



The complex circuitry of interactions determining coexistence among plants and mycorrhizal fungi

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5 **The complex circuitry of interactions determining coexistence**
6 **among plants and mycorrhizal fungi**

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16 Open Research Statement: This paper reports the analysis of a theoretical model. Consequently,
17 no data were generated for this study. Matlab code is available on Figshare at

18 <https://figshare.com/s/f6b0875c7d35e99d6138>. Figshare will be the final open repository.

19

20 Key Words: apparent competition, coexistence, intraguild predation, mutualism, mycorrhizal
21 fungus, resource competition.

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23

24 *Abstract.* We present a mechanistic model of coexistence among a mycorrhizal fungus and
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35 several observed patterns, including shifts in plant-mycorrhizal growth responses and
36 coexistence along nutrient gradients, equivocal results among experiments testing the effect of
37 mycorrhizal fungi on plant diversity, and differences in plant diversity among ecosystems
38 dominated by different mycorrhizal groups.

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41 **Introduction**

42 Different types of species interactions involve varying levels of mechanistic complexity. A
43 direct consumer-resource interaction is simple: individuals of one species consume specific
44 compounds, fluids, tissues, or the entire bodies of individuals of another species (Holling 1959,
45 Murdoch and Oaten 1975, Jeschke, Kopp and Tollrian 2002). Resource competition is more
46 complex, being an indirect interaction in which individuals of two or more species consume the
47 same resource or prey (MacArthur 1969, Tilman 1980, 1982). Likewise, apparent competition is
48 an indirect interaction in which the individuals of two or more species are fed upon by the same
49 consumer (Holt 1977). Even more complex is intraguild predation, an interaction in which
50 predator and prey also compete for the same resource (Holt and Polis 1997). All of these indirect
51 interactions involve more complex circuitries than the basic consumer-resource interaction, and
52 each imposes specific criteria for the interacting species to coexist (McPeck 2022).

53 Basic mutualistic interactions between two species can also be quite complicated, often
54 involving multiple types of direct interaction circuits. Many mutualisms are in fact consumer-
55 resource interactions, but both species gain a fitness benefit despite that consumption (e.g.,
56 Holland et al. 2005, Holland and DeAngelis 2010, Jones, Bronstein and Ferrière 2012). In some,
57 one species feeds on its interaction partner, and in so doing renders a service, such as pollination,
58 seed dispersal, or herbivore protection, that increases the fitness of the partner (Holland and
59 DeAngelis 2010, Bronstein 2015). In others, the two interaction partners feed on one another in
60 ways that increase both their fitnesses (Holland and DeAngelis 2010). The interaction circuitry
61 in this latter mutualism type can be quite complex. One iconic example is the interaction
62 between a plant and a mycorrhizal fungus. Both the plant and fungus forage for mineral
63 nutrients from the environment (Smith and Smith 2011, Näsholm et al. 2013, Püschel et al.
64 2016), and so are resource competitors. The plant extracts these nutrients from the fungus
65 directly (Smith and Smith 2011, Näsholm et al. 2013), and so the plant is a consumer of the
66 fungus. Likewise, the fungus extracts carbon from the plant directly (Smith and Smith 2012,
67 Näsholm et al. 2013), and so the fungus is a consumer of the plant. Because each is

68 simultaneously a consumer and resource competitor of the other, each is an intraguild predator of
69 the other (Figure 1a). Additionally, if the fungus interacts with two plant species, the fungus is
70 both an alternative resource for each plant and a conduit of apparent competition between the
71 two plants (Figure 1b). Given this complex interaction circuitry, the criteria for coexistence of a
72 mycorrhizal fungus with one or two plant species are not obvious.

73 Many theoretical analyses have considered components of this interaction network. Many
74 analyses have explored the consequences of different carbon allocation strategies by plants to
75 support multiple fungal species using both optimal control theory (Bever 2015, Moeller and
76 Neubert 2016, Bachelot and Lee 2018) and market exchange approaches (Noë and Hammerstein
77 1994, Grman, Robinson and Klausmeier 2012, Wyatt et al. 2014, Noë and Kiers 2018). Others
78 have explored the conditions for multiple plant species to coexist with one or more fungal
79 species. Holland and DeAngelis (2010) explored the conditions for the coexistence of two
80 generalized mutualist consumers using simple predator-prey functions. Bever and colleagues
81 showed using generalized models of frequency dependent interactions that coexistence of two
82 plants and two fungi were possible when no species obtained combined higher fitness benefits
83 from both species of the other species type as compared to its competitor (Bever, Westover and
84 Antonovics 1997, Bever 1999). Umbanhowar and McCann (2005) used isocline analyses of
85 generalized functions and concluded that a mycorrhizal fungus would foster the coexistence of
86 two competing plant species if the better plant competitor in the absence of the mycorrhizal
87 fungus receives less benefit from the fungus but gives the fungus more benefit. They did note
88 the similarity of their conclusions to how apparent competition via a shared predator can permit
89 two competing plants to coexist, but this type of interaction circuitry was not part of the model.
90 Explicit environmental nutrient and nutrient-carbon exchange dynamics were also lacking from
91 these studies.

92 Other analyses have included environmental nutrient and exchange dynamics but have not
93 included the full interaction circuitry. Jiang et al. (2017) expanded Tilman's (1980) model of
94 two plants competing for two resources to include a specialist fungus for each. Fungi aided

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95 nutrient uptake by the plants, but nutrient and carbon transfers between plants and their
96 specialized fungi were not included. Benefits from fungi to poorer competitors could permit
97 coexistence with competitively superior plant species, or could shift the competitive dominance
98 hierarchy of plants if these benefits were high enough to inferior competitors (Jiang et al. 2017).
99 Johnson and Bronstein (2019) analyzed a model including explicit environmental nutrient
100 dynamics and exchanges between plants and fungi to show that two competing plants could
101 coexist if one plant extracted environmental nutrient at a higher rate and the other plant extracted
102 the nutrient from the fungus at a higher rate. However, their model did not include competition
103 between either plant and the fungus for the environmental nutrient, and no species paid any
104 fitness cost for having the other extract nutrient or carbon directly from them.

105 To explore the combined consequences of these various interaction components, we analyze
106 a more mechanistic model of the interaction circuitry depicted in Figure 1 to explore the
107 environmental and species properties fostering coexistence of a mycorrhizal fungus with one and
108 two plant species. Our goal is to build a generalized model incorporating these mechanisms and
109 not to make detailed and precise quantitative predictions (Holland and DeAngelis 2010). The
110 dynamics of the abundances and individual nutrient and carbon content are modeled for both
111 plants and fungi. Plants consume the nutrient from the fungus, the fungus consumes carbon from
112 the plant, and all species compete for the nutrient from the environment. We do not include
113 plant and fungal modulation of nutrient and carbon exchanges in the model analyzed here (e.g.,
114 Bever, Westover and Antonovics 1997, Bever 1999); our analysis focuses on the criteria for
115 coexistence of plants and fungi and not whether control mechanisms would match plant and
116 fungal properties that would meet these coexistence criteria. Future analyses will include these
117 controls to explore whether the modulation of exchanges that are adaptive will bring the system
118 to the conditions fostering coexistence that are identified here.

119

120 The Model

121 Begin by considering the dynamics of nutrient uptake and abundances of plant species

122 foraging for a mineral nutrient such as a nitrogen or phosphorus compound from the soil. The
 123 amount of the abiotic nutrient that is available in the environment is N and follows a simple
 124 abiotic renewal function

$$125 \quad \Omega(N) = c(T_N - N), \quad (2)$$

126 where T_N is the maximum amount that can accumulate, and c is the maximum renewal rate
 127 (Tilman 1982, Grover 1997). (All model state variables and parameters are listed in Table 1.)

128 In this analysis we consider the dynamics of two plant species, each has abundance of R_i ,
 129 with $i = 1, 2$ (we use R_1 and R_2 as the abundance state variables and as species identifiers in the
 130 text). Because this model has implications for both community and ecosystem ecology, we use
 131 the term abundance when referring to the plants, which can be conceptualized as either the
 132 number of individuals in a plant population or the total amount of plant biomass among all
 133 individuals in the population. Because the nutrient and carbon amounts in plants and fungi are
 134 resource pools that are consumed by the other species (Figure 1a), we explicitly model the
 135 dynamics of the nutrient and carbon content in plant and fungal biomass. Plant species have a
 136 quantity of the nutrient in their tissues Q_i^N , which is the amount of the nutrient compound in a
 137 unit of plant biomass (Droop 1973a, 1974, Grover 1990, 1991). We think of this as the quantity
 138 of nutrient used as building blocks to construct biomass and fuel to run metabolism, and not as
 139 the total amount of nutrient in the body. A plant acquires the nutrient from the soil nutrient pool
 140 according to a modified version of Michaelis-Menten/Monod dynamics in which its maximum
 141 rate of uptake decreases as its quantity Q_i^N increases:

$$142 \quad P_i(N, Q_i^N) = \frac{\rho_i^N \left(\frac{Q_i^{N \max} - Q_i^N}{Q_i^{N \max} - Q_i^{N \min}} \right) N}{\mathcal{G}_i^N + N}, \quad (3)$$

143 where $Q_i^{N \min}$ and $Q_i^{N \max}$ are the minimum and maximum values of the nutrient quantity allowed,
 144 respectively, \mathcal{G}_i^N is the half-saturation constant for uptake rate, and ρ_i^N is the maximum uptake
 145 rate, which is approached when Q_i^N approaches $Q_i^{N \min}$ and N is very large (Michaelis and
 146 Menten 1913, Monod 1949, Grover 1990, 1991).

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147 Each plant also photosynthesizes to produce carbon compounds; the quantity of carbon in a
 148 unit of plant biomass is given as Q_i^C . As with Q_i^N , we think of Q_i^C as the quantity of carbon
 149 used as building blocks to construct biomass and fuel to run metabolism, and not as the total
 150 amount of carbon in the body. We assume the maximum photosynthetic rate asymptotically
 151 increases with the quantity of nutrient Q_i^N in the plant to a maximum of λ_i , and the parameter ϕ_i
 152 scales the rate of approach to the asymptote. We also assume that plants compete for light, and
 153 so their rate of carbon production due to photosynthesis decreases with increasing plant
 154 abundance according to an exponential function, where α_i scales the rate of decline in carbon
 155 accumulation via photosynthesis with increasing plant abundance of both species. These
 156 assumptions result in the following function:

$$157 \quad \Lambda_i(Q_i^N, R_i) = \frac{\lambda_i Q_i^N}{\phi_i + Q_i^N} e^{-\alpha_i \sum_{j=1}^2 R_j} \quad (4)$$

158 We assume that $\phi_1 = \phi_2$, $\lambda_1 = \lambda_2$ and $\alpha_1 = \alpha_2$, which makes the two plant species equivalent at
 159 producing carbon from sunlight: i.e., in this analysis, plants are equivalent in carbon production
 160 and so differential carbon production capabilities cannot promote their coexistence.

161 The biomass production rate at which the plant grows and reproduces follows the multi-
 162 compound Droop (1973a, b, 1974) formulation, where plants would not produce new biomass if
 163 either quantity was at its minimum, but increases with increasing values of each up to a
 164 maximum production rate of μ_i :

$$165 \quad \Psi_i(Q_i^N, Q_i^C) = \mu_i \left(1 - \frac{Q_i^{N \min}}{Q_i^N}\right) \left(1 - \frac{Q_i^{C \min}}{Q_i^C}\right) \quad (5)$$

166 (see also Sterner and Elser 2002). Plants lose biomass at a rate of f_i . A fraction θ_i of the
 167 nutrient quantity in dead plant biomass is recycled back to the available environmental pool.
 168 Plants also have basal minimum utilization rates of a fraction ε_i^N of their nutrient from their
 169 basal metabolisms and use an amount that scales with biomass production at rate b_i^N for growth
 170 and reproduction. Plants also lose carbon due to metabolic processes at a baseline rate δ_i^C and
 171 increases at a rate of b_i^C that scales with the biomass growth rate to grow and reproduce.

172 This community also contains a mycorrhizal fungus species that has an abundance of M .
 173 Like plants, each unit of fungal biomass has a quantity of the abiotic nutrient Q_M^N and of carbon
 174 Q_M^C , and the dynamics of these quantities are shaped by similar processes as for plants. The
 175 fungus takes up nutrient from the environment according to the same modified version of
 176 Michaelis-Menten/Monod dynamics as used for the plants

$$177 \quad P_M(N, Q_M^N) = \frac{\rho_M^N \left(\frac{Q_M^{N \max} - Q_M^N}{Q_M^{N \max} - Q_M^{N \min}} \right) N}{\mathcal{G}_M^N + N}, \quad (6)$$

178 where $Q_M^{N \min}$ and $Q_M^{N \max}$ are the minimum and maximum values of the nutrient quantity,
 179 respectively, \mathcal{G}_M^N is the half-saturation constant, and ρ_M^N is the maximum uptake rate when Q_M^N
 180 approaches $Q_M^{N \min}$ and N is very large (Michaelis and Menten 1913, Monod 1949, Grover 1990,
 181 1991). The fungus also has a basal minimum utilization rate of a fraction ε_M^N of its nutrient from
 182 its basal metabolism and uses an amount that scales with biomass production at rate b_M^N for
 183 growth and reproduction.

184 The fungus may also extract carbon from the environment according to the equation

$$185 \quad \Lambda_M(M) = \lambda_M e^{-\beta M}, \quad (7)$$

186 where λ_M is the maximum rate of carbon extraction, and β scales the rate at which carbon
 187 extraction declines with fungal abundance (e.g., greater fungal biomass would deplete available
 188 environmental carbon, which is not explicitly included in the model). A value of $\lambda_M = 0$
 189 characterizes arbuscular mycorrhizae and some ectomycorrhizal fungi since they obtain all their
 190 carbon from their plant partners and none from the environment (Lindahl and Tunlid 2015,
 191 Genre et al. 2020). A value of $\lambda_M > 0$ may characterize some ectomycorrhizal, ericoid, and
 192 orchid fungi that can potentially obtain some carbon (and other nutrients) from the environment
 193 by producing enzymes to decompose organic matter (Akroume et al. 2019, Genre et al. 2020).
 194 The fungus loses carbon due to metabolic costs at a baseline rate of δ_M^C that increases with
 195 biomass production at a rate of b_M^C for growth and reproduction. Because of the differences in
 196 carbon production mechanisms between plants and fungi (i.e., photosynthesis versus carbon

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197 extraction from plants or the environment), throughout these analyses λ_i ? λ_M is assumed.

198 The fungus also produces new biomass according to multi-compound Droop dynamics

$$199 \quad \Psi_M(Q_M^N, Q_M^C) = \mu_M \left(1 - \frac{Q_M^{N \min}}{Q_M^N}\right) \left(1 - \frac{Q_M^{C \min}}{Q_M^C}\right), \quad (8)$$

200 where μ_M is the maximum production rate. The fungus also loses biomass at a rate of f_M . A

201 fraction θ_M of the nutrient quantity in dead biomass is recycled back to the available

202 environmental pool.

203 Plants and fungi directly interact with one another by extracting one of the materials from the

204 other species (Figure 1a). A plant extracts nutrient from the fungus at rate

$$205 \quad D_i(Q_M^N, Q_i^N) = \frac{\rho_i^{NM} \left(\frac{Q_i^{N \max} - Q_i^N}{Q_i^{N \max} - Q_i^{N \min}} \right) Q_M^N}{g_i^{NM} + Q_M^N}, \quad (9)$$

206 where g_i^{NM} is the half-saturation constant, and ρ_i^{NM} is the maximum uptake rate from the

207 fungus, which is approached when Q_i^N approaches $Q_i^{N \min}$ and Q_M^N is very large. Likewise, the

208 fungus extracts carbon from each plant at rate

$$209 \quad C_i(Q_i^C, Q_M^C) = \frac{\rho_M^{Ci} \left(\frac{Q_M^{C \max} - Q_M^C}{Q_M^{C \max} - Q_M^{C \min}} \right) Q_i^C}{g_M^{Ci} + Q_i^C}, \quad (10)$$

210 where $Q_M^{C \min}$ and $Q_M^{C \max}$ are the minimum and maximum carbon quantities, respectively, g_M^{Ci} is

211 the half-saturation constant, and ρ_M^{Ci} is the maximum uptake rate from the plants when Q_M^C

212 approaches $Q_M^{C \max}$ and Q_i^C is very large.

213 These assumptions lead to the following set of differential equations describing the changes

214 in the abundances of the abiotic resource, the plant and fungus species, and the nutrient and

215 carbon quantities for each species,

$$216 \quad \frac{dN}{dt} = \Omega(N) - \sum_{i=1}^2 P_i(N, Q_i^N) R_i - P_M(N, Q_M^N) M + \sum_{i=1}^2 \theta_i^N f_i Q_i^N R_i + \theta_M^N f_M Q_M^N M$$

$$217 \quad \frac{dR_i}{dt} = R_i (\Psi_i(Q_i^N, Q_i^C) - f_i)$$

$$218 \quad \frac{dQ_i^N}{dt} = P_i(N, Q_i^N) - (\varepsilon_i^N + b_i^N \Psi_i(Q_i^N, Q_i^C)) Q_i^N + D_i(Q_M^N, Q_i^N) M$$

$$219 \quad \frac{dQ_i^C}{dt} = \Lambda_i(R_i) - (\delta_i^C + b_i^C \Psi_i(Q_i^N, Q_i^C)) Q_i^C - C_i(Q_i^C, Q_M^C) M \quad (11)$$

$$220 \quad \frac{dM}{dt} = M (\Psi_M(Q_M^N, Q_M^C) - f_M)$$

$$221 \quad \frac{dQ_M^N}{dt} = P_M(N, Q_M^N) - (\varepsilon_M^N + b_M^N \Psi_M(Q_M^N, Q_M^C)) Q_M^N - \sum_{i=1}^2 D_i(Q_M^N, Q_i^N) R_i$$

$$222 \quad \frac{dQ_M^C}{dt} = \Lambda_M(M) - (\delta_M^C + b_M^C \Psi_M(Q_M^N, Q_M^C)) Q_M^C + \sum_{i=1}^2 C_i(Q_i^C, Q_M^C) R_i$$

223 where the components are as given in equations (2)-(10).

224 A model of this complexity prohibits mathematical analysis. Therefore, we used computer
 225 simulations (numerical integration of the model using the ode45 solver of Matlab (version
 226 R2023a, Mathworks Inc.)) to analyze patterns emerging from biologically reasonable areas of
 227 parameter space. Matlab code of the model for one and two plant species interacting with a
 228 single fungus species is provided on Figshare (<https://figshare.com/s/f6b0875c7d35e99d6138>,
 229 PlantResourceFungusBaseModel1R1Mv5.m, PlantResourceFungusBaseModel2R1Mv5.m).

230 Simulations were run until the system came to a stable equilibrium (i.e., the abundances of all
 231 species stopped changing to 5 significant digits for 500 iterations) or a stable limit cycle (i.e., a
 232 repeated cycling through the same orbit evaluated visually in a graph of the abundances for 500
 233 iterations). Coexistence is defined as species having abundances $>10^{-5}$ at the equilibrium or
 234 sometime during the limit cycle. Limit cycles were only encountered in narrow ranges of
 235 parameter combinations at some transitions between species being able to coexist in the system
 236 and with environmental nutrient abundance being very low. Also, in the areas of parameter
 237 space we explored, we found no alternative equilibria, based on many replicate simulations using
 238 random initial abundances. Because this model is not meant to mimic quantitative features of the
 239 system, we focus on the general conditions that promote or retard species coexistence and the
 240 qualitative changes in abundances and quantities across various areas of parameter space.

241

242 **Results**

243 *One plant and one fungus*

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244 Coexistence of a plant and a mycorrhizal fungus species cannot be assumed. First, the plant
245 and fungus are competitors for the abiotic environmental nutrient. Because the plant has a
246 substantially greater capacity to acquire carbon, the fungus can coexist with the plant over all but
247 the very lowest range of the environmental nutrient availability gradient if the fungus has a
248 substantially higher environmental nutrient uptake rate than the plant (i.e., $\rho_M^N > \rho_1^N$) (Figure 2).

249 Also, how composition and abundances change along the environmental nutrient gradient
250 depend on whether the nutrient or carbon is more limiting to each species. Plant abundance
251 increases while fungal abundance actually decreases with increasing environmental nutrient
252 availability in the range where the nutrient is more limiting for both species (i.e., low T_N).
253 Remember that the plant is both competing with the fungus for the environmental nutrient pool
254 and extracting nutrient from the fungus directly. At the very low values of T_N , the plant's
255 abundance is not large, and so the total amount of nutrient that the plant extracts from the fungus
256 is not large. As plant abundance increases in this range of T_N , the resulting increases in the
257 combined effects of direct consumption and indirect competition for the limiting nutrient cause
258 the fungal abundance to decline (Figure 2d). Moreover, if the fungus' environmental nutrient
259 uptake rate is only moderately higher than the plant, these combined effects cause fungal
260 abundance to decrease to zero in the intermediate range of T_N (Figure 2c).

261 In contrast, fungal abundance increases and plant abundance decreases at high values of T_N
262 where carbon is more limiting to both species (Figure 2d). In this range, carbon production by
263 the plant is limited by intraspecific competition for light, and carbon extraction by the fungus
264 from the plant becomes the more important direct interaction between them. The increasing
265 fungal abundance with higher nutrient availability causes more carbon to be extracted from the
266 plant, which causes its abundance to decline.

267 If the fungus is able to extract environmental carbon (e.g., $\lambda_M = 0.5$) instead of solely relying
268 on plant subsidy (e.g., $\lambda_M = 0.0$), the fungus can coexist with the plant at lower maximum
269 nutrient uptake rates across the whole nutrient availability gradient (cf. Figures 2a and 2b).

270 The rate at which the plant consumes the fungal nutrient relative to its ability to extract

271 nutrient from the environment also influences whether the plant and fungus can coexist.
272 Coexistence requires that either (1) the plant extracts nutrient from the fungus at a high rate but
273 has a substantially lower environmental nutrient uptake rate than the fungus ($\rho_M^N > \rho_1^N$); or (2)
274 the plant has a higher environmental nutrient extraction rate than the fungus but extracts nutrient
275 from the fungus at a low rate (“ R_1 & M ” area in both panels of Figure 3). Thus, over much of
276 parameter space, coexistence requires that the fungus must be better at extracting the nutrient
277 from the environment than the plant. Even though the plant extracts the environmental nutrient
278 at a slower rate, it coexists because it also extracts the nutrient from the fungus. However, when
279 the plant extracts the environmental nutrient at a faster rate, coexistence requires that it extract
280 little nutrient from the fungus, and the fungus coexists because it extracts carbon from the plant.
281 The plant species can also drive the fungus extinct if it extracts nutrient from the fungus at too
282 high a rate, even when it is significantly poorer at extracting the environmental nutrient as
283 compared to the fungus (“ R_1 only” area in both panels of Figure 3). The rate required for the
284 plant to drive the fungus extinct depends on the fungus’ ability to extract carbon from the
285 environment (λ_M) (Figure 3).

286 Whether the nutrient or carbon is more limiting to plant and fungal growth also defines the
287 areas where the fungus is either a mutualist or parasite to the plant, which further depends on the
288 fungus’ maximum carbon extraction rate from the plant (Figure 4). At low environmental
289 nutrient availabilities where the nutrient is more limiting to both species, the fungus is a
290 mutualist, enhancing the abundance of the plant if they can coexist, regardless of the fungus’
291 carbon extraction rate (Figure 4a-b). In the zone of nutrient availabilities where both species are
292 shifting from nutrient to carbon limitation, the fungus is a mutualist if the fungus’ carbon
293 extraction rate is low, but a parasite depressing plant abundance if the fungus’ carbon extraction
294 rate is high (Figure 4c-d). Finally, in the range of environmental nutrient availabilities where
295 both species are carbon limited, the fungus is a parasite because of carbon consumption from the
296 plant, except at its very lowest carbon extraction rates (Figure 4e-f). The ability of the fungus to
297 extract carbon from the environment does not appreciably affect these trends (cf. panels for each

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298 T_N value with $\lambda_M = 0.0$ versus $\lambda_M = 0.5$).

299 One interesting observation is that the maximum rate at which the plant extracts the nutrient
300 from the fungus has relatively little effect on the plant's abundance over a large parameter range
301 of ρ_1^{NM} (Figure 5a). However, the rate at which the fungus extracts the nutrient from the
302 environment can have a substantial effect on plant abundance; plant abundance increases with
303 ρ_M^N until plant reproduction is limited by carbon and not by the nutrient (Figure 5b). Thus, the
304 environmental nutrient uptake ability of the fungus is a critical determinant of plant abundance
305 when the nutrient limits plant abundance.

306

307 *Two plants and one fungus*

308 A second plant species (R_2) can invade and coexist with the mycorrhizal fungus and the first
309 plant species under restricted conditions. In the comparisons made here, the two plant species
310 being considered have identical parameters except for those being compared explicitly. In the
311 absence of the fungus, the plant species with the higher environmental nutrient extraction rate
312 will drive the other plant extinct, all else being equal (Tilman 1982).

313 The two plant species can coexist if they differ in specific ways in their abilities to extract the
314 nutrient from the environment and from the fungus. Coexistence requires that the relative
315 abilities of the two plant species must trade off within a zone of parameter space where one plant
316 is better at extracting the nutrient from the environment, but the other is better at extracting the
317 nutrient from the fungus (i.e., the R_1, R_2 & M area in Figure 6). If R_2 extracts less from the
318 fungus than R_1 , R_2 must be able to extract proportionally more from the environment. However,
319 R_2 cannot be too good at extracting the environmental nutrient; R_2 will drive R_1 extinct if it
320 extracts the environmental nutrient at too high a rate, even if it is poorer at acquiring the nutrient
321 from the fungus. As expected, one plant always drives the other plant extinct if it has higher
322 maximum extraction rates from both environmental and fungal nutrient pools.

323 In the parameter space where the two plants coexist with the fungus (Figure 6), R_1 (the plant
324 that extracts the nutrient from the environmental pool at a slower rate but from the fungal pool at

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325 a faster rate) has a positive growth response in the presence of the fungus when R_2 is absent (i.e.,
 326 the fungus is a mutualist with R_1). However, R_2 (the plant that extracts nutrient from the
 327 environmental pool at a faster rate but from the fungal pool at a slower rate) has a negative
 328 growth response in the presence of the fungus when R_1 is absent (i.e., the fungus is a parasite of
 329 R_2). More generally from our explorations of large areas of parameter space, when the two
 330 plants coexist, at least one has a parasitic relationship with the fungus. The fungus is typically a
 331 mutualist with the plant that depends more on the fungal nutrient pool, and the fungus is
 332 typically a parasite with the plant that depends more on the environmental nutrient pool.

333 The abilities of the fungus to extract nutrient and carbon from the various sources also shapes
 334 coexistence of the plant species. In the examples presented in Figure 7, R_1 again has a lower
 335 maximum environmental nutrient extraction rate but a higher maximum fungal nutrient
 336 extraction rate than R_2 (i.e., $\rho_1^N < \rho_2^N$ and $\rho_1^{NM} > \rho_2^{NM}$). Also, the fungus has identical
 337 parameters for interactions with both plant species, unless otherwise specified in the example.

338 The relative rates at which the two plant species extract fungal nutrient influence the
 339 coexisting plants' relative frequencies (Figure 7a). Coexistence occurs because the high rate of
 340 fungal nutrient uptake by R_1 offsets the competitive advantage of R_2 for the environmental
 341 nutrient pool. Interestingly, within the parameter range of coexistence, the relative abundances
 342 of the two plant species do not change monotonically. At the lower range of ρ_1^{NM} permitting
 343 plant coexistence, R_2 (the plant with the higher maximum environmental nutrient uptake rate)
 344 decreases in abundance, and R_1 increases. As a result, fungal abundance decreases because R_1 is
 345 now extracting nutrient from it, and the environmental nutrient abundance increases because of
 346 the decreases in R_2 and fungal abundances. However, at higher ρ_1^{NM} values, the changes in
 347 plant relative abundances reverse because fungal abundance is greatly reduced, which more
 348 disadvantages R_1 , and environmental nutrient availability is higher, which advantages R_2 . Here
 349 again, the relative resource competitive abilities of the plants for the environmental and fungal
 350 nutrient pools interact to determine the outcome of these species interactions.

351 The maximum environmental nutrient extraction rate of the fungus will also shift the relative

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352 importance of the two conduits of resource competition between the plants, because this rate
 353 increases the amount of nutrient available to the two plants in the fungal nutrient pool and
 354 decreases the amount in the environmental pool (Figure 7b). At low environmental nutrient
 355 extraction rates for the fungus (i.e., $\rho_M^N < 2.2$), the plant that is less dependent on the fungal
 356 nutrient pool (i.e., R_2) is favored. Where the two plant species coexist (i.e., $2.2 < \rho_M^N < 4.9$),
 357 their relative abundances are determined by the rate at which the fungus extracts the
 358 environmental nutrient. Moreover, at high enough fungal extraction rates (i.e., $\rho_M^N > 4.9$), the
 359 plant species that depends more on the environmental nutrient pool may be unable to coexist,
 360 because the combined effects of the fungus and competing plant species drive the environmental
 361 nutrient availability to a level at which it cannot support a population.

362 The rate at which the fungus can extract environmental carbon also shapes plant coexistence,
 363 because a higher environmental carbon extraction rate elevates fungal abundance (Figure 7c).
 364 Higher values of the maximum environmental carbon extraction rate for the fungus favor the
 365 plant species more dependent on the fungal nutrient pool. Within the range of $0.0 < \lambda_M < 0.15$,
 366 higher values shift the plant species' relative abundances, with R_1 increasing and R_2 decreasing
 367 in relative abundance. Above this range, fungal abundance has increased above a level at which
 368 R_2 can maintain a population. Here, inflation of environmental carbon uptake by the fungus
 369 exacerbates apparent competition between the two plant species and exacerbates resource
 370 competition between R_2 and the fungus. The increase in fungal abundance favors the plant
 371 species that depends more on the fungal nutrient pool. However, if R_1 is absent, R_2 and the
 372 fungus will coexist with $\lambda_M > 0.15$, because fungal abundance will be lower.

373 The maximum rates at which the fungus extracts carbon from the two plant species also
 374 influences plant species coexistence (Figure 7d). In this example, the fungus has the same
 375 maximum carbon extraction rates from both plants (i.e., $\rho_M^{C1} = \rho_M^{C2}$) and does not extract carbon
 376 from the environment $\lambda_M = 0.0$. In the parameter range where the two plant species can coexist
 377 (i.e., $0.19 < \rho_M^{C1} = \rho_M^{C2} < 1.0$), increasing the maximum carbon extraction rates from the two
 378 plants shifts the plant relative frequencies in favor of R_1 , and above this range R_2 cannot coexist.

379 In this case, direct consumption by the fungus shifts the plants' relative abundances, which again
380 favors the plant species that more depends on the fungal nutrient pool. Also note that fungal
381 abundance changes very little as $\rho_M^{C1} = \rho_M^{C2}$ increase, because it becomes nutrient limited.

382

383 **Discussion**

384 As in nature, these model results highlight that the interactions among plants and their
385 mycorrhizal fungal partners are sometimes mutualistic and sometimes antagonistic. These
386 outcomes depend on the abilities of the interacting species, and the shift between mutualism and
387 antagonism occurs along environmental gradients of nutrient availability (Hoeksema et al. 2010,
388 Johnson 2010). Plants and mycorrhizal fungi can be mutualist partners that share resources, but
389 they are also competitors for those resources from the environment and consumers of one
390 another with all the attendant consequences of these interactions. Moreover, a mycorrhizal
391 fungus can be an indispensable community member to promote the coexistence of competing
392 plant species that could not otherwise coexist. However, a fungal partner shared by multiple
393 plant species is also a direct consumer of all, and so a conduit for apparent competition between
394 the plants that may or may not foster coexistence (Simard et al. 1997).

395 *Plant—fungus coexistence*

396 The requirements for coexistence of one plant species with a mycorrhizal fungus species in
397 our model echo the coexistence requirements for an intraguild predator and prey, but with a
398 richer set of possibilities. With intraguild predation, coexistence requires that the intraguild prey
399 consume their shared resource at a faster rate, and that the intraguild predator inflicts only a low
400 to moderate level of mortality on the intraguild prey (Polis and Holt 1992, Holt and Polis 1997,
401 McPeck 2022). Coexistence of a plant and a fungus is possible over a broad range of parameter
402 space if the fungus extracts the environmental nutrient at a higher rate than the plant, and the
403 plant extracts the nutrient at a moderate rate from the fungus. However, the fungus is also a
404 consumer of plant carbon. Consequently, coexistence is also possible if the plant extracts the
405 environmental nutrient at a higher rate than the fungus but extracts relatively little nutrient from

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406 the fungal pool, and if the fungus extracts carbon from the plant above some minimum rate
407 defined by other conditions.

408 Direct measures of environmental nutrient uptake by plants and fungi are difficult, but
409 models suggest that fungi typically have substantially higher nutrient uptake rates than plants
410 because fungi explore a much larger volume of soil and have a much greater surface area for
411 uptake (Schnepf and Roose 2006, Schnepf, Roose and Schweiger 2008, See et al. 2022). Ericoid
412 and some ectomycorrhizal (EcM) fungi can also access various pools of soil nutrients that are
413 inaccessible to plants by producing extracellular enzymes that mine organic matter for nutrients
414 (Koide et al. 2008, Bödeker et al. 2014, Lindahl and Tunlid 2015, Adamczyk et al. 2016, Pellitier
415 and Zak 2018, Akroume et al. 2019, Genre et al. 2020). Furthermore, root colonization by
416 arbuscular mycorrhizae (AM) fungi can reduce the root's ability to take up nutrients (Smith and
417 Smith 2012). These results suggest that fungi in nature may have a much higher environmental
418 nutrient extraction rate than their plant partners in most cases. Plants also derive different
419 nutrient levels from various fungal partners (Smith, Smith and Jakobsen 2003, 2004). Whether
420 any particular plant-fungus pair is coexisting in nature will depend on the balance of these
421 various uptakes and exchanges.

422 Our model results provide a mechanism for how the interaction between a plant and
423 mycorrhizal fungi can shift between mutualism and parasitism. At low environmental nutrient
424 levels, the effect of the fungus on plant abundance is positive, because the plant is more limited
425 by the nutrient. The fungus can also permit the plant to support a population in an ecosystem
426 with nutrient availability too low for the plant to persist by itself. However, at high
427 environmental nutrient levels, plant abundance can be depressed by the fungus because carbon
428 becomes limiting to plants, and the carbon loss to mycorrhizae slows plant growth. The more
429 effective the fungus is at siphoning carbon from the plant, the lower the ambient nutrient
430 availability at which this interaction becomes negative for the plant.

431 These results are consistent with experiments testing plant responses to mycorrhizal fungi
432 presence. The effect of arbuscular mycorrhizal (AM) fungi on plant biomass is positive in low

433 phosphorus soil but negative in high phosphorus soil (Johnson 2010). Similarly, plants are
434 significantly more responsive to mycorrhizal inoculation in unfertilized soil relative to fertilized
435 soil (Hoeksema et al. 2010). In some cases, plants may have adjusted to this negative response:
436 root colonization by AM and ectomycorrhizal (EcM) fungi can decrease as nutrient availability
437 increases, which may decrease the plant's carbon cost for interacting with the fungi (Egerton-
438 Warburton and Allen 2000, Egerton-Warburton, Johnson and Allen 2007, Pellitier et al. 2021).
439 Other resource gradients also affect the mycorrhizal growth response of plants: the interaction
440 can become parasitic at low light levels where carbon should be more limiting (Ibáñez and
441 McCarthy-Neumann 2016). Overall, our model demonstrates how the mycorrhizae-plant
442 interaction exists on a continuum of mutualism to parasitism.

443 Environmental nutrient availability is not the only factor that determines the plant growth
444 response to the presence of mycorrhizal fungi. Plant growth is increased as the fungus' ability to
445 take up nutrients from the environment increases. Plant growth is often dependent on the
446 mycorrhizal species involved (Smith, Smith and Jakobsen 2003, Hoeksema et al. 2018). The
447 growth of ectomycorrhiza-associating trees across Europe increased as the genetic potential of
448 the EcM fungi to take up inorganic nitrogen increased (Anthony et al. 2022). In that study,
449 fungal community composition explained more variation in tree growth than climate or soil
450 factors. The growth response of arbuscular mycorrhiza-associating plants also differs among
451 different AM species (Smith, Smith and Jakobsen 2003, 2004, Bennett and Bever 2007, van der
452 Heijden, Bardgett and van Straalen 2008), but whether these differences are due to differences in
453 the fungi's nutrient uptake capabilities is unknown. Our model provides testable predictions
454 about the mechanisms by which the benefits of the mutualism and costs are dependent on fungal
455 species traits (e.g., Wilson and Hartnett 1997, Klironomos et al. 2000, Klironomos 2002, Bennett
456 and Bever 2007).

457 Whether the mycorrhizae can coexist with the plant depends on its ability to extract nutrients
458 from the environment. In nature, major shifts in EcM assemblage composition occur across
459 nutrient gradients towards fungal species that are better adapted for taking up inorganic nutrients

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460 (Lilleskov, Hobbie and Horton 2011). EcM fungi are polyphyletic and have large differences in
461 their morphology and ability to take up inorganic versus organic nutrients (Avis 2012, Pellitier
462 and Zak 2018). The EcM fungi that produce extracellular enzymes to mine organic matter for
463 nutrients, which is a slower and more energetically costly nutrient acquisition strategy, often
464 decline the most with increasing nitrogen availability. In contrast, hydrophilic, shorter distance
465 exploration types of EcM that are better at taking up inorganic nitrogen from the soil solution
466 increase (Lilleskov, Hobbie and Horton 2011). Our results suggest that competition with plants
467 may be one component of why the EcM species specializing in a slower, more organic-
468 dominated nitrogen cycle are lost as nitrogen availability increases. AM fungal assemblages can
469 also shift as nutrient availability increases depending on ecosystem type and climate (Ma et al.
470 2021, Kasanke et al. 2022). However, the mechanism for this change in AM fungi is more likely
471 due to plants limiting their carbon subsidies in response to a negative mycorrhizal growth
472 response at high nutrient levels (Egerton-Warburton and Allen 2000). We have not incorporated
473 plant control over carbon subsidies to the fungus into this model, but we plan to do so in future
474 versions of the model. Because such controls would decrease the rate of carbon exchange to the
475 fungus, we expect that such controls at high nutrient availability would increase the plant's
476 abundance by mitigating the loss of carbon to the fungus.

477 *Plant coexistence and species diversity*

478 Theory predicts that two resource competitors cannot coexist on a single resource, but they
479 can coexist on two resources if each is better at consuming a different resource (Levin 1970,
480 Tilman 1980, Hsu, Cheng and Hubbell 1981, Tilman 1982). Our results show that the presence
481 of a mycorrhizal fungus can promote the coexistence of two plant species that compete for a
482 single limiting nutrient, and plant coexistence requires that one plant species be better at
483 extracting the nutrient from the environment and the other plant species be better at extracting
484 the nutrient from the fungus (see also Umbanhowar and McCann 2005, Johnson and Bronstein
485 2019). The fungus is not simply a nutrient conduit but rather acts as a separate nutrient pool for
486 the plants, and coexistence results when they trade off the ability to extract the nutrient from the

487 environmental and fungal pools (Umbanhowar and McCann 2005, Johnson and Bronstein 2019).
488 However, the two species must draw the nutrient in relatively equitable but opposite proportions
489 from the two pools (i.e., the area in Figure 6 labeled “ R_1 , R_2 & M ”). These relative nutrient
490 extraction rates between the two plant species also influence the plants’ relative abundances
491 when they do coexist. Thus, quantifying the relative supply of nutrients from the environment
492 and from mycorrhizal fungi for competing plant species will be an essential test of this model.

493 The loss of carbon to the fungus also shapes plant coexistence (Ek, Andersson and
494 Söderström 1997, Hobbie 2006, Kiers et al. 2011, Bever 2015, Genre et al. 2020). Greater
495 maximum carbon extraction rates from the plants by the fungus increases the fungus’ abundance,
496 which (1) exacerbates the plants’ costs, but also (2) provides a larger total fungal nutrient pool
497 available to the plants. Because the fungus is a consumer of both plants, this linkage via carbon
498 supply has two effects: the direct cost of consumption on each plant and the mediation through
499 the fungus of apparent competition between the plants (sensu Holt 1977).

500 Experimental results testing the effect of mycorrhizae on plant coexistence and diversity are
501 equivocal, which suggests a great range of fungal effects on plant competitive performance. In a
502 tallgrass prairie, suppressing mycorrhizal fungi increased plant richness, evenness, and diversity,
503 because competitively dominant plant species decreased in abundance and competitively inferior
504 plant species increased (Hartnett and Wilson 1999, Smith, Hartnett and Wilson 1999). In
505 contrast, in a microcosm experiment, mycorrhizal fungi permitted competitively inferior species
506 to coexist with competitively superior plant species, but the competitive inferiors were excluded
507 in mycorrhizae-free replicates (Grime et al. 1987). Likewise, among 21 plant species in an
508 Ontario old field, species with a greater competitive effect on a common phytometer species had
509 a smaller growth response to the presence of mycorrhizal fungi (Stanescu and Maherali 2017).
510 Thus, in some plant communities, mycorrhizae promote coexistence and in others, they
511 exacerbate competitive differences among species. Our model results predict that these
512 differences in response are due to the relative capabilities of the plants and fungi to extract
513 nutrients and carbon from one another and from the environment.

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514 Mycorrhizae have been shown to promote coexistence when the dominant plants in a
515 community without mycorrhizae have a lower or even negative mycorrhizal growth response
516 than other plants in the community (Grime et al. 1987, Stanescu and Maherali 2017, McHaffie
517 and Maherali 2020). Consistent with these results, our model predicts that the plant species that
518 is better at extracting the nutrient from the environmental pool will have a negative growth
519 response to the presence of the fungus (i.e., a parasitic relationship), and the plant species that is
520 better at extracting the nutrient from the fungal nutrient pool will have a positive mycorrhizal
521 growth response (i.e., a mutualistic relationship). Umbanhowar and McCann (2005) arrived at
522 similar conclusions from analyzing a generalized graphical model of this interaction. This result
523 is also analogous to the criterion for coexistence of two resource competitors that are fed upon by
524 a single consumer (Holt, Grover and Tilman 1994, Leibold 1996, McPeck 1996, 2022).

525 The effect of mycorrhizae on coexistence is also dependent on the abilities of the fungi
526 species present (Wilson and Hartnett 1997, Klironomos et al. 2000, Klironomos 2002, van der
527 Heijden, Bardgett and van Straalen 2008, Vogelsang and Bever 2009). For example, our model
528 predicts that plant coexistence is less likely if the fungus uses carbon from the environment.
529 Consequently, the model predicts arbuscular mycorrhizal fungi, which are obligate biotrophs,
530 should be more capable of fostering plant coexistence than ericoid and orchid mycorrhizae and
531 possibly more than ectomycorrhizal fungi depending on their saprotrophic capabilities. AM
532 systems are generally more diverse than EcM or ericoid systems (Brundrett and Tedersoo 2018).
533 For example, in the tropics, AM forests are quite diverse whereas EcM forests are often
534 dominated by a single species (Corrales, Henkel and Smith 2018). Additionally, the model
535 predicts that the rate at which the fungus can extract the nutrient from the environment strongly
536 influences whether plant species can coexist and their relative abundances if they do. Increasing
537 fungal abundance means a larger fungal nutrient pool from which the plants can draw, but also a
538 greater carbon cost for each plant to pay. It would be interesting to test the predictions of this
539 model result in the field among various ectomycorrhizal communities, which can differ greatly in
540 their nutrient uptake abilities (Pellitier and Zak 2018).

541 Obviously, this model does not include some features of plant-mycorrhizal fungus
542 interactions that may influence plant coexistence. These include when mycorrhizae increase the
543 strength of intraspecific competition (McHaffie and Maherali 2020) and the sharing of carbon
544 through common mycorrhizal networks (Teste and Simard 2008, Klein, Siegwolf and Körner
545 2016, Pickles et al. 2017). In ectomycorrhizal systems, carbon transfer can occur across plant
546 species from the stronger competitor to the poorer competitor via mycorrhizae (Simard et al.
547 1997), reducing interspecific competition. Our model also lacks any control by the plant of
548 carbon subsidy to the mycorrhizae (e.g., Bever 2002, Bever et al. 2009, Bever 2015). Lastly,
549 carbon and nutrients are not coupled in this model. In vivo, plants and fungi maintain their
550 carbon to nutrient ratios within certain bounds, so that nitrogen uptake would be constrained by
551 the amount of carbon in their biomass. Future analyses should explore these additional
552 mechanisms to see how they may alter the model's predictions.

553 *Conclusions*

554 The results of this model show that the coexistence of a plant and a fungus requires that the
555 fungus be substantially better at extracting the environmental nutrient, unless the plant extracts
556 little nutrient from the fungus. The plant can drive the fungus extinct if it extracts too much
557 nutrient from both the environment and the fungus. In contrast, the fungus can drive the plant
558 extinct if it has a higher environmental nutrient uptake rate than the plant and extracts carbon
559 from the plant at a much greater rate than the plant gains nutrient from the fungus. Our model
560 also predicts that the fungus can permit the plant to occupy nutrient-poor environments where it
561 would be incapable of living without the fungus, but that the fungus can become parasitic in
562 nutrient-rich environments where the plant is carbon-limited if it extracts carbon from the plant
563 at a substantial rate.

564 Furthermore, the results showed the presence of a single fungus species can foster the
565 coexistence of two plant species competing for a single environmental resource, because the
566 fungus is a second limiting resource to the plants and is a conduit of "apparent" competition
567 between them. Whether the plant species can coexist depends on 1) the balance among their

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568 relative competitive abilities for the environmental nutrient and for the nutrient from the fungus
569 and the relative amount of carbon extracted by the fungus from each and 2) the ability of the
570 fungus to extract nutrients and carbon from the environment. The ability of the fungus to extract
571 carbon from the environment controls the intensity of apparent competition between the plants.
572 Our analysis highlights several future avenues of inquiry including how the functional
573 capabilities of the mycorrhizal fungi affect competitive interactions between the fungi and plant
574 and between plants. Understanding this complex web of interactions among plants and
575 mycorrhizal fungi should help guide empirical research into new and fruitful directions.

576

577

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587

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813 Table 1. List of state variables, equation terms, and parameters used in the model.

814

815 State variables

816 N abundance of the environmental nutrient: units, nutrient

817 R_1, R_2 abundances of plant species 1 and 2, respectively: units, plant –
818 expressed as either individuals or biomass

819 M abundance of the mycorrhizal fungus: units, fungus – expressed as
820 biomass

821 Q_1^N, Q_2^N, Q_M^N individual quantities of the nutrient in plant species 1 and 2, and the
822 fungus, respectively: units, nutrient/([plant or fungus])

823 Q_1^C, Q_2^C, Q_M^C individual quantities of carbon in plant species 1 and 2, and the fungus,
824 respectively: units, carbon/([plant or fungus])

825 Equation Terms

826 $\Omega(N)$ renewal function for the abiotic nutrient pool: units, nutrient/time

827 $P_1(N, Q_1^N), P_2(N, Q_2^N), P_M(N, Q_M^N)$ uptake function of environmental nutrient by plant
828 species 1 and 2, and the fungus, respectively: units, nutrient/([plant
829 or fungus]·time)

830 $D_1(Q_M^N, Q_1^N), D_2(Q_M^N, Q_2^N)$ rate function for plant species 1 and 2 extracting nutrient
831 from the fungus, respectively: units, nutrient/(plant·fungus·time)

832 $C_1(Q_1^C, Q_M^C), C_2(Q_2^C, Q_M^C)$ rate function for the fungus extracting carbon from plant
833 species 1 and 2, respectively: units, carbon/(plant·fungus·time)

834 $\Lambda_1(R_1), \Lambda_2(R_2), \Lambda_M(M)$ carbon production rate function for plant species 1 and 2
835 and the fungus respectively: units, carbon/([plant or fungus]·time)

836 $\Psi_1(Q_1^N, Q_1^C), \Psi_2(Q_2^N, Q_2^C), \Psi_M(Q_M^N, Q_M^C)$ biomass (or individual) production rate
837 function for plant species 1 and 2, respectively and biomass
838 production rate function for the fungus: units, [plant or
839 fungus]/([plant or fungus]·time)

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840 Parameters

841	T_N	maximum abundance of the environmental nutrient: units, nutrient
842	c	renewal rate of environmental nutrient: units, 1/time
843	$Q_1^{N_{\max}}, Q_2^{N_{\max}}, Q_M^{N_{\max}}$	maximum individual nutrient quantities in plant species 1 and 2, and the
844		fungus, respectively: units, nutrient
845	$Q_1^{N_{\min}}, Q_2^{N_{\min}}, Q_M^{N_{\min}}$	minimum individual nutrient quantities in plant species 1 and 2, and the
846		fungus, respectively: units, nutrient
847	$Q_M^{C_{\max}}$	maximum individual carbon quantities in the fungus: units, carbon
848	$Q_1^{C_{\min}}, Q_2^{C_{\min}}, Q_M^{C_{\min}}$	minimum individual carbon quantities in plant species 1 and 2, and the
849		fungus, respectively: units, carbon
850	$\rho_1^N, \rho_2^N, \rho_M^N$	maximum environmental nutrient uptake rates for plant species 1 and 2,
851		and the fungus, respectively: units, nutrient/time
852	g_1^N, g_2^N, g_M^N	half-saturation constants of environmental nutrient uptake rates for plant
853		species 1 and 2, and the fungus, respectively: units, nutrient
854	ρ_1^{NM}, ρ_2^{NM}	maximum nutrient uptake rates from the fungus by plant species 1 and 2,
855		respectively: units, nutrient/time
856	g_1^{NM}, g_2^{NM}	half-saturation constants of nutrient uptake rates from the fungus for
857		plant species 1 and 2, respectively: units, nutrient
858	ρ_M^{C1}, ρ_M^{C2}	maximum carbon uptake rates from plant species 1 and 2, respectively,
859		by the fungus: units, carbon/time
860	g_M^{C1}, g_M^{C2}	half-saturation constants of carbon uptake rates from plant species 1 and
861		plant species 2, respectively, by the fungus: units, carbon
862	$\lambda_1, \lambda_2, \lambda_M$	maximum rate of carbon production by plant species 1 and 2, and of
863		carbon acquisition by the fungus, respectively: units, carbon/time
864	ϕ_1, ϕ_2	half-saturation constants for photosynthetic rates scaled by Q_1^N and Q_2^N
865		for plant species 1 and 2, respectively: units, nutrient
866	μ_1, μ_2, μ_M	maximum production rate for plant species 1 and 2, and maximum

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867		biomass production by the fungus, respectively: units, [plant or
868		fungus]/time
869	$\alpha_1, \alpha_2, \beta$	scaling parameter for carbon production by plant species 1 and 2, and of
870		carbon acquisition by the fungus, respectively: units, 1/[plant or
871		fungus]
872	$\varepsilon_1^N, \varepsilon_2^N, \varepsilon_M^N$	basal quantities used for growth and reproduction by plant species 1 and
873		2, and the fungus, respectively: units, nutrient/(nutrient·time)
874	b_1^N, b_2^N, b_M^N	nutrient quantities used for growth and reproduction by plant species 1
875		and 2, and the fungus, respectively: units, nutrient/ [plant or fungus]
876	$\delta_1^C, \delta_2^C, \delta_M^C$	basal carbon quantities used for growth and reproduction by plant
877		species 1 and 2, and the fungus, respectively: units,
878		carbon/(carbon·time)
879	b_1^C, b_2^C, b_M^C	carbon quantities used for growth and reproduction each offspring by
880		plant species 1 and 2, and biomass production rate for the fungus,
881		respectively: units, carbon/[plant or fungus]
882	$\theta_1, \theta_2, \theta_M$	fraction of individual nutrient quantity that is recycled to the
883		environmental pool from dead biomass for plant species 1 and 2, and
884		the fungus, respectively: unitless
885	f_1, f_2, f_M	intrinsic death rates for plant species 1 and 2, and intrinsic biomass loss
886		rate of the fungus, respectively: units, [plant or fungus]/([plant or
887		fungus]·time)
888		

889

Figure Legends

890

Figure 1. Conceptual diagrams of the consumption linkages between plants and mycorrhizal

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fungi. Each circle represents an individual of the plant, fungus, or the environmental pool of

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an abiotic nutrient (e.g., a nitrogen or phosphorus compound). The plant and fungus have

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pools of the nutrient N and carbon C in their tissues. Arrows point from the consumed pool

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to the consumer (i.e., the direction of flow of the quantity) and are labeled by the

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corresponding rate functions (see text). Panel (a) illustrates these consumption linkages for

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one plant species and one fungus, and panel (b) illustrates these linkages for two plant

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species and one fungus.

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Figure 2. Areas of coexistence of one plant species and one fungus species along an

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environmental nutrient gradient for various values of maximum nutrient uptake by the fungus

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(ρ_M^N). Panels (a) and (b) identify the areas of parameter space where the two species coexist

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(identified as “ R_1 & M ”), only the plant is present (“ R_1 ”), and a small unlabeled area at very

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low T_N (environmental nutrient) values where neither species can support a population. The

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fungus cannot extract carbon from the environment ($\lambda_M = 0.0$) in panel (a), and it can (

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$\lambda_M = 0.5$) in panel (b). Panels (c) and (d) show the changes in species and environmental

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nutrient abundances and quantities along transects of environmental nutrient availability for

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two different values of maximum environmental nutrient uptake for the fungus. In the top

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panel in each column of (c) and (d), the blue curve is the nutrient equilibrium abundance, the

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orange solid curve is the fungal equilibrium abundance, the green solid curve is the plant

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equilibrium abundance when both species are initially present and interact with one another.

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The green dashed curve is the plant equilibrium abundance in the absence of the fungus. The

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bottom panel in each column gives equilibrium quantities for nutrient (solid curves) and

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carbon (dot-dashed curves) for the plant (green) and fungus (orange). The other parameters

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used in these examples are as follows unless otherwise specified: $c=0.01$, $\mu_1 = \mu_M = 0.2$,

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$Q_1^{N \min} = Q_M^{N \min} = Q_1^{C \min} = Q_M^{C \min} = 0.2$, $Q_1^{N \max} = Q_M^{N \max} = 1.0$, $\rho_1^N = 0.1$, $b_1^N = b_M^N = 0.1$, $g_1^N = g_M^N = g_1^{NM}$

915

$= 25$, $\varepsilon_1^N = \varepsilon_M^N = 0.05$, $\rho_1^{NM} = 0.5$, $\lambda_1 = 100$, $\phi_1 = 0.2$, $\alpha_1 = \beta = 0.1$, $b_1^C = 2.0$, $b_M^C = 0.1$, $\delta_1^C = 0.15$, δ_M^C

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916 $=0.1$, $\rho_M^{C1}=0.3$, $\mathcal{G}_M^{C1}=50$, $f_1=f_M=0.1$, $\theta_1=\theta_M=0.5$.

917 Figure 3. The combinations of maximum nutrient uptake rates for the plant that shape whether
 918 the plant and fungus can coexist. The ordinate axis is the plant maximum uptake rate from
 919 the environment, and the abscissa axis is the plant maximum uptake rate from the fungus.
 920 Panel (a) has a fungus that does not extract carbon from the environment (i.e., $\lambda_M = 0.0$), and
 921 Panel (b) has a fungus with a maximum environmental carbon extraction rate of $\lambda_M = 0.5$.
 922 These parameter spaces are divided into four areas: No species present, because neither
 923 species can support a population with those parameter combinations; M only, where the
 924 fungus outcompetes the plant, so that only the fungus is present; R_1 only, where the plant
 925 outcompetes the fungus, so that only the plant is present; and R_1 & M , where the plant and
 926 fungus coexist. As a reference, the maximum uptake rate of the nutrient from the
 927 environment for the fungus is $\rho_M^N=0.5$ (identified by the dashed line in each panel). The
 928 other parameters are as follows unless otherwise specified: $T_N=50$, $c=0.01$, $\mu_1=\mu_M=0.2$,
 929 $Q_1^{N\min}=Q_M^{N\min}=Q_1^{C\min}=Q_M^{C\min}=0.2$, $Q_1^{N\max}=Q_M^{N\max}=1.0$, $\rho_1^N=0.1$, $b_1^N=b_M^N=0.1$, $\mathcal{G}_1^N=\mathcal{G}_M^N=\mathcal{G}_1^{NM}$
 930 $=25$, $\varepsilon_1^N=\varepsilon_M^N=0.05$, $\rho_1^{NM}=0.5$, $\lambda_1=100$, $\phi_1=0.2$, $\alpha_1=\beta=0.1$, $b_1^C=2.0$, $b_M^C=0.1$, $\delta_1^C=0.15$, δ_M^C
 931 $=0.1$, $\rho_M^{C1}=0.3$, $\mathcal{G}_M^{C1}=50$, $f_1=f_M=0.1$, $\theta_1=\theta_M=0.5$.

932 Figure 4. Carbon extraction rate by the fungus from the plant can shift their interaction from
 933 being mutualistic to parasitic, depending on environmental nutrient availabilities. Each panel
 934 shows the relationship for equilibrium plant abundance when the fungus has different values
 935 of maximum carbon extraction rate from the plant (ρ_M^{C1}). In each panel, the thin dashed line
 936 identifies the plant abundance in the absence of the mutualist. The solid line identifies the
 937 plant abundance. Panels (a), (c), and (e) show results for a fungus that cannot extract carbon
 938 from the environment, and panels (b), (d), and (f) of panels shows results for a fungus that
 939 can extract environmental carbon. Panels (a) and (b) show results at an environmental
 940 nutrient availability of $T_N = 50$, panels (c) and (d) for $T_N = 100$, and panels (e) and (f) for
 941 $T_N = 200$. The fungus cannot support a population below $\rho_M^{C1} = 0.15$, and so the
 942 discontinuity in plant abundance at this point is caused by the fungus now being able to

943 support a population. The other parameters are as follows unless otherwise specified: T_N
 944 $=50$, $c=0.01$, $\mu_1 = \mu_M = 0.2$, $Q_1^{N \min} = Q_M^{N \min} = Q_1^{C \min} = Q_M^{C \min} = 0.2$, $Q_1^{N \max} = Q_M^{N \max} = 1.0$, $\rho_1^N = 0.1$,
 945 $b_1^N = b_M^N = 0.1$, $\mathcal{G}_1^N = \mathcal{G}_M^N = \mathcal{G}_1^{NM} = 25$, $\varepsilon_1^N = \varepsilon_M^N = 0.05$, $\rho_1^{NM} = 0.5$, $\lambda_1 = 100$, $\phi_1 = 0.2$, $\alpha_1 = \beta = 0.1$, b_1^C
 946 $= 2.0$, $b_M^C = 0.1$, $\delta_1^C = 0.15$, $\delta_M^C = 0.1$, $\rho_M^N = 2.5$, $\rho_M^{C1} = 0.3$, $\mathcal{G}_M^{C1} = 50$, $f_1 = f_M = 0.1$, $\theta_1 = \theta_M = 0.5$.

947 Figure 5. Equilibrium abundances for a single plant species interacting with a single fungus
 948 species at various values of (a) the maximum plant uptake rate of nutrient from the fungus,
 949 and (b) the maximum environmental nutrient uptake rate for the fungus. The equilibrium
 950 abundances of the species and nutrient in the environment and the nutrient are identified as in
 951 Figure 2. The other parameters are as follows unless otherwise specified: $T_N = 50$, $c = 0.01$, μ_1
 952 $= \mu_M = 0.2$, $Q_1^{N \min} = Q_M^{N \min} = Q_1^{C \min} = Q_M^{C \min} = 0.2$, $Q_1^{N \max} = Q_M^{N \max} = 1.0$, $\rho_1^N = 0.1$, $b_1^N = b_M^N = 0.1$, \mathcal{G}_1^N
 953 $= \mathcal{G}_M^N = \mathcal{G}_1^{NM} = 25$, $\varepsilon_1^N = \varepsilon_M^N = 0.05$, $\rho_1^{NM} = 0.5$, $\lambda_1 = 100$, $\lambda_M = 0.0$, $\phi_1 = 0.2$, $\alpha_1 = \beta = 0.1$, $b_1^C = 2.0$,
 954 $b_M^C = 0.1$, $\delta_1^C = 0.15$, $\delta_M^C = 0.1$, $\rho_M^N = 2.5$, $\rho_M^{C1} = 0.3$, $\mathcal{G}_M^{C1} = 50$, $f_1 = f_M = 0.1$, $\theta_1 = \theta_M = 0.5$.

955 Figure 6. Areas of parameter space in which two plant species do and do not coexist while
 956 competing for the abiotic nutrient and interacting with a single fungus species. This figure
 957 contrasts plant species 2's maximum rate of nutrient uptake from the environment (ρ_2^N) with
 958 its maximum rate of nutrient uptake from the fungus (ρ_2^{NM}). The comparable parameters for
 959 plant species 1 are identified with the dashed lines. Three areas are identified: where each
 960 plant species coexists with the fungus alone, and where both plant species coexist with the
 961 fungus. Both plants have the same parameters except for those manipulated in the figure.

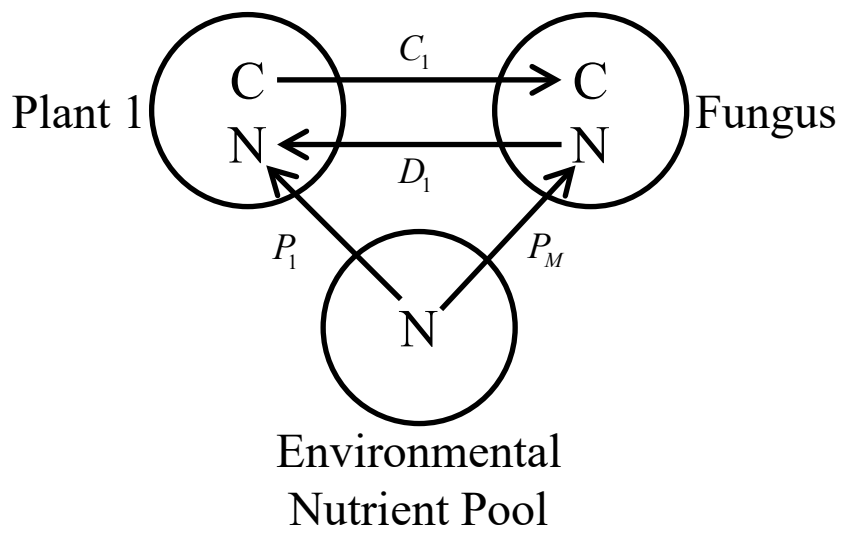
962 The other parameters are as follows unless otherwise specified: $T_N = 50$, $c = 0.01$, $\mu_1 = \mu_2 = \mu_M$
 963 $= 0.2$, $Q_1^{N \min} = Q_2^{N \min} = Q_M^{N \min} = Q_1^{C \min} = Q_2^{C \min} = Q_M^{C \min} = 0.2$, $Q_1^{N \max} = Q_2^{N \max} = Q_M^{N \max} = 1.0$, ρ_1^N
 964 $= 0.05$, $\rho_1^{NM} = 0.25$, $b_1^N = b_2^N = b_M^N = 0.1$, $\mathcal{G}_1^N = \mathcal{G}_2^N = \mathcal{G}_M^N = \mathcal{G}_1^{NM} = \mathcal{G}_2^{NM} = 25$, $\varepsilon_1^N = \varepsilon_2^N = \varepsilon_M^N = 0.05$,
 965 $\rho_1^{NM} = \rho_2^{NM} = 0.5$, $\lambda_1 = \lambda_2 = 100$, $\lambda_M = 0.0$, $\phi_1 = \phi_2 = 0.2$, $\alpha_1 = \alpha_2 = \beta = 0.1$, $b_1^C = b_2^C = 2.0$, $b_M^C = 0.1$,
 966 $\delta_1^C = \delta_2^C = 0.15$, $\delta_M^C = 0.1$, $\rho_M^N = 1.5$, $\rho_M^{C1} = 0.3$, $\mathcal{G}_M^{C1} = 50$, $f_1 = f_2 = f_M = 0.1$, $\theta_1 = \theta_2 = \theta_M = 0.5$.

967 Figure 7. Equilibrium abundances (top panels) and quotas (bottom panels) for two plant species
 968 interacting with a single fungus species at various values of (a) the maximum rate at which
 969 plant species 1 extracts the nutrient from the fungus, (b) the maximum environmental

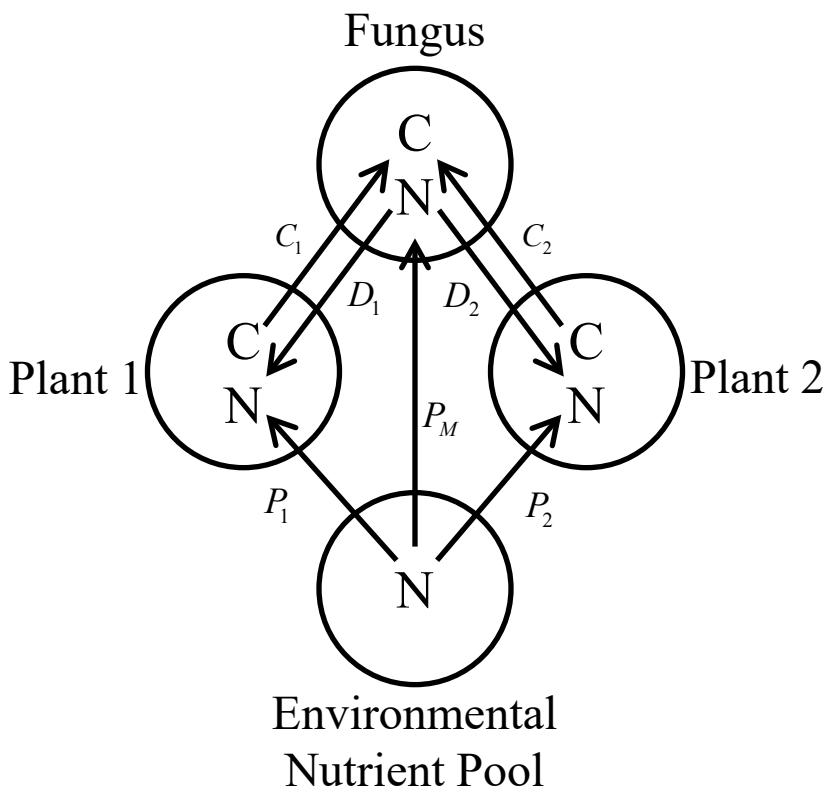
Running Head: Plant-Mycorrhizal Fungus Coexistence

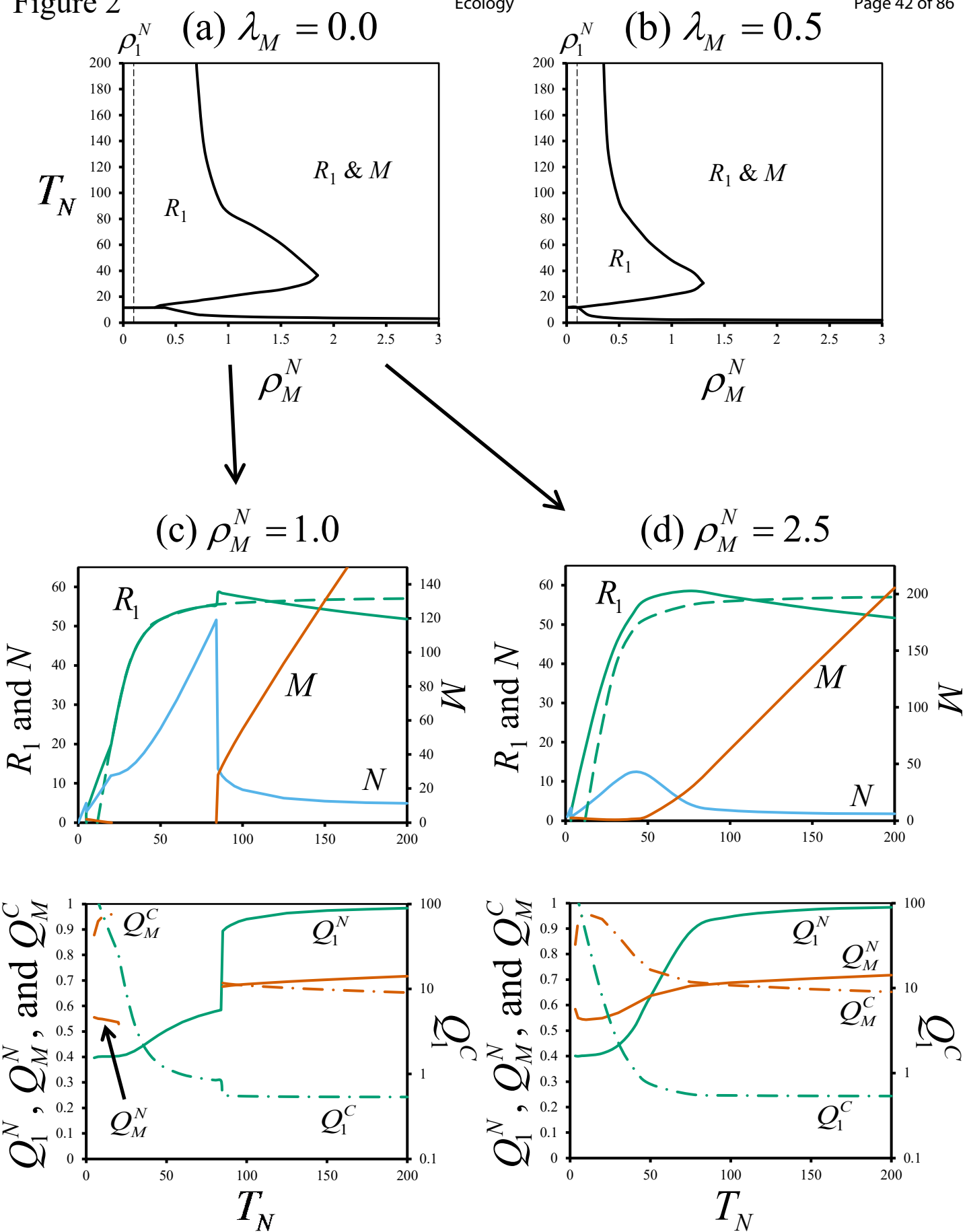
970 nutrient uptake rate for the fungus, (c) the maximum rate at which the fungus extracts carbon
 971 from the environment, and (d) the maximum rates at which the fungus extracts carbon from
 972 each plant for a community potentially consisting of two plants and a fungus. Quantities for
 973 the fungus and nutrient are identified as in Figure 2. Quantities for plant species 1 are given
 974 in dark green and for plant species 2 in light green. The other parameters are as follows
 975 unless otherwise specified: $T_N=50$, $c=0.01$, $\mu_1=\mu_2=\mu_M=0.2$, $Q_1^{N\min}=Q_2^{N\min}=Q_M^{N\min}=Q_1^{C\min}=$
 976 $Q_2^{C\min}=Q_M^{C\min}=0.2$, $Q_1^{N\max}=Q_2^{N\max}=Q_M^{N\max}=1.0$, $\rho_1^N=0.2$, $\rho_2^N=0.5$, $\rho_1^{NM}=1.0$, $\rho_2^{NM}=0.2$, $b_1^N=$
 977 $b_2^N=b_M^N=0.1$, $g_1^N=g_2^N=g_M^N=g_1^{NM}=g_2^{NM}=25$, $\varepsilon_1^N=\varepsilon_2^N=\varepsilon_M^N=0.05$, $\rho_1^{NM}=\rho_2^{NM}=0.5$, $\lambda_1=\lambda_2$
 978 $=100$, $\lambda_M=0.0$, $\phi_1=\phi_2=0.2$, $\alpha_1=\alpha_2=\beta=0.1$, $b_1^C=b_2^C=2.0$, $b_M^C=0.1$, $\delta_1^C=\delta_2^C=0.15$, $\delta_M^C=0.1$,
 979 $\rho_M^N=3.5$, $\rho_M^{C1}=0.3$, $g_M^{C1}=50$, $f_1=f_2=f_M=0.1$, $\theta_1=\theta_2=\theta_M=0.5$.

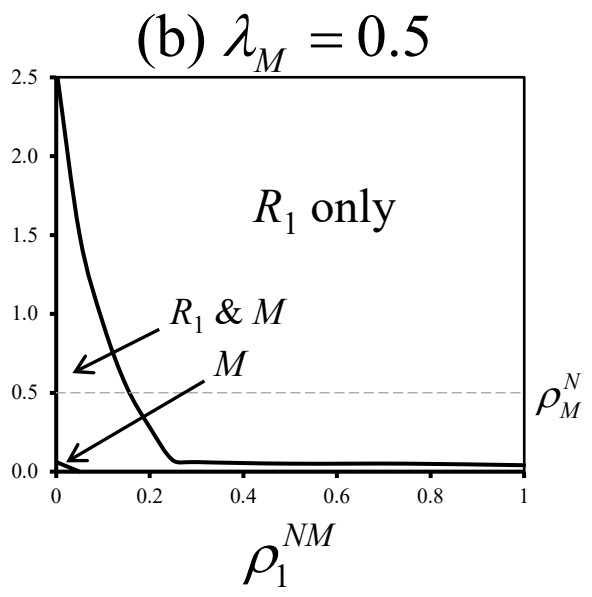
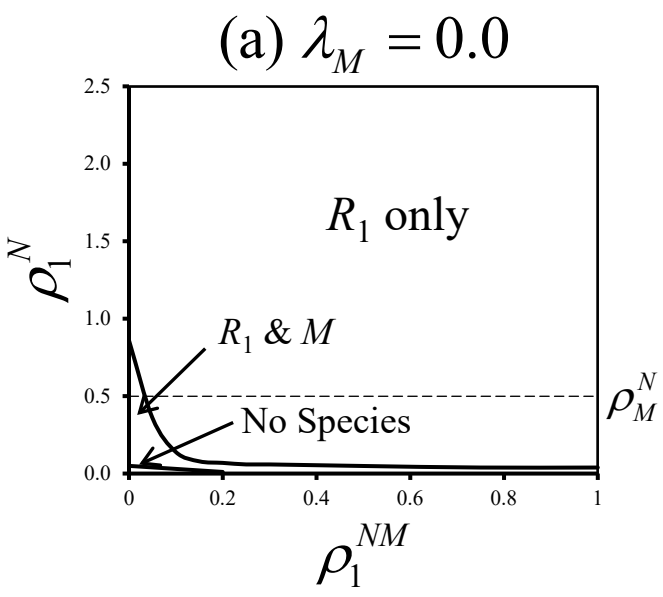
(a) One plant and one fungus



(b) Two plants and one fungus



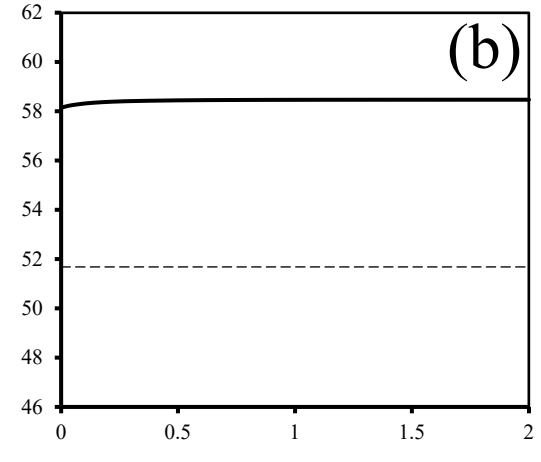
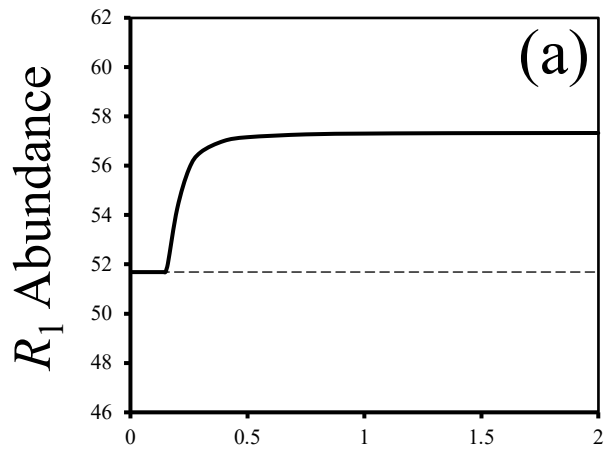




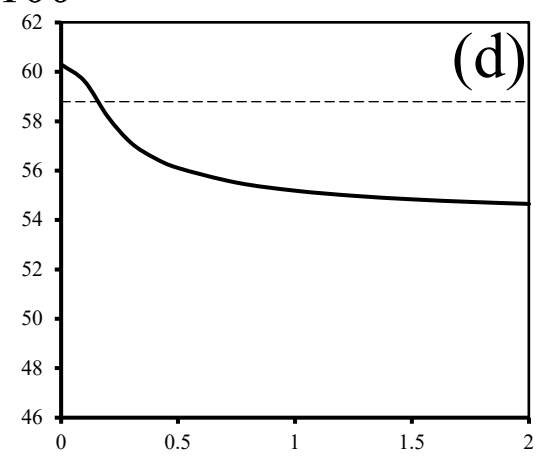
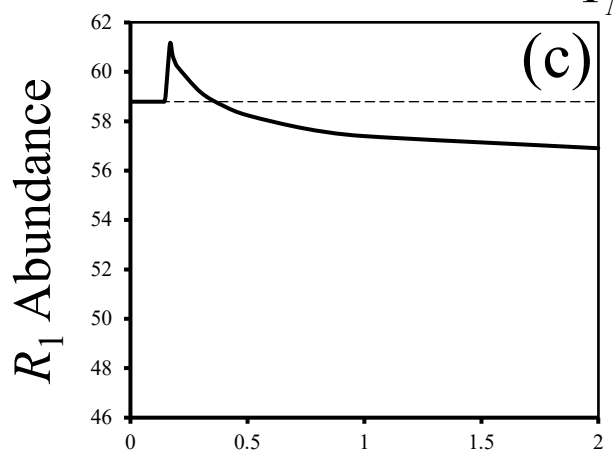
$$\lambda_M = 0.0$$

$$\lambda_M = 0.5$$

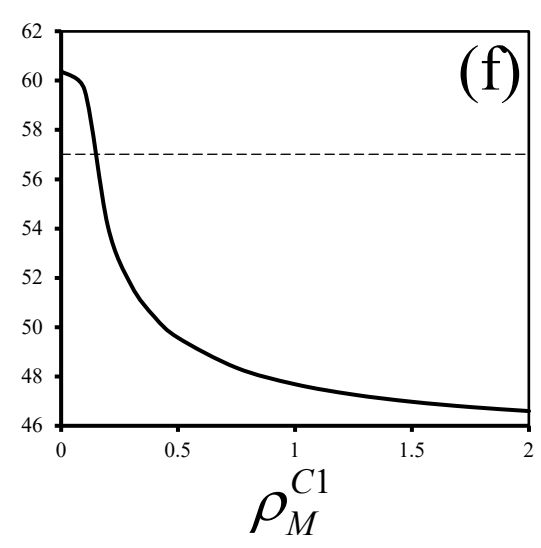
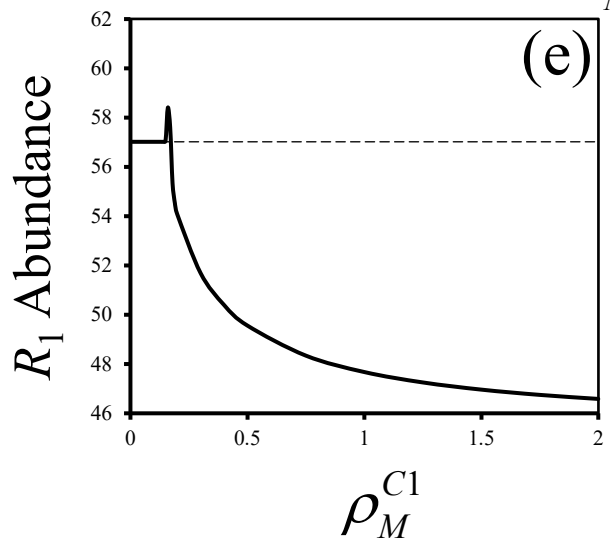
$$T_N = 50$$

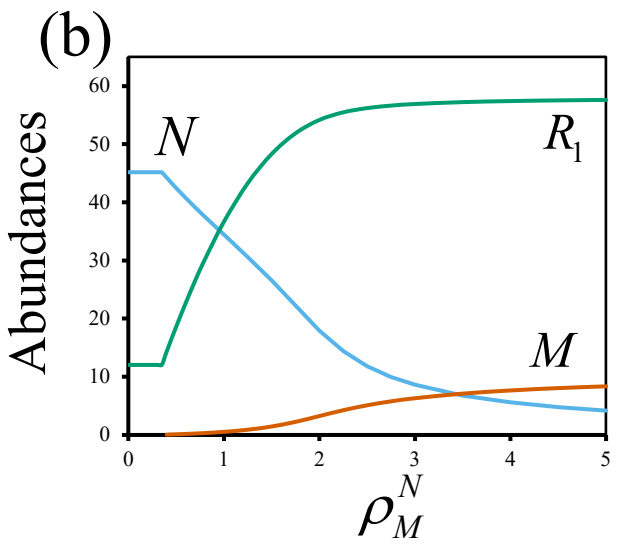
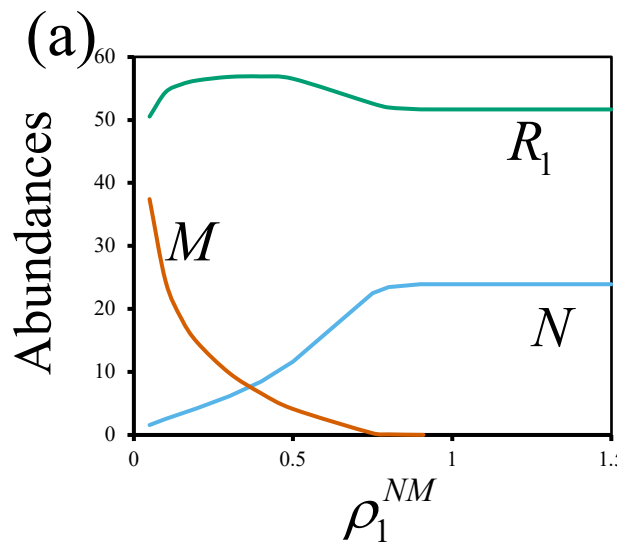


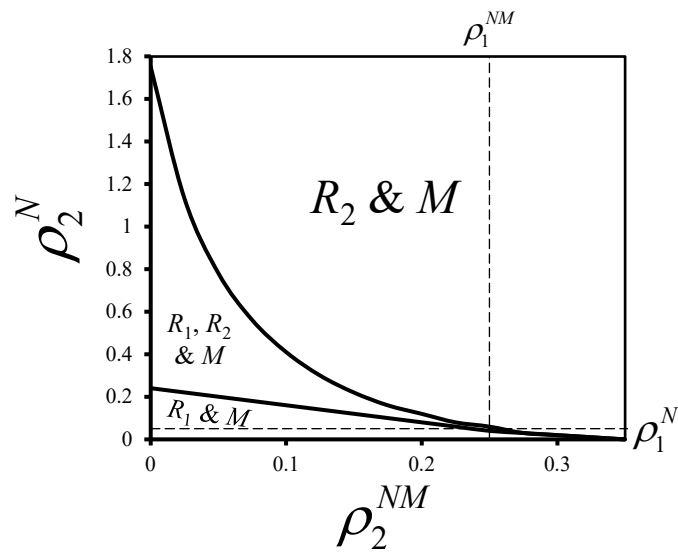
$$T_N = 100$$

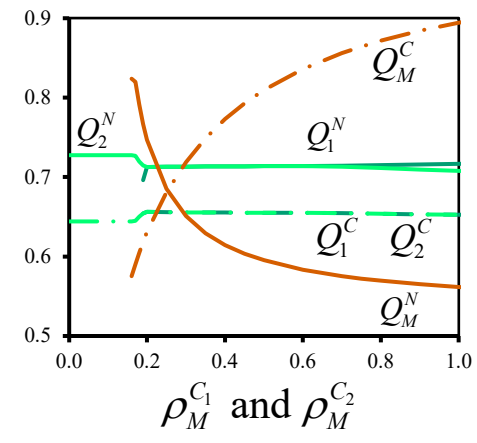
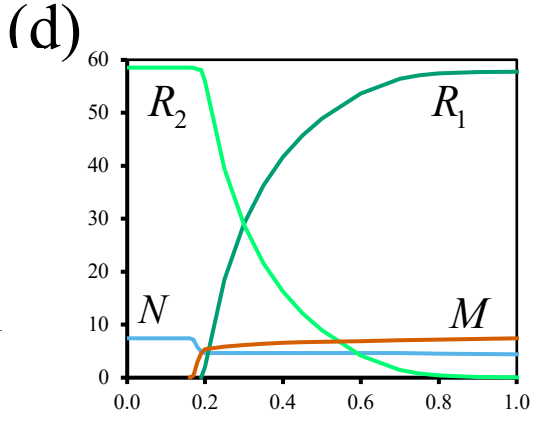
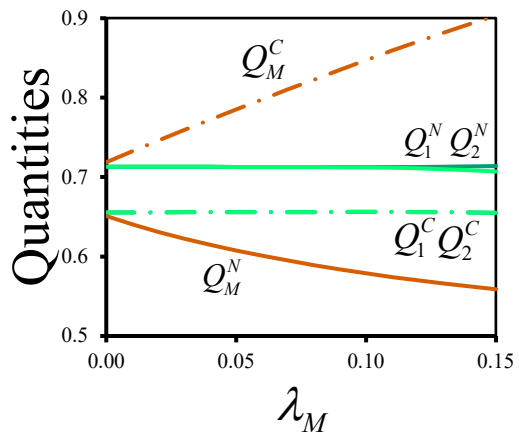
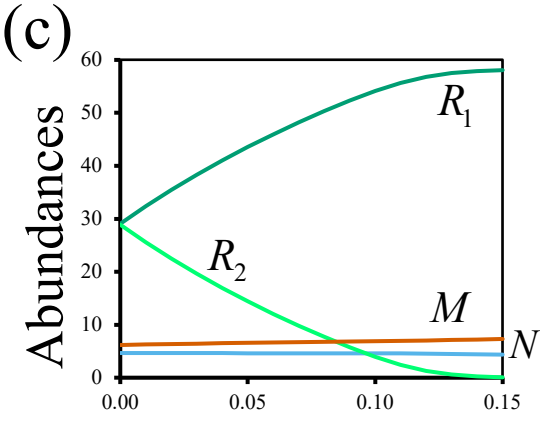
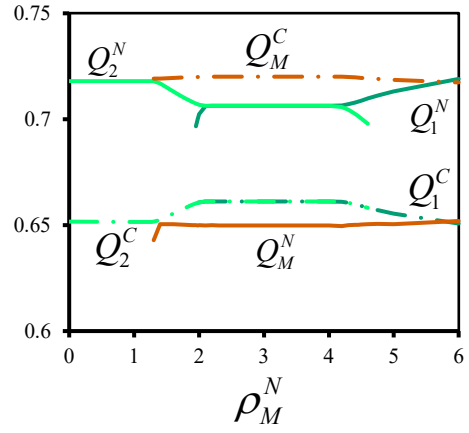
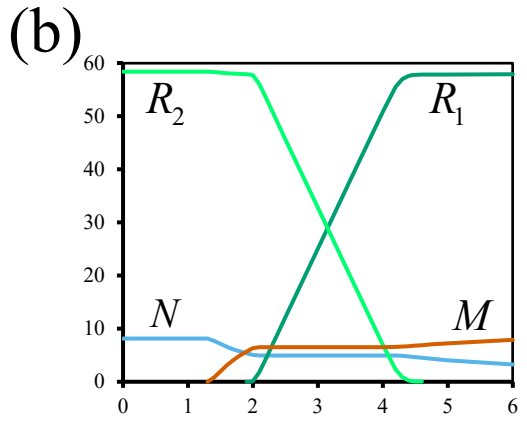
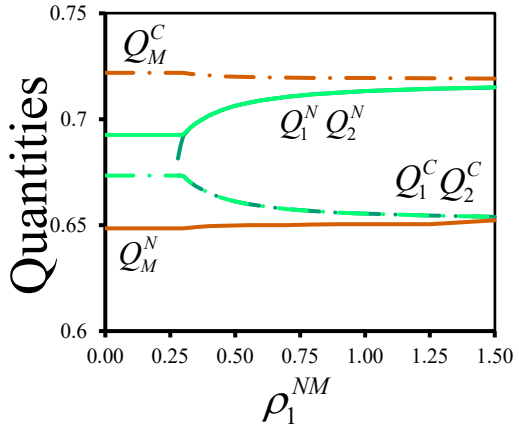
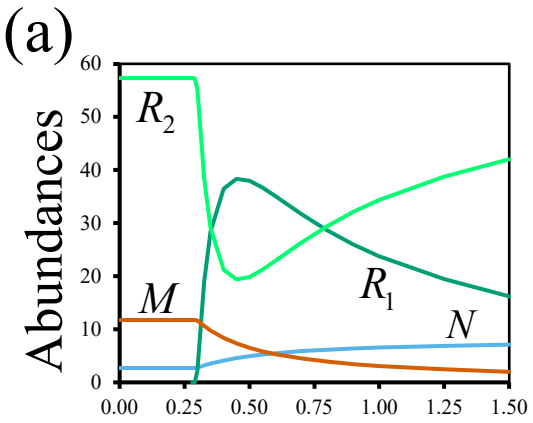


$$T_N = 200$$









1 Journal: Ecology

2 Manuscript type: Article

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5 **The complex circuitry of interactions determining coexistence**
6 **among plants and mycorrhizal fungi**

7

8

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16

17 Open Research Statement: This paper reports the analysis of a theoretical model. Consequently,

18 no data were generated for this study. Matlab code is available on Figshare at

19 <https://figshare.com/s/f6b0875c7d35e99d6138>. Figshare will be the final open repository.

20

21 Key Words: apparent competition, coexistence, intraguild predation, mutualism, mycorrhizal

22 fungus, resource competition.

23

24

25 *Abstract.* We present a mechanistic model of coexistence among a mycorrhizal fungus and
26 one or two plant species that compete for a single nutrient. Plant-fungal coexistence is more
27 likely if the fungus is better at extracting the environmental nutrient than the plant, and the
28 fungus acquires carbon from the plant ~~at an adequate~~above a minimum rate. When they coexist,
29 their interaction can shift from mutualistic to parasitic at high nutrient availability. The fungus is
30 a second nutrient source for the plants and can promote the coexistence of two plant competitors,
31 if one is better at environmental nutrient extraction and the other is better at garnering the
32 nutrient from the fungus. Because it extracts carbon from both plants, the fungus also serves as a
33 conduit of apparent competition between the plants. Consequently, the plant with the lower
34 environmental nutrient extraction rate can drive the plant with the higher environmental nutrient
35 extraction rate extinct at high carbon supply rates. This model illustrates mechanisms to explain
36 several observed patterns, including shifts in plant-mycorrhizal growth responses and
37 coexistence along nutrient gradients, equivocal results among experiments testing the effect of
38 mycorrhizal fungi on plant diversity, and differences in plant diversity among ecosystems
39 dominated by different mycorrhizal groups.

40

41

42 **Introduction**

43 Different types of species interactions involve varying levels of mechanistic complexity. A
44 direct consumer-resource interaction is simple: individuals of one species consume specific
45 compounds, fluids, tissues, or the entire bodies of individuals of another species (Holling 1959,
46 Murdoch and Oaten 1975, Jeschke ~~et al.~~, [Kopp and Tollrian](#) 2002). Resource competition is
47 more complex, being an indirect interaction in which individuals of two or more species
48 consume the same resource or prey (MacArthur 1969, Tilman 1980, 1982). Likewise, apparent
49 competition is an indirect interaction in which the individuals of two or more species are fed
50 upon by the same consumer (Holt 1977). Even more complex is intraguild predation, an
51 interaction in which predator and prey also compete for the same resource (Holt and Polis 1997).
52 All of these indirect interactions involve more complex circuitries than the basic consumer-
53 resource interaction, and each imposes specific criteria for the interacting species to coexist
54 (McPeck 2022).

55 Basic mutualistic interactions between two species can also be quite complicated, often
56 involving multiple types of direct interaction circuits. Many mutualisms are in fact consumer-
57 resource interactions, but both species gain a fitness benefit despite that consumption (e.g.,
58 Holland et al. 2005, Holland and DeAngelis 2010, Jones ~~et al.~~, [Bronstein and Ferrière](#) 2012). In
59 some, one species feeds on its interaction partner, and in so doing renders a service, such as
60 pollination, seed dispersal, or herbivore protection, that increases the fitness of the partner
61 (Holland and DeAngelis 2010, Bronstein 2015). In others, the two interaction partners feed on
62 one another in ways that increase both their fitnesses (Holland and DeAngelis 2010). The
63 interaction circuitry in this latter mutualism type can be quite complex. One iconic example is
64 the interaction between a plant and a mycorrhizal fungus. Both the plant and fungus forage for
65 mineral nutrients from the environment (Smith and Smith 2011, Näsholm et al. 2013, Püschel et
66 al. 2016), and so are resource competitors. The plant extracts these nutrients from the fungus
67 directly (Smith and Smith 2011, Näsholm et al. 2013), and so the plant is a consumer of the
68 fungus. Likewise, the fungus extracts carbon from the plant directly (Smith and Smith 2012,

69 Näsholm et al. 2013), and so the fungus is a consumer of the plant. Because each is
70 simultaneously a consumer and resource competitor of the other, each is an intraguild predator of
71 the other (Figure 1a). Additionally, if the fungus interacts with two plant species, the fungus is
72 both an alternative resource for each plant and a conduit of apparent competition between the
73 two plants (Figure 1b). Given this complex interaction circuitry, the criteria for coexistence of a
74 mycorrhizal fungus with one or two plant species are not obvious.

75 Many theoretical analyses have considered components of this interaction network. Many
76 analyses have explored the consequences of different carbon allocation strategies by plants to
77 support multiple fungal species using both optimal control theory (Bever 2015, Moeller and
78 Neubert 2016, Bachelot and Lee 2018) and market exchange approaches (Noë and Hammerstein
79 1994, Grman ~~et al.~~, Robinson and Klausmeier 2012, Wyatt et al. 2014, Noë and Kiers 2018).
80 Others have explored the conditions for multiple plant species to coexist with one or more fungal
81 species. Holland and DeAngelis (2010) explored the conditions for the coexistence of two
82 generalized mutualist consumers using simple predator-prey functions. Bever and colleagues
83 showed using generalized models of frequency dependent interactions that coexistence of two
84 plants and two fungi were possible when no species had the highest obtained combined higher
85 fitness in all the associations with benefits from both species of the other species type as
86 compared to its competitor (Bever et al. 1997, Bever 1999). (Bever, Westover and Antonovics
87 1997, Bever 1999). Umbanhowar and McCann (2005) used isocline analyses of generalized
88 functions and concluded that a mycorrhizal fungus would foster the coexistence of two
89 competing plant species if the better mycorrhizae-free plant competitor in the absence of the
90 mycorrhizal fungus receives less benefit from the fungus but gives the fungus more benefit.
91 They did note the similarity of their conclusions to how apparent competition via a shared
92 predator can permit two competing plants to coexist, but this type of interaction circuitry was not
93 part of the model. Explicit environmental nutrient and nutrient-carbon exchange dynamics were
94 also lacking from these studies.

95 Other analyses have included environmental nutrient and exchange dynamics but have not

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96 included the full interaction circuitry. Jiang et al. (2017) expanded Tilman's (1980) model of
97 two plants competing for two resources to include a specialist fungus for each. Fungi aided
98 nutrient uptake by the plants, but nutrient and carbon transfers between plants and their
99 specialized fungi were not included. Benefits from fungi to poorer competitors could permit
100 coexistence with competitively superior plant species, or could shift the competitive dominance
101 hierarchy of plants if these benefits were high enough to inferior competitors (Jiang et al. 2017).
102 Johnson and Bronstein (2019) analyzed a model including explicit environmental nutrient
103 dynamics and exchanges between plants and fungi to show that two competing plants could
104 coexist if one plant extracted environmental nutrient at a higher rate and the other plant extracted
105 the nutrient from the fungus at a higher rate. However, their model did not include competition
106 between either plant and the fungus for the environmental nutrient, and no species paid any
107 fitness cost for having the other extract nutrient or carbon directly from them.

108 To explore the combined consequences of these various interaction components, we analyze
109 a more mechanistic model of the interaction circuitry depicted in Figure 1 to explore the
110 environmental and species properties fostering coexistence of a mycorrhizal fungus with one and
111 two plant species. Our goal is to build a generalized model incorporating these mechanisms and
112 not to make detailed and precise quantitative predictions (Holland and DeAngelis 2010). The
113 dynamics of the abundances and individual nutrient and carbon content are modeled for both
114 plants and fungi. Plants consume the nutrient from the fungus, the fungus consumes carbon from
115 the plant, and all species compete for the nutrient from the environment. ~~We do not include
116 plant and fungal modulation of nutrient and carbon exchanges in the model analyzed here (e.g.,
117 Bever et al. 1997, Bever 1999); our analysis focuses on the criteria for coexistence of plants and
118 fungi and not whether control mechanisms would match plant and fungal properties that would
119 meet these coexistence criteria.~~ We do not include plant and fungal modulation of nutrient and
120 carbon exchanges in the model analyzed here (e.g., Bever, Westover and Antonovics 1997,
121 Bever 1999); our analysis focuses on the criteria for coexistence of plants and fungi and not
122 whether control mechanisms would match plant and fungal properties that would meet these

123 coexistence criteria. Future analyses will include these controls to explore whether the
 124 modulation of exchanges that are adaptive will bring the system to the conditions fostering
 125 coexistence that are identified here.

126

127 **The Model**

128 Begin by considering the dynamics of nutrient uptake and abundances of plant species
 129 foraging for a mineral nutrient such as a nitrogen or phosphorus compound from the soil. The
 130 amount of the abiotic nutrient that is available in the environment is N and follows a simple
 131 abiotic renewal function

$$132 \quad \Omega(N) = c(T_N - N), \quad (2)$$

133 where T_N is the maximum amount that can accumulate, and c is the maximum renewal rate
 134 (Tilman 1982, Grover 1997). (All model state variables and parameters are listed in Table 1.)

135 In this analysis we consider the dynamics of two plant species, each has abundance of R_i ,
 136 with $i = 1, 2$ (we use R_1 and R_2 as the abundance state variables and as species identifiers in the
 137 text). Because this model has implications for both community and ecosystem ecology, we use
 138 the term abundance when referring to the plants, which can be conceptualized as either the
 139 number of individuals in a plant population or the total amount of plant biomass among all
 140 individuals in the population. Because the nutrient and carbon amounts in plants and fungi are
 141 resource pools that are consumed by the other species (Figure 1a), we explicitly model the
 142 dynamics of the nutrient and carbon content in plant and fungal biomass. Plant species have a
 143 quantity of the nutrient in their tissues Q_i^N , which is the amount of the nutrient compound in a
 144 unit of plant biomass (Droop 1973a, 1974, Grover 1990, 1991). We think of this as the quantity
 145 of nutrient used as building blocks to construct biomass and fuel to run metabolism, and not as
 146 the total amount of nutrient in the body. A plant acquires the nutrient from the soil nutrient pool
 147 according to a modified version of Michaelis-Menten/Monod dynamics in which its maximum
 148 rate of uptake decreases as its quantity Q_i^N increases:

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$$149 \quad P_i(N, Q_i^N) = \frac{\rho_i^N \left(1 - \frac{Q_i^N}{Q_i^{N \max}}\right) N}{g_i^N + N} \quad P_i(N, Q_i^N) = \frac{\rho_i^N \left(\frac{Q_i^{N \max} - Q_i^N}{Q_i^{N \max} - Q_i^{N \min}}\right) N}{g_i^N + N}, \quad (3)$$

150 where $Q_i^{N \max}$ ~~is~~ $Q_i^{N \min}$ and $Q_i^{N \max}$ are the minimum and maximum value values of the nutrient
 151 quantity allowed, respectively, g_i^N is the half-saturation constant for uptake rate, and ρ_i^N is the
 152 maximum uptake rate ~~when~~ $Q_i^N = 0$, which is approached when Q_i^N approaches $Q_i^{N \min}$ and N
 153 is very large (Michaelis and Menten 1913, Monod 1949, Grover 1990, 1991).

154 Each plant also photosynthesizes to produce carbon compounds; the quantity of carbon in a
 155 unit of plant biomass is given as Q_i^C . As with Q_i^N , we think of Q_i^C as the quantity of carbon
 156 used as building blocks to construct biomass and fuel to run metabolism, and not as the total
 157 amount of carbon in the body. We assume the maximum photosynthetic rate asymptotically
 158 increases with the quantity of nutrient Q_i^N in the plant to a maximum of λ_i , and the parameter ϕ_i
 159 scales the rate of approach to the asymptote. We also assume that plants compete for light, and
 160 so their rate of carbon production due to photosynthesis decreases with increasing plant
 161 abundance according to an exponential function, where α_i scales the rate of decline in carbon
 162 accumulation via photosynthesis with increasing plant abundance of both species. These
 163 assumptions result in the following function:

$$164 \quad \Lambda_i(Q_i^N, R_i) = \frac{\lambda_i Q_i^N}{\phi_i + Q_i^N} e^{-\alpha_i \sum_{j=1}^2 R_j}. \quad (4)$$

165 We assume that $\phi_1 = \phi_2$, $\lambda_1 = \lambda_2$ and $\alpha_1 = \alpha_2$, i.e., which makes the two plant species are
 166 equivalent at producing carbon from sunlight: i.e., in this analysis, plants are equivalent in
 167 carbon production and so differential carbon production capabilities cannot promote their
 168 coexistence.

169 The biomass production rate at which the plant grows and reproduces follows the multi-
 170 compound Droop (1973a, b, 1974) formulation, where plants would not produce new biomass if
 171 either quantity was at its minimum, but increases with increasing values of each up to a
 172 maximum production rate of μ_i :

$$\Psi_i(Q_i^N, Q_i^C) = \mu_i \left(1 - \frac{Q_i^{N\min}}{Q_i^N}\right) \left(1 - \frac{Q_i^{C\min}}{Q_i^C}\right) \quad (5)$$

(see also Sterner and Elser 2002). Plants lose biomass at a rate of f_i . ~~Plants also excrete a~~ fraction $\varepsilon_i^N \theta_i$ of ~~the~~ nutrient ~~quantity in dead plant biomass is recycled~~ back ~~intoto~~ the ~~available~~ environmental ~~pool~~. ~~Plants also have basal minimum utilization rates of a fraction~~ ε_i^N ~~of their~~ nutrient ~~pool at a constant rate from their basal metabolisms~~ and ~~uses the nutrient at a rate~~ b_i^N ~~use~~ ~~an amount~~ that scales with ~~the~~ biomass ~~production at rate~~ b_i^N ~~for growth rate to grow and~~ ~~reproduce~~ reproduction. Plants also lose carbon due to metabolic processes at a baseline rate δ_i^C and increases at a rate of b_i^C that scales with the biomass growth rate to grow and reproduce.

This community also contains a mycorrhizal fungus species that has an abundance of M . Like plants, each unit of fungal biomass has a quantity of the abiotic nutrient Q_M^N and of carbon Q_M^C , and the dynamics of these quantities are shaped by similar processes as for plants. The fungus takes up nutrient from the environment according to the same modified version of Michaelis-Menten/Monod dynamics as used for the plants

$$P_M(N, Q_M^N) = \frac{\rho_M^N \left(1 - \frac{Q_M^N}{Q_M^{N\max}}\right) N}{g_M^N + N} \quad P_M(N, Q_M^N) = \frac{\rho_M^N \left(\frac{Q_M^{N\max} - Q_M^N}{Q_M^{N\max} - Q_M^{N\min}}\right) N}{g_M^N + N}, \quad (6)$$

where $Q_M^{N\max}$ ~~is~~ $Q_M^{N\min}$ ~~and~~ $Q_M^{N\max}$ ~~are~~ the ~~minimum and~~ maximum ~~value~~ values of the nutrient quantity, ~~respectively~~, g_M^N is the half-saturation constant, and ρ_M^N is the maximum uptake rate when $Q_M^N = 0$ ~~approaches~~ $Q_M^{N\min}$ and N is very large (Michaelis and Menten 1913, Monod 1949, Grover 1990, 1991). The fungus also ~~exereteshas a basal minimum utilization rate of a~~ fraction ε_M^N of its nutrient ~~into the environment at a constant rate from its basal metabolism~~ and uses an amount that scales with biomass production at rate b_M^N for growth and reproduction.

The fungus may also extract carbon from the environment according to the equation

$$\Lambda_M(M) = \lambda_M e^{-\beta M}, \quad (7)$$

where λ_M is the maximum rate of carbon extraction, and β scales the rate at which carbon extraction declines with fungal abundance. ~~(e.g., greater fungal biomass would deplete available~~ ~~environmental carbon, which is not explicitly included in the model).~~ A value of $\lambda_M = 0$

Running Head: Plant-Mycorrhizal Fungus Coexistence

198 characterizes arbuscular mycorrhizae and some ectomycorrhizal fungi since they obtain all their
 199 carbon from their plant partners and none from the environment (Lindahl and Tunlid 2015,
 200 Genre et al. 2020). A value of $\lambda_M > 0$ may characterize some ectomycorrhizal, ericoid, and
 201 orchid fungi that can potentially obtain some carbon (and other nutrients) from the environment
 202 by producing enzymes to decompose organic matter (Akroume et al. 2019, Genre et al. 2020).
 203 The fungus loses carbon due to metabolic costs at a baseline rate of δ_M^C that increases with
 204 biomass production at a rate of b_M^C for growth and reproduction. Because of the differences in
 205 carbon production mechanisms between plants and fungi (i.e., photosynthesis versus carbon
 206 extraction from plants or the environment), throughout these analyses $\lambda_i \neq \lambda_M$ is assumed.

207 The fungus also produces new biomass according to multi-compound Droop dynamics

$$208 \quad \Psi_M(Q_M^N, Q_M^C) = \mu_M \left(1 - \frac{Q_M^{N \min}}{Q_M^N}\right) \left(1 - \frac{Q_M^{C \min}}{Q_M^C}\right), \quad (8)$$

209 where μ_M is the maximum production rate. The fungus also loses biomass at a rate of f_M . A
 210 fraction θ_M of the nutrient quantity in dead biomass is recycled back to the available
 211 environmental pool.

212 Plants and fungi directly interact with one another by extracting one of the materials from the
 213 other species (Figure 1a). A plant extracts nutrient from the fungus at rate

$$214 \quad D_i(Q_M^N, Q_i^N) = \frac{\rho_i^{NM} \left(1 - \frac{Q_i^N}{Q_i^{N \max}}\right) Q_M^N}{g_i^{NM} + Q_M^N} \quad D_i(Q_M^N, Q_i^N) = \frac{\rho_i^{NM} \left(\frac{Q_i^{N \max} - Q_i^N}{Q_i^{N \max} - Q_i^{N \min}}\right) Q_M^N}{g_i^{NM} + Q_M^N},$$

215 where g_i^{NM} is the half-saturation constant, and ρ_i^{NM} is the maximum uptake rate from the fungus
 216 when $Q_i^N = 0$, which is approached when Q_i^N approaches $Q_i^{N \min}$ and Q_M^N is very large.

217 Likewise, the fungus extracts carbon from each plant at rate

$$218 \quad C_i(Q_i^C, Q_M^C) = \frac{\rho_{M_1}^{Ci} \left(1 - \frac{Q_M^C}{Q_M^{C \max}}\right) Q_i^C}{g_M^{Ci} + Q_i^C} \quad C_i(Q_i^C, Q_M^C) = \frac{\rho_M^{Ci} \left(\frac{Q_M^{C \max} - Q_M^C}{Q_M^{C \max} - Q_M^{C \min}}\right) Q_i^C}{g_M^{Ci} + Q_i^C},$$

219 where $Q_M^{C \min}$ and $Q_M^{C \max}$ are the minimum and maximum carbon quantities, respectively,

220 g_M^{Ci} is the half-saturation constant, and ρ_M^{Ci} is the maximum uptake rate from the plants when

221 $Q_M^C = 0$ Q_M^C approaches $Q_M^{C\max}$ and Q_i^C is very large.

222 These assumptions lead to the following set of differential equations describing the changes
223 in the abundances of the abiotic resource, the plant and fungus species, and the nutrient and
224 carbon quantities for each species,

$$225 \frac{dN}{dt} = \Omega(N) - \sum_{i=1}^2 P_i(N, Q_i^N) R_i - P_M(N, Q_M^N) M + \sum_{i=1}^2 \varepsilon_i^N Q_i^N R_i + \varepsilon_M^N Q_M^N M$$

$$226 \frac{dN}{dt} = \Omega(N) - \sum_{i=1}^2 P_i(N, Q_i^N) R_i - P_M(N, Q_M^N) M + \sum_{i=1}^2 \theta_i^N f_i Q_i^N R_i + \theta_M^N f_M Q_M^N M$$

$$227 \frac{dR_i}{dt} = R_i (\Psi_i(Q_i^N, Q_i^C) - f_i)$$

$$228 \frac{dQ_i^N}{dt} = P_i(N, Q_i^N) - b_i^N \Psi_i(Q_i^N, Q_i^C) Q_i^N - \varepsilon_i^N Q_i^N + D_i(Q_M^N, Q_i^N) M$$

$$229 \frac{dQ_i^C}{dt} = \Lambda_i(R_i) - b_i^C \Psi_i(Q_i^N, Q_i^C) Q_i^C - \delta_i^C Q_i^C - C_i(Q_i^C, Q_M^C) M \quad \frac{dQ_i^N}{dt} = P_i(N, Q_i^N) - (\varepsilon_i^N + b_i^N \Psi_i(Q_i^N, Q_i^C)) Q_i^N - \delta_i^N Q_i^N + D_i(Q_M^N, Q_i^N) M$$

$$230 \frac{dQ_i^C}{dt} = \Lambda_i(R_i) - (\delta_i^C + b_i^C \Psi_i(Q_i^N, Q_i^C)) Q_i^C - C_i(Q_i^C, Q_M^C) M \quad (11)$$

$$231 \frac{dM}{dt} = M (\Psi_M(Q_M^N, Q_M^C) - f_M)$$

$$232 \frac{dQ_M^N}{dt} = P_M(N, Q_M^N) - b_M^N \Psi_M(Q_M^N, Q_M^C) Q_M^N - \varepsilon_M^N Q_M^N - \sum_{i=1}^2 D_i(Q_M^N, Q_i^N) R_i$$

$$233 \frac{dQ_M^C}{dt} = \Lambda_M(M) - b_M^C \Psi_M(Q_M^N, Q_M^C) Q_M^C - \delta_M^C Q_M^C + \sum_{i=1}^2 C_i(Q_i^C, Q_M^C) R_i$$

$$234 \frac{dQ_M^N}{dt} = P_M(N, Q_M^N) - (\varepsilon_M^N + b_M^N \Psi_M(Q_M^N, Q_M^C)) Q_M^N - \sum_{i=1}^2 D_i(Q_M^N, Q_i^N) R_i$$

$$235 \frac{dQ_M^C}{dt} = \Lambda_M(M) - (\delta_M^C + b_M^C \Psi_M(Q_M^N, Q_M^C)) Q_M^C + \sum_{i=1}^2 C_i(Q_i^C, Q_M^C) R_i$$

236 where the components are as given in equations (2)-(10).

237 A model of this complexity prohibits mathematical analysis. Therefore, we used computer
238 simulations (numerical integration of the model using the ode45 solver of Matlab (version
239 R2023a, Mathworks Inc.)) to analyze patterns emerging from biologically reasonable areas of
240 parameter space. Matlab code of the model for one and two plant species interacting with a
241 single fungus species is provided on Figshare (<https://figshare.com/s/f6b0875c7d35e99d6138>,
242 PlantResourceFungusBaseModel1R1Mv5.m, PlantResourceFungusBaseModel2R1Mv5.m).

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243 Simulations were run until the system came to a stable equilibrium (i.e., the abundances of all
 244 species stopped changing to 5 significant digits for 500 iterations) or a stable limit cycle- (i.e., a
 245 repeated cycling through the same orbit evaluated visually in a graph of the abundances for 500
 246 iterations). Coexistence is defined as species having ~~positive~~ abundances $>10^{-5}$ at the
 247 equilibrium or sometime during the limit cycle. Limit cycles were only encountered in narrow
 248 ranges of parameter combinations at some transitions between species being able to coexist in
 249 the system and with environmental nutrient abundance being very low. Also, ~~we found no~~ in the
 250 areas of parameter space ~~that had we explored, we found no~~ alternative equilibria, based on
 251 many replicate simulations using random initial ~~species~~ abundances. Because this model is not
 252 meant to mimic quantitative features of the system, we focus on the general conditions that
 253 promote or retard species coexistence and the qualitative changes in abundances and quantities
 254 across various areas of parameter space.

255

256 **Results**257 *One plant and one fungus*

258 Coexistence of a plant and a mycorrhizal fungus species cannot be assumed, ~~because of their~~
 259 ~~complex interaction circuitry.~~ First, the plant and fungus are competitors for the abiotic
 260 environmental nutrient. Because the plant has a substantially greater capacity to acquire carbon,
 261 the fungus can coexist with the plant over all but the very lowest range of the environmental
 262 nutrient availability gradient if the fungus has a substantially higher environmental nutrient
 263 uptake rate than the plant (i.e., $\rho_M^N > \rho_1^N$) (Figure 2).

264 Also, how composition and abundances change along the environmental nutrient gradient
 265 depend on whether the nutrient or carbon is more limiting to each species. Plant abundance
 266 increases while fungal abundance actually decreases with increasing environmental nutrient
 267 availability in the range where the nutrient is more limiting for both species (i.e., low T_N).

268 Remember that the plant is both competing with the fungus for the environmental nutrient pool
 269 and extracting nutrient from the fungus directly. At the very low values of T_N , the plant's

270 abundance is not large, and so the total amount of nutrient that the plant extracts from the fungus
271 is not large. As plant abundance increases in this range of T_N , the resulting increases in the
272 combined effects of direct consumption and indirect competition for the limiting nutrient cause
273 the fungal abundance to decline (Figure 2d). Moreover, if the fungus' environmental nutrient
274 uptake rate is only moderately higher than the plant, these combined effects cause fungal
275 abundance to decrease to zero in the intermediate range of T_N (Figure 2c).

276 In contrast, fungal abundance increases and plant abundance decreases at high values of T_N
277 where carbon is more limiting to both species (Figure 2d). In this range, carbon production by
278 the plant is limited by intraspecific competition for light, and carbon extraction by the fungus
279 from the plant becomes the more important direct interaction between them. The increasing
280 fungal abundance with higher nutrient availability causes more carbon to be extracted from the
281 plant, which causes its abundance to decline.

282 If the fungus is able to extract environmental carbon (e.g., $\lambda_M = 0.5$) instead of solely relying
283 on plant subsidy (e.g., $\lambda_M = 0.0$), the fungus can coexist with the plant at lower maximum
284 nutrient uptake rates across the whole nutrient availability gradient (cf. Figures 2a and 2b).

285 The rate at which the plant consumes the fungal nutrient relative to its ability to extract
286 nutrient from the environment also influences whether the plant and fungus can coexist.
287 Coexistence requires that either (1) the plant extracts nutrient from the fungus at a high rate but
288 has a substantially lower environmental nutrient uptake rate than the fungus ($\rho_M^N > \rho_1^N$); or (2)
289 the plant has a higher environmental nutrient extraction rate than the fungus but extracts nutrient
290 from the fungus at a low rate ("R₁ & M" area in both panels of Figure 3). Thus, over much of
291 parameter space, coexistence requires that the fungus must be better at extracting the nutrient
292 from the environment than the plant. Even though the plant extracts the environmental nutrient
293 at a slower rate, it coexists because it also extracts the nutrient from the fungus. However, when
294 the plant extracts the environmental nutrient at a faster rate, coexistence requires that it extract
295 little nutrient from the fungus, and the fungus coexists because it extracts carbon from the plant.
296 The plant species can also drive the fungus extinct if it extracts nutrient from the fungus at too

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297 high a rate, even when it is significantly poorer at extracting the environmental nutrient as
298 compared to the fungus (“ R_1 only” area in both panels of Figure 3). The rate required for the
299 plant to drive the fungus extinct depends on the fungus’ ability to extract carbon from the
300 environment (λ_M) (Figure 3).

301 Whether the nutrient or carbon is more limiting to plant and fungal growth also defines the
302 areas where the fungus is either a mutualist or parasite to the plant, which further depends on the
303 fungus’ maximum carbon extraction rate from the plant (Figure 4). At low environmental
304 nutrient availabilities where the nutrient is more limiting to both species, the fungus is a
305 mutualist, enhancing the abundance of the plant if they can coexist, regardless of the fungus’
306 carbon extraction rate (Figure 4a-b). In the zone of nutrient availabilities where both species are
307 shifting from nutrient to carbon limitation, the fungus is a mutualist if the fungus’ carbon
308 extraction rate is low, but a parasite depressing plant abundance if the fungus’ carbon extraction
309 rate is high (Figure 4c-d). Finally, in the range of environmental nutrient availabilities where
310 both species are carbon limited, the fungus is a parasite because of carbon consumption from the
311 plant, except at its very lowest carbon extraction rates (Figure 4e-f). The ability of the fungus to
312 extract carbon from the environment does not appreciably affect these trends (cf. panels for each
313 T_N value with $\lambda_M = 0.0$ versus $\lambda_M = 0.5$).

314 One interesting observation is that the maximum rate at which the plant extracts the nutrient
315 from the fungus has relatively little effect on the plant’s abundance over a large parameter range
316 of ρ_1^{NM} (Figure 5a). However, the rate at which the fungus extracts the nutrient from the
317 environment can have a substantial effect on plant abundance; plant abundance increases with
318 ρ_M^N until plant reproduction is limited by carbon and not by the nutrient (Figure 5b). Thus, the
319 environmental nutrient uptake ability of the fungus is a critical determinant of plant abundance
320 when the nutrient limits plant abundance.

321

322 *Two plants and one fungus*

323 A second plant species (R_2) can invade and coexist with the mycorrhizal fungus and the first

324 plant species under restricted conditions. In the comparisons made here, the two plant species
325 being considered have identical parameters except for those being compared explicitly. In the
326 absence of the fungus, the plant species with the higher environmental nutrient extraction rate
327 will drive the other plant extinct, all else being equal (Tilman 1982).

328 The two plant species can coexist if they differ in specific ways in their abilities to extract the
329 nutrient from the environment and from the fungus. Coexistence requires that the relative
330 abilities of the two plant species must trade off within a zone of parameter space where one plant
331 is better at extracting the nutrient from the environment, but the other is better at extracting the
332 nutrient from the fungus (i.e., the R_1 , R_2 & M area in Figure 6). If R_2 extracts less from the
333 fungus than R_1 , R_2 must be able to extract proportionally more from the environment. However,
334 R_2 cannot be too good at extracting the environmental nutrient; R_2 will drive R_1 extinct if it
335 extracts the environmental nutrient at too high a rate, even if it is poorer at acquiring the nutrient
336 from the fungus. As expected, one plant always drives the other plant extinct if it has higher
337 maximum extraction rates from both environmental and fungal nutrient pools.

338 In the parameter space where the two plants coexist with the fungus (Figure 6), R_1 (the plant
339 that extracts the nutrient from the environmental pool at a slower rate but from the fungal pool at
340 a faster rate) has a positive growth response in the presence of the fungus when R_2 is absent (i.e.,
341 the fungus is a mutualist with R_1). However, R_2 (the plant that extracts nutrient from the
342 environmental pool at a faster rate but from the fungal pool at a slower rate) has a negative
343 growth response in the presence of the fungus when R_1 is absent (i.e., the fungus is a parasite of
344 R_2). More generally from our explorations of large areas of parameter space, when the two
345 plants coexist, at least one has a parasitic relationship with the fungus. The fungus is typically a
346 mutualist with the ~~coexisting~~ plant that depends more on the fungal nutrient pool, and the fungus
347 is typically a parasite with the ~~coexisting~~ plant that depends more on the environmental nutrient
348 pool.

349 The abilities of the fungus to extract nutrient and carbon from the various sources also shapes
350 coexistence of the plant species. In the examples presented in Figure 7, R_1 again has a lower

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351 maximum environmental nutrient extraction rate but a higher maximum fungal nutrient
 352 extraction rate than R_2 (i.e., $\rho_1^N < \rho_2^N$ and $\rho_1^{NM} > \rho_2^{NM}$). Also, the fungus has identical
 353 parameters for interactions with both plant species, unless otherwise specified in the example.

354 The relative rates at which the two plant species extract fungal nutrient influence the
 355 coexisting ~~plants~~ plants' relative frequencies (Figure 7a). Coexistence occurs because the high
 356 rate of fungal nutrient uptake by R_1 offsets the competitive advantage of R_2 for the
 357 environmental nutrient pool. Interestingly, within the parameter range of coexistence, the
 358 relative abundances of the two plant species do not change monotonically. At the lower range of
 359 ρ_1^{NM} permitting plant coexistence, R_2 (the plant with the higher maximum environmental
 360 nutrient uptake rate) decreases in abundance, and R_1 increases. As a result, fungal abundance
 361 decreases because R_1 is now extracting nutrient from it, and the environmental nutrient
 362 abundance increases because of the decreases in R_2 and fungal abundances. However, at higher
 363 ρ_1^{NM} values, the changes in plant relative abundances reverse because fungal abundance is
 364 greatly reduced, which more disadvantages R_1 , and environmental nutrient availability is higher,
 365 which advantages R_2 . Here again, the relative resource competitive abilities of the plants for the
 366 environmental and fungal nutrient pools interact to determine the outcome of these species
 367 interactions.

368 The maximum environmental nutrient extraction rate of the fungus will also shift the relative
 369 importance of the two conduits of resource competition between the plants, because this rate
 370 increases the amount of nutrient available to the two plants in the fungal nutrient pool and
 371 decreases the amount in the environmental pool (Figure 7b). At low environmental nutrient
 372 extraction rates for the fungus (i.e., $\rho_M^N < 2.2$), the plant that is less dependent on the fungal
 373 nutrient pool (i.e., R_2) is favored. Where the two plant species coexist (i.e., $2.2 < \rho_M^N < 4.9$),
 374 their relative abundances are determined by the rate at which the fungus extracts the
 375 environmental nutrient. Moreover, at high enough fungal extraction rates (i.e., $\rho_M^N > 4.9$), the
 376 plant species that depends more on the environmental nutrient pool may be unable to coexist,
 377 because the combined effects of the fungus and competing plant species drive the environmental

378 nutrient availability to a level at which it cannot support a population.

379 The rate at which the fungus can extract environmental carbon also shapes plant coexistence,
380 because a higher environmental carbon extraction rate elevates fungal abundance (Figure 7c).
381 Higher values of the maximum environmental carbon extraction rate for the fungus favor the
382 plant species more dependent on the fungal nutrient pool. Within the range of $0.0 < \lambda_M < 0.15$,
383 higher values shift the plant species' relative abundances, with R_1 increasing and R_2 decreasing
384 in relative abundance. Above this range, fungal abundance has increased above a level at which
385 R_2 can maintain a population. Here, inflation of environmental carbon uptake by the fungus
386 exacerbates apparent competition between the two plant species and exacerbates resource
387 competition between R_2 and the fungus. The increase in fungal abundance favors the plant
388 species that depends more on the fungal nutrient pool. However, if R_1 is absent, R_2 and the
389 fungus will coexist with $\lambda_M > 0.15$, because fungal abundance will be lower.

390 The maximum rates at which the fungus extracts carbon from the two plant species also
391 influences plant species coexistence (Figure 7d). In this example, the fungus has the same
392 maximum carbon extraction rates from both plants (i.e., $\rho_M^{C1} = \rho_M^{C2}$) and does not extract carbon
393 from the environment $\lambda_M = 0.0$. In the parameter range where the two plant species can coexist
394 (i.e., $0.19 < \rho_M^{C1} = \rho_M^{C2} < 1.0$), increasing the maximum carbon extraction rates from the two
395 plants shifts the plant relative frequencies in favor of R_1 , and above this range R_2 cannot coexist.
396 In this case, direct consumption by the fungus shifts the plants' relative abundances, which again
397 favors the plant species that more depends on the fungal nutrient pool. Also note that fungal
398 abundance changes very little as $\rho_M^{C1} = \rho_M^{C2}$ increase, because it becomes nutrient limited.

399

400 Discussion

401 As in nature, these model results highlight that the interactions among plants and their
402 mycorrhizal fungal partners are sometimes mutualistic and sometimes antagonistic. These
403 outcomes depend on the abilities of the interacting species, and the shift between mutualism and
404 antagonism occurs along environmental gradients of nutrient availability (Hoeksema et al. 2010,

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405 Johnson 2010). Plants and mycorrhizal fungi can be mutualist partners that share resources, but
406 they are also competitors for those resources from the environment and consumers of one
407 another with all the attendant consequences of these interactions. Moreover, a mycorrhizal
408 fungus can be an indispensable community member to promote the coexistence of competing
409 plant species that could not otherwise coexist. However, a fungal partner shared by multiple
410 plant species is also a direct consumer of all, and so a conduit for apparent competition between
411 the plants that may or may not foster coexistence (Simard et al. 1997).

412 *Plant–fungus coexistence*

413 The requirements for coexistence of one plant species with a mycorrhizal fungus species in
414 our model echo the coexistence requirements for an intraguild predator and prey, but with a
415 richer set of possibilities. With intraguild predation, coexistence requires that the intraguild prey
416 consume their shared resource at a faster rate, and that the intraguild predator inflicts only a low
417 to moderate level of mortality on the intraguild prey (Polis and Holt 1992, Holt and Polis 1997,
418 McPeck 2022). Coexistence of a plant and a fungus is possible over a broad range of parameter
419 space if the fungus extracts the environmental nutrient at a higher rate than the plant, and the
420 plant extracts the nutrient at a moderate rate from the fungus. However, the fungus is also a
421 consumer of plant carbon. Consequently, coexistence is also possible if the plant extracts the
422 environmental nutrient at a higher rate than the fungus but extracts relatively little nutrient from
423 the fungal pool, and if the fungus extracts carbon from the plant ~~at an adequate rate above some~~
424 minimum rate defined by other conditions.

425 Direct measures of environmental nutrient uptake by plants and fungi are difficult, but
426 models suggest that fungi typically have substantially higher nutrient uptake rates than plants
427 because fungi explore a much larger volume of soil and have a much greater surface area for
428 uptake (Schnepf and Roose 2006, Schnepf ~~et al.~~, Roose and Schweiger 2008, See et al. 2022).
429 Ericoid and some ectomycorrhizal (EcM) fungi can also access various pools of soil nutrients
430 that are inaccessible to plants by producing extracellular enzymes that mine organic matter for
431 nutrients (Koide et al. 2008, Bödeker et al. 2014, Lindahl and Tunlid 2015, Adamczyk et al.

432 2016, Pellitier and Zak 2018, Akroume et al. 2019, Genre et al. 2020). Furthermore, root
433 colonization by arbuscular mycorrhizae (AM) fungi can reduce the root's ability to take up
434 nutrients (Smith and Smith 2012). These results suggest that fungi in nature may have a much
435 higher environmental nutrient extraction rate than their plant partners in most cases. Plants also
436 derive different nutrient levels from various fungal partners (Smith ~~et al.~~, [Smith and Jakobsen](#)
437 2003, 2004). Whether any particular plant-fungus pair is coexisting in nature will depend on the
438 balance of these various uptakes and exchanges.

439 Our model results provide a mechanism for how the interaction between a plant and
440 mycorrhizal fungi can shift between mutualism and parasitism. At low environmental nutrient
441 levels, the effect of the fungus on plant abundance is positive, because the plant is more limited
442 by the nutrient. The fungus can also permit the plant to support a population in an ecosystem
443 with nutrient availability too low for the plant to persist by itself. However, at high
444 environmental nutrient levels, plant abundance can be depressed by the fungus because carbon
445 becomes limiting to plants, and the carbon loss to mycorrhizae slows plant growth. The more
446 effective the fungus is at siphoning carbon from the plant, the lower the ambient nutrient
447 availability at which this interaction becomes negative for the plant.

448 These results are consistent with experiments testing plant responses to mycorrhizal fungi
449 presence. The effect of arbuscular mycorrhizal (AM) fungi on plant biomass is positive in low
450 phosphorus soil but negative in high phosphorus soil (Johnson 2010). Similarly, plants are
451 significantly more responsive to mycorrhizal inoculation in unfertilized soil relative to fertilized
452 soil (Hoeksema et al. 2010). In some cases, plants may have adjusted to this negative response:
453 root colonization by AM and ectomycorrhizal (EcM) fungi can decrease as nutrient availability
454 increases, which may decrease the plant's carbon cost for interacting with the fungi (Egerton-
455 Warburton and Allen 2000, Egerton-Warburton ~~et al.~~, [Johnson and Allen](#) 2007, Pellitier et al.
456 2021). Other resource gradients also affect the mycorrhizal growth response of plants: the
457 interaction can become parasitic at low light levels where carbon should be more limiting
458 (Ibáñez and McCarthy-Neumann 2016). Overall, our model demonstrates how the mycorrhizae-

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459 plant interaction exists on a continuum of mutualism to parasitism.

460 Environmental nutrient availability is not the only factor that determines the plant growth
461 response to the presence of mycorrhizal fungi. Plant growth is increased as the fungus' ability to
462 take up nutrients from the environment increases. Plant growth is often dependent on the
463 mycorrhizal species involved (Smith ~~et al.~~, [Smith and Jakobsen](#) 2003, Hoeksema et al. 2018).
464 The growth of ectomycorrhiza-associating trees across Europe increased as the genetic potential
465 of the EcM fungi to take up inorganic nitrogen increased (Anthony et al. 2022). In that study,
466 fungal community composition explained more variation in tree growth than climate or soil
467 factors. The growth response of arbuscular mycorrhiza-associating plants also differs among
468 different AM species (Smith ~~et al.~~, [Smith and Jakobsen](#) 2003, 2004, Bennett and Bever 2007, van
469 der Heijden ~~et al.~~, [Bardgett and van Straalen](#) 2008), but whether these differences are due to
470 differences in the fungi's nutrient uptake capabilities is unknown. Our model provides testable
471 predictions about the mechanisms by which the benefits of the mutualism and costs are
472 dependent on fungal species traits (e.g., Wilson and Hartnett 1997, Klironomos et al. 2000,
473 Klironomos 2002, Bennett and Bever 2007).

474 Whether the mycorrhizae can coexist with the plant depends on its ability to extract nutrients
475 from the environment. In nature, major shifts in EcM assemblage composition occur across
476 nutrient gradients towards fungal species that are better adapted for taking up inorganic nutrients
477 (~~Lilleskov et al. 2011~~); ([Lilleskov, Hobbie and Horton 2011](#)). EcM fungi are polyphyletic and
478 have large differences in their morphology and ability to take up inorganic versus organic
479 nutrients (Avis 2012, Pellitier and Zak 2018). The EcM fungi that produce extracellular
480 enzymes to mine organic matter for nutrients, which is a slower and more energetically costly
481 nutrient acquisition strategy, often decline the most with increasing nitrogen availability. In
482 contrast, hydrophilic, shorter distance exploration types of EcM that are better at taking up
483 inorganic nitrogen from the soil solution increase (~~Lilleskov et al. 2011~~); ([Lilleskov, Hobbie and
484 Horton 2011](#)). Our results suggest that competition with plants may be one component of why
485 the EcM species specializing in a slower, more organic-dominated nitrogen cycle are lost as

486 nitrogen availability increases. AM fungal assemblages can also shift as nutrient availability
487 increases depending on ecosystem type and climate (Ma et al. 2021, Kasanke et al. 2022).
488 However, the mechanism for this change in AM fungi is more likely due to plants limiting their
489 carbon subsidies in response to a negative mycorrhizal growth response at high nutrient levels
490 (Egerton-Warburton and Allen 2000). We have not incorporated plant control over carbon
491 subsidies to the fungus into this model, but we plan to do so in future versions of the model.
492 Because such controls would decrease the rate of carbon exchange to the fungus, we expect that
493 such controls at high nutrient availability would increase the plant's abundance by mitigating the
494 loss of carbon to the fungus.

495 *Plant coexistence and species diversity*

496 Theory predicts that two resource competitors cannot coexist on a single resource, but they
497 can coexist on two resources if each is better at consuming a different resource (Levin 1970,
498 Tilman 1980, Hsu ~~et al.~~, [Cheng and Hubbell](#) 1981, Tilman 1982). Our results show that the
499 presence of a mycorrhizal fungus can promote the coexistence of two plant species that compete
500 for a single limiting nutrient, and plant coexistence requires that one plant species be better at
501 extracting the nutrient from the environment and the other plant species be better at extracting
502 the nutrient from the fungus (see also Umbanhowar and McCann 2005, Johnson and Bronstein
503 2019). The fungus is not simply a nutrient conduit but rather acts as a separate nutrient pool for
504 the plants, and coexistence results when they trade off the ability to extract the nutrient from the
505 environmental and fungal pools (Umbanhowar and McCann 2005, Johnson and Bronstein 2019).
506 However, the two species must draw the nutrient in relatively equitable but opposite proportions
507 from the two pools (i.e., the area in Figure 6 labeled " R_1 , R_2 & M "). These relative nutrient
508 extraction rates between the two plant species also influence the plants' relative abundances
509 when they do coexist. Thus, quantifying the relative supply of nutrients from the environment
510 and from mycorrhizal fungi for competing plant species will be an essential test of this model.

511 The loss of carbon to the fungus also shapes plant coexistence (Ek ~~et al.~~, [Andersson and](#)
512 [Söderström](#) 1997, Hobbie 2006, Kiers et al. 2011, Bever 2015, Genre et al. 2020). Greater

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513 maximum carbon extraction rates from the plants by the fungus increases the fungus' abundance,
514 which (1) exacerbates the plants' costs, but also (2) provides a larger total fungal nutrient pool
515 available to the plants. Because the fungus is a consumer of both plants, this linkage via carbon
516 supply has two effects: the direct cost of consumption on each plant and the mediation through
517 the fungus of apparent competition between the plants (sensu Holt 1977).

518 Experimental results testing the effect of mycorrhizae on plant coexistence and diversity are
519 equivocal, which suggests a great range of fungal effects on plant competitive performance. In a
520 tallgrass prairie, suppressing mycorrhizal fungi increased plant richness, evenness, and diversity,
521 because competitively dominant plant species decreased in abundance and competitively inferior
522 plant species increased (Hartnett and Wilson 1999, Smith ~~et al.~~, [Hartnett and Wilson](#) 1999). In
523 contrast, in a microcosm experiment, mycorrhizal fungi permitted competitively inferior species
524 to coexist with competitively superior plant species, but the competitive inferiors were excluded
525 in mycorrhizae-free replicates (Grime et al. 1987). Likewise, among 21 plant species in an
526 Ontario old field, species with a greater competitive effect on a common phytometer species had
527 a smaller growth response to the presence of mycorrhizal fungi (Stanescu and Maherali 2017).
528 Thus, in some plant communities, mycorrhizae promote coexistence and in others, they
529 exacerbate competitive differences among species. Our model results predict that these
530 differences in response are due to the relative capabilities of the plants and fungi to extract
531 nutrients and carbon from one another and from the environment.

532 Mycorrhizae have been shown to promote coexistence when the dominant plants in a
533 community without mycorrhizae have a lower or even negative mycorrhizal growth response
534 than other plants in the community (Grime et al. 1987, Stanescu and Maherali 2017, McHaffie
535 and Maherali 2020). Consistent with these results, our model predicts that the plant species that
536 is better at extracting the nutrient from the environmental pool will have a negative growth
537 response to the presence of the fungus (i.e., a parasitic relationship), and the plant species that is
538 better at extracting the nutrient from the fungal nutrient pool will have a positive mycorrhizal
539 growth response (i.e., a mutualistic relationship). Umbanhowar and McCann (2005) arrived at

540 similar conclusions from analyzing a generalized graphical model of this interaction. This result
541 is also analogous to the criterion for coexistence of two resource competitors that are fed upon by
542 a single consumer (Holt ~~et al.~~, [Grover and Tilman](#) 1994, Leibold 1996, McPeck 1996, 2022).

543 The effect of mycorrhizae on coexistence is also dependent on the abilities of the fungi
544 species present (Wilson and Hartnett 1997, Klironomos et al. 2000, Klironomos 2002, van der
545 Heijden ~~et al.~~, [Bardgett and van Straalen](#) 2008, Vogelsang and Bever 2009). For example, our
546 model predicts that plant coexistence is less likely if the fungus uses carbon from the
547 environment. Consequently, the model predicts arbuscular mycorrhizal fungi, which are obligate
548 biotrophs, should be more capable of fostering plant coexistence than ericoid and orchid
549 mycorrhizae and possibly more than ectomycorrhizal fungi depending on their saprotrophic
550 capabilities. AM systems are generally more diverse than EcM or ericoid systems (Brundrett
551 and Tedersoo 2018). ~~For example, in the tropics, AM forests are quite diverse whereas EcM~~
552 ~~forests are often dominated by a single species (Corrales et al. 2018).~~ For example, in the tropics,
553 AM forests are quite diverse whereas EcM forests are often dominated by a single species
554 (Corrales, Henkel and Smith 2018). Additionally, the model predicts that the rate at which the
555 fungus can extract the nutrient from the environment strongly influences whether plant species
556 can coexist and their relative abundances if they do. Increasing fungal abundance means a larger
557 fungal nutrient pool from which the plants can draw, but also a greater carbon cost for each plant
558 to pay. It would be interesting to test the predictions of this model result in the field among
559 various ectomycorrhizal communities, which can differ greatly in their nutrient uptake abilities
560 (Pellitier and Zak 2018).

561 Obviously, this model does not include some features of plant-mycorrhizal fungus
562 interactions that may influence plant coexistence. These include when mycorrhizae increase the
563 strength of intraspecific competition (McHaffie and Maherali 2020) and the sharing of carbon
564 through common mycorrhizal networks (Teste and Simard 2008, Klein ~~et al.~~, [Siegwolf and](#)
565 [Körner](#) 2016, Pickles et al. 2017). In ectomycorrhizal systems, carbon transfer can occur across
566 plant species from the stronger competitor to the poorer competitor via mycorrhizae (Simard et

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567 al. 1997), reducing interspecific competition. Our model also lacks any control by the plant of
568 carbon subsidy to the mycorrhizae (e.g., Bever 2002, Bever et al. 2009, Bever 2015). Lastly,
569 carbon and nutrients are not coupled in this model. In vivo, plants and fungi maintain their
570 carbon to nutrient ratios within certain bounds, so that nitrogen uptake would be constrained by
571 the amount of carbon in their biomass. Future analyses should explore these additional
572 mechanisms to see how they may alter the model's predictions.

573 *Conclusions*

574 The results of this model show that the coexistence of a plant and a fungus requires that the
575 fungus be substantially better at extracting the environmental nutrient, unless the plant extracts
576 little nutrient from the fungus. The plant can drive the fungus extinct if it extracts too much
577 nutrient from both the environment and the fungus. In contrast, the fungus can drive the plant
578 extinct if it has a higher environmental nutrient uptake rate than the plant and extracts carbon
579 from the plant at a much greater rate than the plant gains nutrient from the fungus. Our model
580 also predicts that the fungus can permit the plant to occupy nutrient-poor environments where it
581 would be incapable of living without the fungus, but that the fungus can become parasitic in
582 nutrient-rich environments where the plant is carbon-limited if it extracts carbon from the plant
583 at a substantial rate.

584 Furthermore, the results showed the presence of a single fungus species can foster the
585 coexistence of two plant species competing for a single environmental resource, because the
586 fungus is a second limiting resource to the plants and is a conduit of "apparent" competition
587 between them. Whether the plant species can coexist depends on 1) the balance among their
588 relative competitive abilities for the environmental nutrient and for the nutrient from the fungus
589 and the relative amount of carbon extracted by the fungus from each and 2) the ability of the
590 fungus to extract nutrients and carbon from the environment. The ability of the fungus to extract
591 carbon from the environment controls the intensity of apparent competition between the plants.
592 Our analysis highlights several future avenues of inquiry including how the functional
593 capabilities of the mycorrhizal fungi affect competitive interactions between the fungi and plant

594 and between plants. Understanding this complex web of interactions among plants and
595 mycorrhizal fungi should help guide empirical research into new and fruitful directions.

596

597

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611

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836

837

838 Table 1. List of state variables, equation terms, and parameters used in the model.

839

840 State variables

841 N abundance of the environmental nutrient: units, nutrient

842 R_1, R_2 abundances of plant species 1 and 2, respectively: units, plant –
843 expressed as either individuals or biomass

844 M abundance of the mycorrhizal fungus: units, fungus – expressed as
845 biomass

846 Q_1^N, Q_2^N, Q_M^N individual quantities of the nutrient in plant species 1 and 2, and the
847 fungus, respectively: units, nutrient/([plant or fungus])

848 Q_1^C, Q_2^C, Q_M^C individual quantities of carbon in plant species 1 and 2, and the fungus,
849 respectively: units, carbon/([plant or fungus])

850 Equation Terms

851 $\Omega(N)$ renewal function for the abiotic nutrient pool: units, nutrient/time

852 $P_1(N, Q_1^N), P_2(N, Q_2^N), P_M(N, Q_M^N)$ uptake function of environmental nutrient by plant
853 species 1 and 2, and the fungus, respectively: units, nutrient/([plant
854 or fungus]·time)

855 $D_1(Q_M^N, Q_1^N), D_2(Q_M^N, Q_2^N)$ rate function for plant species 1 and 2 extracting nutrient
856 from the fungus, respectively: units, nutrient/(plant·fungus·time)

857 $C_1(Q_1^C, Q_M^C), C_2(Q_2^C, Q_M^C)$ rate function for the fungus extracting carbon from plant
858 species 1 and 2, respectively: units, carbon/(plant·fungus·time)

859 $\Lambda_1(R_1), \Lambda_2(R_2), \Lambda_M(M)$ carbon production rate function for plant species 1 and 2
860 and the fungus respectively: units, carbon/([plant or fungus]·time)

861 $\Psi_1(Q_1^N, Q_1^C), \Psi_2(Q_2^N, Q_2^C), \Psi_M(Q_M^N, Q_M^C)$ biomass (or individual) production rate
862 function for plant species 1 and 2, respectively and biomass
863 production rate function for the fungus: units, [plant or
864 fungus]/([plant or fungus]·time)

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865 Parameters

866	T_N	maximum abundance of the environmental nutrient: units, nutrient
867	c	renewal rate of environmental nutrient: units, 1/time
868	$Q_1^{N_{\max}}, Q_2^{N_{\max}}, Q_M^{N_{\max}}$	maximum individual nutrient quantities in plant species 1 and 2, and the
869		fungus, respectively: units, nutrient
870	$Q_1^{N_{\min}}, Q_2^{N_{\min}}, Q_M^{N_{\min}}$	minimum individual nutrient quantities in plant species 1 and 2, and the
871		fungus, respectively: units, nutrient
872	$Q_M^{C_{\max}}$	maximum individual carbon quantities in the fungus: units, carbon
873	$Q_1^{C_{\min}}, Q_2^{C_{\min}}, Q_M^{C_{\min}}$	minimum individual carbon quantities in plant species 1 and 2, and the
874		fungus, respectively: units, carbon
875	$\rho_1^N, \rho_2^N, \rho_M^N$	maximum environmental nutrient uptake rates for plant species 1 and 2,
876		and the fungus, respectively: units, nutrient/time
877	g_1^N, g_2^N, g_M^N	half-saturation constants of environmental nutrient uptake rates for plant
878		species 1 and 2, and the fungus, respectively: units, nutrient
879	ρ_1^{NM}, ρ_2^{NM}	maximum nutrient uptake rates from the fungus by plant species 1 and 2,
880		respectively: units, nutrient/time
881	g_1^{NM}, g_2^{NM}	half-saturation constants of nutrient uptake rates from the fungus for
882		plant species 1 and 2, respectively: units, nutrient
883	ρ_M^{C1}, ρ_M^{C2}	maximum carbon uptake rates from plant species 1 and 2, respectively,
884		by the fungus: units, carbon/time
885	g_M^{C1}, g_M^{C2}	half-saturation constants of carbon uptake rates from plant species 1 and
886		plant species 2, respectively, by the fungus: units, carbon
887	$\lambda_1, \lambda_2, \lambda_M$	maximum rate of carbon production by plant species 1 and 2, and of
888		carbon acquisition by the fungus, respectively: units, carbon/time
889	ϕ_1, ϕ_2	half-saturation constants for photosynthetic rates scaled by Q_1^N and Q_2^N
890		for plant species 1 and 2, respectively: units, nutrient
891	μ_1, μ_2, μ_M	maximum production rate for plant species 1 and 2, and maximum

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892		biomass production by the fungus, respectively: units, [plant or
893		fungus]/time
894	$\alpha_1, \alpha_2, \beta$	scaling parameter for carbon production by plant species 1 and 2, and of
895		carbon acquisition by the fungus, respectively: units, 1/[plant or
896		fungus]
897	$\varepsilon_1^N, \varepsilon_2^N, \varepsilon_M^N$	<u>nutrient excretion rate</u> <u>basal quantities used for growth and reproduction</u>
898		by plant species 1 and 2, and the fungus, respectively: units,
899		nutrient/(nutrient·time)
900	b_1^N, b_2^N, b_M^N	nutrient quantities used for growth and reproduction by plant species 1
901		and 2, and the fungus, respectively: units, nutrient/ [plant or fungus]
902	$\delta_1^C, \delta_2^C, \delta_M^C$	<u>basal carbon metabolic loss rate</u> <u>quantities used for growth and</u>
903		<u>reproduction</u> by plant species 1 and 2, and the fungus, respectively:
904		units, carbon/(carbon·time)
905	b_1^C, b_2^C, b_M^C	carbon quantities used for growth and reproduction each offspring by
906		plant species 1 and 2, and biomass production rate for the fungus,
907		respectively: units, carbon/[plant or fungus]
908	<u>$\theta_1, \theta_2, \theta_M$</u>	<u>fraction of individual nutrient quantity that is recycled to the</u>
909		<u>environmental pool from dead biomass for plant species 1 and 2, and</u>
910		<u>the fungus, respectively: unitless</u>
911	f_1, f_2, f_M	intrinsic death rates for plant species 1 and 2, and intrinsic biomass loss
912		rate of the fungus, respectively: units, [plant or fungus]/([plant or
913		fungus]·time)
914		

915 **Figure Legends**

916 Figure 1. Conceptual diagrams of the consumption linkages between plants and mycorrhizal
 917 fungi. Each circle represents an individual of the plant, fungus, or the environmental pool of
 918 an abiotic nutrient (e.g., a nitrogen or phosphorus compound). The plant and fungus have
 919 pools of the nutrient N and carbon C in their tissues. Arrows point from the consumed pool
 920 to the consumer (i.e., the direction of flow of the quantity) and are labeled by the
 921 corresponding rate functions (see text). Panel **A(a)** illustrates these consumption linkages for
 922 one plant species and one fungus, and panel **B(b)** illustrates these linkages for two plant
 923 species and one fungus.

924 Figure 2. Areas of coexistence of one plant species and one fungus species along an
 925 environmental nutrient gradient for various values of maximum nutrient uptake by the fungus
 926 (ρ_M^N). Panels **A(a)** and **B(b)** identify the areas of parameter space where the two species
 927 coexist (identified as “ R_1 & M ”), only the plant is present (“ R_1 ”), and a small unlabeled area
 928 at very low T_N (**environmental nutrient**) values where neither species can support a
 929 population. The fungus cannot extract carbon from the environment ($\lambda_M = 0.0$) in panel
 930 **A(a)**, and it can ($\lambda_M = 0.5$) in panel **B(b)**. Panels **C(c)** and **D(d)** show the changes in
 931 species and environmental nutrient abundances and quantities along transects of
 932 environmental nutrient availability for two different values of maximum environmental
 933 nutrient uptake for the fungus. In the top panel in each column of **C(c)** and **D(d)**, the blue
 934 curve is the nutrient equilibrium abundance, the **redorange** solid curve is the fungal
 935 equilibrium abundance, the green solid curve is the plant equilibrium abundance when both
 936 species are initially present and interact with one another. The green dashed curve is the
 937 plant equilibrium abundance in the absence of the fungus. The bottom panel in each column
 938 gives equilibrium quantities for nutrient (solid curves) and carbon (dot-dashed curves) for **the**
 939 **plant individuals** (green) and **fungus individuals** (**redorange**). The other parameters used in
 940 these examples are as follows unless otherwise specified: $c=0.01$, $\mu_1 = \mu_M = 0.2$, $Q_1^{N\min} =$
 941 $Q_M^{N\min} = Q_1^{C\min} = Q_M^{C\min} = 0.2$, $Q_1^{N\max} = Q_M^{N\max} = 1.0$, $\rho_1^N = 0.1$, $b_1^N = b_M^N = 0.1$, $g_1^N = g_M^N = g_1^{NM} = 25$,

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942 $\varepsilon_1^N = \varepsilon_M^N = 0.05$, $\rho_1^{NM} = 0.5$, $\lambda_1 = 100$, $\phi_1 = 0.2$, $\alpha_1 = \beta = 0.1$, $b_1^C = 2.0$, $b_M^C = 0.1$, $\delta_1^C = 0.15$, $\delta_M^C = 0.1$,
 943 $\rho_M^{C1} = 0.3$, $\mathcal{G}_M^{C1} = 50$, $f_1 = f_M = 0.1$, $\theta_1 = \theta_M = 0.5$.

944 Figure 3. The combinations of maximum nutrient uptake rates for the plant that shape whether
 945 the plant and fungus can coexist. The ordinate axis is the plant maximum uptake rate from
 946 the environment, and the abscissa axis is the plant maximum uptake rate from the fungus.
 947 Panel **A(a)** has a fungus that does not extract carbon from the environment (i.e., $\lambda_M = 0.0$),
 948 and Panel **B(b)** has a fungus with a maximum environmental carbon extraction rate of
 949 $\lambda_M = 0.5$. These parameter spaces are divided into four areas: No species present, because
 950 neither species can support a population with those parameter combinations; M only, where
 951 the fungus outcompetes the plant, so that only the fungus is present; R_1 only, where the plant
 952 outcompetes the fungus, so that only the plant is present; and R_1 & M , where the plant and
 953 fungus coexist. As a reference, the maximum uptake rate of the nutrient from the
 954 environment for the fungus is $\rho_M^N = 0.5$ (identified by the dashed line in each panel). **All other**
 955 **parameters are as given in Figure 2. The other parameters are as follows unless otherwise**
 956 **specified:** $T_N = 50$, $c = 0.01$, $\mu_1 = \mu_M = 0.2$, $Q_1^{N \min} = Q_M^{N \min} = Q_1^{C \min} = Q_M^{C \min} = 0.2$, $Q_1^{N \max} = Q_M^{N \max}$
 957 $= 1.0$, $\rho_1^N = 0.1$, $b_1^N = b_M^N = 0.1$, $\mathcal{G}_1^N = \mathcal{G}_M^N = \mathcal{G}_1^{NM} = 25$, $\varepsilon_1^N = \varepsilon_M^N = 0.05$, $\rho_1^{NM} = 0.5$, $\lambda_1 = 100$, $\phi_1 = 0.2$,
 958 $\alpha_1 = \beta = 0.1$, $b_1^C = 2.0$, $b_M^C = 0.1$, $\delta_1^C = 0.15$, $\delta_M^C = 0.1$, $\rho_M^{C1} = 0.3$, $\mathcal{G}_M^{C1} = 50$, $f_1 = f_M = 0.1$, $\theta_1 = \theta_M$
 959 $= 0.5$.

960 Figure 4. Carbon extraction rate by the fungus from the plant can shift their interaction from
 961 being mutualistic to parasitic, depending on environmental nutrient availabilities. Each panel
 962 shows the relationship for equilibrium plant abundance when the fungus has different values
 963 of maximum carbon extraction rate from the plant— $\rho_M^{C1} = (\rho_M^{C1})$. In each panel, the thin
 964 dashed line identifies the plant abundance in the absence of the mutualist. The solid line
 965 identifies the plant abundance. Panels **A**, **C**, **(a)**, **(c)**, and **E** **(e)** show results for a fungus that
 966 cannot extract carbon from the environment, and panels **B**, **D**, **(b)**, **(d)**, and **F** **(f)** of panels
 967 shows results for a fungus that can extract environmental carbon. Panels **A** **(a)** and **B** **(b)** show
 968 results at an environmental nutrient availability of $T_N = 50$, panels **C** **(c)** and **D** **(d)** for

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969 $T_N = 100$, and panels **E(e)** and **F(f)** for $T_N = 200$. ~~In panels A, C, and E the~~The fungus
 970 cannot support a population below $\rho_M^{C1} = 0.15$, and so the discontinuity in plant abundance at
 971 this point is caused by the fungus now being able to support a population. ~~All other~~
 972 ~~parameters are as specified in Figure 2, and~~ $\rho_M^N = 2.5$. ~~The other parameters are as follows~~
 973 ~~unless otherwise specified:~~ $T_N = 50, c = 0.01, \mu_1 \equiv \mu_M = 0.2, Q_1^{N\min} \equiv Q_M^{N\min} \equiv Q_1^{C\min} \equiv Q_M^{C\min} = 0.2,$
 974 $Q_1^{N\max} \equiv Q_M^{N\max} = 1.0, \rho_1^N = 0.1, b_1^N \equiv b_M^N = 0.1, \mathcal{G}_1^N \equiv \mathcal{G}_M^N \equiv \mathcal{G}_1^{NM} = 25, \varepsilon_1^N \equiv \varepsilon_M^N = 0.05, \rho_1^{NM} = 0.5, \lambda_1$
 975 $= 100, \phi_1 = 0.2, \alpha_1 \equiv \beta = 0.1, b_1^C = 2.0, b_M^C = 0.1, \delta_1^C = 0.15, \delta_M^C = 0.1, \rho_M^N = 2.5, \rho_M^{C1} = 0.3, \mathcal{G}_M^{C1} = 50,$
 976 $f_1 \equiv f_M = 0.1, \theta_1 \equiv \theta_M = 0.5.$

977 Figure 5. Equilibrium abundances for a single plant species interacting with a single fungus
 978 species at various values of (**Aa**) the maximum plant uptake rate of nutrient from the fungus,
 979 and (**Bb**) the maximum environmental nutrient uptake rate for the fungus. The equilibrium
 980 abundances of the species and nutrient in the environment and the nutrient are identified as in
 981 Figure 2. ~~All other parameters are as given in Figure 3. The other parameters are as follows~~
 982 ~~unless otherwise specified:~~ $T_N = 50, c = 0.01, \mu_1 \equiv \mu_M = 0.2, Q_1^{N\min} \equiv Q_M^{N\min} \equiv Q_1^{C\min} \equiv Q_M^{C\min} = 0.2,$
 983 $Q_1^{N\max} \equiv Q_M^{N\max} = 1.0, \rho_1^N = 0.1, b_1^N \equiv b_M^N = 0.1, \mathcal{G}_1^N \equiv \mathcal{G}_M^N \equiv \mathcal{G}_1^{NM} = 25, \varepsilon_1^N \equiv \varepsilon_M^N = 0.05, \rho_1^{NM} = 0.5, \lambda_1$
 984 $= 100, \lambda_M = 0.0, \phi_1 = 0.2, \alpha_1 \equiv \beta = 0.1, b_1^C = 2.0, b_M^C = 0.1, \delta_1^C = 0.15, \delta_M^C = 0.1, \rho_M^N = 2.5, \rho_M^{C1}$
 985 $= 0.3, \mathcal{G}_M^{C1} = 50, f_1 \equiv f_M = 0.1, \theta_1 \equiv \theta_M = 0.5.$

986 Figure 6. Areas of parameter space in which two plant species do and do not coexist while
 987 competing for the abiotic nutrient and interacting with a single fungus species. This figure
 988 contrasts R_2 's plant species 2's maximum rate of nutrient uptake from the environment (ρ_2^N)
 989 with its maximum rate of nutrient uptake from the fungus (ρ_2^{NM}). The comparable
 990 parameters for R_1 plant species 1 are identified with the dashed lines. Three areas are
 991 identified: where each plant species coexists with the fungus alone, and where both plant
 992 species coexist with the fungus. ~~All parameters are as given in Figure 2 for both plant~~
 993 ~~species and the fungus, except~~ $\lambda_M = 0.0, \rho_1^N = 0.05, \rho_1^{NM} = 0.25, \rho_M^N = 1.5,$ and those being
 994 manipulated. Also, both plants have the same parameters except for those manipulated in the
 995 figure. ~~Both plants have the same parameters except for those manipulated in the figure. The~~

996 other parameters are as follows unless otherwise specified: $T_N=50, c=0.01, \mu_1 \equiv \mu_2 \equiv \mu_M$
 997 $=0.2, Q_1^{N \min} \equiv Q_2^{N \min} \equiv Q_M^{N \min} \equiv Q_1^{C \min} \equiv Q_2^{C \min} \equiv Q_M^{C \min} =0.2, Q_1^{N \max} \equiv Q_2^{N \max} \equiv Q_M^{N \max} =1.0, \rho_1^N$
 998 $=0.05, \rho_1^{NM} =0.25, b_1^N \equiv b_2^N \equiv b_M^N =0.1, \mathcal{G}_1^N \equiv \mathcal{G}_2^N \equiv \mathcal{G}_M^N \equiv \mathcal{G}_1^{NM} \equiv \mathcal{G}_2^{NM} =25, \varepsilon_1^N \equiv \varepsilon_2^N \equiv \varepsilon_M^N =0.05,$
 999 $\rho_1^{NM} \equiv \rho_2^{NM} =0.5, \lambda_1 \equiv \lambda_2 =100, \lambda_M =0.0, \phi_1 \equiv \phi_2 =0.2, \alpha_1 \equiv \alpha_2 \equiv \beta =0.1, b_1^C \equiv b_2^C =2.0, b_M^C =0.1,$
 1000 $\delta_1^C \equiv \delta_2^C =0.15, \delta_M^C =0.1, \rho_M^N =1.5, \rho_M^{C1} =0.3, \mathcal{G}_M^{C1} =50, f_1 \equiv f_2 \equiv f_M =0.1, \theta_1 \equiv \theta_2 \equiv \theta_M =0.5.$

1001 Figure 7. Equilibrium abundances (top panels) and quotas (bottom panels) for two plant species
 1002 interacting with a single fungus species at various values of (**Aa**) the maximum rate at which
 1003 plant species 1 extracts the nutrient from the fungus, (**Bb**) the maximum environmental
 1004 nutrient uptake rate for the fungus, (**Cc**) the maximum rate at which the fungus extracts
 1005 carbon from the environment, and (**Dd**) the maximum rates at which the fungus extracts
 1006 carbon from each plant for a community potentially consisting of two plants and a fungus.

1007 Quantities for the fungus and nutrient are identified as in Figure 2. Quantities for R_1 are
 1008 given in light green and for R_2 in dark green. All parameters are as given in Figure 6, except
 1009 for $\rho_1^N =0.2, \rho_1^{NM} =0.5, \rho_2^N =0.5, \rho_2^{NM} =0.2, \rho_M^N =3.5$, and those being manipulated. plant
 1010 species 1 are given in dark green and for plant species 2 in light green. The other parameters
 1011 are as follows unless otherwise specified: $T_N=50, c=0.01, \mu_1 \equiv \mu_2 \equiv \mu_M =0.2, Q_1^{N \min} \equiv Q_2^{N \min} \equiv$
 1012 $Q_M^{N \min} \equiv Q_1^{C \min} \equiv Q_2^{C \min} \equiv Q_M^{C \min} =0.2, Q_1^{N \max} \equiv Q_2^{N \max} \equiv Q_M^{N \max} =1.0, \rho_1^N =0.2, \rho_2^N =0.5, \rho_1^{NM} =1.0,$
 1013 $\rho_2^{NM} =0.2, b_1^N \equiv b_2^N \equiv b_M^N =0.1, \mathcal{G}_1^N \equiv \mathcal{G}_2^N \equiv \mathcal{G}_M^N \equiv \mathcal{G}_1^{NM} \equiv \mathcal{G}_2^{NM} =25, \varepsilon_1^N \equiv \varepsilon_2^N \equiv \varepsilon_M^N =0.05, \rho_1^{NM} \equiv \rho_2^{NM}$
 1014 $=0.5, \lambda_1 \equiv \lambda_2 =100, \lambda_M =0.0, \phi_1 \equiv \phi_2 =0.2, \alpha_1 \equiv \alpha_2 \equiv \beta =0.1, b_1^C \equiv b_2^C =2.0, b_M^C =0.1, \delta_1^C \equiv \delta_2^C$
 1015 $=0.15, \delta_M^C =0.1, \rho_M^N =3.5, \rho_M^{C1} =0.3, \mathcal{G}_M^{C1} =50, f_1 \equiv f_2 \equiv f_M =0.1, \theta_1 \equiv \theta_2 \equiv \theta_M =0.5.$