

Spatial coexistence of coinvasive communities with mutualism and competition

Naven Narayanan Venkatanarayanan¹, Peter Lutz¹, and Allison Shaw¹

¹University of Minnesota Twin Cities

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Abstract

All interactions between multiple species invading together (coinvasion) must be accounted for to predict species coexistence patterns across space. Mutualisms, particularly, are known to influence species' population dynamics and their invasive ability (e.g. mycorrhizal fungi with partner plants). Yet, while modelling coinvasion, their role in mediating coexistence is overlooked. We build a spatial model of coinvasion of two competing plant species with a shared fungal mutualist to study how mutualism and competition shape the spatial coexistence of competitors. We find that mutualist presence engenders regional (spatial) coexistence between competitors even when local coexistence between them is impossible. Further, increasing mutualist dispersal results in sharp transitions in competitor coexistence outcomes. Finally, differences in mutualist partner dependence and competitive ability interact to produce a variety of local and regional coexistence outcomes. Thus, incorporating mutualism dependence and dispersal behaviour into coinvasion models offers new insights into spatial coexistence and invasive species distributions.

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Naven Narayanan^{1*}, Peter Lutz¹, Allison K. Shaw¹

^{1.} Department of Ecology, Evolution, Behavior, University of Minnesota
Twin Cities, Saint Paul, MN, 55108, USA ; * Corresponding author

Contact for corresponding author: venka210@umn.edu

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Introduction

¹⁸ Understanding the drivers of species coexistence, both local and regional (i.e. spatial) is essential to understand the biogeography of communities and the distribution of its constituent species. Traditional biotic drivers of local and
²¹ spatial coexistence proposed consist interactions with natural enemies or herbivores, life-history, and competition-colonisation tradeoffs among others (Tilman, 1982; MacArthur, 1970; Chesson, 1994; Janzen, 1970; Amarasekare, 2003; Fagan et al., 2005). Biotic interactions shaping spatial coexistence, in particular,
²⁴ has often been limited to pairwise competition or predator-prey dynamics where competition between invading species leads to either local coexistence or species
²⁷ replacement and the predator behaviour (generalism or specialism) can generate range overlaps or limits of the species (Case and Taper, 2000; Holt, 1984; Hochberg and Ives, 1999; Lutscher, 2019). However, more recently, the role of
³⁰ positive interactions has also been shown to shape the local coexistence between competing species.

Mutualisms are ubiquitous ecological interactions between two or more species
³³ that reciprocally increase each others' growth rates and thus their respective abundances (Vandermeer and Boucher, 1978; Bronstein, 2015). The degree to which species attribute their growth to partner benefits is termed as 'mutualism dependence' (Douglas and Smith, 1989; Ollerton, 2006; Janos, 2007). Mutualism dependence often evolves to maximise usage of partner benefits but tradeoffs can lead to trait loss resulting in reduced growth of a species when the partner
³⁶ is absent (Siefert et al., 2019; Chomicki et al., 2020; Visser et al., 2010; Ellers et al., 2012). Thus, differences in mutualism dependence could lead to competitors obtaining different magnitudes of benefits from a shared mutualist partner.
³⁹ Differential benefits obtained by competitors from a shared mutualists has been shown to stabilise the local coexistence of competitors (Bever et al., 1997; Bever,
⁴²

1999; Umbanhowar and McCann, 2005; Heijden et al., 2008).

In addition to influencing local coexistence by shaping competitor population growth, mutualisms also shape the spatial dynamics of competing species. Across a variety of taxa, the coinvasion of two or more species arise through mutualistic interactions resulting in repeated, successful invasions in a phenomenon termed ‘invasional meltdown’ (Simberloff and Von Holle, 1999). This hypothesis has been borne out in several empirical examples including legume-rhizobial mutualisms and plant-fungal mutualisms (Lopez et al., 2021; Simonsen et al., 2017; Nuñez et al., 2009). For instance, the invasion and range expansion of pine species in parts of South America and New Zealand are known to proceed only in the presence of their mutualist ectomycorrhizal fungi (EM) (A. Dickie and Reich, 2005; Dickie et al., 2017; Traveset and Richardson, 2014; Richardson et al., 2000). Indeed, increased dependence on their fungal partner is known to increase the invasive abilities of a tree species (Moyano et al., 2020, 2021). This dependence-invasion correlation can arise when more dependent species morphologically adapt to produce smaller seeds or lower seed wing loading (among other adaptations broadly termed Long Distance Dispersal (LDD) Syndrome) that disperse further even at the cost of reduced competitive ability (Groom, 2010; Greene and Johnson, 1993). Indeed, it has been shown that mycorrhizal plants are more likely to have structures enabling LDD than non-mycorrhizal plants (Correia et al., 2018; Vargas et al., 2012; Zhang et al., 2019). Differential dispersal due to variation in LDD traits could shape invasion dynamics of competitors through priority effects and putatively spatial coexistence through reduced spatial niche overlap (Fukami, 2015; Hess et al., 2019; Vannette and Fukami, 2014; Plough et al., 2020). Yet, we do not completely understand the conditions under which mutualisms shape local and regional (or spatial) coexistence of co-invading competitor species.

Here, we build a spatially explicit mathematical model of two coinvasive
competitors (for e.g. congeneric plant species) with a shared mutualist partner
(for e.g. EM fungi) to understand the conditions under which the competitors
coexist locally, regionally, or both. We model the role of mutualistic dependence
on competitor population dynamics and on their dispersal ability and study their
interplay in driving coexistence outcomes. We also consider scenarios where the
shared mutualist disperses faster or slower than the competitors to identify how
relative dispersal abilities of the three interacting species ultimately drive the
coexistence and spatial distribution of the community.

Methods

Model

We build a system agnostic model of competition and mutualism, drawing inspiration from plant-fungal and legume-rhizobial models of mutualisms. We
consider two very similar competing species (e.g. congeneric plant species) such
that they have similar resource requirements, habitat requirements, and share
the same mutualist partner species (rhizobia or EM fungi).

We model our system using a set of Integro-Difference Equations (IDEs) that incorporate growth, species interactions, and dispersal of species. The growth and dispersal phases repeat in a cycle, over discrete time steps across continuous one-dimensional space. Growth occurs from t to $t + T$, followed by dispersal at $t + 1$, where t is a given year or generation. ‘ T ’ is some period of time less than a year (or generation) i.e. $0 < T < 1$. Growth is modelled by coupled Ordinary Differential Equations (ODEs) for the three species while the dispersal of each species is governed by their own dispersal kernel (Naven Narayanan and Shaw, 2023 (in press)). We track the speed at which species expand into new regions

⁹⁶ in space along with how their populations densities are spatially distributed.

In our model species F_1 and F_2 are the focal plant species competitors and P is the partner mutualist of both F_1 and F_2 . F_1 and F_2 differ both in their dependence on P (and thus receive different magnitudes of mutualistic benefits) and in competitive ability. We arbitrarily assume, without loss of generality, that F_1 depends more on P than F_2 (see Figure 1). The general functional form ⁹⁹ of our IDEs are as follows:

$$P_{t+1}(x) = \int_{-\infty}^{\infty} k_P(x-y) M_P(P_t(y), F_{1,t}(y), F_{2,t}(y)) dy \quad (1a)$$

$$F_{1,t+1}(x) = \int_{-\infty}^{\infty} k_{F_1}(x-y) M_{F_1}(P_t(y), F_{1,t}(y), F_{2,t}(y)) dy \quad (1b)$$

$$F_{2,t+1}(x) = \int_{-\infty}^{\infty} k_{F_2}(x-y) M_{F_2}(P_t(y), F_{1,t}(y), F_{2,t}(y)) dy \quad (1c)$$

where k_i represents the dispersal kernel of species 'i' ($i = P, F_1, F_2$), x and y are spatial coordinates after and before dispersal respectively, and M_i is the ¹⁰⁵ nonlinear growth function describing the growth of species 'i' at a point in space.

Growth Functions

We model growth of the three species at a given point in the landscape using ¹⁰⁸ a set of Ordinary Differential Equations (ODEs). We model competition between F_1 and F_2 using classic Lotka-Volterra dynamics with linear functional responses. Mutualisms between P and F_1 (or F_2) are modelled as bi-directional ¹¹¹ consumer-resource interactions sensu (Holland and DeAngelis, 2009, 2010). The benefits obtained are modelled as a saturating function with partner density which captures physiological limits to uptake or handling of resources. Such

¹¹⁴ saturation has been observed in fig-fig wasp, ant-treehopper, ant-aphid mutualisms (Wright, 1989; Addicott, 1981; Morales, 2000; Bronstein, 2001). In the absence of mutualists and competitors, a single species grows logistically to a ¹¹⁷ carrying capacity. The equations are given as

$$\frac{dP}{dt} = P \left[(r_P + \left(\frac{\alpha_{PF_1} F_1}{h_P + F_1} + \frac{\alpha_{PF_2} F_2}{h_P + F_2} \right) - d_P P \right] \quad (2a)$$

$$\frac{dF_1}{dt} = F_1 \left[(1 - \delta_{F_1}) r_{F_1} + \delta_{F_1} \left(\frac{\alpha_{F_1 P} P}{h_{F_1} + P} \right) - d_{F_1} F_1 - \tau_{12} F_2 \right] \quad (2b)$$

$$\frac{dF_2}{dt} = F_2 \left[(1 - \delta_{F_2}) r_{F_2} + \delta_{F_2} \left(\frac{\alpha_{F_2 P} P}{h_{F_2} + P} \right) - d_{F_2} F_2 - \tau_{21} F_1 \right] \quad (2c)$$

and are integrated from time ‘t’ to ‘t+T’ to obtain M_P, M_{F_1}, M_{F_2} respectively. δ_i represents the mutualist partner dependence of species F_i . The total growth ¹²⁰ of a species (say F_1) is the sum of its own intrinsic growth and partner benefits weighted by its degree of dependence (δ_{F_1}) resulting in some tradeoff between intrinsic growth versus benefit uptake from partner. Such tradeoffs between re- ¹²³ production and root architecture have been observed in invasive forbs with different degrees of dependence on their mycorrhizal fungal partner (Seifert et al., 2009). r_i is the intrinsic birth rates of species ‘i’, α_{ij} is the maximal benefit received from species ‘j’ by species ‘i’, h_i is the half-saturation constant of species ‘i’, d_i s are the species’ intrinsic death rates, and τ_{ij} is the competitive effect on species ‘i’ by species ‘j’. In our model, we do not explicitly model mutualism ¹²⁶ costs. We assume that benefits exchanged are ‘net benefits’ and thus the costs of mutualism (i.e. resource acquisition of carbon, phosphorous, or nitrogen) are embedded in the expression itself.

¹³² **Dispersal Kernel**

Species dispersal is governed by their dispersal kernel, a probability density function describing the probability of an individual dispersing to and establishing at a location ‘x’ given it started at another location ‘y’. We assume that ¹³⁵ each species has a Gaussian dispersal kernel given as

$$k_P(x - y) = \frac{1}{\sqrt{2\pi\sigma_P^2}} e^{-\frac{(x-y)^2}{2\sigma_P^2}} \quad (3a)$$

$$k_{F_i}(x - y) = \frac{1}{\sqrt{2\pi\delta_{F_i}\sigma_i^2}} e^{-\frac{(x-y)^2}{2\delta_{F_i}\sigma_i^2}} \quad (3b)$$

where σ_P^2 is the variance of P and $\sigma_{F_i}^2$ s are the variances of the dispersal kernel of the competitors. While implementing dependence-dispersal tradeoffs in our simulations, the kernels of the competitors are asymmetric. When these tradeoffs are not implemented, we ignore their δ_{F_i} values and set them to 1 thus ¹³⁸ making the kernels symmetric. ¹⁴¹

Simulations

To simulate the spatial dynamics of the model, we initialize a one-dimensional landscape. All simulations begin with very low population densities for each species ($P = F_1 = F_2 = 0.1$) at the center of the landscape with symmetric coinvasion in both directions. Each species’ growth phase occurs for an arbitrary T time steps; changing this number does not qualitatively affect results. ¹⁴⁴ Dispersal then occurs thus completing a single iteration of the simulation. We ran each simulation for 500 iterations by which time steady state was reached, ¹⁴⁷ which we defined as when all three species reached a constant range expansion speed at the edge and the population density of species behind their range edge reached equilibrium. We determined range expansion speed by subtracting ¹⁵⁰

153 the range edge location for the previous iteration from the one for the current
 154 iteration. We also defined a metric for range overlap ρ which allowed us to de-
 155 termine what type of coexistence arose between the the competitors. We define
 156 ρ as $\frac{R_{F_1} - R_{F_2}}{R_{F_1} \cup R_{F_2}}$ where R_{F_1} and R_{F_2} are the ranges of the F_1 and F_2 respectively.
 157 The numerator describes the difference in the range size between the two species
 158 while the denominator depicts the size of space where either F_1 or F_2 is present.
 159 Based on ρ 's value, we can identify what sort of coexistence outcome can be
 160 expected between the competitors (see Appendix S1: Table S1 for expected
 161 ranges of ρ for different coexistence outcomes). Table 1 includes the parameter
 162 values used in all simulations.

Scenarios

We ran four sets of simulations: Set 1 - We compare the coexistence outcomes
 163 between competitors in cases where a mutualist coinvades with them versus is
 164 absent from the landscape. Here we assume that the dispersal kernels of all
 165 species are equal. Set 2 - To understand how increasing dispersal ability of
 166 P altered coexistence of competitors under different competitive abilities (i.e.
 167 strong, intermediate, and weak competition coefficients (τ_{ij})), we swept over
 168 $\sigma_P^2 \in [0.001, 0.75]$ with step size 0.001 and calculated their range overlap ρ .
 169 Set 3 - Next, for a given dispersal ability (variance in dispersal kernel i.e. σ_P^2)
 170 of P , we ask how differences in competitive ability influence the spatial coexis-
 171 tence outcomes of F_1 and F_2 when P spreads a) slower than, b) equal to, or c)
 172 faster than F_1 and F_2 while the competitors have equal dispersal abilities (i.e.
 173 $\sigma_{F_1} = \sigma_{F_2}$). These kernel asymmetries between mutualist partners are often
 174 observed in tree-fungal mutualisms where tree seeds are often wind-dispersed
 175 $\sim 100 - 200\text{m}$ whereas fungal spores typically disperse in the order of $\sim 1 - 10\text{m}$
 176 (Galante et al., 2011; Peay et al., 2012; Greene and Johnson, 1993) Set 4 - We

next incorporate dependence-dispersal tradeoffs which generates asymmetry in
180 the dispersal ability of the competitors themselves to study its interplay with P's
dispersal ability in determining the spatial coexistence of F_1 and F_2 . We fixed
values of dependence $(\delta_{F_1}, \delta_{F_2}) = (0.6, 0.4)$ on P. The difference in dependence
183 modified the dispersal kernels of the competitors and more dependent competi-
tors disperse further (see Equation 3). Our results are robust to changes in the
values of dependence (which vary from 0 to 1). In this set of simulations, the
186 dispersal kernels of all three species were different from one another. We ran all
simulations across a wide range of competitive abilities of F_1 and F_2 (see Table
1 for values chosen).

189 Outcomes

We classified the coexistence outcome of each simulation when a steady state
was reached. If the population of F_2 was zero across all points in the landscape,
192 we defined this as *F_1 dominance or win* i.e. competitive exclusion of F_2 and
vice versa for F_1 . When the fraction of the total combined species range jointly
occupied by both F_1 and F_2 was > 0.95 we defined it as *local coexistence*. In
195 instances where F_1 or F_2 excluded the other over a fraction (≥ 0.05) of the total
occupied range with local coexistence over the remaining range, we termed this
as *local coexistence with F_1 or F_2 dominance*. Finally, when we found F_1 and F_2
198 each exclusively occupying separate portions of the total occupied range due to
either exclusion of differential dispersal abilities, we defined this as *regional or
spatial coexistence* (See Figure 2 for illustrations of each coexistence outcome).

201 **Results**

Coinvasion of shared mutualist with competitors promotes their regional coexistence

204 We first ran simulations (Set 1) with coinvasion of F_1 and F_2 in the absence
of P . We found that for all possible combinations of competition coefficients
 (τ_{12}, τ_{21}) pairs, species F_2 always excluded F_1 across the landscape resulting in
207 its complete extinction. Due to F_1 's increased dependence of partner relative
to F_2 , its growth and competitive effect on F_2 was low leading to its extinction.
We then ran these coinvasion simulations in the presence of spreading
210 P . We found that P 's presence altered coexistence outcomes (Figure 3). When
 $\tau_{12} \gg \tau_{21}$, we find similar to earlier that F_2 locally and spatially excludes F_1 .
On the other hand, when $\tau_{12} \ll \tau_{21}$, F_1 wins and excludes F_2 across its range.
213 Here, F_1 receives more benefits from P than F_2 and this, combined with its bet-
ter competitive ability excludes F_2 . When both species are weak competitors
 $\tau_{12} \approx \tau_{21} \in [0, 0.07]$, locally coexistence due to P providing unequal buffers to
216 each competitor's growth. Finally, when $\tau_{12} \gtrapprox \tau_{21}$, we observe regional coexis-
tence where F_2 always outcompetes F_1 in regions of common occurrence but F_1
spreads faster across space thereby partially escaping competition from F_2 . P
219 provides benefits which increases F_1 's growth resulting in greater dispersal and
increased speed. Thus, mutualisms promote both local and regional coexistence
between competitors in scenarios where exclusion might have occurred in their
222 absence.

Increasing mutualist dispersal leads to qualitatively different coexistence outcomes in different competitive environments

225

Next, we relaxed the assumption that all species had the same dispersal kernel and ran simulations to identify how mutualist dispersal ability could shape spatial coexistence outcomes (Set 2). Differences in dispersal ability between mutualistic partners of different taxonomic groups (for e.g. plant and fungi) have been well documented and can vary to multiple orders of magnitude (Galante et al., 2011; Peay et al., 2012). We modified the variance of P's dispersal kernel (σ_P^2) from 0.001 (extremely low dispersal relative to competitors) to 0.099 (extremely high dispersal ability) and studied its effect on spatial coexistence of the competitors by measuring the overlap of their ranges. We found that when competitive abilities of both species were intermediate or high, increasing mutualist dispersal resulted in sharp transitions between outcomes from exclusion of more dependent species (F_1) to less dependent species (F_2) with a narrow region of intermediate values of σ_P^2 resulting in regional coexistence (Figure 4).

On the other hand, when F_1 and F_2 were weak competitors, there was a slight increase in ρ with increasing σ_P^2 but neither competitor excluded the other. Rather, increasing σ_P^2 simply altered which species dominated at the edge of the co-invading community's range but maintained local coexistence at the core of their ranges. Determining whether competition led to regional coexistence or local coexistence with one dominant species at the range edge required comparing the observed ρ for these simulations with expected ρ s from either of the aforementioned coexistence outcomes (Appendix S2: Figure S1).

Differences in competitive ability result in different coexistence outcomes of the competitors with symmetric kernels

²⁴⁹ In our previous result, we found that spatial coexistence was influenced by P's dispersal as well as overall strength of competition between F_1 and F_2 . Here, we relaxed the assumption that F_1 and F_2 were equivalent competitors
²⁵² and explored how differences in competitive ability between F_1 and F_2 could influence coexistence outcomes (Figure 5 a-c). We chose to study these outcomes for three different values of dispersal for P (i.e. $\sigma_P^2 = 0.01, 0.05, 0.075$) (Set 3).

²⁵⁵ We found that results greatly varied based on F_1 and F_2 's relative competitive ability. When P's dispersal was slower than the competitors ($\sigma_P^2 < \sigma_{F_1}^2 = \sigma_{F_2}^2$), there were three possible outcomes. When $\tau_{12} > \tau_{21}$, F_2 excluded F_1 across space due to its lower dependence on P for growth and its relatively equal (if not greater) competitive ability to F_1 . When competition was weak i.e. ($\tau_{12} \approx \tau_{21} \in [0, 0.07]$), F_2 locally coexisted with F_1 yet excluded it at F_2 's range edge. However, when $\tau_{12} < \tau_{21}$, we find that both species regionally coexist. In these simulations, F_2 spreads faster than F_1 due to lesser dependence on the slow spreading P but get excluded behind their range front by F_1 . Here, F_2 is not a strong competitor and F_1 growth is buffered by P.
²⁶⁴

When P's dispersal is equal to the competitors ($\sigma_P^2 = \sigma_{F_1}^2 = \sigma_{F_2}^2$), we see a shift in coexistence. While we still see F_2 excluding F_1 when $\tau_{12} \gg \tau_{21}$, ²⁶⁷ we also see regions where F_1 excludes F_2 when $\tau_{12} \ll \tau_{21}$. When competition is very low, both species locally coexist across their ranges while for slightly higher values of τ_{21} , local coexistence with F_1 dominance at its range edge is observed. The zone of regional coexistence shrinks to only occupy regions where $\tau_{12} \gtrsim \tau_{21}$ or $\tau_{12} \lesssim \tau_{21}$. Interestingly, these are qualitatively different forms of regional coexistence. In the former, F_1 is present on the edge of the invasion but F_2 outcompetes F_1 behind the expansion front while the reverse pattern is
²⁷³

observed in the latter case.

When P's dispersal is greater the competitors ($\sigma_P^2 > \sigma_{F_1}^2 = \sigma_{F_2}^2$), there was
another abrupt shift in the coexistence outcomes. When $\tau_{12} < \tau_{21}$, as opposed
to regional coexistence (seen above), we find F_1 excluding F_2 . Although we find
cases where local and regional coexistence arise, we do not find scenarios where
 F_2 excludes F_1 .

Dispersal-Dependence tradeoffs increase zone of regional coexistence of the competitors

Finally, we incorporate asymmetries in the dispersal kernels of the competitors
that arise from adaptations correlated with degree of dependence on P and
perform simulations for different dispersal abilities of P (Set 4). Here, too
we see an abrupt transition in coexistence outcomes based on P's dispersal
ability (Figure 5 d-f). When P's dispersal was slower than the competitors
($\sigma_P^2 < \sigma_{F_2}^2 < \sigma_{F_1}^2$), we see either local coexistence with F_2 dominance, F_1
exclusion, or regional coexistence similar to the case when the competitors'
dispersal kernels were similar (Figure 5a). However, when P's dispersal ability
was intermediate ($\sigma_{F_1}^2 > \sigma_P^2 > \sigma_{F_2}^2$), there is a shift in coexistence outcomes
where F_1 excludes F_2 when $\tau_{12} < \tau_{21}$ but the competitors regionally coexist
when F_2 is the better competitor with local coexistence (with F_1 dominance)
occurring when both τ_{12} and τ_{21} were low. This pattern was recapitulated even
as we increased P's dispersal ability i.e. ($\sigma_P^2 > \sigma_{F_1}^2 > \sigma_{F_2}^2$). Thus, we find
that differential competitor dispersal creates a sharper transition between the
coexistence patterns that are generated with increasing σ_P^2 .

Discussion

There is growing theoretical and empirical evidence of the role mutualisms have in shaping the outcomes of local coexistence between competitors as well as shaping the invasion and range expansion speeds of participating species (Umbanhowar and McCann, 2005; Siefert et al., 2019; Lewis et al., 2002; Nuñez et al., 2009; Lopez et al., 2021). However, we have yet to completely understand how these two phenomena interact to shape the spatial coexistence of competing, dispersing species. In this paper, we sought to understand how the mutualisms shaped the coexistence of two coinvasive competitor species.

Our model goes beyond past theory to consider several species invading together in line with growing biological evidence of coinvasion seen across a number of aquatic and terrestrial taxa (Johnson et al., 2009; Preston et al., 2012; Kuebbing and Nuñez, 2015; Jackson, 2015; Carrasco et al., 2018). When these coinvasive species are mutualists, the invasion meltdown hypothesis posits that species invasion is accelerated. Successful invasions can then result in downstream ecosystem impacts on native community structure and interactions (Prior et al., 2015; Christian, 2001; Rudgers and Clay, 2008). However, multi species coinvasions often include other biotic interactions, which are often negative (Kuebbing and Nuñez, 2015; Jackson, 2015). By incorporating these additional negative interactions in our model, we find first that variation in mutualism traits i.e. dependence engenders both local coexistence (by buffering against competitive exclusion of weaker species at a location in space) as well as regional coexistence (by providing benefits which in turn increase growth and range expansion speeds of the more dependent species). We also find that competition acts alongside species spread resulting in the constriction of the range size of the poorer competitor. In the absence of a mutualist, invasion into a region where the better competitor is present is not possible. Competition is

³²⁴ a common mechanism invoked to generate species range borders (Yodzis, 2013;
Fowler and Levin, 1984; Case and Taper, 2000). However, unlike past models
³²⁷ with only antagonistic interactions, co-invasion with the mutualist and regional
coexistence by the weaker competitor if it is a more dependent species. This
is due to differential benefits obtained by the competitors as well as mutualism
mediated seed trait evolution (modelled here as dispersal-dependence tradeoffs).

³³⁰ We next find that the dispersal ability of the mutualist influences the range
of possible coexistence outcomes between the competitors. We find that increasing
dispersal ability of P results in a transition from the more dependent to the
³³³ less dependent species getting excluded when competition between F_1 and F_2
is roughly equivalent and interspecific reduction of growth rates are high. On
the other hand, when competition is weak ($\tau_{12}, \tau_{21} < 0.05$), increased dispersal
³³⁶ of P does not change patterns of coexistence but alters which species dominates
at the range edge (Figure 4). Greater dispersal of P leads to mutualists being
present at high densities at a new habitat prior to either competitor reaching it.
³³⁹ We also observe that differences in competitive ability between F_1 and F_2 also
lead to different coexistence patterns for a fixed value of P's dispersal ability.
Thus, we find that mutualism, competition, and dispersal interact to generate
³⁴² three qualitatively different types of coexistence outcomes based on whether
the mutualist is faster, slower, or similar in dispersal ability to the competi-
tors (Figure 5). We also find that incorporating dispersal-dependence tradeoffs,
³⁴⁵ sharpens the transition between the coexistence patterns that are generated by
P's dispersal ability (Figure 5d and 5e).

³⁴⁸ The absence or reduced density of mutualist partners has been shown to to
slow down and hinder species range expansions paticularly in plant-microbial in-
teractions (Wilkinson, 1998; Stanton-Geddes and Anderson, 2011; Nuñez et al.,
2009). However, in the presence of a competitor, our model predicts that more

dependent species are not just slowed down (due to lower intrinsic growth rates) but more likely to go extinct during the invasion process (Figure 3). This is in contrast to scenarios where the mutualist is a far better disperser than the competitors, where the more dependent species (F_1) benefits more than its competitor in expanding into ranges its partner is present in. Here, the less dependent species is more likely to be outcompeted even in cases where it is a better competitor (i.e. $\tau_{12} > \tau_{21}$). This is because, F_1 spreads faster and grows to higher densities before F_2 can invade these regions. Evidence for more dependent plant species showing greater invasive ability has been shown in pine-EM fungal mutualisms (Moyano et al., 2021, 2020). Hence, F_2 is excluded through priority effects mediated by F_1 's significantly higher densities in regions F_2 is newly invading to. Our model also predicts that the set of coexistence (or exclusion) outcomes is more diverse when the dispersal ability of the mutualist is equal to the competitors (Figure 5). Here, the mutualist is present at low densities (similar to the competitors) at their range front and all three species are in the transient phase of their growth. This transience allows for several equilibria to be accessed based on the species' relative competitive abilities and mutualist dependence.

Our model could also be interpreted in the context of mutualism trait evolution during invasion. By considering F_1 and F_1 as two variants (within a species) with different degrees of investment into mutualism traits, our results identify conditions during coinvasion in which mutualism should be selected for (i.e. F_1 dominance across space). On one hand, selection could favour increasing dependence on mutualism during invasion if these interactions provide F_1 a fitness advantage over the less dependent (F_2) conspecific invading with it or being present in the native community (Rodríguez-Echeverría et al., 2009; Rodríguez-Echeverría et al., 2012). On the other hand, selection for lesser

³⁷⁸ mutualism dependence could arise particularly in the presence of competitors,
reduced mutualist availability in novel habitats or life-history tradeoffs (Shelby
et al., 2016; terHorst et al., 2018; Seifert et al., 2009). Indeed, evolution during
³⁸¹ invasion could lead to mutualism breakdowns between plant and symbiont and
result in more exploitative symbiont phenotypes (Wendlandt et al., 2021).

³⁸⁴ Although not presented explicitly, our model implicitly predicts outcomes
of invader-native plant competition in the presence of a common mutualist.
Such competitive interactions are observed globally with outcomes of these in-
teractions potentially modifying future communities through soil legacy effects
³⁸⁷ (Reinhart and Callaway, 2006; Fahey and Flory, 2022; Van der Putten et al.,
2010). In our model, scenarios where $\sigma_P^2 > \sigma_{F_1}^2 > \sigma_{F_2}^2$ are equivalent to F_2
invading a native plant-fungal mutualism and outcomes of local and regional
³⁹⁰ coexistence should proceed similar results presented in Figure 5c (or 5e).

³⁹³ There are several possible extensions to our model one of which is relax-
ing the assumption that the landscape across which species spread is homoge-
neous. This implies our model does not generate coexistence patterns that arise
due spatial heterogeneity such as spatial storage effects (Chesson, 2000; Ama-
rasekare, 2003). Abiotic variation across space is also an important generator
³⁹⁶ of dispersing species' range limits. In our model, range limits are generated
purely through competition, a commonly observed biotic factor generating lim-
its (Fowler and Levin, 1984; Case and Taper, 2000; Case et al., 2005). Further,
³⁹⁹ mutualisms can themselves be context dependent and vary across space in how
much benefits are exchanged between species (Cunning and Baker, 2014; Drew
and King, 2022; Chamberlain et al., 2014). We aim to extend our work to focus
⁴⁰² on the effects of spatial variation in mutualistic benefit exchange which can then
shape coexistence outcomes of invasive species.

In conclusion, we show that extending models of co-invasion to include mul-

⁴⁰⁵ tiple biotic interactions can give rise to an array of local and regional coexistence outcomes through both population dynamic effects and modification of dispersal abilities. Particularly, even in the absence of stable equilibria between
⁴⁰⁸ competitors locally, we find conditions where coexistence between competitors occurs globally due to unequal acquisition of mutualist benefits and dependence-dispersal tradeoffs. We hope the theoretical framework presented here fosters
⁴¹¹ further research into the role of mutualism as an important biotic driver of local and regional coexistence of co-invading communities.

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Figures

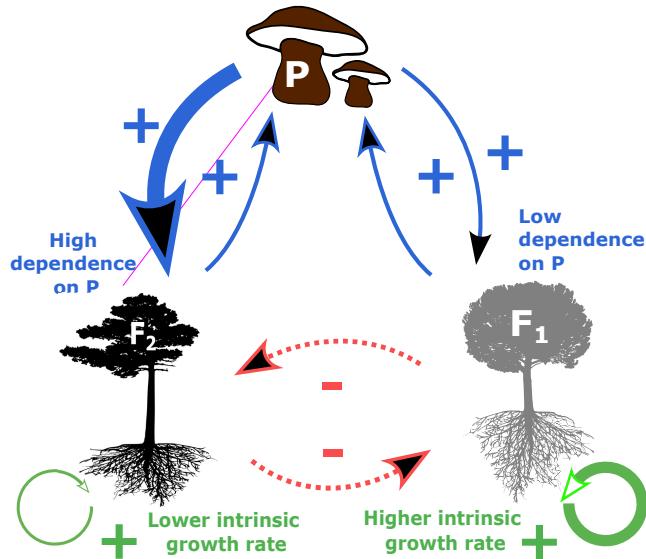


Figure 1: Schematic representation of interactions in the model. Species F_1 and F_2 are the focal competitor species (congeneric plant species) with shared mutualist P (fungal partner) where all species disperse and coinvoke new territory. F_1 has greater dependence on mutualist partner P (in blue) but also lower intrinsic growth rate (in green) than F_2 . Interspecific competition is denoted by dotted red arrows

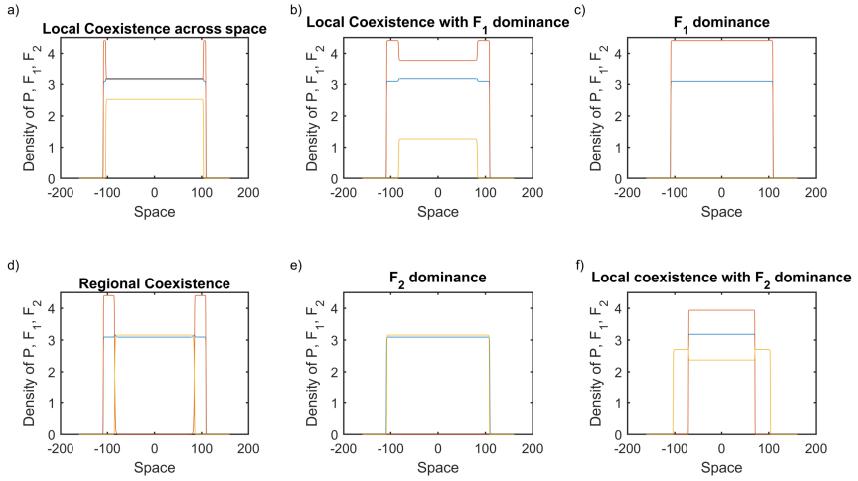


Figure 2: Illustration of different qualitative outcomes observed. All figures are density versus space plots with species P in blue, species F_1 in orange and F_2 in yellow. Subpanel a) shows local coexistence of competitors, b) shows local coexistence with exclusion of F_2 by F_1 at their range edges, c) shows competitive exclusion of F_2 across space, d) shows regional coexistence of both species (but not local coexistence), e) shows local coexistence with F_2 excluding F_1 at the edges, and f) shows F_2 competitively excluding F_1 across all space. Parameter values used for these simulations are: $r_i = 0.3 (i = P, F_1, F_2)$, $\delta_{F_1} = 0.6$, $\delta_{F_2} = 0.4$, $\sigma_{F_1}^2 = \sigma_{F_2}^2 = \sigma_P^2 = 0.05$ ($\sigma_P^2 = 0.02$ for subpanel f), $(\tau_{12}, \tau_{21}) = (0.05, 0.02), (0.05, 0.05), (0.05, 0.15), (0.15, 0.05), (0.3, 0.2), (0.02, 0.02)$

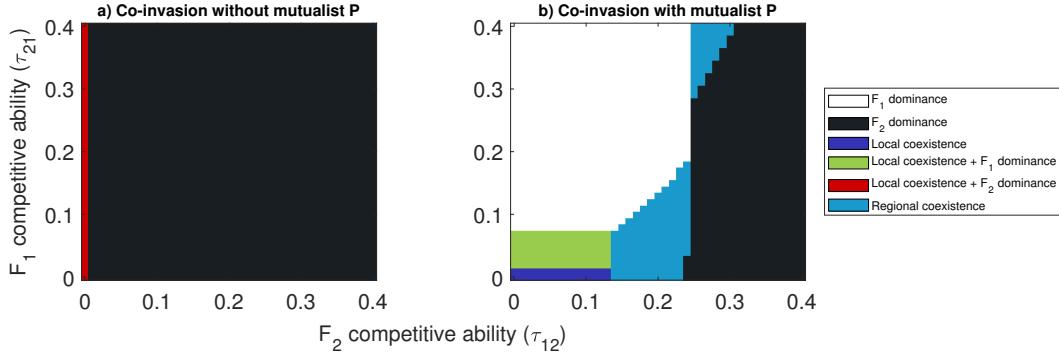


Figure 3: Coexistence of competitors of differing dependence arises in the presence of a co-invading mutualist. Panel a) shows competitive exclusion of the more dependent F_1 without a mutualist while b) shows different possible coexistence outcomes between the competitors in the presence of P for differing relative competitive abilities. Parameters: $r_i = 0.3(i = P, F_1, F_2)$, $\delta_{F_1} = 0.6, \delta_{F_2} = 0.4, \sigma_{F_1}^2 = \sigma_{F_2}^2 = \sigma_P^2 = 0.05$ (only for b)

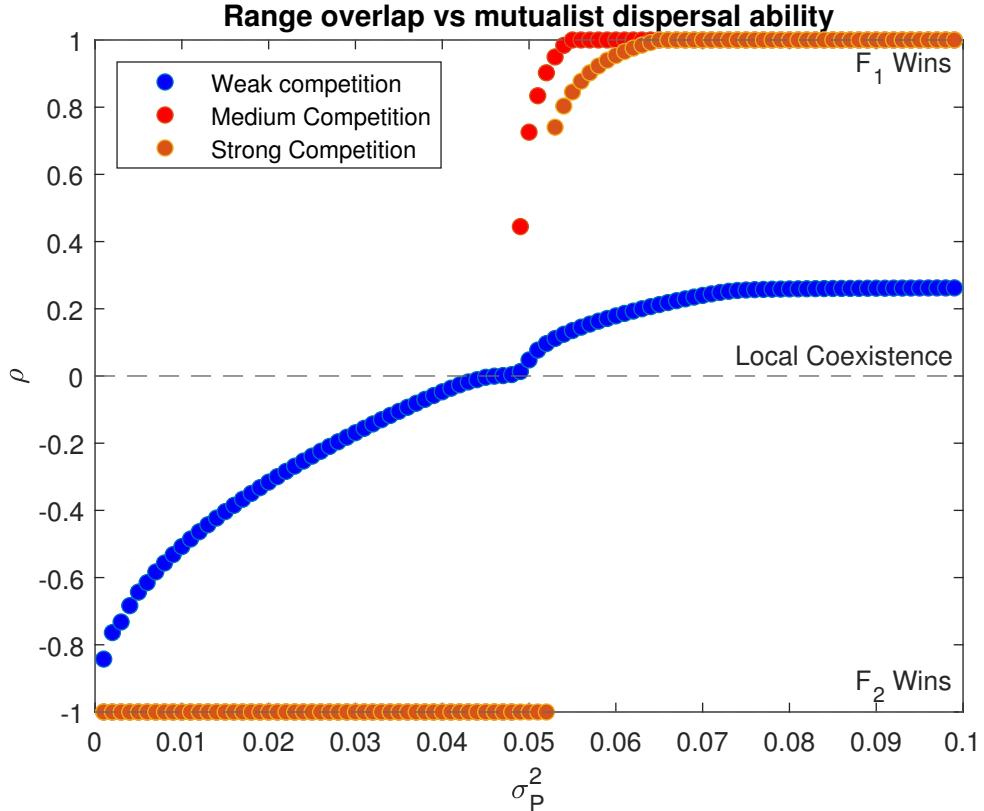


Figure 4: Increasing mutualist dispersal ability alters coexistence type in qualitatively different manners based on strength of competition. When strength of competition is weak (blue), spatial coexistence outcome (denoted by ρ , the range overlap) shifts from F_1 exclusion to local coexistence with F_1 dominance. When the competition strength is intermediate (red) or strong (orange), there is more abrupt shift from F_1 exclusion to F_2 exclusion with regions of regional coexistence for small regions of σ_P^2 . Parameters chosen: $r_i = 0.3 (i = P, F_1, F_2)$, $\delta_{F_1} = 0.6$, $\delta_{F_2} = 0.4$, $\sigma_{F_1}^2 = \sigma_{F_2}^2 = 0.05$ ($\tau_{12}, \tau_{21} = (0.02, 0.02), (0.2, 0.15), (0.37, 0.29)$) for weak, intermediate, and strong competition respectively.

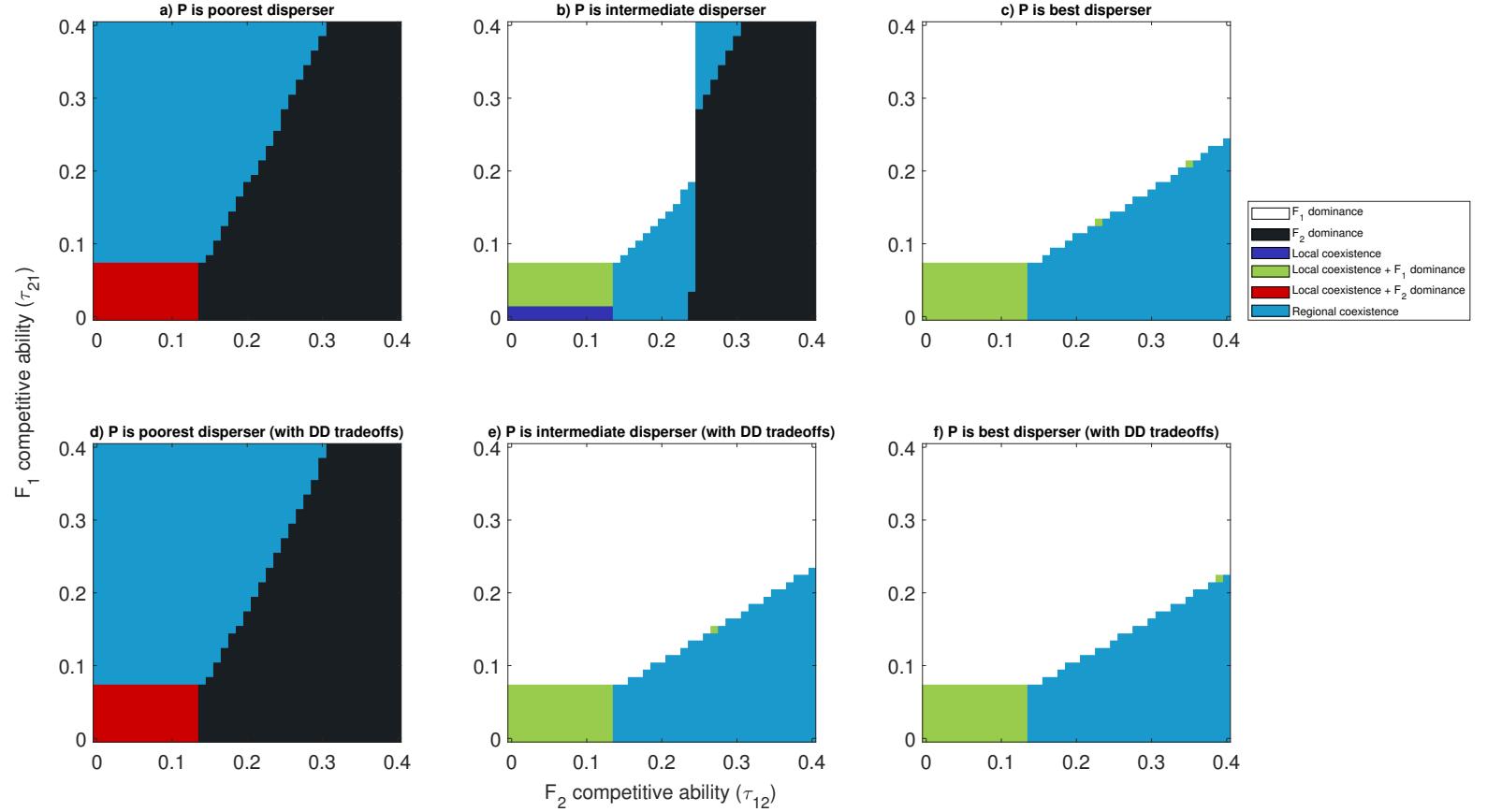


Figure 5: Set of coexistence outcomes shaped by mutualist's dispersal ability and asymmetry in competitors' dispersal kernels arising from dependence-dispersal tradeoffs. In subpanels a), b), and c), we assume both F_1 and F_2 have symmetric dispersal kernels ($\sigma_{F_1}^2 = \sigma_{F_2}^2$) and in d), e), and f) assume F_1 and F_2 have asymmetric dispersal kernels ($\sigma_{F_1}^2 \neq \sigma_{F_2}^2$). We consider P to have lower ($\sigma_P^2 < \sigma_{F_1}^2, \sigma_{F_2}^2$), similar ($\sigma_P^2 \approx \sigma_{F_1}^2, \sigma_{F_2}^2$), and greater ($\sigma_P^2 > \sigma_{F_1}^2, \sigma_{F_2}^2$) dispersal ability than the competitors. When competitors are asymmetric dispersers, only two outcomes are observed. Parameters: $r_i = 0.3(i = P, F_1, F_2)$, $\delta_{F_1} = 0.6$, $\delta_{F_2} = 0.4$. For first row: $\sigma_P^2 = (0.01(a), 0.05(b), 0.075(c))$; For second row: $\sigma_{F_1}^2 = 0.03$, $\sigma_{F_2}^2 = 0.02$, $\sigma_P^2 = 0.01(a), 0.025(b), 0.075(c)$.

Tables

Table 1: Model parameters and values used in simulations

Symbol	Description	Simulation values
P	Population density of species P	...
F_1	Population density of species F_1	...
F_2	Population density of species F_2	...
τ_{ij}	Competition coefficient of species F_j on F_i ($i,j = 1,2; i \neq j$)	$0 \leq \tau_{ij} \leq 0.4$
δ_{F_1}	Dependence on mutualism for growth of species F_1	0.6
δ_{F_2}	Dependence on mutualism for growth of species F_2	0.4
r_i	Intrinsic growth rate of species i ($i = P, F_1, F_2$)	0.3
α_{iP}	Mutualist benefits provided by species P to F_i ($i = F_1, \text{ or } F_2$)	0.5
α_{Pj}	Mutualist benefits provided by species F_i to P ($j = F_1, \text{ or } F_2$)	0.01
h_i	Half saturation constant of benefits provided to species i ($i = P, F_1, F_2$)	0.3
d_i	Death rate of species i ($i = P, F_1, F_2$)	0.1
σ_i^2	Variance of dispersal kernel for species i ($i = F_1, F_2$)	0.05
σ_P^2	Variance of dispersal kernel for species P (low, intermediate, high)	(0.01, 0.05, 0.1)