

# A BIOLOGICAL MARKET ANALYSIS OF THE PLANT-MYCORRHIZAL SYMBIOSIS

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It has been argued that cooperative behavior in the plant-mycorrhizal mutualism resembles trade in a market economy and can be understood using economic tools. Here, we assess the validity of this “biological market” analogy by investigating whether a market mechanism—that is, competition between partners over the price at which they provide goods—could be the outcome of natural selection. Then, we consider the conditions under which this market mechanism is sufficient to maintain mutualistic trade. We find that: (i) as in a market, individuals are favored to divide resources among trading partners in direct relation to the relative amount of resources received, termed linear proportional discrimination; (ii) mutualistic trade is more likely to be favored when individuals are able to interact with more partners of both species, and when there is a greater relative difference between the species in their ability to directly acquire different resources; (iii) if trade is favored, then either one or both species is favored to give up acquiring one resource directly, and vice versa. We then formulate testable predictions as to how environmental changes and coevolved responses of plants and mycorrhizal fungi will influence plant fitness (crop yields) in agricultural ecosystems.

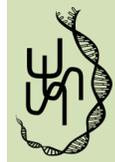
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Mutualistic cooperation between species poses a problem for evolutionary theory (Sachs et al. 2004; Foster and Wenseleers 2006; Leigh 2010). The problem is that—all else being equal—cheats who reduce their investment in a cooperative trait, while enjoying the benefits of others’ investment, will be favored by natural selection (West et al. 2007; Ghoul et al. 2014). Consequently, natural selection will act to disfavor costly cooperation. Within a species, genetic relatedness between social partners may result in kin selection that directly favors selflessness (Hamilton 1964), whereas the emergence and stability of cooperation between species requires additional mechanisms (Foster and Wenseleers 2006, but see Frank 1994; Wyatt et al. 2013).

A number of empirical studies have shown that mutualistic cooperation can be stabilized when one of the partners exerts control over the other (Agrawal and Karban 1997; Korb and Aanen 2003; Edwards et al. 2006; Johnstone and Bshary 2008; McFall-Ngai 2008). That is, members of the controlled species either irreversibly commit to their mutualistic partner or cannot choose

at all, and the controlling partner employs some mechanism to enforce or select for cooperation (Noë 1990; Bull and Rice 1991; Pellmyr and Huth 1994; West and Herre 1994; West et al. 2002a, b; Kiers et al. 2003; Freaan and Abraham 2004; Goto et al. 2010; Jander and Herre 2010; Archetti et al. 2011). For example, legume species invest fewer resources into root nodules containing rhizobia that fix less nitrogen (Kiers et al. 2003; Simms et al. 2006; Oono et al. 2009, 2011; Regus et al. 2014).

In contrast, in the mutualism formed between plants and mycorrhizal fungi, neither partner wields total control. Here, every individual may interact with multiple partners simultaneously: multiple mycorrhizal fungi can colonize a single plant host, and each of these fungal individuals can potentially interact with multiple plant hosts (Selosse et al. 2006; Kiers and Denison 2008). Empirical work has shown that plants supply more carbohydrates to fungal partners that provide more phosphorus, and vice versa (Hammer et al. 2011; Kiers et al. 2011; Fellbaum et al. 2012, 2014). Biological market theory has emerged as a tool to study



how cooperation can be stabilized in many-to-many interactions (Noë et al. 1991; Noë 1992; Noë and Hammerstein 1994, 1995; Werner et al. 2014), having originally been applied to systems where control is wielded by a single partner class (Selten and Shmida 1991; Peleg and Shmida 1992; Peleg et al. 1992). The strength of biological market theory is to make networks of two-way trading connections tractable by treating them as if partners were trading goods within a central marketplace (Noë and Hammerstein 1994).

However, the validity of this biological market approach in analyzing many-to-many interactions has yet to be formally evaluated. First, previous theory assumes the reward functions used by at least one class of partner (Schwartz and Hoeksema 1998; Hoeksema and Schwartz 2001, 2003; Kummel and Salant 2006). The question of which rewarding schemes natural selection will lead to has not been addressed. Natural selection could easily lead to consistent pricing across partners, or it could instead lead to discriminatory pricing, where different individuals face a different reward function. Second, previous theoretical models have assumed that mutually beneficial trade is made, rather than investigating when trade would be evolutionarily stable (Schwartz and Hoeksema 1998; Hoeksema and Schwartz 2001, 2003; Grman et al. 2012). There are many situations where trade or cooperation would be mutually beneficial but is not favored by natural selection, as famously illustrated by the Prisoner's Dilemma. Third, previous biological market models have assumed that markets comprise either very few or else infinitely many traders (Schwartz and Hoeksema 1998; Hoeksema and Schwartz 2001, 2003; Akçay and Roughgarden 2007; de Mazancourt and Schwartz 2010; Akçay and Simms 2011; Grman et al. 2012). Incorporating the more realistic assumption of finite markets with a variable number of participants may lead to single individuals exerting partial control over the overall supply of a good—termed “bargaining power” (Johnson et al. 2012). This could lead to the collapse of trade (Baldwin 1948; Rieber 1982).

Here, we assess the validity of the biological market analogy, developing a market model based on current knowledge of the mycorrhizal symbiosis. We derive the conditions under which individuals receive the same market exchange rate for their goods and under which trade is maintained. When these conditions are satisfied, we apply an economic model where individuals compete to supply goods and services in biological settings. We use our market model to explore the selective forces behind specialization in mutualisms. Finally, we consider the specific application of our model to the mycorrhizal symbiosis and the implications for agricultural scenarios. Specifically, we examine the consequences of: (i) variation in the number of trading partners of each species; (ii) the addition of phosphorus fertilizers; and (iii) rising CO<sub>2</sub> levels.

## Model and Analyses

We develop a model for the cooperative exchange of two resources between two species. We phrase our model in terms of the plant-mycorrhizal mutualism in which carbon from the host is exchanged for phosphorus from the fungus. Here, we consider only exchange of these two resources, although in reality the fungal partner can provide other nutrients, such as nitrogen. While we examine cases of particular relevance to that interaction, our aim is to keep our overall model general so that it can be applied to other mutualisms. Consequently, in the general formulation of our model we allow mycorrhizal fungi to acquire carbon directly, even though in the arbuscular mycorrhizal (AM) symbiosis, the fungal partner is an obligate biotroph that is completely dependent on its host for carbon (Parniske 2008). Our approach allows us to explore the reasons natural selection has favored reliance on host-derived carbon. To explain why mycorrhizal fungi do not acquire carbon directly, we must work out the fitness consequences for hypothetical fungi that can directly obtain carbon and show that natural selection will have eliminated them. This approach of considering a wider range of possibilities leads to a better understanding of the phenomena actually observed (Eddington 1928).

### DIRECT RESOURCE ACQUISITION

We consider a population of plants and mycorrhizal fungi that require carbon and phosphorus for growth. We assume that there is a linear trade-off between the resources invested into carbon and phosphorus acquisition, although other trade-offs would yield qualitatively identical solutions (Hoeksema and Schwarz 2003). Specifically, we assume that individuals acquire a proportion  $x$  of the maximum amount of carbon that they can acquire and a proportion  $1-x$  of the maximum amount of phosphorus. These maximum amounts are  $C_p$  and  $P_p$  for plants, and  $C_m$  and  $P_m$  for mycorrhizae (in practice,  $C_m = 0$  for mycorrhizal fungi). In principle, increased growth in mutualism could mean that these maximum amounts increase. We neglect such effects because the primary purpose of our model is to investigate the influence of partner discrimination in mutualisms. Hence, plants acquire  $x_p C_p$  units of carbon and  $(1-x_p)P_p$  units of phosphorus, whilst mycorrhizal fungi acquire  $x_m C_m$  units of carbon and  $(1-x_m)P_m$  units of phosphorus. The maximum amount of a resource that an individual can acquire depends on two factors—the availability of that resource in the environment and the inherent ability of individuals of that species to acquire it. For biological realism, we also give mycorrhizal fungi a small initial endowment of carbon,  $I$ . This reflects the trace amounts of carbon that fungal spores require to develop, as well as their ability to maintain at least some carbon independence from trade with specific host plants, for example by drawing down from common mycorrhizal networks (Giovannetti et al. 2004; Sbrana et al.

2011). Nonetheless, it is clear that this amount must be small as mycorrhizal fungi grow poorly except in symbiosis.

### MUTUALISTIC TRADE

In addition to acquiring carbon and phosphorus directly, we allow plants and mycorrhizal fungi to engage in mutualistic trade. Each plant has  $n_m$  mycorrhizal fungi as trading partners and each fungus has  $n_p$  plants. Plants transfer a proportion  $q_p$  of their directly acquired carbon to mycorrhizal partners and the fungi transfer a proportion  $q_m$  of their directly acquired phosphorus to plants.

What strategy for sharing resources between trading partners does natural selection favor? In principle, an individual could transfer all traded resources to one partner, could share equally between all partners, or could use any intermediate strategy. To determine the optimal sharing strategy across all partners, we only need to work out the relative amounts transferred to any pair of partners. This works because it allows us to consider the amount allocated to any given partner versus any other. With this information, we can calculate the ratios allocated between a sequence of as many partners as a focal individual has (a:b:c:d:e:f etc.). A plant is favored to allocate a proportion  $f_{p1}$  of an amount of carbon  $C_t$  to fungus  $m_1$  and a proportion  $1-f_{p1}$  of the amount  $C_t$  to  $m_2$ , so as to maximize phosphorus received in return. The phosphorus received from each fungus is a proportion,  $f_{m1}$  or  $f_{m2}$ , of the phosphorus that each fungus trades,  $P_{t1}$  and  $P_{t2}$ , respectively. The proportions  $f_{m1}$  and  $f_{m2}$  are functions of the focal plant's ( $f_{p1}C_t$  or  $(1-f_{p1})C_t$ ) and all other plants' ( $C_{re1}$  or  $C_{re2}$ ) carbon allocation to that fungus. The focal plant maximizes its phosphorus from trade when the equation  $P_r = f_{m1}(f_{p1}C_t, C_{re1})P_{t1} + f_{m2}((1-f_{p1})C_t, C_{re2})P_{t2}$  is maximized. In the Appendix we show that:

**Result 1**—Individuals are favored use a rule that allocates resources among partners of the other species in direct proportion to the relative amount of benefits they receive from each partner, when others do likewise. Specifically, a linear “proportional discrimination” (Tang-Martinez 2001) allocation is an evolutionarily stable strategy (ESS, Maynard Smith and Price 1973).

To illustrate, we find that in populations using linear proportional discrimination, if a plant receives two-thirds of the benefits it acquires through trade from one mycorrhizal fungus and one-third from another, it sends two-thirds of the total carbon it allocates for trade to the former and one-third to the latter. No other strategy arising in such a population can invade. Plants that either allocate all carbon to one partner or split carbon equally between all partners would have a lower fitness and hence be eliminated by natural selection. Linear proportional discrimination leads to individuals that receive the same exchange rate for resources or services traded in many mutualistic contexts, including our model (see Appendix for details). We still need to show that quantities

traded in our model can be nonzero. We do this by showing that when members of both species are simultaneously maximizing their fitness, their evolved strategy includes sending resources to members of the other species. Henceforth, we assume that all individuals adopt a linear proportional discrimination allocation, as it is an ESS.

### EVOLUTION OF RESOURCE ACQUISITION AND TRANSFER

After acquisition and trading of resources, each individual has a final amount of carbon ( $C_f$ ) and phosphorus ( $P_f$ ). These amounts jointly determine fitness. We choose fitness functions so that: (i) an individual's fitness is zero unless they possess both resources; (ii) increasing the level of either resource gives diminishing marginal fitness returns; (iii) there are constant returns to scale, so that a change in fitness due to different trading dynamics can be measured against a consistent baseline as resource availability changes. Specifically, we assume that plant fitness is given by  $w_p = C_f^a P_f^{1-a}$ , and mycorrhizal fitness is given by  $w_m = C_m^b P_m^{1-b}$ , where the exponents  $0 < a < 1$  and  $0 < b < 1$  mediate the marginal fitness effects of additional resources. These functions are commonly used to satisfy the above requirements in the economics literature and are termed “Cobb-Douglas functions” (Cobb and Douglas 1928).

We now re-write these fitness functions, replacing the final amounts of carbon and phosphorus ( $C_f$  and  $P_f$ ) with explicit expressions for the amounts acquired and traded for (see Table 1 for a list of parameters and evolved strategies used in the analysis). We consider a focal plant with a strategy pair  $(x_p, q_p)$ , which may not be the ESS, in a population with mean proportions of carbon acquired  $x'_p$  and  $x'_m$ , and allocations to trade  $q'_p$  and  $q'_m$  where resource acquisition and trading allocations are uncorrelated.

The plant acquires an amount  $x_p C_p$  of carbon and retains a fraction  $1-q_p$  of this, so that it has a final quantity of carbon given by  $C_{fp} = x_p C_p (1-q_p)$ . The plant also acquires an amount of phosphorus  $(1-x_p)P_p$  directly and receives an amount of phosphorus  $P_r = P_t n_m s_p$  via trade, where  $P_t$  is the quantity phosphorus each mycorrhizal fungus trades,  $n_m$  is the total number of mycorrhizal fungi hosted by the plant and  $s_p$  is the share of the traded phosphorus the focal plant acquires (see Appendix for a derivation of  $s_p$  in terms of model parameters and strategies). Mycorrhizal fungi each acquire, on average, a quantity  $(1-x'_m)P_m$  of phosphorus and allocate a proportion  $q'_m$  of it to trade. Hence, the average quantity of phosphorus allocated to trade by each fungus is  $P_t = (1-x'_m)P_m q'_m$ . This means that the total quantity of phosphorus the focal plants trades for is  $P_r = (1-x'_m)P_m q'_m n_m s_p$ . The final quantity of phosphorus available to plants is the sum of the quantity they take up from the soil and the quantity they acquire via trade, so  $P_{fp} = (1-x_p)P_p + (1-x'_m)P_m q'_m n_m s_p$ . Now, we replace  $C_{fp}$  and  $P_{fp}$  in the focal plant's

**Table 1.** Parameters and evolved strategies used in the analysis.

Symbol:	Definition:
$C_{p/m}$ :	Quantity of carbon available for an individual plant/mycorrhizal fungus to acquire
$C_i$ :	Quantity of carbon traded by an individual plant
$C_{re}$ :	Quantity of phosphorus received in trade by an individual mycorrhizal fungus, excluding what it receives from the focal plant
$I$ :	Initial carbon endowment of mycorrhizal fungi
$P_{p/m}$ :	Quantity of phosphorus available for an individual plant/mycorrhizal fungus to acquire
$P_r$ :	Quantity of phosphorus received in trade by an individual plant
$P_i$ :	Quantity of phosphorus traded by an individual mycorrhizal fungus
$n_{p/m}$ :	The number of heterospecific trading partners available to each plant/mycorrhizal fungus
$a$ :	Exponent that mediates the marginal effect of additional carbon or phosphorus on plant fitness
$b$ :	Exponent that mediates the marginal effect of additional carbon and phosphorus on mycorrhizal fungus fitness
$x_{p/m}$ :	Proportion of resources that plants/mycorrhizal fungi allocate to acquiring carbon. They allocate the remainder of their resources to acquiring phosphorus. ' denotes the average across the population
$q_{p/m}$ :	Proportion of carbon/phosphorus that plants/mycorrhizal fungi allocate to trade. ' denotes the average across the population

fitness function with the equations in this paragraph to yield

$$w_p = (x_p C_p (1 - q_p))^a ((1 - x_p) P_p + n_m (1 - x'_m) P_m q'_m s_p)^{(1-a)}. \quad (1a)$$

Similarly, a focal mycorrhizal fungus' fitness is

$$w_m = (I + x_m C_m + n_p x'_p C_p q'_p s_m)^b ((1 - x_m) P_m (1 - q_m))^{(1-b)}. \quad (1b)$$

We then study the evolution of the four variables that determine resource acquisition ( $x_p$  and  $x_m$ ) and transfer ( $q_p$  and  $q_m$ ). We find the ESSs ( $x_p^*$ ,  $q_p^*$ ) for plants and ( $x_m^*$ ,  $q_m^*$ ) for fungal partners. The ESS for plants determines that for mycorrhizal fungi and vice versa, so we denote pairs of coevolutionary ESSs as ( $x_p^*$ ,  $q_p^*$ ,  $x_m^*$ ,  $q_m^*$ ). Four ESS scenarios are possible: (i) there is no mutualistic trade ( $q_p = q_m = 0$ ); (ii) plants acquire only carbon directly ( $x_p = 1$ ) and mycorrhizal fungi acquire only phosphorus directly ( $x_m = 0$ ); (iii) plants acquire only carbon directly ( $x_p = 1$ ), but mycorrhizal fungi acquire both phosphorus and carbon directly ( $0 < x_m < 1$ ); (iv) plants acquire both phosphorus and carbon directly ( $0 < x_p < 1$ ), but mycorrhizae acquire only phosphorus directly ( $x_m = 0$ ) (see Appendix for details). Scenario (iii) cannot occur in nature, but as discussed above it is essential to consider the scenario in order to explain why it does not occur.

We use our model and the ESSs it yields to explore three questions. First, when is mutualistic trade evolutionarily stable? Second, when is one of the partners favored to acquire only one resource, and hence rely completely on the other species for the other resource? Third, what are the consequences for agricultural yields due to changes in partner numbers ( $n_p$  and  $n_m$ ), atmospheric carbon concentrations ( $C_p$  and  $C_m$ ), and phosphorus fertilizer availability ( $P_p$  and  $P_m$ )?

### *Under what conditions do individuals engage in mutualistic trade?*

We find a pair of coevolutionary ESSs with trade ( $q_p, q_m > 0$ ) when

$$\frac{b C_p P_m}{P_p ((1 - b) I + b C_m)} > \frac{n_p n_m}{(n_p - 1)(n_m - 1)}. \quad (2)$$

This result shows that a market analogy is valid, as natural selection can both maintain trade and lead to all individuals receiving the same market exchange rate for their goods in our model. The result also shows that we should only expect trade when ecological parameters satisfy the conditions in inequality (2), even though mutually beneficial trade is possible under all parameter values in our model.

**Result 2**—Mutualistic trade is promoted when individuals in both species have less access to the resource that they can acquire by trade ( $P_p$ ,  $C_m$ , or  $I$  decreases) or are more efficient at acquiring the resource that they cannot acquire by trade ( $C_p$  or  $P_m$  increases) (Fig. 1). These changes increase the benefit of acquiring resources by trade.

Result 2 is in line with previous predictions that mutual dependence increases the likelihood of mutualistic cooperation (Foster and Wenseleers 2006; Leigh 2010) and trade (Cordella and Gabszewicz 1997).

**Result 3**—Mutualistic trade is promoted when the number of potential competitors in each species ( $n_p$  or  $n_m$ ) increases (Fig. 1). The increase in mycorrhizal partner numbers decreases a single individual's control over total phosphorus traded (i.e., its bargaining power). With this increase, a focal mycorrhizal fungus benefits less from manipulating the total amount of phosphorus

in the market to increase its value (Cordella and Gabszewicz 1998). Instead, it benefits relatively more from competing intensely for carbon by trading phosphorus, thus promoting trade.

To illustrate result 3, consider the scenario where  $n$  mycorrhizal fungi providing an equal amount of phosphorus to a plant. Each fungus therefore gets a fraction  $1/n$  of the traded carbon. Now suppose that one mycorrhizal fungus doubles its supply of phosphorus to the plant, thus receiving  $2/(n+1)$  of the traded carbon in return. The carbon returned to that fungus is increased by a factor  $2n/(n+1)$ , which increases with larger  $n$  (Fig. 2). A similar result has already been derived in the economics literature (Cordella and Gabszewicz 1997). However, it runs counter to widespread thinking in biology that cooperation is more likely to be outcompeted by selfishness as the number of social partners increases (Frank 1994).

**Result 4**—The absence of trade is always evolutionarily stable, except when at least one species can acquire only one resource without trading ( $C_p$ ,  $P_p$ ,  $C_m$ , and  $I$ , or  $P_m = 0$ ). In general, if individuals in one of the species are not trading, it does not pay for members of the other species to engage in mutualistic trade. However, if individuals in one species cannot acquire one resource by other means, they must trade to survive. This illustrates that biological cooperation is easier to maintain than to initiate, as has been shown elsewhere (Axelrod and Hamilton 1981).

#### When does selection favor specialization?

We now explore the conditions that favor specialization. Here, we use specialization to mean when individuals of a species acquire only one resource, and rely on trade for the other.

**Result 5**—Whenever trade is favored, either one or both species are favored to stop acquiring one resource directly, and only acquire it through trade ( $x_p = 1$  or  $x_m = 0$  at each pair of trading ESSs). The reverse also holds. Whenever individuals in one species are favored to adopt a strategy where they forsake acquiring one resource directly, trade is favored.

We find that when trade is favored, plants are favored to acquire carbon, but not phosphorus, when

$$P_p \leq \frac{bC_p(n_p - 1)(n_p - 1 + a)(n_m - 1)n_m P_m}{n_p((1 - a)C_p(n_p - 1)n_p n_m + I(1 - b)(n_p - 1 + a)n_m^2 - (1 - a)bC_p(n_p - 1)n_p)} \quad (3a)$$

(Fig. 3). When trade is favored, mycorrhizal fungi are favored to acquire phosphorus, but not carbon, when

$$C_p \geq \frac{(bC_m - I(1 - b))(n_p - 1 + a)n_m^2}{(1 - a)(n_p - 1)n_p(n_m - b)}. \quad (3b)$$

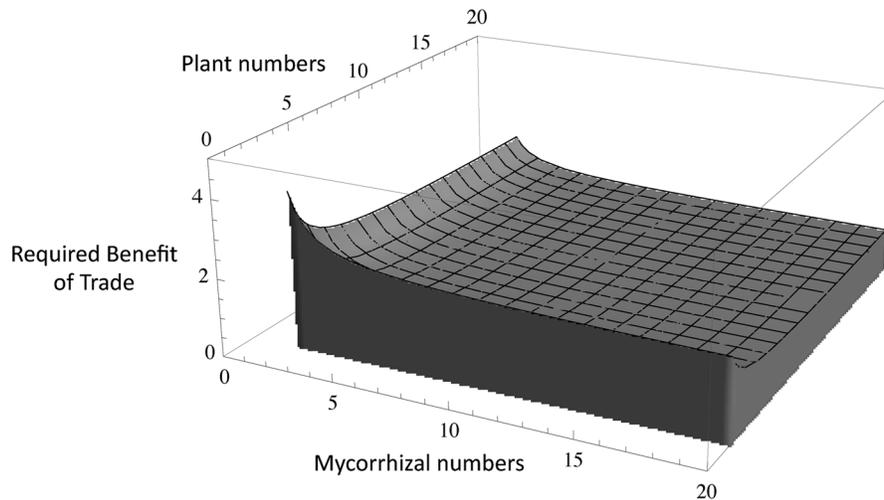
**Result 6**—Specialization is more favored as individuals become less efficient at acquiring the resource they trade for ( $P_p$ ,  $C_m$ , and/or  $I$  are small relative to  $P_m$  and/or  $C_p$ ). These changes increase the marginal benefit of acquiring more of the resource that they cannot acquire through trade.

**Result 7**—Specialization is more favored when individuals interact with fewer members of the other species, or when individuals of the other species interact with more trading partners. For example, decreasing the number of plants ( $n_p$ ) or increasing the number of mycorrhizal fungi ( $n_m$ ) increases the total quantity of phosphorus relative to the total quantity of carbon in the market. This increases the scarcity, and therefore value, of the carbon. This favors plants that invest relatively more in carbon acquisition, whether for their own use or to benefit from its increased value in trade.

These results demonstrate why mycorrhizal fungi are, in general, not favored to acquire carbon directly. Once the fungus is engaged in a stable mutualistic relationship where it is a specialized partner, it gains no fitness benefits from the ability to acquire carbon directly. Consequently, mycorrhizal fungi are likely to lose any adaptations related to direct (nonhost) carbon acquisition. The results in this section capture one of the central predictions of trade under comparative advantage: at least one class of trader will specialize completely, and individuals will be more likely to specialize the greater their relative disadvantage in acquiring one resource (Ricardo 1817). We highlight the generality of this principle, as it has also been recovered in other models where individuals are able to acquire two resources (Hoeksema and Schwartz 2003, Grman et al. 2012).

#### AGRICULTURAL CONSEQUENCES

We now explore three scenarios with relevance to agriculture. We consider how coevolutionary changes combine to determine variation in agricultural yields (i.e., plant fitness,  $f_p$ ) and mycorrhizal cooperativeness (which we define as the proportion



**Figure 1.** Condition for the stability of mutualistic trade. Above the threshold surface,  $bC_p P_m / (P_p((1-b)I + bC_m)) = n_p n_m / ((n_p - 1)(n_m - 1))$ , the benefit of specialization and trade is large enough that individuals benefit from maintaining resource transfer. This condition becomes easier to satisfy as the number of individuals in each species,  $n_p$  or  $n_m$ , increases.

of their phosphorus that they send to plants,  $q_m$ ) in response to: (i) changes in the number of mutualistic partners; (ii) the application of phosphorus fertilizers (higher  $P_m$  and/or  $P_p$ ); (iii) an increase in atmospheric carbon (which is never available to mycorrhizae,  $C_m = 0$ ).

#### Partner numbers

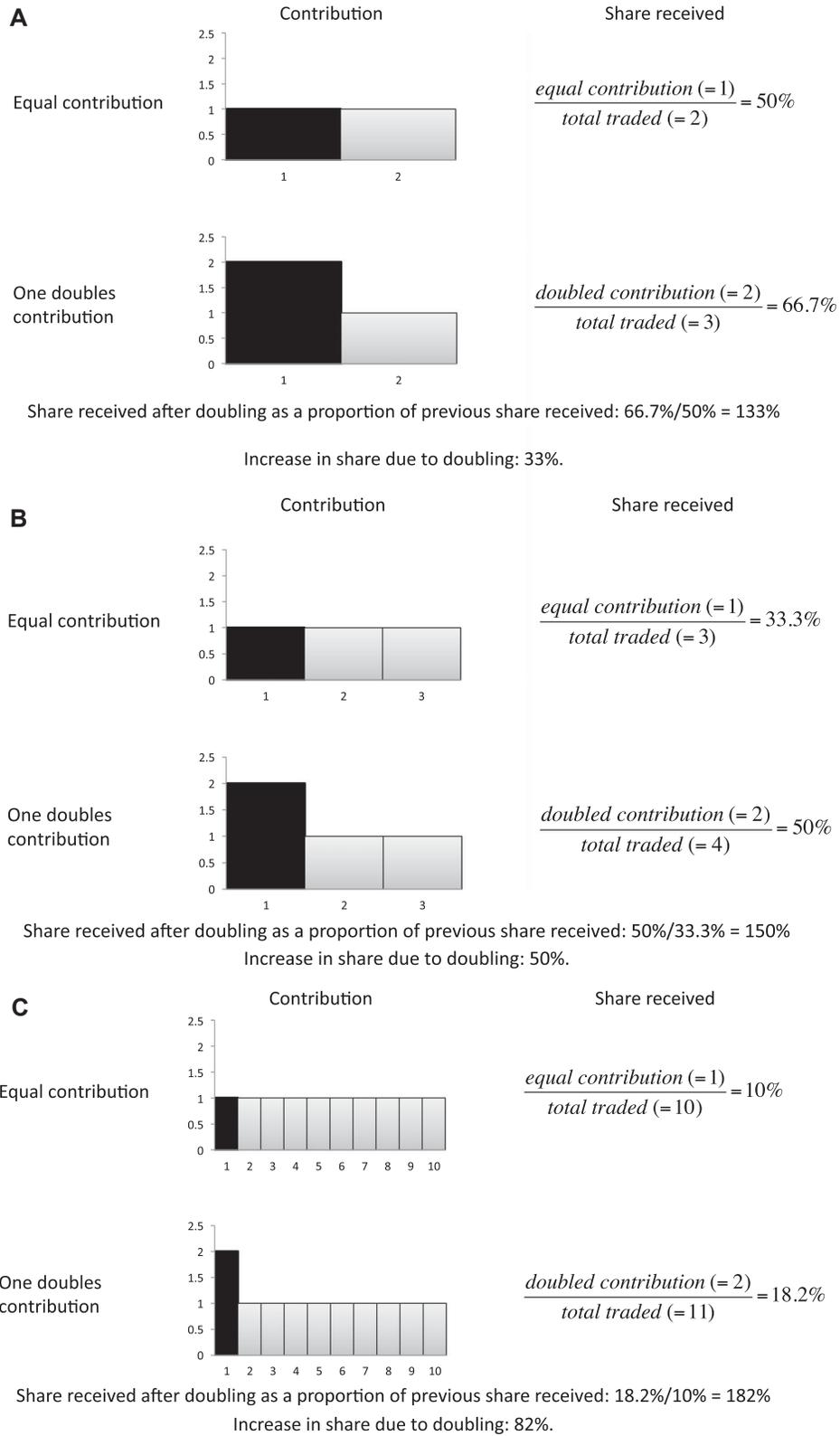
When host plants are grown as agricultural crops, this can alter plant density in a way that alters the number of available trading partners for each individual plant and mycorrhizal fungus. We assume that there is no initial cost to setting up a trading link. Such a cost might be important in the evolutionary origin of a de novo mutualism, but need not be if the mutualism arises from a preexisting association between plants and fungi. Moreover, we are not considering the origin of mutualism but its maintenance and elaboration, and the costs of setting up a trading link are likely negligible relative to the quantity of resources flowing through the network (Mikkelsen et al. 2008).

**Result 8**—An increase in the number of mycorrhizal partners per plant ( $n_m$ ) increases both the cooperativeness of each mycorrhizal fungus ( $q_m$ ) and the fitness of each plant ( $f_p$ ). This is because the same plant carbon becomes shared between more mycorrhizal partners, increasing the marginal benefit of additional carbon for each mycorrhizal fungus. They are favored to transfer more phosphorus to compete for this carbon, thus increasing plant fitness. When plants acquire both resources before trade (condition 4a is not satisfied), the increase in fitness is slow because plants compete for phosphorus by increasing their investment in carbon acquisition and transferring that carbon to the fungal partner. When plants acquire only carbon directly,

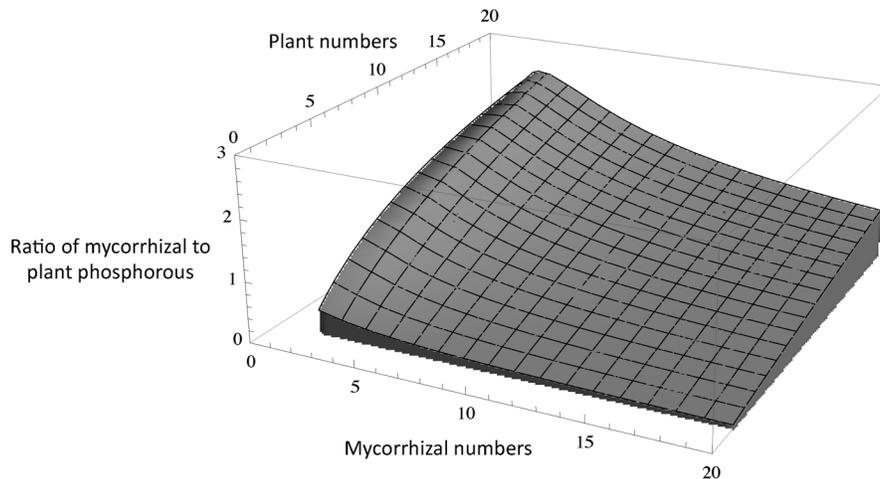
they cannot acquire any more of it to compete for mycorrhizal phosphorus. Therefore, plant fitness begins to increase rapidly, but at a diminishing rate (Fig. 4).

The increase in plant fitness caused by an increase in fungal numbers follows easily from the consequences of market supply and demand. The principle has been verbally applied to biological settings by Noe and Hammerstein (1994), but ours is the first model to quantify this effect. Grman et al. (2012) identify a similar trend that increased fungal biomass will lead to increased plant fitness because phosphorus becomes more readily available, but their model only considers one trader of each type, so the added impact on plant fitness of increased fungal cooperativeness is not captured. The predicted increase in fungal cooperativeness is also novel in the economic literature. Previous work suggests that less phosphorus may be supplied per fungus due to falling phosphorus prices because suppliers, in this case mycorrhizal fungi, increase in number (Amir and Lambson 2000).

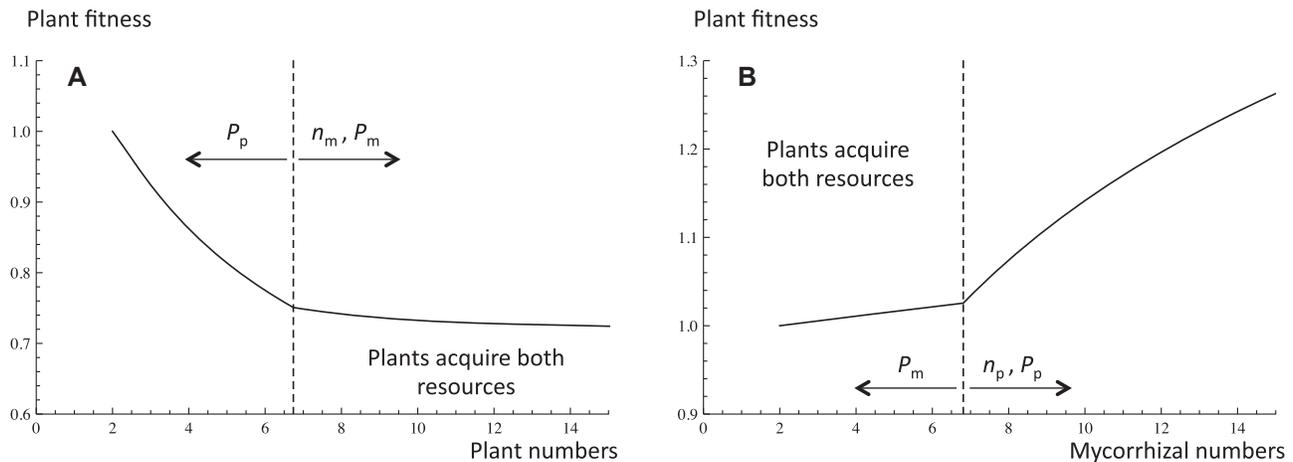
**Result 9**—An increase in the number of plant partners per mycorrhiza ( $n_p$ ) has a small positive effect on mycorrhizal cooperativeness, proportional to the size of the mycorrhizal carbon endowment ( $I$ ). The impact on cooperativeness is small because two effects oppose. (i) The quantity of carbon that each mycorrhizal fungus receives, given the amount of phosphorus it sends, increases. This effect selects for more cooperative mycorrhizal fungi as trading away phosphorus yields a greater carbon return. (ii) Each mycorrhizal fungus receives more plant carbon, so the marginal value of an additional unit is lower, thus decreasing the quantity of phosphorus it trades. Overall, plant fitness decreases because more plants compete for a quantity of phosphorus that increases at a slow rate. This results in less phosphorus per



**Figure 2.** Mutualistic trade and the number of trading partners. The proportional increase in resources returned to the black individual for doubling its contribution increases with the number of same species competitors, as illustrated by an increase from two (A), to three (B), to ten (C).



**Figure 3.** Specialisation and partner numbers. Above the surface, condition (3a) is satisfied. Plants acquire only carbon directly. Below it, plants acquire both resources directly. This surface is the critical ratio of mycorrhizal phosphorus to plant phosphorus, above which plants are favored to rely completely on mycorrhizal fungi for phosphorus (In graph,  $a = 0.6$ ,  $b = 0.4$ ,  $C_p = 1$ ,  $l = 0.1$ ).



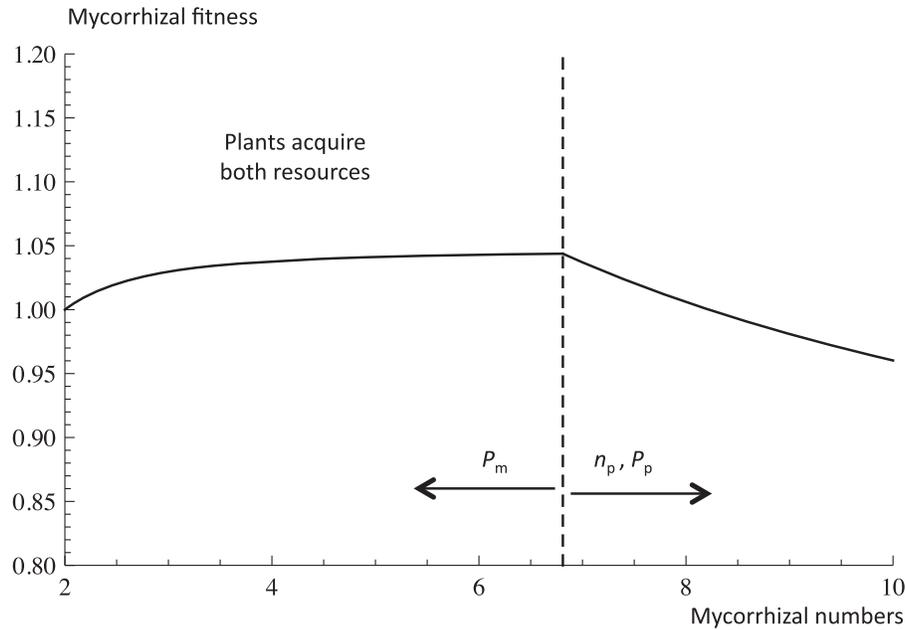
**Figure 4.** Effect of number of partners on plant fitness. (A) Plant fitness decreases with the number of plants. When plants acquire both resources directly (left of dashed line), the rate of fitness decrease slows dramatically as plants are no longer reliant on mycorrhizae for phosphorus. (In graph,  $n_p = 10$ ,  $C_p = 1$ ,  $P_p = 0.5$ ,  $P_m = 1$ ,  $a = 0.7$ ,  $b = 0.3$ ,  $l = 0.1$ ). (B) Plant fitness increases with the number of mycorrhizal partners,  $n_m$ . When plants acquire only carbon directly (right of dashed line), fitness increases more rapidly as plants can no longer compete with each other by increasing the resources they allocate to acquiring carbon directly. (In graph,  $n_m = 5$ ,  $C_p = 1$ ,  $P_p = 0.5$ ,  $P_m = 1$ ,  $a = 0.7$ ,  $b = 0.3$ ,  $l = 0.1$ ).

individual plant. When there are few plants, the decrease in fitness is rapid. However, the plants become self-reliant on phosphorus when there are many (condition 4a is not satisfied). Hence, further decreases in plant fitness are small (Fig. 5).

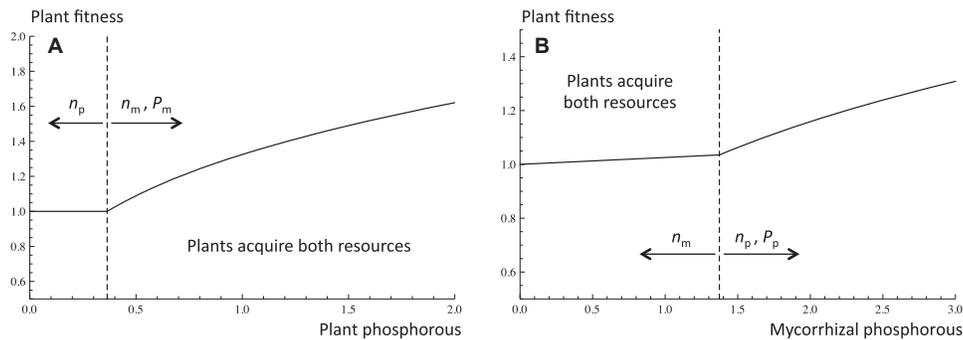
While the loss in fitness per plant with an increase in plant numbers follows directly from supply and demand predictions, the increase in fungal cooperativeness is again a novel and unexpected result.

Results 8 and 9 predict opposite effects on plant fitness because, all else being equal, having more competitors is bad for a

focal individual's fitness. In contrast, having more trading partners competing against each other is good for the focal individual's fitness. Overall, extending plant-mycorrhizal networks (adding both plant and mycorrhizal partners) can have conflicting effects on agricultural yields: plants lose fitness when mycorrhizae make connections with more plant partners, but gain fitness as they make connections with more mycorrhizal partners (Fig. 4, Weremijewicz and Janos 2013). In addition, our model highlights potential for conflict over network size and composition as mycorrhizal fungi can benefit from increases in the number of both mycorrhizal fungi and plants, leading to different fitness optima in the two species (Fig. 6).



**Figure 5.** Effect of mycorrhizal numbers on mycorrhizal fitness. When there are few mycorrhizal fungi, their fitness increases as with their numbers. This occurs because they can induce plants to acquire more carbon and less phosphorus directly, thus lowering the phosphorus price of carbon. However, once plants acquire only carbon directly (right of dashed line), mycorrhizae lose fitness as their numbers increase. (In graph,  $n_p = 10$ ,  $C_p = 1$ ,  $P_p = 0.5$ ,  $P_m = 1$ ,  $a = 0.7$ ,  $b = 0.3$ ,  $I = 0.1$ ).



**Figure 6.** Effect of phosphorus availability on plant fitness. (A) Plants only benefit from an increase in phosphorus they can acquire directly once they start acquiring it (right of dashed line). (In graph,  $n_p = 10$ ,  $n_m = 5$ ,  $C_p = 1$ ,  $P_m = 1$ ,  $a = 0.7$ ,  $b = 0.3$ ,  $I = 0.1$ ). (B) Plant fitness always increases with the quantity of phosphorus available to mycorrhizae. Fitness increases much more rapidly once plants acquire only carbon directly (right of dashed line, condition (6a) is satisfied) and therefore cannot compete with each other for phosphorus by acquiring more carbon directly. (In graph,  $n_p = 10$ ,  $n_m = 5$ ,  $C_p = 1$ ,  $P_p = 0.5$ ,  $a = 0.7$ ,  $b = 0.3$ ,  $I = 0.1$ ).

### Phosphorus fertilizer availability

An increase in phosphorus fertilizer availability will increase the amount of phosphorus available to plants ( $P_p$ ), the amount of phosphorus available to mycorrhizal fungi ( $P_m$ ), or both. In practice, scenarios where phosphorus availability increases to each plant (but not to each mycorrhizal fungus) are likely only when the quantity of mycorrhizal fungi increases as well, thus forcing the fungi to compete amongst each other for the increased phosphorus. However, our model can tease apart the separate effects of increase in phosphorus available to plants and mycorrhizal fungi. The effect of a simultaneous increase in both is a combination of

the two separate effects that can be determined through empirical parametrization of our model.

**Result 10**—An increase in phosphorus available exclusively to plants decreases mycorrhizal cooperativeness, whereas an increase in phosphorus availability to mycorrhizae increases their cooperativeness. Again, these effects will be small, proportional to the fungi's initial carbon endowment  $I$ , because two effects oppose: (i) if additional phosphorus is available, it is relatively less valuable in trade than if consumed by the mycorrhizal fungi. This selects mycorrhizal fungi to transfer less phosphorus; (ii)

the increased levels of phosphorus increase the marginal benefit of a unit of carbon, so mycorrhizal fungi are selected to transfer more phosphorus in exchange for this carbon.

**Result 11**—Increases in phosphorus availability, whether to plants or mycorrhizal fungi, increase plant fitness. However, this effect is threshold dependent. When plants acquire only carbon directly, they do not benefit from an increase in the phosphorus directly available to them ( $P_p$ ), as they do not use this source. Plants benefit from an increase in either phosphorus source when they acquire both resources directly, as is most biologically realistic (Fig. 7). However, in this scenario, they benefit very little from an increase in phosphorus available to mycorrhizal fungi ( $P_m$ ). They compete for this additional phosphorus by acquiring more carbon directly and transferring it to the fungal partner. Plants benefit more from an increase in phosphorus available to mycorrhizal fungi when they are fully reliant on mycorrhizal phosphorus (Fig. 8).

Result 10 analyses how strategies change with changes in phosphorus availability. Here, our model differs significantly from the model of Grman et al. (2012). Their model predicts a significantly less cooperative symbiont at high phosphorus availability to fungi because their single mycorrhizal fungus exploits monopoly power. In our model that allows multiple mycorrhizal individuals, as is most likely in the natural world, competition prevents this outcome. Result 11 analyses changes in plant fitness with phosphorus availability and highlights the same expected threshold dependencies found previously (Grman et al. 2012).

While the plants gain fitness even when additional phosphorus is not available to them except through trade, mycorrhizae lose fitness when plants can acquire more phosphorus directly. This is because plants become less reliant on them.

**Result 12**—When phosphorus availability to plants,  $P_p$ , reaches sufficiently high levels, trade between plants and mycorrhizae ceases. However, plant fitness does not suffer once this happens. When phosphorus is so easily available to plants, it is cheaper for the plants to acquire it directly than to acquire it through trade.

Hoeksema and Schwarz (2003) provide a more comprehensive analysis of conditions when mutualistic trade is not beneficial, although our model extends this by also showing when mutually beneficial trade fails to evolve due to public goods dilemmas. This outcome has already been shown in the economics literature (Bacchiaga 2013).

### *Atmospheric carbon concentrations*

How will rising CO<sub>2</sub> levels influence trade between plants and their mycorrhizae?

**Result 13**—Rising CO<sub>2</sub> concentrations increase plant fitness because plants are able to acquire more carbon directly ( $C$  increases). In addition, rising CO<sub>2</sub> levels increase mycorrhizal cooperativeness, although the effect will again be proportion to the mycorrhizal carbon endowment  $I$ , and hence small, because two effects oppose: (i) mycorrhizae are selected to transfer more phosphorus because plants can transfer more carbon in return; (ii) more carbon is available, which decreases its marginal value, and selects for mycorrhizae to transfer less phosphorus.

The diminishing marginal returns for an increase in availability limiting resource found in Result 13 are the default prediction in both economics and biology.

## *Discussion*

Our work builds on previous research in biological market theory and its predictions. We demonstrate the validity of the market analogy and extend predictions on specialization and trade in mutualisms. We then use the biological market framework to make predictions about the agricultural consequences of ecological change.

### **BIOLOGICAL MARKETS**

The plant-mycorrhizal mutualism consists of two-way trading connections between individuals. We have shown that this system can lead to the equivalent outcome as a central marketplace to which all individuals must bring the goods they trade. Specifically, we found that natural selection can lead to all individuals receiving the same market exchange rate for their goods and maintain trade. We derived our results using preexisting frameworks in the economics literature used for analyzing trade, termed “noncooperative trading games” (see Online Supplementary Material 1). Within species interactions were analyzed using frameworks for competition between suppliers of a particular good, where these suppliers must compete by adjusting quantities they bring to markets. This competitive structure is termed “Cournot competition” (Cournot 1838, see Online Supplementary Material 1).

Our results depend on linear proportional discrimination being an evolutionarily stable strategy for sharing resources. This is not a problem in economics, where it is typically assumed that individuals receive goods in proportion to the amount of money they pay, but it was not obvious that natural selection could lead to the same outcome. Linear proportional discrimination is stable when the ratio of benefits traded to benefits received is the same for any individual in each species. The ratio of exchange need not be 1:1 for the resources, but it must remain consistent across trades in that particular population. The optimal foraging theory literature on Ideal Free Distributions suggests that this ratio is often consistent, especially whenever individuals differ only

in their competitive ability to acquire resources and are free to engage with whatever mutualistic partners they choose or whenever individuals acquiring more resources grow faster (Whitham 1980; Harper 1982; Sutherland and Parker 1985; Parker and Sutherland 1986; Houston and McNamara 1988; Sutherland et al. 1988; Inman 1990; Kacelnik et al. 1992; Krivan 1997). While plants and arbuscular mycorrhizal fungi have been shown to allocate more carbon resources to individuals offering more phosphorus in return (Bücking and Shachar-Hill 2005; Bever et al. 2009; Kiers et al. 2011), it is not known if they actually use a linear proportional discrimination rule. One confounding factor is that while plants trade only carbon with fungal partners, the fungal partners can trade additional resources, such as nitrogen and trace elements (Chen et al. 2003; Tanaka and Yano 2005). How this asymmetry in the diversity of goods offered by the two species affects proportional discrimination is unknown. Tracking and quantifying the exchange of multiple resources in mycorrhizal networks remains empirically difficult.

We have also shown that trade can only be maintained by linear proportional discrimination when individuals are exposed to enough potential competitors of the same species. As the number of competitors goes up, this increases competition for the resources provided by the mutualistic partner, and hence favors transferring more resources to the other species to earn a greater share of trade. If there are too few competitors, then a decrease in resources transferred can always be favored, and trade can even collapse altogether (Fig. 1). Empirical work in the mycorrhizal symbiosis suggests that individuals most often trade in large networks of partners (Giovannetti et al. 2004; Montesinos-Navarro et al. 2012), and so discriminating between individuals (and allocating resources accordingly) is likely to be a useful mechanism for maintaining cooperation (Fig. 2). The exact physiology of how this discrimination could take place is the focus of on-going work. It has been shown, for example, that an increase in host plant carbon can trigger the uptake of nutrients, such as nitrogen, by the fungal partner (Fellbaum et al. 2012). Vice versa, fungal partners can discriminate among adjacent roots differing in carbon resources (Bücking and Shachar-Hill 2005; Kiers et al. 2011), even allocating more nutrients to plants grown under sun rather than shade conditions (Fellbaum et al. 2014). However, such examples of fair-trade are not always the norm (e.g., Merckx and Bidartondo 2008; Walder et al. 2012).

### *Trade and specialization*

A link between trade and specialization has long been recognized in economics (Ricardo 1817), and the tendency for specialization to drive trade has been explored in the biological market literature (Schwartz and Hoeksema 1998; Hoeksema and Schwartz 2001; Grman et al. 2012). Indeed, mutualisms tend to evolve more easily when species are highly specialized on a partner, as the benefits

of trade are greater (Poisot et al. 2011). In our model, we recover and extend these results, suggesting that trade and specialization will go hand in hand: specialization evolves when mutualistic trade is present, and vice versa. In biological settings, it was unclear whether or not trade would drive specialization. Mycorrhizal fungi could have potentially benefited from retaining the ability to acquire carbon directly (rather than being dependent on the host), thus retaining bargaining power with plants (Bergmüller et al. 2007). However, physiological evidence suggests that whilst mycorrhizal fungi have not lost all of their saprophytic abilities, they do not possess the key genes to obtain carbon directly (e.g., genes to degrade plant cell walls, Tisserant et al. 2014). Instead, they have clearly evolved a dependence on host plant carbon, only expressing their full genetic potential when in symbiosis (Corradi and Bonfante 2012). An explanation suggested by our model is that mycorrhizal fungi compete most fiercely with other mycorrhizal fungi for plant carbon. As a result, only adaptations that will help them acquire more of the host carbon can be favored by natural selection even if these adaptations entail greater dependence on the host. This feedback loop may help explain how the mycorrhizal symbiosis and other mutualisms evolve from facultative to obligate (Aanen and Hoekstra 2007).

### *Ecological change and agricultural consequences*

We have found that the impact of the number of social partners on plant fitness (and thus potentially crop yields) is threshold dependent (Fig. 4). Initially, increasing the number of mycorrhizal fungi per plant has only a small beneficial effect on per plant fitness. However, once plants start relying entirely on trade for phosphorus, per plant fitness increases rapidly, even though mycorrhizal cooperativeness increases at a diminishing rate throughout. In contrast, as plant number per fungal partner rises, per plant fitness falls rapidly but then levels off, even though mycorrhizal cooperativeness remains constant. Therefore our model suggests that large networks are likely to be better for plants, as the variety of suppliers means that plants can rely on mycorrhizae for phosphorus and enjoy the fitness gains associated with specializing on acquiring carbon.

The benefits of an increase in phosphorus availability are similarly threshold dependent (Fig. 6). When plants do not acquire phosphorus from the soil, only an increase in phosphorus available to mycorrhizae ( $P_m$ ) increases plant fitness. On the other hand, when plants acquire both carbon and phosphorus directly, only an increase in phosphorus available directly to plants ( $P_p$ ) significantly increases plant fitness. We also predict that mycorrhizal fungi lose fitness when plants can acquire more phosphorus directly, as plants become less reliant on them. This effect has the potential to select for mycorrhizal fungi that prevent, whether partially or completely, plants from acquiring phosphorus directly. There is some evidence that mycorrhizal fungi have evolved ways

to suppress the direct nutrient uptake pathway of their host plants. The apparent deactivation of the direct pathway in plants colonized by mycorrhizal fungi is hypothesized to be a result of downregulation of the plant phosphorus transporters in root epidermis and root hairs (Smith et al. 2011). While our model shows that changing phosphorus conditions do not necessarily have a major effect on cooperativeness (i.e., the proportion of fungal phosphorus allocated to trade), it does suggest that there is room for the fungal partner to evolve greater control of soil resources.

Predicting the effects of increasing atmospheric CO<sub>2</sub> concentration on crop yields is difficult, and remains a hotly debated topic (Jaggard et al. 2010). While carbon becomes more readily available to plants, the increase in fitness directly attributable to increased carbon is likely to show diminishing returns, as other resources become more limiting. Our model suggests that this benefit is enhanced by interactions with symbionts. Mycorrhizal fungi will be competing for a larger pool of plant carbon, which encourages them to transfer more phosphorus, although this will be moderated by the increasingly limiting role of phosphorus throughout the system. Consistent with these predictions, long-term studies, such as the free air CO<sub>2</sub> enrichment (FACE) experiment in Switzerland suggest that increasing CO<sub>2</sub> can drive strong selection pressures in mycorrhizal fungi (Staddon et al. 2004). Within 8 years, mycorrhizal fungal isolates (e.g., *Glomus* sp.) from plots treated with elevated CO<sub>2</sub> improved the nitrogen nutrition of their host plants significantly more than those in plots treated with ambient CO<sub>2</sub> (Gamper et al. 2005). These experiments demonstrate the potential for harnessing evolved mutualistic strategies in order to increase crop yields. An improved understanding of the coevolutionary dynamics, with a particular emphasis on identifying thresholds beyond which plant growth increases rapidly, is a key part of a “Darwinian Agricultural” strategy to increase crop yields in a more sustainable manner (Denison et al. 2003; Denison 2013).

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## Appendix A: Linear proportional discrimination

Here, we prove that linear proportional discrimination is an evolutionarily stable strategy. Assume that a focal plant interacts with two mycorrhizae using linear proportional discrimination,  $m_1$  and  $m_2$ . The amount of phosphorus that  $m_1$  allocates for trade is  $P_{t1}$ , while the amount that partner  $m_2$  allocates is  $P_{t2}$ . These mycorrhizae receive total amounts of carbon  $C_{re1}$  and  $C_{re2}$  respectively from all of their other plant trading partners (i.e., not including the focal plant). The focal plant then shares an amount of carbon allocated for trade,  $C_t$ , between the two mycorrhizae, giving a proportion  $C_t f_1$  and a proportion  $C_t(1-f_1)$  of that amount to  $m_1$  and  $m_2$ , respectively. In return, the plant receives a total amount of phosphorus  $P_r$ , as determined by the linear proportional discrimination functions of the two mycorrhizae:

$$P_r = \frac{C_t f_1}{C_t f_1 + C_{re1}} P_{t1} + \frac{C_t(1-f_1)}{C_t(1-f_1) + C_{re2}} P_{t2}. \quad (4)$$

We denote the shares of phosphorus  $C_t f_{p1}/(C_t f_{p1} + C_{r1})$  and  $C_t(1-f_1)/(C_t(1-f_1) + C_{re2})$  received by the plant as  $s_1$  and  $s_2$ . We now calculate  $\partial P_r/\partial f_1$  and  $\partial^2 P_r/\partial f_1^2$  from equation 4. We then evaluate these derivatives at the value of  $f_1$  determined by linear proportional discrimination, which must satisfy

$$\frac{f_1}{1-f_1} = \frac{s_1 P_{t1}}{s_2 P_{t2}}. \quad (5)$$

We simplify the resulting expressions and find that phosphorus received is maximized when

$$\frac{C_{re1}}{P_{t1}} = \frac{C_{re2}}{P_{t2}}. \quad (6)$$

Hence, linear proportional discrimination maximizes phosphorus received, and allocating amongst partners according to this rule is therefore an ESS when equation 6 is satisfied. This is always true in our model, where all individuals in a species are identical. Note that we have not demonstrated that linear proportional discrimination is the only ESS of our model, but we do demonstrate that allocating all resources to the best trading partner or sharing

equally between all partners are not evolutionarily stable in the mutualistic system (see Online Supplementary Material 2).

We also note that across the population, equation 6 will be satisfied on average. That is, the expected ratio of carbon sent to phosphorus received is the same for any individual. Hence, if the resource sharing strategy is genetically encoded, or if individuals cannot measure whether or not an alternative sharing strategy yields an increase in resources returned, they cannot do better than also adopt linear proportional discrimination.

### Appendix B: Conditions for existence of trading ESS and equilibrium allocations

We take plant fitness from equation (1a), and substitute model parameters and evolved strategies for the proportion of traded phosphorus acquired by the focal plant,  $s_p$ , which is equal to the share of total traded carbon that the plant acquires which we now write down in terms of model parameters. The numerator of  $s_p$  is the total amount of carbon that the focal plant provides in trade that is the proportion of acquired carbon that the focal plant allocates to trade,  $C_t = x_p C_p q_p$ . The denominator of  $s_p$  is the total amount of carbon traded by all competing plants, including the focal individual. There are  $n_p - 1$  competitors, and the average amount of carbon each trades is the average proportion of the average total amount of carbon that each plant acquires,  $x'_p C_p q'_p$ . We add this across all of the competitors and add the amount of carbon provided by the focal individual, so the denominator is  $((n_p - 1)x'_p C_p q'_p + x_p C_p q_p)$ . Hence, the proportion of total traded phosphorus that the plant acquires is  $s_p = (x_p C_p q_p) / ((n_p - 1)x'_p C_p q'_p + x_p C_p q_p)$ . This means that equation (1a) is now entirely expressed in terms of model parameters and evolved strategies. The same approach allows us to express equation (1b) in the same way.

We now calculate the fixed points with respect to allocation to direct carbon acquisition and trade,  $\partial w_p / \partial x_p = \partial w_p / \partial q_p = 0$ .

$$(x'_p, q'_p, x'_m, q'_m) = \left( 1, \frac{(1-a)(n_p-1)}{n_p-1+a}, \frac{(bC_m - (1-b)I)(n_p-1+a)n_m^2 - (1-a)C_p(n_p-1)n_p(n_m-b)}{C_m(n_p-1+a)n_m^2}, \frac{(1-a)C_p(n_p-1)n_p(n_m-1)}{(1-b)(I+C_m)(n_p-1+a)n_m^2 + (1-a)C_p(n_p-1)n_p(n_m-b)} \right). \tag{9}$$

At an ESS, any focal plant receives population mean fitness to first order, so we take its strategy to be the population average ( $q_p = q'_p, x_p = x'_p$ ). Substituting, we find that at a fixed point

$$q'_p = \frac{(1-a)q'_m(1-x'_m)(n_p-1)n_m P_m}{a(1-x'_p)n_p^2 P_p + q'_m(1-x'_m)(n_p-1+a)n_m P_m} \tag{7a}$$

$$x'_p = a + \frac{q'_m(1-x'_m)(n_p-1+a)n_m P_m}{n_p^2 P_p}. \tag{7b}$$

Similarly, we find that the fixed-point values of trade and direct carbon acquisition for mycorrhizae are

$$q'_m = \frac{bC_p x'_p q'_p n_p (n_m - 1)}{(n_m - b)C_p x'_p q'_p n_p + (1 - b)(I + C_m x'_m) n_m^2} \tag{7c}$$

$$x'_m = \frac{bC_p x'_p q'_p n_p - (C_p x'_p q'_p n_p + I n_m) n_m + b(I + C_m) n_m^2}{C_m n_m^2}. \tag{7d}$$

We find that there is a unique solution that satisfies equation (7a-d)

$$(x'_p, q'_p, x'_m, q'_m) = \left( a, 0, b + \frac{I(1-b)}{C_m}, 0 \right). \tag{8}$$

Any mutant in either species that uses a different strategy to the one specified in equation (8) has lower fitness as long as individuals in both species can acquire both resources directly, hence equation (8) defines a pair of ESSs when  $C_p, C_m$  or  $I, P_p$ , and  $P_m$  are positive.

In addition, plants and mycorrhizae are constrained to allocations to direct carbon acquisition and trade between 0 and 1. We look for other pairs of ESSs that are constrained maxima on this boundary. We eliminate  $x'_p = 0$  and  $q'_p = 1$  as this would leave plants without carbon, and  $x'_m = 1$  and  $q'_m = 1$  as this would leave mycorrhizae without phosphorus. We first set  $x'_p = 1$  and work out the evolved best response values for the other variables if all other individuals use the same strategy:

We verify whether fitness at  $x_p = 1$  is greater than at  $x_p < 1$ , given the corresponding values of  $q'_p, x'_m$ , and  $q'_m$ :

$$\frac{\partial w_p}{\partial x_p} |_{x'_p=1} > 0 \Leftrightarrow \frac{C_p P_m}{P_p((1-b)I + bC_m)} > \frac{n_p n_m}{(n_p - 1)(n_m - 1)}. \tag{10}$$

In the parameter region from equation (10), the best response values in equation (9) are feasible (and eq. 9 is thus a pair of ESSs) if

$$C_p \geq \frac{(bC_m - I(1 - b))(n_p - 1 + a)n_m^2}{(1 - a)(n_p - 1)n_p(n_m - b)}. \tag{11}$$

We can also set  $x'_m = 0$  and find a pair of ESSs by the same method with

$$(x'_p, q'_p, x'_m, q'_m) = \left( \frac{e}{C_p(n_p - 1)n_p^2(n_m - b)P_p}, \frac{(n_p - 1)n_m(bC_p(n_p - 1)(n_m - 1)P_m - I(1 - b)n_p n_m P_p)}{e}, 0, \frac{(n_p n_m - n_p - n_m + 1)P_m C_p b - I(1 - b)n_p n_m P_p}{C_p(n_p - 1)(n_m - b)P_m} \right) \tag{12}$$

$$P_p \leq \frac{bC_p(n_p - 1)(n_p - 1 + a)(n_m - 1)n_m P_m}{n_p((1 - a)C_p(n_p - 1)n_p n_m + I(1 - b)(n_p - 1 + a)n_m^2 - (1 - a)bC_p(n_p - 1)n_p)}. \tag{13}$$

Finally, we set  $x'_p = 1$  and  $x'_m = 0$ . We find that

$$(x'_p, q'_p, x'_m, q'_m) = \left( 1, \frac{(1 - a)(n_p - 1)}{n_p - 1 + a}, 0, \frac{(1 - a)bC_p(n_p - 1)n_p(n_m - 1)}{(1 - a)C_p(n_p - 1)n_p(n_m - b) + I(1 - b)(n_p - 1 + a)n_m^2} \right). \tag{14}$$

These strategies are a pair of ESSs when both inequality (11) and inequality (13) are satisfied.

where expression

$$e = n_p (a (n_m - b) C_p (n_p - 1) n_p - I (1 - b) (n_p - 1 + a) n_m^2) P_p + b C_p (n_p - 1) (n_p - 1 + a) (n_m - 1) n_m P_m.$$

Fitness is also maximized at  $x'_m = 0$  in the parameter region defined by equation (10), given the best response values in equation (12). These are feasible when

### Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

**Supporting information 1.** Economic Background and Future Avenues.

**Supporting information 2.** Alternative Resource Sharing Rules.

**Figure S1.** Probability distribution of  $C_{t1}$  and  $C_{t2}$ .