When Does Mutualism Offer a Competitive Advantage? A Game-Theoretic Analysis of Host-Host Competition in Mutualism

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Abstract

Questions: Can resource-resource trade mutualism offer a competitive advantage to plants? If so, what are the conditions that give mutualism an advantage especially with regard to the size of the neighborhood?

Hypothesis: We hypothesized that mutualism could offer a competitive advantage if the benefits outweighed the costs. We also hypothesized that this competitive advantage could lead to coexistence between mutualist and non-mutualist strategies within the same population. We also hypothesize that local neighborhood size (the number of competitors at a given moment) would change this response, though the specific direction of change was unclear to us.

Method: We created an evolutionary game theoretic model in which a plant could either be a mutualist or non-mutualist that incorporated nutrients freely available to the plant, nutrients obtained only through mutualism with microbes, the cost of producing roots, the cost of trade with microbes, and neighborhood size. We sought ESS solutions as defined by the Nash equilibrium criterion.

Key Assumptions: 1) Costs and benefits are fixed for all plants. 2) Freely available nutrients are equally shared between all competing plants in a local neighborhood. 3) Microbially obtained nutrients are shared equally between mutualistic plants in the local neighborhood.

Conclusion: We found that mutualism could offer a competitive advantage if the net benefit was positive. Coexistence between mutualist strategies in our model happens because of competition between mutualists over the microbially available nutrient. Coexistence was more likely with greater neighborhood size but at the expense of mutualist fixation.

Introduction

Mutualisms are an important aspect of plant ecology. The non-motile nature of plants means that they frequently rely on other organisms to carry out functions such as seed dispersal, pollination, and nutrient acquisition on their behalf (Howe & Westley, 1990). Two key nutrient acquisition strategies for plants include microbial symbioses with mycorrhizae (in 80% of plant species and 92% of plant families (Simon et al., 1993; Wang & Qiu, 2006)), and the associations with symbiotic nitrogen-fixing bacteria (in a smaller subset of families (de FARIA et al., 1989; Sprent, 2005)). In these mutualisms, the partners trade resources, that is, the plants trade carbon in the form of carbohydrates and lipids while receiving nutrients like nitrogen and phosphorous (Hawkins et al., 2000; Hodge et al., 2001; Leigh et al., 2009; Sawada et al., 2003; Sessitsch et al., 2002). Across the plant kingdom, the commonality of partnering with microbial mutualists implies that doing so often offers a fitness benefit to plants (Hartnett et al., 1993). However, it is also known that the costs and benefits of mutualism depend upon ecological and evolutionary factors such as nutrient availability (nitrogen and phosphorous) and genotype (Bronstein, 2009; Chamberlain et al., 2014; Heath & Tiffin, 2007; Lu & Hedin, 2019; Peng et al., 1993). These variations in benefits can have knock-on effects at larger scales leading to the variation in the presence or absence of the mutualist partnership among lineages (de FARIA et al., 1989; Maherali et al., 2016; Werner et al., 2015). In this paper, we sought to determine how various ecological, evolutionary, and environmental contexts can promote or exclude the microbial mutualistic partnership and ultimately lead to its evolution in a species.

To understand how ecological context determines evolution of the microbial mutualist partnership, we turned to mathematical analysis. Mathematical analyses have been widely used to understand the evolution and persistence of mutualism (Akçay & Roughgarden, 2007; Akçay

& Simms, 2011; Ferriere et al., 2002; Hoeksema & Kummel, 2003; Noë & Hammerstein, 1995; West et al., 2002). Typically, the focus of these models has been on the stability and maintenance of interactions between partners, the host and the symbiont, with reasons such as partner selection (Akçay & Roughgarden, 2007; Akçay & Simms, 2011; West et al., 2002) and spatial structure given (see (Wilson et al., 2003) for a model of seed dispersal). That said, intraspecific individual competition is a necessary component of evolution by natural selection as the adaptations of more fit individuals become common within the population (Darwin, 1859). As such, mutualism must also offer a competitive advantage to a host if it is to evolve (Jones et al., 2012). We wanted to explore how host-host competition affects the evolution of mutualism. To do so, we turned to evolutionary game theory. Originally developed to understand animal behavior, evolutionary game theory is a mathematical tool that examines how strategies perform in terms of fitness against other interacting strategies (Brown, 2016; Geritz et al., 1998; Smith & Price, 1973). It has been applied widely across taxa; for plants, it has been used to understand properties such as defense against herbivory and biomass allocation with competition (Augner et al., 1991; T. J. Givnish, 1982; Thomas J Givnish, 1995; McNickle et al., 2016). Recently, evolutionary game theoretic host-host competition has been used to understand the global distribution of nutrient acquisition strategies worldwide (Lu & Hedin, 2019). Viewing the partnership with microbes (and its complement, non-partnership) as strategies in an evolutionary game should allow us to narrow our focus to just the competitive interactions between hosts and the ecological and environmental contexts that benefit one strategy over the other.

To this end, we created a simple 2×2 matrix game how the ecological contexts of nutrient availability, frequency of alternate strategies, and competitor density may or may not offer an intraspecific competitive advantage to a plant that partners with a microbe to obtain

nutrients. In our model, we assume that using mutualism itself is a strategy, the equivalent of a functional trait (Violle et al., 2007), where a plant can either be a non-mutualist and only acquire benefits from freely available nutrients in the soil or be a mutualist and receive additional benefits from microbially derived nutrients. All plants must pay a cost to acquire the freely available nutrients with mutualists paying an additional cost for the microbially derived nutrients. Besides these four parameters, we also included competitor number as a parameter to see how density-dependence may influence selection of strategy (Clarke, 1972). We analyzed our game for coexistence of mutualist and non-mutualist strategies and the fixation of either strategy; we then discuss our results mean for the evolution of and variation in mutualist strategies in plant-microbe systems.

Model Analysis

Competition with one plant

In our model, we start out by assuming there are two pools of nutrients available to a plant, one that is freely available AN and one that is only available through microbial mutualism MN. These nutrients provide fitness benefits of B_{AN} and B_{MN} respectively to a plant. Some proportion of the population are genotypes of plants have the ability to partner with microbial mutualists, while the remainder are made up of genotypes that cannot (we hereafter refer to those genotypes as mutualists and non-mutualists respectively). Mutualist plants get the fitness benefit of the freely available nutrients and the microbially obtained nutrients while non-mutualists only get the benefit of freely available nutrients. Mutualists however have to pay an additional fitness cost through trade and other mechanisms (e.g. allocation of biomass to nodules) represented by c_t to obtain the microbial nutrients. All plants can also produce roots to obtain the AN type of nutrient at a cost of c_r. Finally, we begin by assuming only two competing plants with equal

competitive ability. From these assumptions, we construct the following fitness matrix for each type of plant:

		Resident	
		Non-Mutualist	Mutualist
Focal Invader	Non-Mutualist	$\frac{B_{AN}}{2} - c_r$	$\frac{B_{AN}}{2} - c_r$
	Mutualist	$\frac{B_{AN}}{2} - c_r + B_{MN} - c_t$	$\frac{B_{AN}}{2} - c_r + \frac{B_{MN}}{2} - c_t$

Since all individuals have access to freely available nutrients and must produce roots, all individuals get a net fitness benefit of $\frac{B_{AN}}{2} - c_r$ regardless of strategy due to competition over the same pool of resources. If a mutualist competes with a non-mutualist, the mutualist gets the full benefit of the microbially obtained nutrients while paying the cost of trade $B_{MN} - c_t$; however, when competing with another mutualist, both have to share the microbially obtained nutrients and have a net benefit of $\frac{B_{MN}}{2} - c_t$.

Since all individuals receive the exact same fitness benefit from the freely available nutrient and pay the exact same cost for the roots ($\frac{B_{AN}}{2} - c_r$), these terms can be removed to arrive at the simpler payoff matrix below:

		Resident	
		Non-Mutualist	Mutualist
Focal Invader	Non-Mutualist	0	0
	Mutualist	$B_{MN} - c_t$	$\frac{B_{MN}}{2} - c_t$

From this simplified matrix, we can quickly arrive at conditions for fixation of mutualist or non-mutualist varieties. Specifically, if the cost of trade outweighs the total benefit of microbially obtained nutrients $c_t > B_{MN}$, then mutualist do worse, and non-mutualism is the dominant strategy (Fig 1a,d). This is intuitive and true of any trait: when the fitness costs outweigh the benefits, no trait should be favoured by natural selection. However, if the benefits

of microbially obtained nutrients after competition with other mutualist plants in the population is greater than the cost of trade $\frac{B_{MN}}{2} > c_t$, then mutualists always do better and so become the dominant strategy (Fig 1 c,f). Interestingly, the difference between B_{MN} and $\frac{B_{MN}}{2}$ creates a region of the fitness landscape where mutualists and non-mutualists can coexist within a population. Indeed, if the total benefit of microbially obtained nutrients is greater than the cost of trade but the benefit of microbially obtained nutrients under competition is lower than the cost of trade (i.e. $B_{MN} > c_t > \frac{B_{MN}}{2}$), then both genotypes coexist in the same shared space (Figure 1b,e). Our analysis also allows us to reveal the equilibrium proportion of mutualists in each population given by $x^* = 2\left(1 - \frac{c_t}{B_{MN}}\right)$ (Figure 2). This coexistence of different strategies is proven to be a stable equilibrium (Figure 1e).

Competition with multiple plants

Above, we assumed that plants competed with only one other individual at any given time. While the non-motile nature of plants means that they compete on local spatial scales, this neighborhood of competitive interactions is more often than not greater than one neighbour. This can be especially true when resources are scare and individuals have to draw from the same pool of resources. Having more competitors means that individuals should take up a smaller share of the resources. This is especially compounded for the microbially available nutrients for which the share will also depend on the frequency of mutualists in the neighborhood, and ultimately the frequency of mutualists in the population. Therefore, we next modify our game to have competition among any number of plant individuals in their local neighborhood. We can generalize our fitness matrix such that

	Resident Neighbourhood (n)		
	Purely Non-Mutualist	Mixed Neighbourhood	Purely Mutualist

Focal Invader	Non-Mutualist	$\frac{B_{AN}}{n+1} - c_r$	$\frac{B_{AN}}{n+1} - c_r$	$\frac{B_{AN}}{n+1} - c_r$
	Mutualist	$\frac{B_{AN}}{n+1} - c_r + B_{MN} - c_t$	$\frac{B_{AN}}{n+1} - c_r + \frac{B_{MN}}{xn+1} - c_t$	$\frac{B_{AN}}{n+1} - c_r + \frac{B_{MN}}{n+1} - c_t$

where n is the number of interactions per plant, i.e., the size of their local neighborhood, and x is the proportion of mutualists in that neighborhood. Like before, fitness benefits from available nitrogen are invariant with strategy of the focal invader and neighborhood residents. Therefore, it can be subtracted from each expression to arrive at the simpler matrix below.

		Resident Neighbourhood (n)		
		Purely Non-Mutualist	Mixed Neighbourhood	Purely Mutualist
Focal Invader	Non-Mutualist	0	0	0
	Mutualist	$B_{MN} - c_t$	$\frac{B_{MN}}{xn+1} - c_t$	$\frac{B_{MN}}{n+1} - c_t$

Following from Hauert et al.(2006), we derive overall fitness of a mutualist plant to be $\frac{B_{MN}\left(1-(1-x)^{n+1}\right)}{x(n+1)} - c_t$ (see SI for derivation). Interestingly, with a larger neighborhood of interaction, the criterion for non-mutualist fixation is unchanged and still requires that the cost of mutualism without mutualist competitors must be greater than the benefits $c_t > B_{MN}$. Fixation of the mutualist strategy requires that the benefit of mutualism when solely competing with mutualist must be greater than the costs $\frac{B_{MN}}{1+n} > c_t$. We can express this later criterion in terms of cost benefit ratio, that is, $\frac{B_{MN}}{c_t} > n + 1$. From this we can see that as n increases, there needs to be more benefits relative to the costs, reducing the possibility of fixation. This means that mutualist strategy is more likely to appear in coexistence with the non-mutualist strategy with an increasing number of competitors (Figure 3). Solving for this coexistence equilibrium proportion of mutualists is significantly harder with multiple competitors, and is analytically impossible with five or more individuals, but we can arrive at the solution $x^* = \frac{1}{2}\left(3 - \sqrt{12\frac{c_t}{B_{MN}} - 3}\right)$ when there is a neighborhood of two plant competitors (see SI for the solution for three competitors).

Discussion

In this study, we wanted to see how various contexts could lead to an intraspecific competitive advantage when partnering with microbe. Many models that determine the theoretical conditions of mutualism evolution focus on the stability of the plant-microbe partnership with a focus on microbial cheating and the overall maintenance of beneficial variants (Akçay & Roughgarden, 2007; Akçay & Simms, 2011; West et al., 2002). Host-host interactions are usually not a focus in these models of evolution and are done so implicitly (Bergstrom & Lachmann, 2003) (however see (Lu & Hedin, 2019)). Our model explicitly focuses on host-host competition to see when partnering with a microbial mutualist offers a competitive advantage for a host plant. Using evolutionary game theory, we found that if the cost of mutualism outweighed the benefit, then non-mutualists would entirely exclude mutualist while if the benefit of mutualism was greater than the cost under at least some conditions, then mutualism would be a viable strategy. That evolution favours traits with higher benefits compared to costs is well known, but by expanding the neighbourhood size, we gained precise insight into how benefits and costs combined within the context of intraspecific plant competition to shape the evolution of mutualism. In particular, the evolution of mutualism was heavily influenced by the number of plants with which an individual would compete in the local neighborhood as fixation of the mutualism strategy became significantly harder with a larger local neighborhood, leading instead to coexistence between mutualist and non-mutualist strategies. Alternatively, the evolution of a non-mutualist strategy was invariant with the size of the neighbourhood (Fig 3).

Our model was simple. It assumed that the benefits and costs of obtaining nutrients were constant regardless of strategy, only changing due to competition between host plants. Because all host plants competed equally for the same freely available nutrients regardless of strategy, it

had no effect on the competitive advantage of mutualism. All that mattered was the net benefit of mutualism. This conflicts with empirical studies that have shown that increasing nitrogen availability leads to a reduction in the mutualist partnership (McCoy et al., 2018; Taylor & Menge, 2018; Vitousek et al., 1997; Weese et al., 2015) (but see (Simonsen et al., 2015)). This suggests that microbial mutualism does not simply occur as an added benefit to the plant. Instead, there must be some kind of tradeoff between using freely available resources and microbially obtained nutrients. This could be due to a fixed resource budget on the part of the plant – anywhere between 4% and 20% of total plant carbon is traded to mychorrhizal partners – (Johnson et al., 1997; Taylor & Menge, 2018; Voisin et al., 2003), varying marginal costs of investment in the sources of the nutrients, preference for the form the nutrient comes in (Falkengren-Grerup, 1995), or some combination of the three.

One interesting result of our model is that coexistence only happened if mutualists competed for the same microbially obtained nutrients. If they did not compete, then it would lead to fixation of either strategy as either would be competitively dominant. We know that some microbial based mutualisms differ in their nutrient sources. Mycorrhiza obtain their traded nutrients such as phosphorous and nitrogen from organic sources (Hawkins et al., 2000; Hodge et al., 2001; Leigh et al., 2009), a depletable resource likely shared between mutualist competitors. Rhizobia, on the other hand, get their traded nitrogen from fixing atmospheric nitrogen, an essential infinite resource that is not locally depletable (Sawada et al., 2003; Sessitsch et al., 2002). In the rhizobial mutualism, benefits may not change in the presence of competitors with the same strategy. This lack of sharing the microbially derived resources may add to the explanation as to why legumes are so dominant in mutualistic invasions compared to mycorrhizal associated plants (Castro-Díez et al., 2014; Richardson et al., 2000). If a mutualist

invader must share its resources with other competitors, it becomes limited by its own success; with more individuals using the same strategy, frequency dependence puts an upper limit on how successful an invader can be, especially with a larger neighborhood of competition. By not having to share resources, invading legumes may represent a purely dominant strategy at least when in the right conditions. That coexistence is a possibility only when resources are shared could explain variation in mutualism at higher taxa. Mycorrhizal associations are formed more widely among plant species while rhizobium mutualisms are relatively rare and largely found in specific lineages (de FARIA et al., 1989; Simon et al., 1993; Sprent, 2005; Wang & Qiu, 2006; Werner et al., 2015). There are probably numerous reasons as to why mycorrhizal associations are more common than rhizobial including but not limited to the time these mutualisms first appeared (Lu & Hedin, 2019; Maherali et al., 2016), phylogenetic inertia, the possibly lower costs of the mycorrhizal mutualism (assuming the specialized nodule structure has high initial fixed costs), the ease of deriving nitrogen from organic sources instead of the more expensive nitrogen fixation (Downie, 2014; Hoffman et al., 2014).

We note that additions to this model can be made to reveal other aspects of mutualism evolution. For example, we assumed that a plant either was a mutualist (and so fully invested in mutualism) or was not a mutualist regardless of whether net benefits were positive or negative. This is likely true at larger scales and interactions at the intertaxonomic level where entire lineages show the presence or absence of mutualism strategies (Sprent, 2005; Werner et al., 2015). However, at smaller scales of the individual and population, variation in mutualism is likely to present itself in a more continuous and quantitative fashion (Heath & Stinchcombe, 2014). The abstract nature of mathematical modelling does mean that our equilibrium proportion x^* could be understood as the proportion of mutualists in a population or community depending

on whether the interactions are thought to be intra- or interspecific respectively as well as probability of any individual using the mutualism strategy. However, different processes and properties operate on these different scales (Jablonski, 2008). At the individual level, timescales are within a lifetime, and the response is governed at the anatomy and physiology specific to that organism. At the population and community level, timescales operate over generations with variation between individuals leading to variations in fitness and reproduction which drive the response. Both scales are unique but influence each other; seeing how plasticity at the individual level drives variation at the population/community level and vice versa would certainly reveal much about the dynamics of mutualism evolution. Such a model of plasticity in the amount of trade would require more than just fitness benefits of nutrients, it would require a second resource (i.e. carbon) for the plant to trade. We suggest that this model would have to be a more process based model of plant growth that includes photosynthesis to acquire carbon for trade, as well as nutrient dynamics in soil. A number of models of plant growth with limitation from multiple essential resources exist (Craine et al., 2005; Dybzinski et al., 2011; McNickle et al., 2016; Pacala & Tilman, 1994). Future work could explore introducing some of the insights gained in our simple model into those more complex models of plant growth and allocation. In particular, it would be interesting to examine how the prevalence of mutualism in the population/community relates to individual investment in mutualism or if there are scenarios where they diverge (high prevalence with low investment and vice versa).

This simplicity of our model does offer an advantage in that it can be easily translated to an experimental setup which can be used to falsify it. One way could be through pot experiments between mutualists and non-mutualists (McNickle et al., 2020). Some plant species have loss of function mutants that allow for resource mutualisms to be turned on or off such as *DMI1* in

Medicago and *sym8* in *Pisum* (Ané et al., 2004; Balaji et al., 1994; Guinel & Geil, 2002; Markwei & LaRue, 1992). One could grow the mutants and wildtype of the same species together in the same space with different densities and nutrient limitations to see how they respond. Measures such as seed and flower number, average seed size, height, and root and shoot biomass could all be used as proxies of fitness for comparisons between wildtype and mutants (subsequent statistical analyses would have to take into account intrinsic fitness differences between wildtype and mutant as wildtype typically have greater fitness than mutants). Because these mutants do not express mutualisms with both mycorrhizae and rhizobia, comparisons between different microbial partners can also be made.

Conclusion

Our model, though simple, reveals the potential for a competitive advantage to be gained from a hosting using mutualism as a strategy, leading to mutualism's evolution and fixation in a lineage. It also points to the possibility of coexistence of mutualist strategies in a population of plants. The results elucidate the basic conditions of positive net benefit and low local competition needed for this competitive advantage, why mutualisms may be prevalent yet variable and how this prevalence and variation depends on sharing of resources. We suggest that future models begin to incorporate mutualism into process-based models of plant growth.

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Fig. 1 Evolutionary dynamics as seen through best response curves (a, b, c) and directional fields (d, e, f) for the three qualitative different scenarios. In the first scenario (a, d), the cost of mutualism outweighs any benefit, regardless of the opposing player's strategy. In the second scenario (b, e), the benefit of mutualism outweighs the cost only when the opposing player is a non-mutualist. Results are shown for $x^* = 0.5$ ($c_t = 1$ and $B_{MN} = 4$) but generally apply to $0 > x^* > 1$. In the third scenario (c, f), the benefit of mutualism outweighs the cost regardless of the opposing player's strategy. For the best response curves (a, b, c), x_i indicates the strategy played by the i-th player with greater values of x_i indicating mutualism. Solid lines are the best response for player 1 and dashed lines for player 2. As this is an intraspecific evolutionary game, the dotted line indicates the feasible set of solutions as the game occurs within a single population and therefore $x_1 = x_2$. Actual solutions for x^* are the intersection of all three lines for the three different results: (a) The best response leads to a pure Nash equilibrium of non-mutualism fixation. (b) The best response leads to a mixed Nash equilibrium with coexistence between mutualism and non-mutualist types. (c) The best response leads to a pure Nash equilibrium of mutualism fixation. Replicator dynamics show the same result (d, e, f). The only difference is that fixation of either strategy is an equilibrium but the stability of those two equilibria varies according to the cost-benefit ratio.

Fig. 2 A plot of the proportion of mutualists in a population x^* for combinations of B_{MN} and c_t. Orange-red indicates non-mutualist fixation, blue indicates mutualist fixation, and magenta indicates coexistence. Solid black lines demarcate the values of B_{MN} and c_t that separate fixation of either strategy from coexistence.

Fig. 3 Plots of how the results of our model change with the neighborhood of competitors. The colors remain the same as Figure 2. (a) Neighborhood of one competitor (b) Neighborhood of

two competitors. (c) Neighborhood of four competitors (d) Neighborhood of nine competitors. The region of fixation for the non-mutualist strategy does not change with neighborhood size. However, fixation of the mutualist strategy becomes less likely, expanding the region of coexistence between strategies when the neighborhood of competitors increases.

Fig. 1

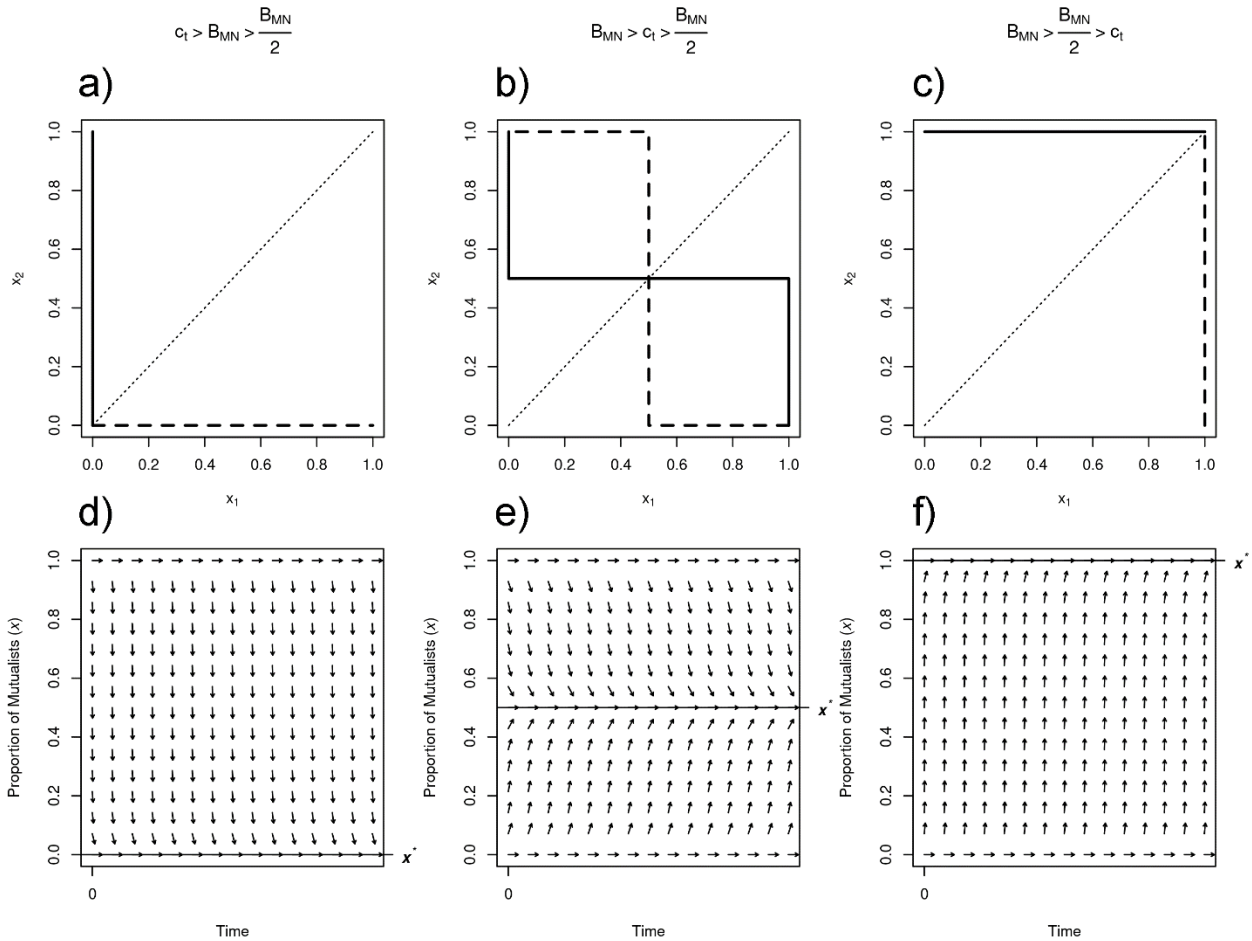

$c_t > B_{MN} > \frac{B_{MN}}{2}$
$B_{MN} > c_t > \frac{B_{MN}}{2}$
$B_{MN} > \frac{B_{MN}}{2} > c_t$
a)
b)
c)
d)
e)
f)
x_1
x_2
Proportion of Mutualists (x)
Proportion of Mutualists (x)
Proportion of Mutualists (x)
x^*
x^*
x^*
0
Time
Time
Time

Fig. 2

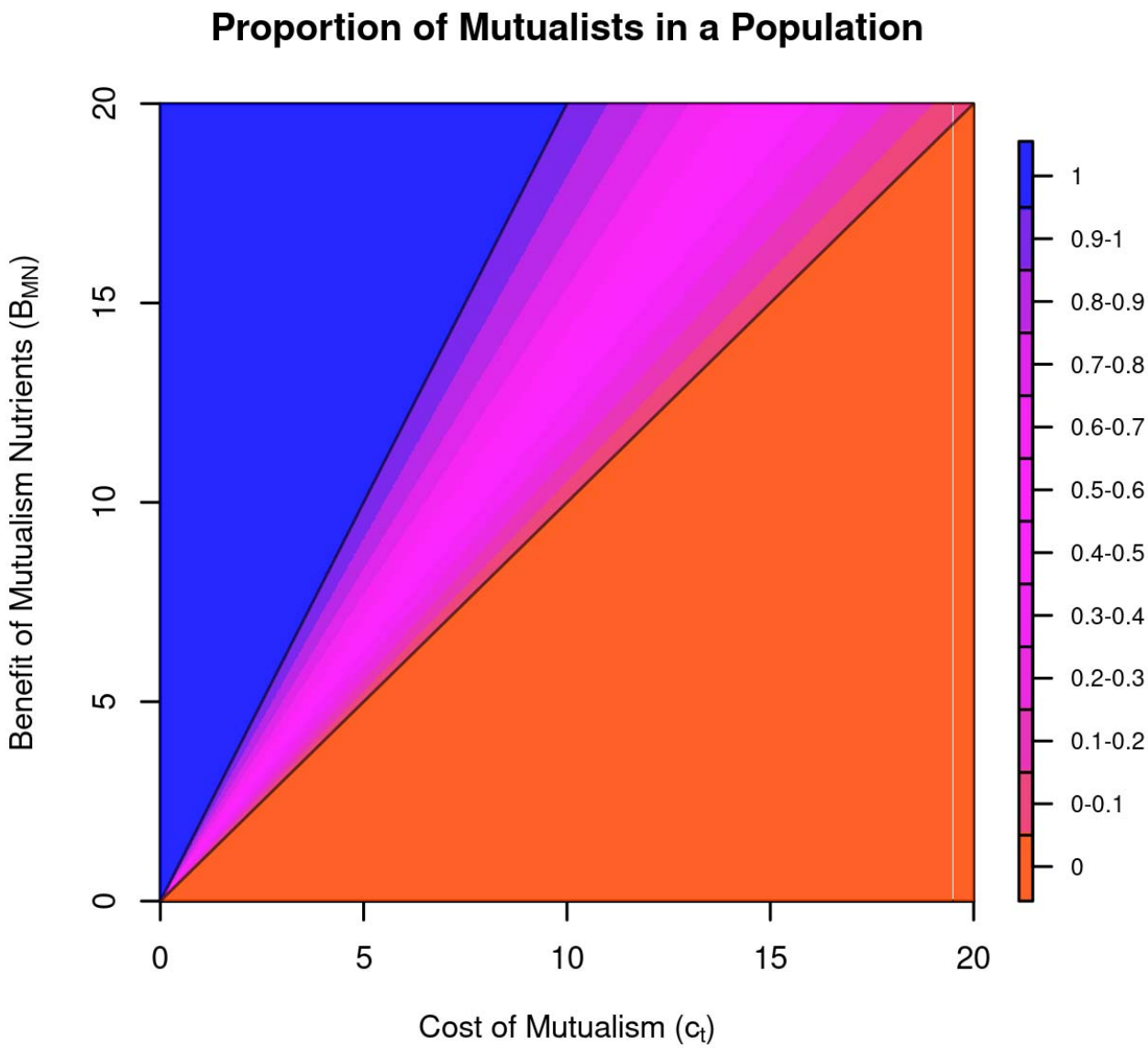
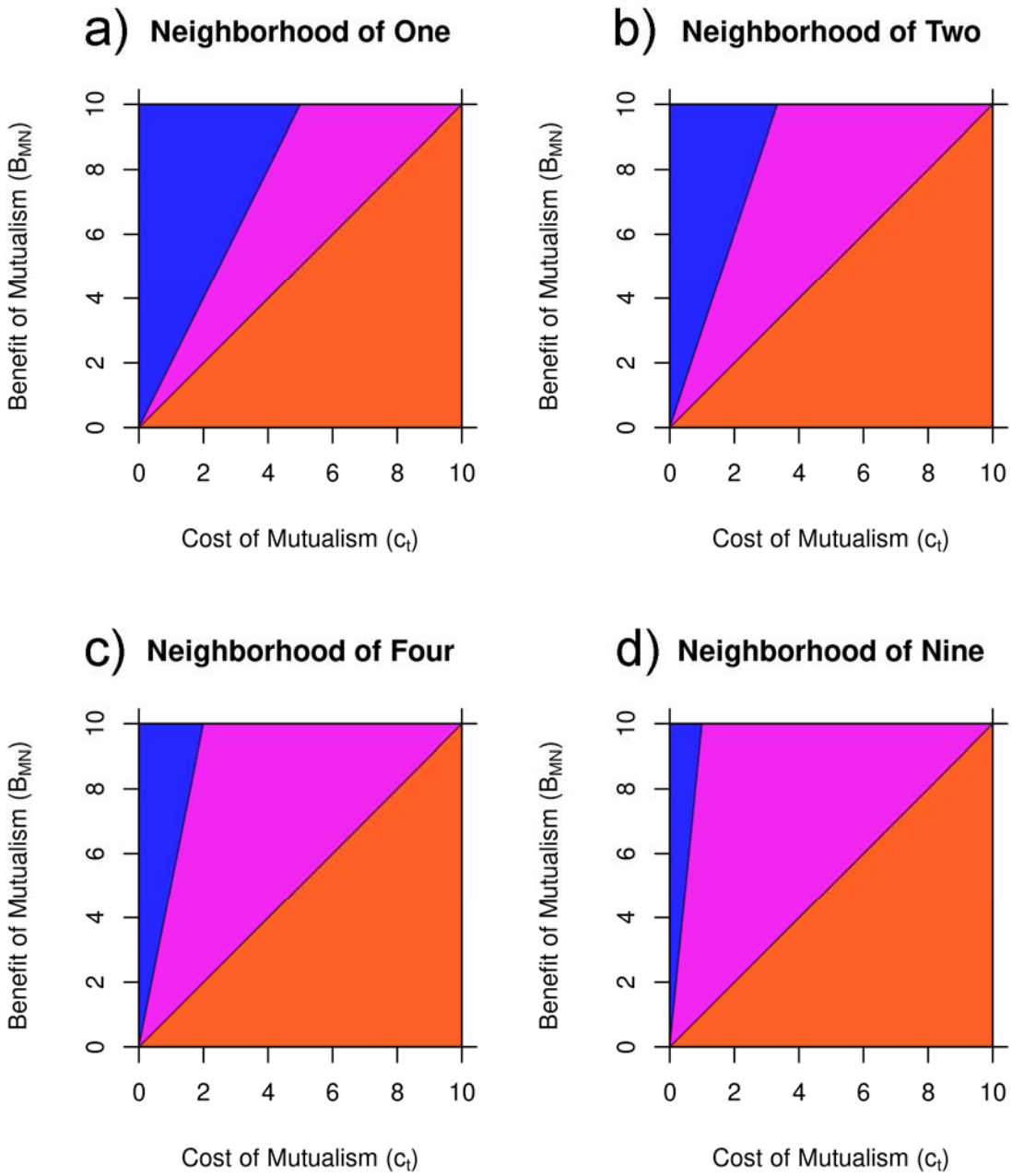

Proportion of Mutualists in a Population
Benefit of Mutualism Nutrients (B_{MN})
Cost of Mutualism (c_t)
0
5
10
15
20
1
0.9-1
0.8-0.9
0.7-0.8
0.6-0.7
0.5-0.6
0.4-0.5
0.3-0.4
0.2-0.3
0.1-0.2
0-0.1
0

Fig. 3


a) Neighborhood of One
b) Neighborhood of Two
c) Neighborhood of Four
d) Neighborhood of Nine
Benefit of Mutualism (B_{MN})
Cost of Mutualism (c_t)
0
2
4
6
8
10