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Partner selection in the mycorrhizal mutualism

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Summary

Partner selection in the mycorrhizal symbiosis is thought to be a key factor stabilising the mutualism. Both plant hosts and mycorrhizal fungi have been shown to preferentially allocate resources to higher quality partners. This can help maintain underground cooperation, although it is likely that different plant species vary in the spatial precision with which they can select partners. Partner selection in the mycorrhizal symbiosis is presumably context-dependent and can be mediated by factors like (relative) resource abundance and resource fluctuations, competition among mycorrhizas, arrival order and cultivation history. Such factors complicate our current understanding of the importance of partner selection and its effectiveness in stimulating mutualistic cooperation.

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I. Introduction

Mutualisms are vulnerable to exploitation by less cooperative partners because it is beneficial for individuals to obtain the benefits of cooperation, while not paying the full cost of cooperation (Ghoul *et al.*, 2014). This is particularly true when there are multiple partners on both sides of the interaction, such as in the plant–mycorrhizal mutualism. Here, multiple fungi interact with individual plant hosts (Johnson *et al.*, 2012) and multiple plants can tap into a mycorrhizal network (Weremijewicz & Janos, 2013) making it potentially difficult to evaluate the contribution of an

individual partner. Why is the mycorrhizal–plant partnership one of the world's most ancient and widespread symbioses if partners can potentially exploit the benefits provided by others?

Here, we discuss the role of partner selection in stabilising the mycorrhizal symbiosis, including mechanisms of preferential allocation that divert resources to high-quality partners. Partner selection allows individuals on both side of the exchange to associate preferentially with high-quality partners: this creates a selective pressure to invest in your mutualistic partner, which can counteract incentives for cheating (Noë & Hammerstein, 1994) and is especially important in stabilising mutualisms involving

symbiotic partners acquired directly from the environment. We review the evidence for partner selection in the mycorrhizal symbiosis, both on the plant and fungal sides, largely focusing on the arbuscular mycorrhizal fungi (AMF). We interpret this in a biological market framework (i.e. the idea that mutualists exchange commodities in a manner similar to human economic markets), ask about the mechanisms that could mediate such partner discrimination, and identify factors that can impact on its strength and importance.

II. Bidirectional partner selection in the arbuscular mycorrhizal symbiosis

The most common type of mycorrhizal symbiosis is between plants and arbuscular mycorrhizal fungi, in which the fungal partner trades soil nutrients – primarily phosphorus – for carbohydrates with plants (Parniske, 2008). In the field, plant hosts associate with multiple AMF that can differ in terms of the growth benefits that they provide to the host (Johnson *et al.*, 2012), so a major question concerns the role of plant partner selection in determining the success of these fungi.

In a seminal study, Bever *et al.* (2009) used radioactively labelled carbon in a split-root system to demonstrate that *Allium vineale* plants preferentially allocated photosynthate to the side of the root system colonized by a more mutualistic AMF, which resulted in a higher spore production compared with a nonbeneficial AMF species. However, this effect disappeared when the fungi were mixed on the same root system, stimulating the question: at what spatial scale can hosts discriminate among different fungi? To study host allocation patterns on a smaller scale, Kiers *et al.* (2011) used molecular markers and stable isotope probing to track carbon flow from *Medicago truncatula* hosts into fungal RNA when roots were colonized by mixed fungal communities. They found that the RNA of the more beneficial AMF species was significantly more enriched with host carbon, suggesting that preferential host allocation can operate at small spatial scales in some plants. A follow-up multi-generational study in *Plantago lanceolata* revealed that partner selection was actually more efficient in well-mixed soil, suggesting that host selection in some plants can operate at fine spatial scales (Verbruggen *et al.*, 2012). The potential variation among host species in precision of selection remains an open question (Fig. 1a). For example, variation may be based on plant traits such as degree of root coarseness, with coarser roots (such as in *Allium* sp.) showing a decreased ability for fine-scaled partner selection.

Like host plants, mycorrhizal fungi are also under selection to maximize nutrient uptake. Allocating more resources to hosts providing more carbon can help achieve this. Experiments using root organ culture have shown that AMF will preferentially allocate phosphorus to root clusters providing more carbon (Lekberg *et al.*, 2010; Kiers *et al.*, 2011). Because of the artificial nature of root organ cultures, these ‘fungal choice’ experiments were recently scaled up to whole plants, where host quality was varied by shading one of the two plants in a common mycelium network. Testing two different species of AMF, Fellbaum *et al.* (2014) found that both fungal species preferentially allocated nitrogen and phosphorus to

nonshaded plants over shaded plants. However, patterns of fungal choice are not consistent across all systems. Walder *et al.* (2012) found that fungi allocated more nutrients to flax (*Linum usitatissimum*) than to sorghum (*Sorghum bicolor*) when connected by a single fungus, despite sorghum’s higher carbon investment in the mycorrhizal network. Whether fungal allocation patterns can be strictly correlated to host quality will require a series of elegant experiments that employ a larger range of plant–fungal combinations. The trick will be to standardize for all variables, for example fungal colonization levels (e.g. Fellbaum *et al.*, 2014), while varying only host quality.

III. Nutrient transport and partner selection

Although evidence of preferential allocation has emerged over the last 5 yr, the mechanisms behind these patterns are still unknown. Pioneering research is beginning to elucidate the role of transporters in mediating nutrient transfer across the plant–mycorrhizal interface. Such research is revealing fine-scaled regulation of transporter genes, potentially even at the level of individual cells colonized by arbuscules, influenced by local nutrient concentrations in and around these cells (Doidy *et al.*, 2012; Gutjahr & Parniske, 2013; Koegel *et al.*, 2013; Xie *et al.*, 2013). Such dynamics could give rise to positive coupling of nutrient transport from plant to AMF, effectively resulting in quality-based bidirectional partner selection. A major question is whether such partner selection is based on absolute amounts of nutrients or relative contributions, allowing a comparison of competing AMF. If there are absolute thresholds levels, are these thresholds fixed or variable with the environment? Across what scales can AMF preferentially allocate resources to physically separated plant hosts (Fellbaum *et al.*, 2014)? How and over which distance are plants and mycorrhizal fungi able to integrate information about partner quality and use this information to act accordingly (Werner *et al.*, 2014a)? These are pressing questions that will require research using very fine-scale manipulations of nutrient movement.

IV. Mycorrhizal partner selection: an underground biological market?

One area that has shown continuous progress is our theoretical understanding of what drives partner selection dynamics (e.g. Steidinger & Bever, 2014). Borrowing from economic theory, recent work has explored how the mycorrhizal mutualism can function in a way that is analogous to a human economic market (Franklin *et al.*, 2014; Wyatt *et al.*, 2014). If both plants and mycorrhizal fungi allocate resources based on which partner offers the best ‘price’ per unit of the invested resource, this can lead to stable resource trading in a ‘biological market’ (Noë & Hammerstein, 1994). Such competition among partners over the price they provide goods can be driven by natural selection and result in ‘linear proportional discrimination’ as an evolutionarily stable strategy (Wyatt *et al.*, 2014). This means that individuals are favoured to allocate resources in direct proportion to the relative amount of benefits they receive from each partner, when others do

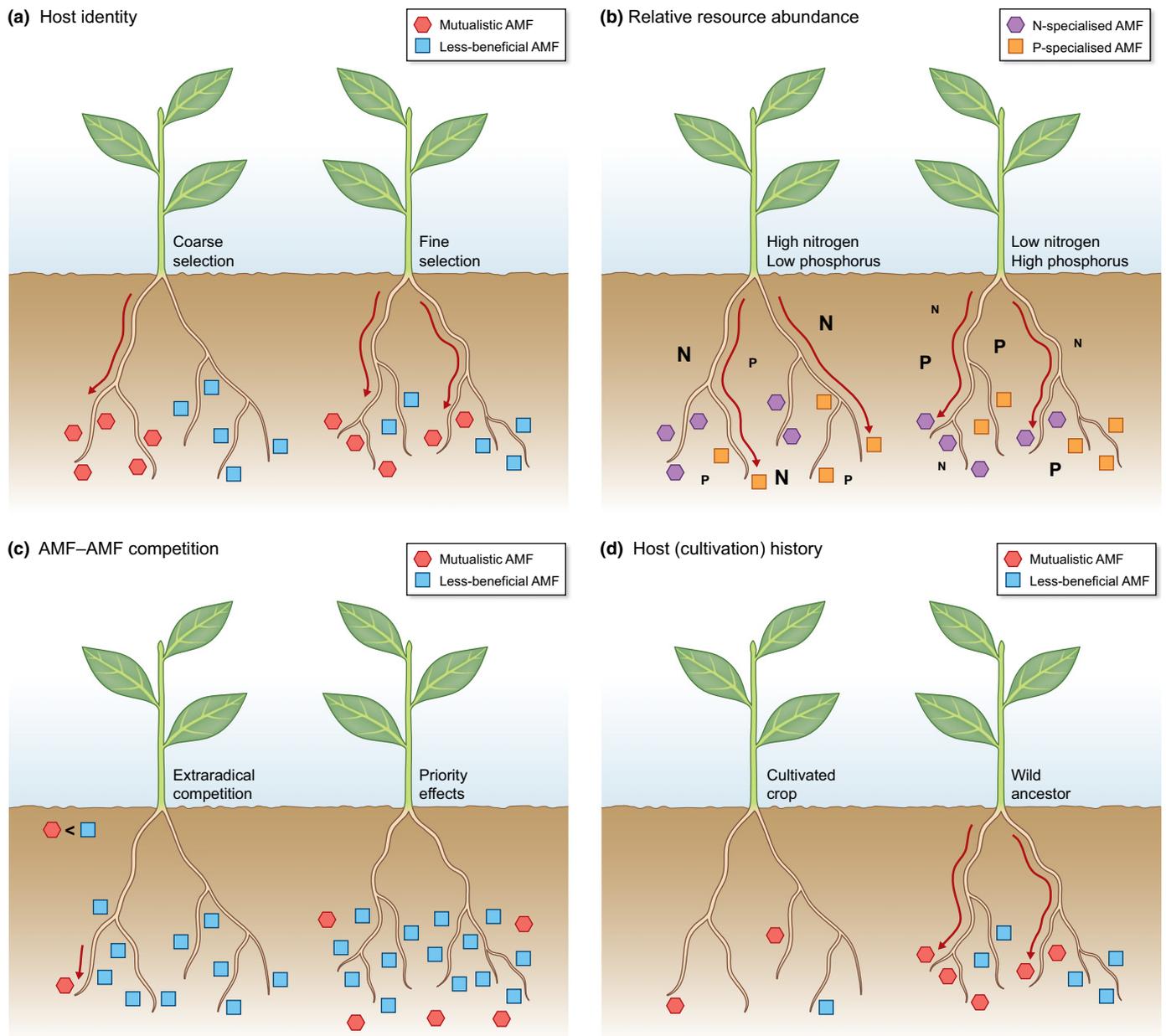


Fig. 1 Potential factors influencing partner selection in the plant-mycorrhizal symbiosis. Red arrows indicate the preferential allocation of photosynthate to mutualistic (red) over less-beneficial (blue) arbuscular mycorrhizal fungi (AMF). (a) The spatial precision of partner selection potentially varies by host plant. Some host plants, such as *Allium vineale* (Bever *et al.*, 2009), are thought to only discriminate spatially segregated AMF (coarse selection), whereas others, such as *Medicago truncatula* and *Plantago lanceolata* (Kiers *et al.*, 2011; Verbruggen *et al.*, 2012) can select mycorrhizal partners that are mixed at very fine spatial scales (fine selection). A host plant only capable of coarse partner selection probably cannot effectively select its mycorrhizal partner in a field setting where AMF are usually mixed. Potentially, such plants experience more mycorrhizal cheating. (b) Relative resource abundances can affect plant selection of AMF (Johnson *et al.*, 2013). In phosphorus (P)-limiting conditions (left), plants are expected to select AMF species offering the best P to carbon (C) exchange ratio (orange), whereas in nitrogen (N)-limiting conditions (right) they would preferentially select AMF specialised in providing nitrogen (purple). (c) Competition among AMF can affect plant partner selection. To the left, a hypothetical case is depicted where a less-beneficial AMF is superior to the mutualistic AMF in extraradical competition, directly reducing the abundance of the mutualistic AMF at the roots and limiting the potential for preferential allocation of photosynthate. In this case, plant partner selection and extraradical competition are counteracting forces: the ultimate success of both AMF species will depend on their relative strength. To the right, a scenario is shown where a prior arriving AMF has already fully colonized the host (priority effects), preventing further colonization by a second (in this case more beneficial) AMF. (d) Host (cultivation) history could also affect partner selection. Compared with wild plants (right), bred cultivars (left) often have reduced interactions with mycorrhizal fungi (Xing *et al.*, 2012) and potentially a reduced ability to select high-quality AMF, like in other root mutualisms (Kiers *et al.*, 2007).

likewise. Additionally, theoretical models predict that traders can specialise to such an extent that they lose the capacity to independently acquire the resource obtained through trade

(Schwartz & Hoeksema, 1998; Grman *et al.*, 2012; Wyatt *et al.*, 2014). This prediction is thought to have occurred in the AMF that specialise in acquiring soil nutrients and have lost the capacity to

autonomously obtain carbon, becoming obligate biotrophs (Parniske, 2008).

Market theory can also help in explaining the benefits of interacting with multiple partners, rather than selecting a single AMF. Like human markets, external variation, for example access to resources, can drive changes in prices (Noë & Hammerstein, 1994; Werner *et al.*, 2014a). Similar dynamics emerge in the mycorrhizal mutualism: partner benefits are both context-dependent and temporally variable. A market model revealed that, under the biologically realistic assumption that mycorrhizal resource price depends on the amount of resources exchanged, plants are favoured to maintain multiple mycorrhizal partners (Kummel & Salant, 2006). In fact, trade is more likely to be favoured when individuals are able to interact with more partners of both species (Wyatt *et al.*, 2014). Additionally, it is well known that AMF provide a range of benefits from phosphorus and nitrogen nutrition, to pathogen and stress protection (Parniske, 2008), making it difficult to define the exact parameters of a 'high-quality' fungus. The relative importance of these different benefits to the plant might differ over time: currently nonbeneficial AMF might become useful partners when the environment changes.

Ultimately, environmental context is key in any market model (Noë & Hammerstein, 1994). If biological markets are an accurate representation of mycorrhizal–plant resource exchanges, the resulting 'price' of resources should depend on environmental fluctuations in the availability of partners and resources; that is, on the fluctuating balance between supply and demand. This could be tested, for example, by varying phosphorus concentration and asking whether the amount of carbon allocated per unit of phosphorus (or the phosphorus 'price') falls with increasing phosphorus supply, as predicted by market models. This also raises the intriguing question of what factors most strongly influence the strength of partner selection. If, like general colonization suppression (Grman, 2012; Grman & Robinson, 2013), partner selection is a plastic trait, we expect its importance to depend on environmental factors. We now briefly discuss three potential environmental and evolutionary factors that could affect partner selection (Fig. 1b–d).

V. Potential factors influencing partner selection in the mycorrhizal symbiosis

Resource abundance

The abundance of nutrients in an ecosystem, particularly the relative availability of phosphorus and nitrogen, is of crucial importance for mycorrhizal functioning (Johnson *et al.*, 2013). In phosphorus-poor but nitrogen-rich conditions, a unit of phosphorus is relatively valuable and will fetch a high price in terms of plant carbon: plants should actively select mycorrhizal partners efficient at extracting and providing phosphorus (Fig. 1b). A similar reasoning applies to fluctuations in the availability of carbon. Factors that increase the amount of available carbon, such as elevated atmospheric CO₂ concentration or high light intensity, increase the relative value of soil nutrients to plants. When modelled in a market framework, mycorrhizal fungi are predicted to be competing for a larger pool of

plant carbon under high CO₂ concentrations, encouraging them to transfer more phosphorus, although this will be moderated by the increasingly limiting role of phosphorus throughout the system. This could select for stronger partner selection and higher mycorrhizal cooperativeness (Wyatt *et al.*, 2014).

Competition among mycorrhizal fungi

Although the host (and host selection dynamics) plays a large role in mediating the success of the mycorrhizal symbionts, fungal fitness does not depend only on plant partner selection (Kennedy, 2010). Instead, AMF also face direct competition from other AMF, both intraradically and in the soil (Engelmoer *et al.*, 2014; Thonar *et al.*, 2014). The outcome of this competition can affect the level and efficiency of partner selection by plants (Fig. 1c). For instance, if a mycorrhizal species is very successful in extraradical competition, this could limit the potential pool of species to choose from, reducing the effectiveness of partner selection (Verbruggen & Kiers, 2010). High diversity of fungal partners, however, may not be consistently good for partner selection. In one experiment, low-quality strains were found to be able to 'hide in a crowd' of highly beneficial AMF (Hart *et al.*, 2012), suggesting that high fungal diversity on a root system can also have drawbacks.

A second way that competition among mycorrhizal fungi can affect partner selection is through priority effects. Priority effects occur when a species can outcompete another competitively dominant species by arriving in the ecosystem earlier and have been observed in ectomycorrhizal fungi (ECM) (Kennedy *et al.*, 2009; Kennedy, 2010) and in laboratory studies with AMF (Werner & Kiers, 2014). Such differences in arrival order can limit the potential for plant partner choice because arriving sequentially rather than simultaneously could prevent host comparison of mycorrhizal phosphorus prices, forcing the plant to 'take or leave' the available offer (Werner & Kiers, 2014).

Plant and fungal identity: evolutionary and cultivation history

Whether or not partner selection operates in other mycorrhizal mutualisms, such as ectomycorrhizas, is still unknown (Franklin *et al.*, 2014). In extreme cases, such as in nonphotosynthetic mycoheterotrophic plants, hosts have escaped fungal discrimination mechanisms and there is no strict control in the exchange of phosphorus for carbon (Selosse & Rousset, 2011). In AMF, partner selection has been found to be variable in the few plant species where it has been studied so far (Bever *et al.*, 2009; Kiers *et al.*, 2011; Verbruggen *et al.*, 2012). One way forward is to ask: is there a relationship between host selectiveness and host (evolutionary) history? A good place to study this phenomenon is in crops bred for agricultural systems. Typical high-nutrient conditions in intensive agriculture can reduce mycorrhizal benefit (Verbruggen & Kiers, 2010), and have resulted in reduced mycorrhizal dependence in some cultivars (Xing *et al.*, 2012). Does reduced dependence also mean reduced ability to discriminate, as has been found in another plant–microbe mutualism (Fig. 1d; Kiers *et al.*, 2007)?

VI. Conclusions

Research into partner selection in the mycorrhizal symbiosis is still in its infancy. Even defining a 'high-quality' partner is difficult because quality varies with environmental conditions (Johnson & Graham, 2012; Smith & Smith, 2013) and encompasses many possible benefits. We can begin to overcome these challenges by cataloguing partner quality (nutrient provisioning but also other benefits such as water uptake and pathogen protection) over a range of well-defined conditions. We know from artificial systems like root organ cultures (Lekberg *et al.*, 2010; Hammer *et al.*, 2011; Kiers *et al.*, 2011) and glasshouse experiments (Bever *et al.*, 2009; Fellbaum *et al.*, 2014) that partner selection can exist on both sides of the partnership, and has the potential to produce an underground market (Kiers *et al.*, 2011; Grman *et al.*, 2012; Franklin *et al.*, 2014; Steidinger & Bever, 2014; Wyatt *et al.*, 2014). However, the field of mycorrhizal partner selection needs more data on its strength and importance in natural settings. This should include analyses of less common hosts, such as mycoheterotrophic plants.

Why are some species more precise or efficient at partner selection than others, and how does this relate to their evolutionary histories? One approach to answering this question is to catalogue partner selection occurrence across the plant phylogeny and to test hypotheses of its genetic and ecological correlates using a comparative phylogenetic framework (e.g. Werner *et al.*, 2014b). Lastly, we argue for more extensive theoretical analysis to derive quantitative and testable hypotheses regarding the evolution of mycorrhizal partner selection (e.g. Steidinger & Bever, 2014; Wyatt *et al.*, 2014). For instance, is partner selection more important in mycorrhiza-dependent plant species because of a high fitness cost associated with low-quality partners, or less important because any mycorrhizal partner is better than none? We need theoretical work analysing the relative costs and benefits of selectiveness under diverse conditions, followed by experimental testing of these predictions. Overall, we expect the emerging field of partner selection to be an important component of mycorrhizal research, as it can help us interpret the history, evolution, ecology of this mutualism, including its agricultural applications.

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