Bio-*
553 *chemistry*, 41(6):1173–1179.
- 554 Murray, J. D. (1993). *Biological Waves: Multi-Species Reaction Diffusion Models*, pages 311–
555 359. Springer, Berlin, Heidelberg.
- 556 Niwa, R., Koyama, T., Sato, T., Adachi, K., Tawarayama, K., Sato, S., Hirakawa, H., Yoshida, S.,
557 and Ezawa, T. (2018). Dissection of niche competition between introduced and indigenous
558 arbuscular mycorrhizal fungi with respect to soybean yield responses. *Scientific Reports*, 8.
- 559 Odenbaugh, J. (2005). Idealized, inaccurate but successful: A pragmatic approach to evalu-
560 ating models in theoretical ecology. *Biology and Philosophy*, 20(2-3):231–255.
- 561 Okubo, A., Maini, P. K., Williamson, M. H., and Murray, J. D. (1989). On the spatial spread
562 of the grey squirrel in Britain. *Proceedings of the Royal Society of London. B. Biological*
563 *Sciences*, 238(1291):113–125.
- 564 Omirou, M., Fasoula, D. A., and Ioannides, I. M. (2016). Bradyrhizobium inoculation al-
565 ters indigenous AMF community assemblages and interacts positively with AMF inoculum to
566 improve cowpea performance. *Applied Soil Ecology*, 108:381–389.
- 567 Peay, K. G. and Bruns, T. D. (2014). Spore dispersal of basidiomycete fungi at the landscape
568 scale is driven by stochastic and deterministic processes and generates variability in plant–
569 fungal interactions. *New Phytologist*, 204(1):180–191.
- 570 Peay, K. G., Schubert, M. G., Nguyen, N. H., and Bruns, T. D. (2012). Measuring ecto-
571 mycorrhizal fungal dispersal: macroecological patterns driven by microscopic propagules.
572 *Molecular Ecology*, 21(16):4122–4136.
- 573 Pellegrino, E., Bedini, S., Avio, L., Bonari, E., and Giovannetti, M. (2011). Field inocu-
574 lation effectiveness of native and exotic arbuscular mycorrhizal fungi in a Mediterranean
575 agricultural soil. *Soil Biology and Biochemistry*, 43(2):367–376.
- 576 Pellegrino, E., Turrini, A., Gamper, H. A., Cafà, G., Bonari, E., Young, J. P. W., and Gio-
577 vannetti, M. (2012). Establishment, persistence and effectiveness of arbuscular mycorrhizal
578 fungal inoculants in the field revealed using molecular genetic tracing and measurement of
579 yield components. *New Phytologist*, 194(3):810–822.
- 580 Pozo, M. J. and Azcón-Aguilar, C. (2007). Unraveling mycorrhiza-induced resistance. *Current*
581 *Opinion in Plant Biology*, 10(4):393–398.
- 582 Real, L. A. and Biek, R. (2007). Spatial dynamics and genetics of infectious diseases on
583 heterogeneous landscapes. *Journal of the Royal Society Interface*, 4(16):935–948.
- 584 Ricciardi, A., Blackburn, T. M., Carlton, J. T., Dick, J. T., Hulme, P. E., Iacarella, J. C.,
585 Jeschke, J. M., Liebhold, A. M., Lockwood, J. L., MacIsaac, H. J., et al. (2017). Invasion
586 science: a horizon scan of emerging challenges and opportunities. *Trends in Ecology &*
587 *Evolution*, 32(6):464–474.

- 588 Roques, L., Hosono, Y., Bonnefon, O., and Boivin, T. (2015). The effect of competition
589 on the neutral intraspecific diversity of invasive species. *Journal of Mathematical Biology*,
590 71(2):465–489.
- 591 Ryan, M. H. and Graham, J. H. (2002). Is there a role for arbuscular mycorrhizal fungi in
592 production agriculture? *Plant and Soil*, 244(1-2):263–271.
- 593 Säle, V., Aguilera, P., Laczko, E., Mäder, P., Berner, A., Zihlmann, U., van der Heijden,
594 M. G., and Oehl, F. (2015). Impact of conservation tillage and organic farming on the
595 diversity of arbuscular mycorrhizal fungi. *Soil Biology and Biochemistry*, 84:38–52.
- 596 Schnoor, T. K., Lekberg, Y., Rosendahl, S., and Olsson, P. A. (2011). Mechanical soil dis-
597 turbance as a determinant of arbuscular mycorrhizal fungal communities in semi-natural
598 grassland. *Mycorrhiza*, 21(3):211–220.
- 599 Schwartz, M. W., Hoeksema, J. D., Gehring, C. A., Johnson, N. C., Klironomos, J. N., Abbott,
600 L. K., and Pringle, A. (2006). The promise and the potential consequences of the global
601 transport of mycorrhizal fungal inoculum. *Ecology Letters*, 9(5):501–515.
- 602 Smith, S. E. and Read, D. J. (2010). *Mycorrhizal symbiosis*. Academic Press.
- 603 Soubeyrand, S., Held, L., Höhle, M., and Sache, I. (2008). Modelling the spread in space
604 and time of an airborne plant disease. *Journal of the Royal Statistical Society: Series C*
605 (*Applied Statistics*), 57(3):253–272.
- 606 Streeter, J. G. (1994). Failure of inoculant rhizobia to overcome the dominance of indigenous
607 strains for nodule formation. *Canadian Journal of Microbiology*, 40(7):513–522.
- 608 Šýkorová, Z., Börstler, B., Zvolenská, S., Fehrer, J., Gryndler, M., Vosátka, M., and Re-
609 decker, D. (2012). Long-term tracing of rhizophagus irregularis isolate beg140 inoculated
610 on phalaris arundinacea in a coal mine spoil bank, using mitochondrial large subunit rDNA
611 markers. *Mycorrhiza*, 22(1):69–80.
- 612 Symanczik, S., Courty, P.-E., Boller, T., Wiemken, A., and Al-Yahya’ei, M. N. (2015). Impact
613 of water regimes on an experimental community of four desert arbuscular mycorrhizal fungal
614 (amf) species, as affected by the introduction of a non-native amf species. *Mycorrhiza*,
615 25(8):639–647.
- 616 Thiet, R. K. and Boerner, R. (2007). Spatial patterns of ectomycorrhizal fungal inoculum in
617 arbuscular mycorrhizal barrens communities: implications for controlling invasion by *Pinus*
618 *virginiana*. *Mycorrhiza*, 17(6):507–517.
- 619 Thomsen, C. N. and Hart, M. M. (2018). Using invasion theory to predict the fate of arbuscular
620 mycorrhizal fungal inoculants. *Biological Invasions*, 20(10):2695–2706.
- 621 Tyson, R., Stern, L., and LeVeque, R. J. (2000). Fractional step methods applied to a
622 chemotaxis model. *Journal of Mathematical Biology*, 41(5):455–475.
- 623 Vellinga, E. C., Wolfe, B. E., and Pringle, A. (2009). Global patterns of ectomycorrhizal
624 introductions. *New Phytologist*, 181(4):960–973.
- 625 Verbruggen, E., van der Heijden, M. G., Rillig, M. C., and Kiers, E. T. (2013). Mycorrhizal
626 fungal establishment in agricultural soils: factors determining inoculation success. *New*
627 *Phytologist*, 197(4):1104–1109.

- 628 Wagg, C., Barendregt, C., Jansa, J., and Heijden, M. G. (2015). Complementarity in both
629 plant and mycorrhizal fungal communities are not necessarily increased by diversity in the
630 other. *Journal of Ecology*, 103(5):1233–1244.
- 631 Warner, N. J., Allen, M. F., and MacMahon, J. A. (1987). Dispersal agents of vesicular-
632 arbuscular mycorrhizal fungi in a disturbed arid ecosystem. *Mycologia*, 79(5):721–730.
- 633 Zhang, S., Lehmann, A., Zheng, W., You, Z., and Rillig, M. C. (2019). Arbuscular mycorrhizal
634 fungi increase grain yields: a meta-analysis. *New Phytologist*, 222(1):543–555.

636 **Supplementary information**637 **A model for investigating the persistence and spread**
638 **of fungal resident**

639 To investigate the persistence and spread of the introduction of a commercial fungal inoculant (m_c) into a field inhabited by a resident fungal community (m_{w_j} , where $j = 1..N$),
640 we extend the model developed by [Martignoni et al. \(2020b\)](#) to explicitly consider random
641 fungal dispersal. In the model, plant and fungal coupled growth is determined by the density
642 dependent functions $f_p(p, m_c, m_{w_j})$, for plant growth, $f_{m_c}(p, m_c, m_{w_j})$, for inoculum growth,
643 and $f_{m_{w_j}}(p, m_c, m_{w_j})$, for the growth of the resident fungal community, defined in [Martignoni](#)
644 [et al. \(2020b\)](#). The complete model can be written as

$$\left\{ \begin{array}{l} \frac{\partial p}{\partial t} = q_{hp}r_p p + q_{hp} \left(\alpha_c m_c + \sum_j \alpha_{w_j} m_{w_j} \right) \frac{p}{d+p} - q_{cp} \left[\beta_c m_c \left(\frac{\sum_j a_{w_j c} m_{w_j}}{\sum_j a_{w_j c} m_{w_j} + (\sum_j m_{w_j})^2} \right) \right. \\ \quad \left. + \sum_j \beta_{w_j} m_{w_j} \left(\frac{a_{cw_j} m_c + \sum_{i \neq j} a_{w_i w_j} m_{w_i}}{a_{cw} m_c + \sum_{i \neq j} a_{w_i w_j} m_{w_i} + (m_c + \sum_{i \neq j} m_{w_i})^2} \right) \right] p - \mu_p p^2, \quad (6a) \\ \frac{\partial m_c}{\partial t} = D_c \frac{\partial^2 m_c}{\partial x^2} + q_{cm_c} \beta_c p m_c \left(\frac{\sum_j a_{w_j c} m_{w_j}}{\sum_j a_{w_j c} m_{w_j} + (\sum_j m_{w_j})^2} \right) - q_{hm_c} \alpha_c \frac{p}{d+p} m_c - \mu_{m_c} m_c^2, \quad (6b) \\ \frac{\partial m_{w_j}}{\partial t} = D_{w_j} \frac{\partial^2 m_{w_j}}{\partial x^2} + q_{cm_{w_j}} \beta_{w_j} p m_{w_j} \left(\frac{a_{cw_j} m_c + \sum_{i \neq j} a_{w_i w_j} m_{w_i}}{a_{cw} m_c + \sum_{i \neq j} a_{w_i w_j} m_{w_i} + (m_c + \sum_{i \neq j} m_{w_i})^2} \right) \\ \quad - q_{hm_{w_j}} \alpha_{w_j} \frac{p}{d+p} m_{w_j} - \mu_{m_{w_j}} m_{w_j}^2. \quad (6c) \end{array} \right.$$

646 A description of the model parameters with respective measurement unit is provided in Table
647 S1.

648 To simplify the analysis, we will assume that the competition strength between the com-
649 mercial fungus m_c and individuals of the wild community m_{w_j} and between individuals of the
650 wild community are the same for all fungi (i.e. $a_{w_j c} = a_{wc}$, $a_{cw_j} = a_{cw}$ and $a_{w_i w_j} = a_{ww}$). We
651 will further assume that all fungal parameters are the same, except for the phosphorus and
652 carbon exchange ability (α 's and β 's parameters). With these simplifications, the model of
653 Eq. (6) becomes

$$\left\{ \begin{array}{l} \frac{\partial p}{\partial t} = q_{hp}r_p p + q_{hp} \left(\alpha_c m_c + N \alpha_w m_{w_j} \right) \frac{p}{d+p} - q_{cp} \left[\beta_c m_c \frac{a_{wc}}{a_{wc} + N m_{w_j}} + \right. \\ \quad \left. N \left(\beta_w m_{w_j} \frac{a_{cw} m_c + a_{ww} (N-1) m_{w_j}}{a_{cw} m_c + a_{ww} (N-1) m_{w_j} + (m_c + (N-1) m_{w_j})^2} \right) \right] p - \mu_p p^2, \quad (7a) \\ \frac{\partial m_c}{\partial t} = D_c \frac{\partial^2 m_c}{\partial x^2} + q_{cm} \beta_c p m_c \left(\frac{a_{wc}}{a_{wc} + N m_{w_j}} \right) - q_{hm} \alpha_c \frac{p}{d+p} m_c - \mu_m m_c^2, \quad (7b) \\ \frac{\partial m_{w_j}}{\partial t} = D_w \frac{\partial^2 m_{w_j}}{\partial x^2} + q_{cm} \beta_w p m_{w_j} \left(\frac{a_{cw} m_c + a_{ww} (N-1) m_{w_j}}{a_{cw} m_c + a_{ww} (N-1) m_{w_j} + (m_c + (N-1) m_{w_j})^2} \right) \\ \quad - q_{hm} \alpha_w \frac{p}{d+p} m_{w_j} - \mu_m m_{w_j}^2. \quad (7c) \end{array} \right.$$

654

655

656

657

658

659

660

661

662

663

664

665

666

667

668

669

670

671

672

673

674

675

676

We will use Eq. (7) to study how the competition strength between the inoculant and resident fungal species affect fungal spread. We will consider a community of coexisting weakly competing fungi (i.e., a_{ww} is large), competing with the inoculated fungal species m_c . The scenarios considered are sketched in Table. 2. In case (A), competition between the inoculant and the resident community is weak (i.e., a_{wc} and a_{cw} are large). In cases (B) and (C) competition between the inoculant and the resident community is asymmetric, where either the inoculant or the resident community is a superior competitor (i.e., $a_{cw} > a_{wc}$ or $a_{cw} < a_{wc}$). In case (D) competition between the inoculant and the resident fungal community is strong (i.e., a_{wc} and a_{cw} are small). Additionally, we will determine how the spreading speed is affected by the dispersal ability of the inoculant (parameter D_c), by its mutualist quality (α_c/β_c ratio), and by the number of fungal species present in the resident community.

Model outputs will be analysed through traveling wave analysis and numerical simulations.

As discussed in the manuscript, the output of case (D) depends on the initial distribution of inoculant; in case (Da) the inoculant is introduced over a small proportion of the field, while in case (Db) the inoculant is introduced over a large proportion of the field. In our traveling wave analysis, we will be looking at the spread of inoculants from a region with positive inoculant density into a region where the inoculant is absent (see boundary conditions given in Eq. (10)). These initial distribution of inoculants allows us to investigate case (Da) analytically. Case (Db) is analytically intractable. Numerical simulations are run in Matlab R2017a. Solutions are found by using a semi-implicit scheme (Tyson et al., 2000), where the reaction term is solved explicitly and the diffusion term is solved implicitly. The discretization used for the space is $dx = 0.05$, and the discretion used for the time is $dt = 0.05$.

677 Model analysis

We are interested in understanding whether the introduction of a new fungal species (m_c) in the presence of an existing fungal community (m_{wj}) will result in a spread of the new species into the field. To tackle this problem, we will look at travelling wave solution of Eq. (7), which are particular solutions describing the invasion of one steady state by an other one at constant speed c . More precisely, we assume that the solution of Eq. (7) are of the form $p(t, x) = P(x - ct) = P(z)$, $m_c(t, x) = M_c(x - ct) = M_c(z)$ and $m_{wj}(t, x) = M_{wj}(x - ct) = M_{wj}(z)$ for an unknown speed $c \in \mathbb{R}$. By replacing these expressions into Eq. (7) we obtain

$$\begin{cases} -c \frac{dP}{dz} = F_P(P, M_c, M_{wj}), & (8a) \\ -c \frac{dM_c}{dz} = D_c \frac{d^2 M_c}{dz^2} + F_{M_c}(P, M_c, M_{wj}), & (8b) \\ -c \frac{dM_{wj}}{dz} = D_w \frac{d^2 M_{wj}}{dz^2} + F_{M_{wj}}(P, M_c, M_{wj}). & (8c) \end{cases}$$

678

679

680

In order to lighten the notations, we define the vector $\mathbf{U}(x - ct) = \mathbf{U}(z) = (P, M_c, M_{wj})$, the diffusion matrix $\mathbf{D} = \text{diag}(0, D_c, D_w)$ and the interaction function $\mathbf{F}(\mathbf{U}(z)) = (F_P, F_{M_c}, F_{M_{wj}})$. Then Eq. (8) can be written as

681

$$\mathbf{D}\mathbf{U}''(z) + c\mathbf{U}'(z) + \mathbf{F}(\mathbf{U}(z)) = \mathbf{0}. \quad (9)$$

682

683

We will focus on three particular steady states which stability have been already investigated in Martignoni et al. (2020b):

684

- Community only: $\mathbf{U}_w^* = (P_w^*, 0, M_{wj}^*)$,

685 - Coexistence: $\mathbf{U}_{cw}^{**} = (P_{cw}^{**}, M_c^{**}, M_{wj}^{**})$,

686 - Inoculant only: $\mathbf{U}_c^* = (P_c^*, M_c^*, 0)$.

687 The stability of these steady states depends on the strength of the competitive interactions
688 between the fungi. As shown in Table S2, in case (A), competition between the inoculant and
689 the resident community is weak. In cases (B) and (C) competition between the inoculant and
690 the resident community is asymmetric, where either the inoculant or the resident community
691 is a superior competitor. In case (D) competition between the inoculant and the resident
692 fungal community is strong. From the analysis of the non-spatial model (Martignoni et al.,
693 2020b) we know that

694 • Case (A): \mathbf{U}_{cw}^{**} stable, \mathbf{U}_w^* unstable,

695 • Case (B): \mathbf{U}_c^* unstable, \mathbf{U}_w^* stable,

696 • Case (C): \mathbf{U}_c^* stable, \mathbf{U}_w^* unstable,

697 • Case (D): \mathbf{U}_c^* stable, \mathbf{U}_w^* stable *.

698 We will consider on the right of the domain a steady state where the inoculant biomass
699 density is zero (i.e. $M_c(\infty) = 0$) and only the resident community and the plant are present.
700 On the left we will assume that the steady state has a positive density of a commercial
701 inoculant ($M_c(-\infty) > 0$), plant biomass density is positive and the biomass density of the
702 resident community can be zero or positive depending on which scenario has been investigated.
703 This situation corresponds to investigating whether the steady state \mathbf{U}_w^* can be invaded by
704 a steady state with a positive density of the inoculant (i.e. either \mathbf{U}_{cw}^{**} or \mathbf{U}_c^*). Thus the
705 boundary conditions can be expressed as

$$706 \quad \mathbf{U}(-\infty) = \begin{cases} \mathbf{U}_{cw}^{**} & \text{Case (A)} \\ \mathbf{U}_c^* & \text{Cases (B) - (Da)} \end{cases} \quad \text{and} \quad \mathbf{U}(+\infty) = \mathbf{U}_w^* \quad (10)$$

707 The solutions to Eq. (9) satisfy boundary conditions for P , M_{wj} and M_c . The stability of the
708 steady states involved in the boundary conditions, may help us to describe the speed at which
709 the solution moves.

710 When one stable steady state and one unstable steady state are present (cases (A)-(C))
711 the stable state will invade the unstable state at constant speed c . In this case, there is a
712 monostable traveling waves and one may expect an estimate of the minimal speed of propa-
713 gation using the linearized problem around the unstable steady state. In case (Da), a bistable
714 traveling wave connects two stable steady state. In this case it is difficult to determine the
715 actual speed of invasion, however, there are some techniques to estimate the sign of the propa-
716 gation speed, to determine which of steady states will invade the other. We will first analyse
717 the three monostable cases, and then investigate the bistable one. In order to gain more
718 insight into the results of the analysis, We will explore numerically how the invasion speed
719 varies as a function of diversity of the resident community, as well as a function of different
720 characteristic of the inoculant, such as dispersal ability (D_c) and mutualist quality (α_c/β_c).

*In the spatial case, investigated in this paper, case (D) can have two different outcomes, depending on the initial distribution of inoculants. We will refer to these as case (Da) and case (Db.)

721 Monostable traveling waves

722 **Cases (A) and (C):** In these cases, the unstable steady state \mathbf{U}_w^* will be invaded by a
 723 steady state that contains the commercial inoculant, where either coexistence of the inocu-
 724 lant with the resident community is observed (\mathbf{U}_{cw}^{**} , case (A)) or the resident community is
 725 displaced by the inoculant (\mathbf{U}_c^* , case (C)). To find an estimate for the minimal propagation
 726 speed c , we linearize Eq. (9) around the unstable steady state \mathbf{U}_w^* and obtain

$$\left\{ \begin{array}{l} -cP' = F_P \Big|_{\mathbf{U}_w^*} + \frac{\partial F_P}{\partial P} \Big|_{\mathbf{U}_w^*} P + \frac{\partial F_P}{\partial M_c} \Big|_{\mathbf{U}_w^*} M_c + \frac{\partial F_P}{\partial M_{wj}} \Big|_{\mathbf{U}_w^*} M_{wj} \end{array} \right. \quad (11a)$$

$$\left\{ \begin{array}{l} -cM'_c = D_c M''_c + F_{M_c} \Big|_{\mathbf{U}_w^*} + \frac{\partial F_{M_c}}{\partial P} \Big|_{\mathbf{U}_w^*} P + \frac{\partial F_{M_c}}{\partial M_c} \Big|_{\mathbf{U}_w^*} M_c + \frac{\partial F_{M_c}}{\partial M_{wj}} \Big|_{\mathbf{U}_w^*} M_{wj} \end{array} \right. \quad (11b)$$

$$\left\{ \begin{array}{l} -cM'_{wj} = D_w M''_{wj} + F_{M_{wj}} \Big|_{\mathbf{U}_w^*} + \frac{\partial F_{M_{wj}}}{\partial P} \Big|_{\mathbf{U}_w^*} P + \frac{\partial F_{M_{wj}}}{\partial M_c} \Big|_{\mathbf{U}_w^*} M_c + \frac{\partial F_{M_{wj}}}{\partial M_{wj}} \Big|_{\mathbf{U}_w^*} M_{wj} \end{array} \right. \quad (11c)$$

727 Because $F_{M_c}|_{\mathbf{U}_w^*} = 0$ and $\frac{\partial F_{M_c}}{\partial P}|_{\mathbf{U}_w^*} = \frac{\partial F_{M_c}}{\partial M_{wj}}|_{\mathbf{U}_w^*} = 0$, we can observe that the component
 728 M_c of the linearized problem of Eq. (11) satisfies

$$729 \quad D_c M''_c + cM'_c + F_c^* M_c = 0, \quad (12)$$

730 where

$$731 \quad F_c^* = P_w^* \left(\frac{q_{cm}\beta_c a_{wc}}{a_{wc} + NM_w^*} - \frac{q_{hm}\alpha_c}{P_w^* + d} \right). \quad (13)$$

732 From the analysis of the non spatial version of the model (Martignoni et al., 2020b), we know
 733 that $F_c^* > 0$ for cases (A) and (C). Hence, one can conclude that a lower bound for the
 734 propagation speed $c_c^* \leq c$ is given by (Murray, 1993; Li et al., 2005)

$$735 \quad c_c^* = 2\sqrt{D_c F_c^*} = 2\sqrt{D_c P_w^* \left(\frac{q_{cm}\beta_c a_{wc}}{a_{wc} + NM_w^*} - \frac{q_{hm}\alpha_c}{P_w^* + d} \right)}. \quad (14)$$

736 Thus in cases (A) and (C) the commercial inoculant invade a field inhabited by a resi-
 737 dent community at a minimal speed that increases with increasing dispersal ability of the
 738 commercial fungus and decreases with increasing diversity of the resident fungal community.
 739 Additionally, the minimal propagation speed increases if the commercial fungus can be re-
 740 garded as a cheater, i.e. when α_c is small and β_c is large. These findings are supported
 741 by numerical simulations. In Fig. S1, the theoretically predicted linear speed of Eq. (14) is
 742 compared with the speed resulting from numerical simulations, for different dispersal ability
 743 and mutualist quality of the inoculant, and for increasing diversity of the resident community.
 744 The speed resulting from the numerical simulations does not depend on whether the resident
 745 community is displaced (case (C)) or the inoculant coexist with the community (case (A)), as
 746 anticipated by the traveling wave analysis.

747 **Case (B):** In this case, the resident community competes strongly against the inoculant.
 748 The steady state \mathbf{U}_w^* is stable while the unstable steady state is now \mathbf{U}_c^* . We linearize therefore
 749 Eq. (9) around \mathbf{U}_c^* . Because $F_{M_{wj}}|_{\mathbf{U}_c^*} = 0$ and $\frac{\partial F_{M_{wj}}}{\partial P}|_{\mathbf{U}_c^*} = \frac{\partial F_{M_{wj}}}{\partial M_{wj}}|_{\mathbf{U}_c^*} = 0$, all components
 750 M_{wj} of the linearized problem satisfy

$$751 \quad D_w M''_w + cM'_w + F_w^* M_w = 0 \quad (15)$$

753 where

$$754 \quad F_w^* = P_c^* \left(\frac{q_{cm}\beta_w a_{cw}}{a_{cw} + M_c^*} - \frac{q_{hm}\alpha_w}{P_c^* + d} \right) \quad (16)$$

755 It is known that $F_w^* > 0$ for case (B) (Martignoni et al., 2020b). A lower bound for the
756 propagation speed $c_w^* \leq c$ is thus given by

$$757 \quad c_w^* = 2\sqrt{D_w F_w^*} = 2\sqrt{D_w P_c^* \left(\frac{q_{cm}\beta_w a_{cw}}{a_{cw} + M_c^*} - \frac{q_{hm}\alpha_w}{P_c^* + d} \right)}. \quad (17)$$

758 One can conclude that in case (B) the commercial inoculant is displaced by the resident
759 community at a minimal speed c_w^* . The speed increases with increasing mutualist quality of
760 the inoculant (i.e., with larger α_c/β_c ratio, determining the value of P_c^* and M_c^*) and with
761 decreasing competitive strength of the inoculant (a_{cw}), and it is independent on the dispersal
762 ability of the inoculant. The linear speed of Eq. (17) seems to be a good approximation when
763 the competitive ability of the inoculant is small (i.e., a_{cw} is large, see Fig. S2c), and when the
764 mutualist quality of the inoculant is low (i.e., the ratio α_c/β_c is small, see Fig. S2b). However
765 the speed c_w^* appears to be non-linear for higher competitive ability and mutualist quality of
766 the inoculant.

767 5.0.1 Bistable traveling wave

768 **Case (Da), when $N > 1$:** In this case competition between the inoculant and the resident
769 community is strong, and the steady state \mathbf{U}_w^* and \mathbf{U}_c^* are both stable. We will first discuss
770 the case where $N > 1$, i.e., the resident community consists of two or more fungal species.
771 To understand which steady state will invade the other, we will determine the sign of the
772 propagation speed c . For this purpose, we multiply Eq. (8b) by M_c' and integrate over the
773 whole z -domain. We obtain the equation

$$774 \quad \int_{-\infty}^{\infty} [D_c M_c'' M_c' + c M_c'^2 + F_{M_c} M_c'] dz = 0. \quad (18)$$

775 We know that $M_c' = 0$ when $z \rightarrow \pm\infty$. Hence $\int_{-\infty}^{\infty} M_c'' M_c' dz = \int_{-\infty}^{\infty} 1/2((M_c')^2)' dz = 0$ and
776 Eq. (18) can be rewritten as

$$777 \quad c \underbrace{\int_{-\infty}^{\infty} (M_c')^2 dz}_{>0} = - \int_{-\infty}^{\infty} F_{M_c} M_c' dz. \quad (19)$$

778 The sign of the wave speed c depends therefore on the sign of the integral on the right-hand
779 side of Eq. (19). We can observe that

$$780 \quad - \int_{-\infty}^{\infty} F_{M_c} M_c' dz = - \int_{-\infty}^{\infty} \frac{F_{M_c}}{M_c} M_c' M_c dz = - \int_{-\infty}^{\infty} \frac{F_{M_c}}{2M_c} (M_c^2)' dz. \quad (20)$$

781 According to the boundary conditions of Eq. (10),

$$782 \quad \frac{F_{M_c}}{M_c}(-\infty) = \frac{F_{M_c}}{M_c}(\mathbf{U}_c^*) = 0, \quad \text{and} \quad \frac{F_{M_c}}{M_c}(+\infty) = \frac{F_{M_c}}{M_c}(\mathbf{U}_w^*) = F_c^*. \quad (21)$$

783 From Martignoni et al. (2020b) we know that, for case (D), $F_c^* < 0$. Additionally, from
784 numerical simulations one can notice that the slope of M_c is really steep (see Table S2) and
785 thus the integral of Eq. (20) can be approximated by

$$786 \quad - \int_{-\infty}^{\infty} \frac{F_{M_c}}{2M_c} (M_c^2)' dz = \frac{1}{2} \left(\frac{F_{M_c}}{M_c}(\infty) - \frac{F_{M_c}}{M_c}(-\infty) \right) = \frac{1}{2} F_c^* < 0. \quad (22)$$

787 Hence, the integral on the right side of Eq. (20) is always negative. We can conclude that
 788 the propagation speed c is negative, and therefore the stable steady state \mathbf{U}_w^* is expected to
 789 invade the state \mathbf{U}_c^* . In other words, the commercial inoculant is displaced by the resident
 790 fungal community.

791 To gain more insights into the speed at which the commercial inoculant is displaced, we
 792 explore the dependence of the speed on diversity of the resident community, and on the dis-
 793 persal ability and mutualist quality of the inoculant numerically (see Fig. S3). We find that
 794 the speed at which the inoculant is displaced increases with increasing diversity in the resi-
 795 dent community, and decreases with increased dispersal ability and with decreasing mutualist
 796 quality of the inoculant.

797 For a combination of low resident fungal density and high propagule pressure, the spatial
 798 dynamics follows a multi-step process illustrated in Fig. 1, case (Da), that is:

- 799 • The inoculant can temporarily establish and spread from its initial location. This
 800 initial spread prevents the growth of resident fungi in areas where the density of fungal
 801 inoculant is high, but at the same time plant growth is accelerated by the large presence
 802 of the inoculant (Fig. 1, case (Da), $T = 20$).
- 803 • Beyond the dispersal range of the inoculant, the density of resident fungi increases and
 804 so does plant productivity, eventually reaching a higher density than when only the
 805 inoculant is present (Fig. 1, case (Da), $T = 30$ and $T = 40$).
- 806 • A higher plant density determines higher resource availability, what gives a competi-
 807 tive advantage to the resident community with respect to the inoculant. The resident
 808 community is able to recolonize the portion of field taken by the inoculant leading the
 809 inoculated population to extinction (Fig. 1, case (Da), $T = 60$ and $T = 100$).

810 The speed at which the inoculant is displaced increases with increasing diversity of the resident
 811 fungal community, and decreases with increasing dispersal ability of the inoculant and with
 812 decreasing mutualist quality (see Fig. 2, case (Da)). For higher proportion of field occupied
 813 by the inoculant, resident fungi may not be able to recolonize the field (see Fig. 1, case (Db)).

814 **Case (Da), when $N = 1$:** We consider now the case where a strong competing inoculant
 815 m_c is introduced in the field is inhabited by a single resident fungal species m_w , that is a
 816 strong competitor as well. In this case, the competitive exclusion steady states \mathbf{U}_w^* (only m_w)
 817 and \mathbf{U}_c^* (only m_c) are both stable. If m_c and m_w have different parameters, the strongest
 818 competitor will invade the other. A competitive advantage can be given by larger initial
 819 propagule density, lower mutualist quality (i.e., smaller α/β ratio) or lower maintenance cost
 820 (i.e., smaller μ_m). A larger diffusion constant (i.e., larger D_c or D_w), can drive the invasion
 821 of a species only if the domain was previously unoccupied by the other species.

822 If the two fungi are identical, none of the species has a competitive advantage over the
 823 other and stationary solutions will be observed. To explore this scenario numerically, we
 824 consider on the left of the domain a steady state where m_w is zero, and on the right a steady
 825 state a steady state where m_c is zero. In this case, neither m_w nor m_c will prevail over the
 826 other. At the boundary between the two domains, where the two fungal species meet, we
 827 observe an increase in plant biomass density due to the partial presence of both species (see
 828 Fig. S4). The increase in plant biomass density is less pronounced for stronger competition
 829 between the fungi.

Table S1: Description of variables and parameters of the model given in (6), with respective measurement units.

Symbol	Description	Unit
p	Plant	plant biomass density
m_c	Fungal inoculant	fungal biomass density
m_w	resident fungal species	fungal biomass density
D_c	Diffusion coefficient of m_c	$\frac{\text{space}}{\text{time}}$
D_w	Diffusion coefficient of m_w	$\frac{\text{space}}{\text{time}}$
a_{wc}	Competition parameter (m_w toward m_c)	fungal biomass density
a_{cw}	Competition parameter (m_c toward m_w)	fungal biomass density
a_{ww}	Competition parameter (m_w toward m_w)	fungal biomass density
d	Half-saturation constant	plant biomass density
r_p	Intrinsic growth rate	$\frac{\text{phosphorus}}{\text{plant biomass density} \times \text{time}}$
α	Phosphorus exchange ability	$\frac{\text{phosphorus}}{(\text{time}) \times (\text{fungal biomass density})}$
β	Carbon exchange ability	$\frac{\text{carbon}}{(\text{time}) \times (\text{fungal biomass density}) \times (\text{plant biomass density})}$
μ_p	Plant maintenance rate	$\frac{1}{(\text{time}) \times (\text{plant biomass density})}$
μ_m	Fungal maintenance rate	$\frac{1}{(\text{time}) \times (\text{fungal biomass density})}$
q_{hm}	Conversion phosphorus to fungal biomass density	fungal biomass density/ phosphorus
q_{hp}	Conversion phosphorus to plant biomass density	plant biomass density/ phosphorus
q_{cm}	Conversion carbon to fungal biomass density	fungal biomass density/ carbon
q_{cp}	Conversion carbon to plant biomass density	plant biomass density/ carbon

Table S2: Cases A-D indicate the four possible scenarios occurring when varying the competition strength between the introduced fungal inoculant (m_c) and resident fungal species (m_{w_j}), where all fungi share a resource supplied by the same plant. Interactions between the fungi and the plant are mutualistic, while interactions between fungal species are competitive. In the top row, arrow thickness represents the strength of the interactions. The second row summarises the predictions on inoculum establishment discussed in [Martignoni et al. \(2020b\)](#). The third and four rows illustrate the predictions on inoculum spread in each of the four cases. The output of case (D) depends on the initial density of the inoculant, as shown in Fig. 1. The outcome shown for case (D) here corresponds to case (Da). The big arrows in the bottom row indicate the spread direction and on the left of each arrow are the plant, inoculant and resident community densities expected after inoculation.

Case	(A)	(B)	(C)	(D)
Interactions				
Stable steady states (no diffusion)	Coexistence $(\tilde{p}^*, \tilde{m}_c^*, \tilde{m}_{w1}^*, \dots, \tilde{m}_{wN}^*)$	Community only $(p^*, 0, m_{w1}^*, \dots, m_{wN}^*)$	Inoculant only $(\tilde{p}^*, m_c^*, 0, \dots, 0)$	Bistability $(\tilde{p}^*, m_c^*, 0, \dots, 0)$ and $(p^*, 0, m_{w1}^*, \dots, m_{wN}^*)$
Spread	from $(p^*, 0, \tilde{m}_{w1}^*, \dots, \tilde{m}_{wN}^*)$ to $(\tilde{p}^*, \tilde{m}_c^*, \tilde{m}_{w1}^*, \dots, \tilde{m}_{wN}^*)$	from $(\tilde{p}^*, m_c^*, 0, \dots, 0)$ to $(p^*, 0, m_{w1}^*, \dots, m_{wN}^*)$	from $(p^*, 0, m_{w1}^*, \dots, m_{wN}^*)$ to $(\tilde{p}^*, m_c^*, 0, \dots, 0)$	from $(\tilde{p}^*, m_c^*, 0, \dots, 0)$ to $(p^*, 0, m_{w1}^*, \dots, m_{wN}^*)$
Sketch of the spread				

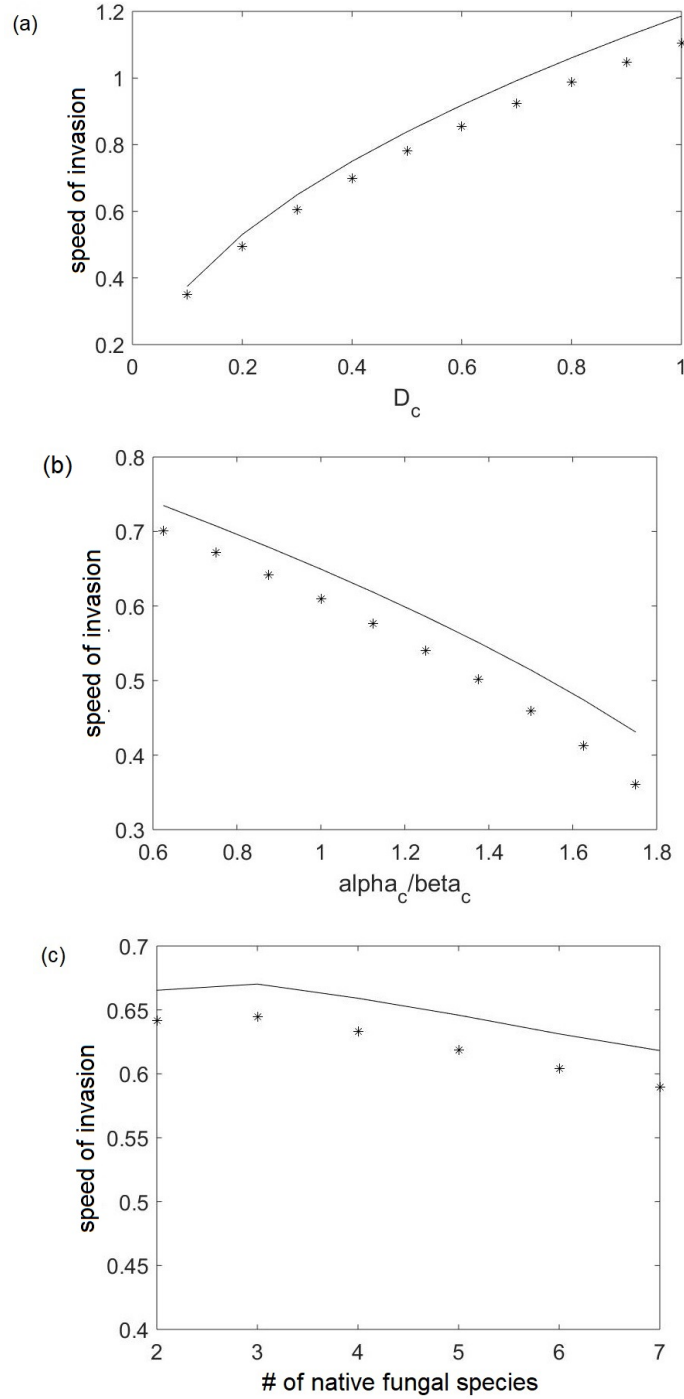


Fig. S1: Speed of invasion of the inoculant in a weak competing resident community (cases (A) and (C)) as a function of (a) the diffusion constant of the inoculant, (b) the mutualist quality of the inoculant, and (c) the number of species present in the resident community. The solid lines are the theoretically predicted lower bounds (see Eq. (14)) while the scattered plots are the results of the numerical simulations. The speed of invasion does not depend on whether the inoculant coexist with the resident community (case (A)) or displace the resident community (case (C)). In figures (a) and (b) competition parameters are $a_{ww} = a_{wc} = 2.2$, $a_{cw} = 0.3$, $\alpha_w = \beta_w = 0.4$. In figure (c) $a_{ww} = a_{wc} = 3.0$, $a_{cw} = 0.1$, $\alpha_w = 0.7$ and $\beta_w = 0.3$. Other parameter values are $q_{hp} = 3$, $q_{cm} = 2$, $q_{hm} = q_{cp} = 1$, $\mu_p = \mu_m = 0.3$, $d = 1.2$, $r_p = 0.02$, $D_w = 0.3$.

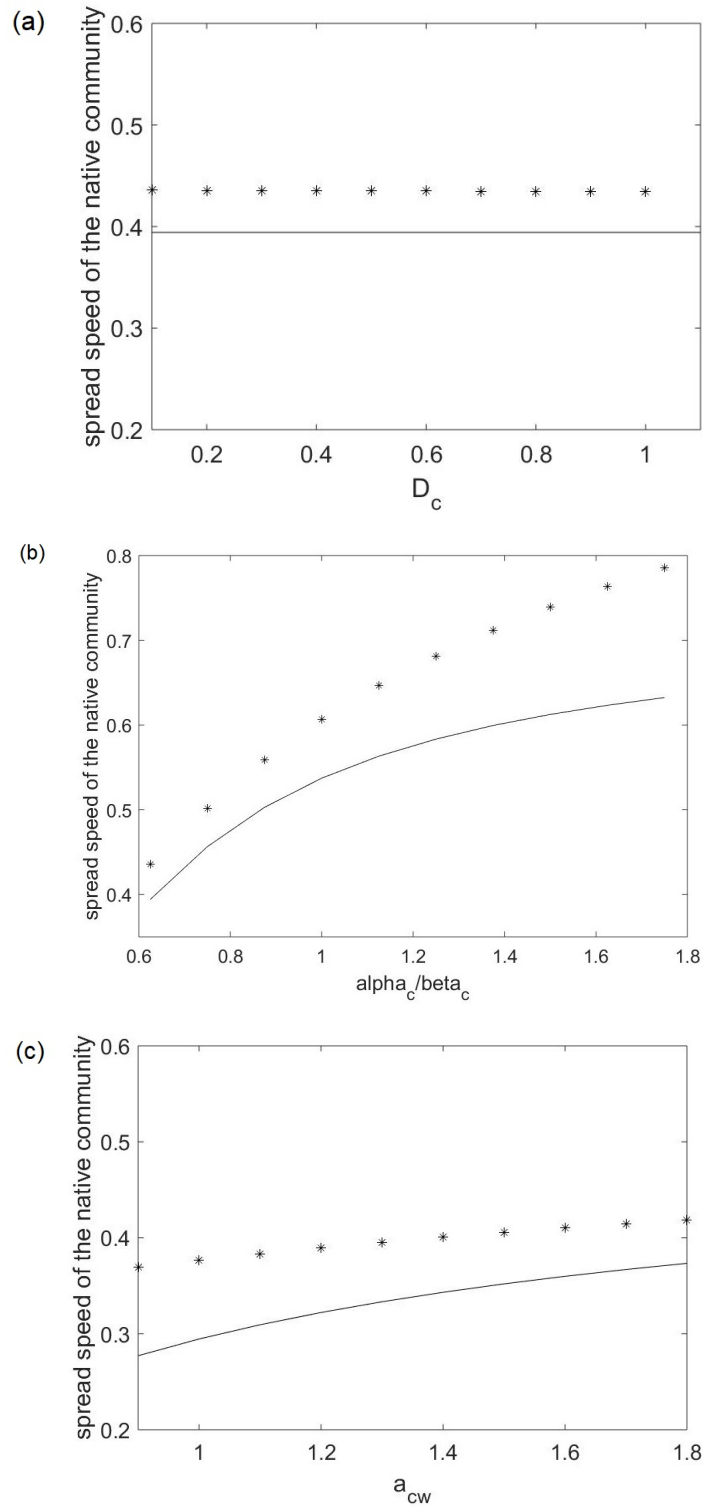


Fig. S2: Numerical simulations representing the speed at which a weakly competing inoculant is displaced by the resident community (case (B)). The solid lines are the theoretically predicted lower bounds (see Eq. (17)) while the scattered plots are the results of the numerical simulations. The speed is plot as a function of (a) the diffusion constant of the inoculant, (b) the mutualist quality of the inoculant, and (c) the competitive strength of the inoculant. Competition parameters are $a_{ww} = 2.2$, $a_{wc} = 0.3$. Other parameters correspond to those of Fig. S1a.

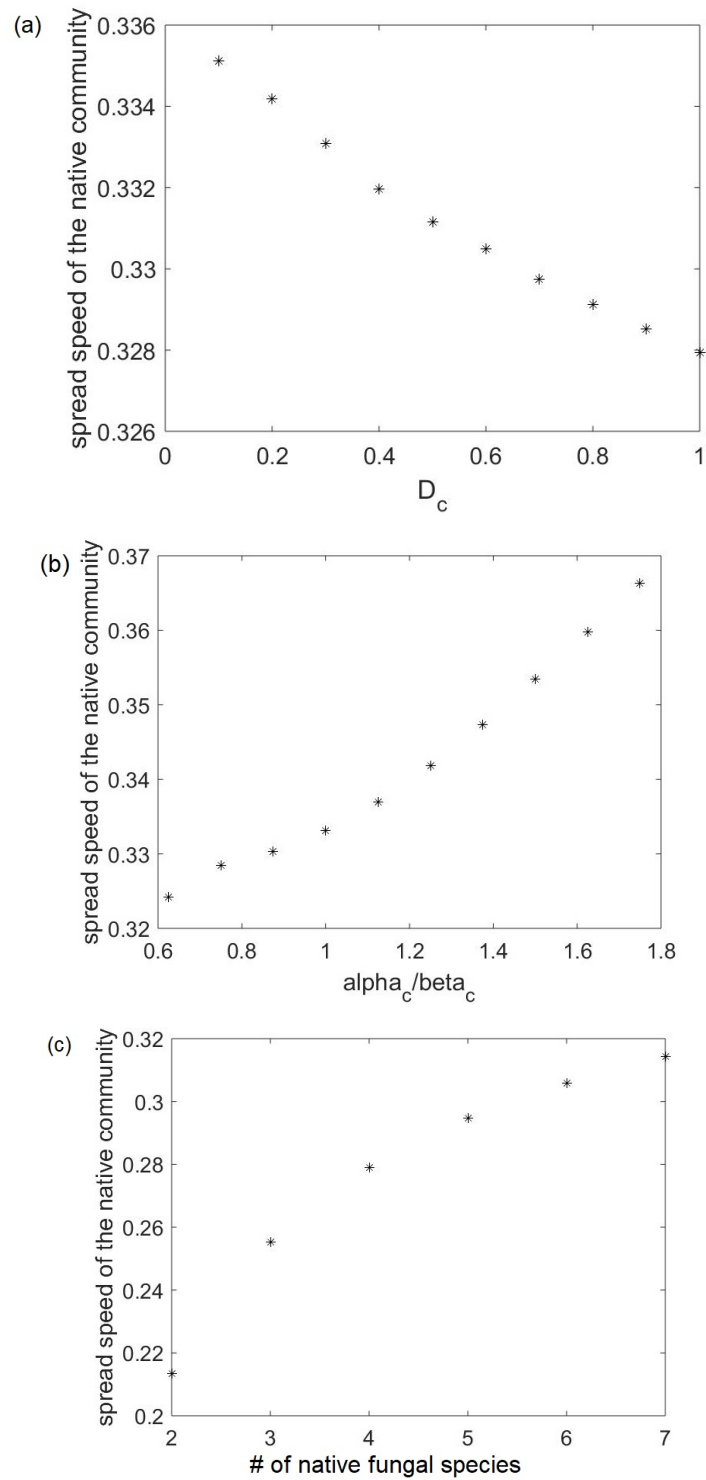


Fig. S3: Numerical simulations representing the speed at which a competitive inoculant is displaced by a strongly competing resident community (case (Da), for $N > 1$), as a function of (a) the diffusion constant of the inoculant, (b) the mutualist quality of the inoculant, and (c) the number of species present in the resident community. Competition parameters are $a_{ww} = 2.2$, $a_{wc} = a_{cw} = 0.3$. Other parameters correspond to those of Fig. S1a.

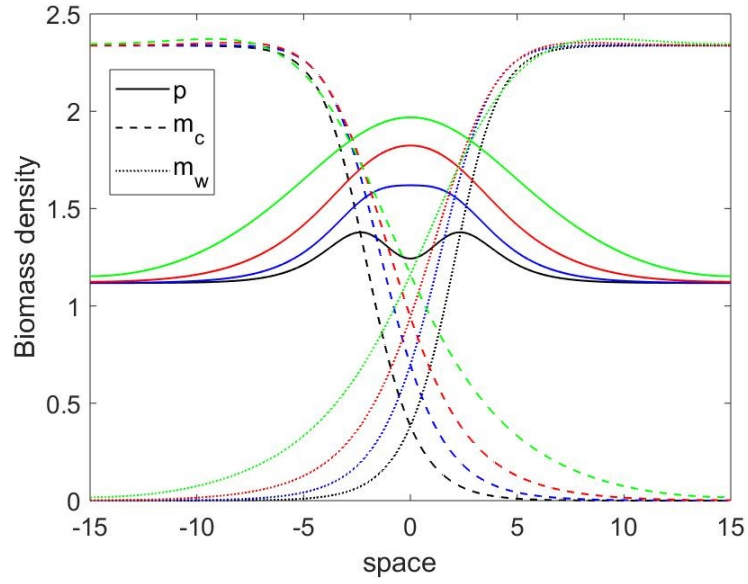


Fig. S4: Numerical simulation showing the plant (solid lines) and fungal biomass density distribution resulting from the encounter of two strongly competing fungi (m_c , scattered line, and m_w , dotted line), for different competition strengths (case (D), for $N = 1$). Competition parameters a_{cw} and a_{wc} have the same value and they are varies from 0.1 (strongest competition observed, black curves) to 0.7 (weakest competition observed, green curves) in steps of 0.2. Other parameters correspond to those of Fig. S1.