



Review in Advance first posted online
on September 23, 2009. (Minor changes may
still occur before final publication
online and in print.)

Mycorrhizal Symbioses and Plant Invasions

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Annu. Rev. Ecol. Evol. Syst. 2009. 40:699–715

The *Annual Review of Ecology, Evolution, and Systematics* is online at ecolsys.annualreviews.org

This article's doi:
10.1146/annurev.ecolsys.39.110707.173454

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1543-592X/09/1201-0699\$20.00

Key Words

arbuscular mycorrhizal, conservation biology, ectomycorrhizal, fungi

Abstract

The factors that influence a plant's ability to invade are not well understood. Many mechanisms are involved and the relative importance of different mechanisms depends on the specific invasion. Here we consider one factor—mycorrhizal symbioses. These symbioses are ubiquitous interactions involving the plants and soil fungi of most terrestrial ecosystems. We develop a conceptual framework for considering mycorrhizal symbioses in plant species invasions. The most critical aspects of this framework are: (a) the mycorrhizal status and (b) the growth response of the invading plant, (c) the ability of the plant to associate with different fungi, (d) the quality of the plant as a host for local fungi and feedback dynamics, (e) the biogeography and dispersal of the fungi, (g) the introduction and spread of the fungi, and (g) the ecological consequences of the creation of novel mycorrhizas. These aspects can critically influence the trajectory of a plant invasion, and this symbiosis deserves more attention in plant invasion biology.

AM: arbuscular
mycorrhizal

EM: ectomycorrhizal

INTRODUCTION

Many plant species have been introduced to new habitats throughout the world, and some also grow in abundance and extend beyond original points of introduction (Lockwood et al. 2007). Plant species that spread extensively in their novel habitats are termed invasive. Some invasive plants may have repercussions on the local, native, community and impact rare and threatened species (Wilcove & Master 2005, but see Gurevitch & Padilla 2004) or influence ecosystem properties (Razaida et al. 2008). When an invasive plant becomes a target of concern, management plans are drafted for its control. However, to craft an effective management plan, it is important to understand the mechanisms involved in the invasion process.

A vast literature on plant invasions makes clear that no single mechanism can explain invasiveness. The potential for a plant species to become invasive can be influenced by its niche, competitive ability, reproductive potential, and the evolution of these traits in the novel habitat (Leger & Rice 2003, Blair & Wolfe 2004). A species' ability to invade can also be influenced by characteristics of the habitat being invaded, including the novel biotic interactions that may occur in a new range (Mitchell et al. 2006). Specialist herbivores and pathogens have been the focus of research directed at these novel biotic interactions, and form the basis of the enemy release hypothesis (Mitchell & Power 2003, Torchin et al. 2003). Much less work has focused on the potential for mutualistic interactions to alter invasion success [but see reviews by Richardson et al. (2000) and Mitchell et al. (2006)]. Even so, mutualisms can be the central force shaping a species' ecology (Herre et al. 1999), and mutualisms between pairs of exotic species may be at least as common as parasitisms (Simberloff & Von Holle 1999). As a result, the introduction of one species may facilitate subsequent invasions by other species (Mandon-Dalger et al. 2004).

In this review, we focus on a common symbiosis that involves most plant species, the mycorrhizal symbiosis, and discuss how this symbiosis may affect the ability of a plant species to invade. When a plant species is associated with mycorrhizal fungi the symbiosis may constrain or facilitate the spread of the plant. Understanding if and how the mycorrhizal association influences plant invasion may be a key aspect of the ecology and management of invasive plant species, as well as the conservation biology of native habitats.

Mycorrhizas are symbioses between plants and fungi. The association is ancient; fossil symbioses date to 460 Mya (Redecker et al. 2000). Nearly 95% of the world's plant species belong to families that are characteristically mycorrhizal, and although the mycorrhizal status of most species has not been explicitly probed, 80% of surveyed land plant species are mycorrhizal (Smith & Read 2008, Trappe 1987, Wang & Qiu 2006). The fungi involved in the symbiosis are not a monophyleticity and associations may involve any of four different fungal phyla. The symbioses are often classed as either arbuscular mycorrhizal (AM) or ectomycorrhizal (EM), and the different types are defined by both the taxonomy of the fungi as well as the structures formed in or around plant roots (Smith & Read 2008). In addition to AM and EM symbioses, mycorrhizal associations include arbutoid, monotropoid, ericoid, and orchid forms. Mycorrhizal symbioses are generally considered as mutualisms. Plants and fungi trade resources, often exchanging photosynthetically derived C for P and N scavenged from soils. Other benefits have been ascribed to the mutualism, for example, protection from soil pathogens (Borowicz 2001) and enhanced tolerance to drought (Augé 2001). As with most other mutualisms, the degree of benefit derived by each partner depends on the particular context of an association, and in some cases the symbiosis is a parasitism (Johnson et al. 1997, Jones & Smith 2004).

We identify critical aspects of the symbioses of plants and mycorrhizal fungi that will influence the trajectory of a plant species' invasion. These aspects include:

1. *The mycorrhizal status of the invading plant.* Does it form mycorrhizas? A number of plants do not form mycorrhizal symbioses, and many invasive plants are nonmycorrhizal.
2. *The growth response of the invading plant.* If the plant does normally form mycorrhizas, is the association obligate, and does the plant require a fungus for germination and growth? Or is the association facultative? If facultative, is the plant less responsive to infection, as compared to native plant species? Which contexts maximize the exchange of benefits?
3. *The ability of the invading plant to associate with different fungi.* Does the plant require specific fungi to form a mycorrhizal symbiosis? Or is it flexible, and can it form the association with a phylogenetically diverse array of fungi? If the plant requires a specific fungus in the novel habitat and the fungus is not locally available, the mycorrhizal symbiosis will serve as a constraint.
4. *The benefit a plant provides to a mycorrhizal fungus and feedback dynamics in plant invasions.* Is the invading plant species a quality host for all fungal species or for particular fungal species? The quality of the interactions among plants and fungi, both fungal responses to plant hosts and plant responses to infection by mycorrhizal fungi, will determine the plant-fungal feedback dynamics, which can greatly influence plant invasion dynamics.
5. *The biogeography and dispersal biology of the fungi.* If every species of mycorrhizal fungus were evenly distributed across the globe, the mycorrhizal association would never serve as a constraint. Of course, fungi do have more restricted ranges, and emerging knowledge of fungal biogeography is of particular importance when discussing the invasion biology of plant species that may specialize and require specific fungi. The dispersal biology of mycorrhizal fungi is also relevant, as fungi that can easily disperse may independently reach the novel habitats of introduced plant species.
6. *Introductions of mycorrhizal fungi.* Very recent work has focused on the transport of mycorrhizal fungi by humans; humans have in many cases moved plants with intact root systems and so packaged the mycorrhizal association as a portable symbiosis. When mycorrhizal fungi are introduced to a habitat with introduced mycorrhizal plants those plants may more easily spread. Whether the fungi that are moved to novel habitats commonly persist and establish independently of introduced plants remains an open question.
7. *Community and ecosystem consequences of the creation of novel mycorrhizas.* Does the arrival of novel fungi, and the creation of novel combinations of plants and fungi, influence the local community and its functioning?

Before discussing each of these ideas in more detail, we provide a simple conceptual framework of mycorrhizas in plant invasions. Although the framework is intended to focus our discussion of mycorrhizal controls on plant invasions, aspects of the framework can be used to understand the constraints imposed by any symbiosis on any species invasion.

A CONCEPTUAL FRAMEWORK FOR CONSIDERING MYCORRHIZAS IN PLANT INVASIONS

In this framework a plant is classified according to three criteria: (a) It either does or does not require a mycorrhizal fungus to germinate and grow, and is either obligate or facultative; (b) it either requires a specific fungus or can associate with a phylogenetically diverse array of fungi, and is either specific or flexible; and (c) it is either transported with or independently of its mycorrhizal fungus; the mycorrhizal association is either transportable or not transportable (**Figure 1**).

Each of the criteria can be combined to give a specific prediction for whether a plant that is, for example, as in Case 1, a nonmycorrhizal or facultatively mycorrhizal plant (regardless

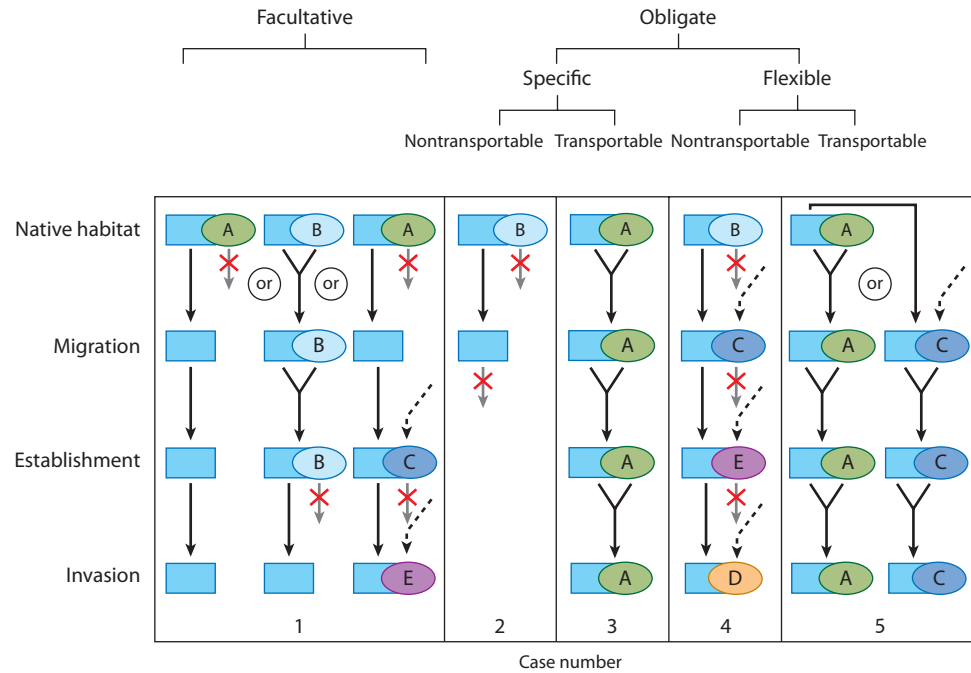


Figure 1

In this schema a square depicts a plant and an oval depicts an associated root fungus. Colors and numbers designate different species. For example, the facultative case depicts a plant species that can grow without symbionts or associate with a variety of fungal species; it emigrates alone or is planted in a novel habitat as a seedling with its symbiont, and may subsequently establish and spread without fungal associates, or with the original, or a third or fourth mycorrhizal species (*Case 1*). In contrast, when a plant associated in an obligate, specific, and nontransportable mycorrhizal association is introduced to a novel habitat without its mycorrhizal fungus, it cannot establish or spread (*Case 2*). Plants associated in obligate symbioses but moved with mycorrhizal associations intact may more easily spread because the symbiosis is transportable (*Case 3*); plant species that are generalists and flexible will associate with a diversity of fungal species and may also spread (*Case 4*). Obligate and flexible plant species may be moved with intact symbioses but will also spread with local fungal symbionts (*Case 5*).

of whether the plant is specific or obligate, and the mycorrhizal association transportable or not transportable) can successfully invade (**Figure 1**). A prediction of the framework is that mutualism will pose no barrier to the invasion of a nonmycorrhizal or facultative mutualist. In contrast, in *Case 2*, plants associated in obligate and specific mycorrhizal associations will not successfully establish or spread within a novel habitat unless they are moved with intact symbioses (*Case 3*). A plant that obligately requires the mycorrhizal association may also successfully invade if it is flexible (*Case 4*), and can associate with local fungi. Finally, in *Case 5*, a plant that obligately requires the mycorrhizal association but is both flexible and also moved with intact symbioses is very likely to be a successful invasive species.

The criteria can be used to formulate three hypotheses:

1. An invasive plant is likely to be a nonmycorrhizal or a facultative symbiont.
2. An invasive plant that is obligately dependent on the mycorrhizal association is likely to be flexible as regards the species with which mutualism is formed and will associate with local fungi. Empirical work related to this prediction is discussed by Richardson et al. (2000); typically, invasive plant species requiring pollinator or other microbial mutualists are



generalists and can associate with a diverse array of symbionts. This prediction is also made by Rejmanek (2000).

3. An invasive plant that is obligately dependent on specific fungi is likely to have been moved with its symbionts intact, or will spread in habitats where appropriate mutualists already grow, or after symbionts are independently introduced.

The framework and associated examples illustrate general points on the theme of mutualism and invasion: invasion is facilitated when organisms are not associated in mutualism, or are facultative mutualists; invasion may be hindered by an organism's association in an obligate mutualism. The impact of an obligate mutualism on the trajectory of an invasion can be mitigated if the species is either flexible, and associates with local biota (and in this case mutualism may even facilitate invasion), or if the species is moved with its symbiont, or moved to territory where the symbiont is already established. Predicting whether or not an introduced species will invade is a major ecological priority (Grotkopp et al. 2002, Kolar & Lodge 2001, Mack et al. 2000). According to this framework, a mutualism's influence on the invasion process can be predicted by an organism's association in facultative, flexible, or transportable mutualisms.

We now use the framework to explore each of our seven key points:

1. *The mycorrhizal status of the invading plant.* The very limited data available suggest that, as predicted by the framework, many invasive plants do not associate with mycorrhizal fungi, or employ a flexible strategy and can be mycorrhizal or not depending on context, or associate with different types of mycorrhizal fungi (e.g., AM and EM species). To reach this conclusion we used the database held by NatureServe (<http://www.natureserve.org/explorer>) and generated a list of vascular plants with a U.S. Invasive Species Impact Rank (I-Rank) of "high." The list includes a total of 82 species. Each species' mycorrhizal status was checked using Wang & Qiu (2006). Not surprisingly, the mycorrhizal status of most of these invasive species is unknown. Data are available for only 33 species, of which 15 associate with AM fungi, and 18 are either nonmycorrhizal, facultatively mycorrhizal, or associated with multiple kinds of mycorrhizal fungi.

To understand whether more destructive invasive plants show a pattern different from species with minimal impacts we did the same analysis with the 74 exotic species listed as having an I-Rank of "insignificant." Unfortunately, there is no information in Wang & Qiu (2006) for 61 of the 74 plant species; data are available for only 13 species. Seven of these plants associate with AM fungi and the rest are nonmycorrhizal or employ a mixed strategy. Although the data suggests that invasives with low impact are more likely to be obligately mycorrhizal than invasives of great impact (45% of "high" impact invasive plant species are obligately mycorrhizal; 53% of "insignificant" impact invasives are obligately mycorrhizal), there is not enough data to suggest a trend. It is fairly simple to determine the mycorrhizal status of a plant, and because mycorrhizal fungi can influence the trajectory of the invasion process (Vogelsang & Bever 2009), one useful direction for future research would be to collect data on the mycorrhizal associations of invasive plant species.

We also found evidence for a greater proportion of native species associating with mycorrhizal fungi, as compared to introduced species. For this analysis we turned to lists of the introduced species of California and California's native flora (Hickman 1993). A greater proportion of California's naturalized plant species are from plant families that typically do not associate with mycorrhizal fungi (Gerdemann 1968, Newman & Reddell 1987, Tester et al. 1987, Wang & Qiu 2006), as compared to the native flora (**Figure 2**). The same pattern holds in local floras within the western USA (J.D. Bever, unpublished manuscript). Despite known variability in the mycorrhizal status of species within a plant family (Miller et al. 1999, Wang & Qiu 2006), the pattern nevertheless suggests that reduced dependency on mycorrhizal fungi may be an important dimension of the success of some naturalized plant species. However, this pattern does not hold in Great



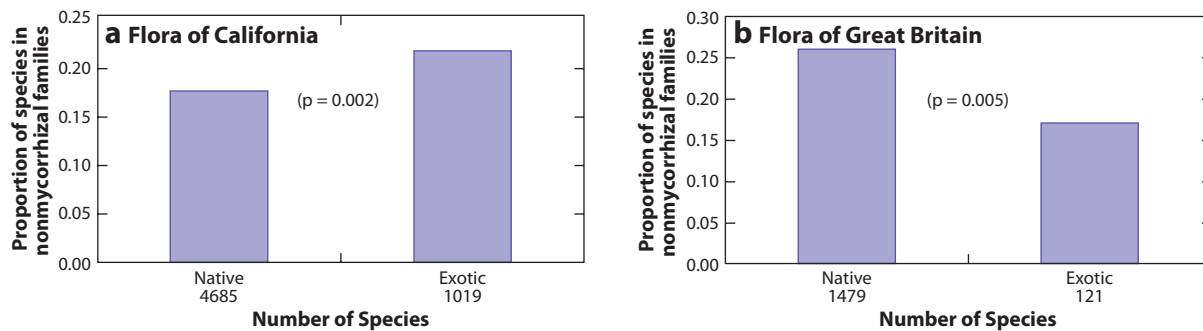


Figure 2

Patterns of nonmycorrhizal species in native and naturalized floras in California and Great Britain. (a) A greater proportion of the naturalized flora in California belongs to nonmycorrhizal families, as compared to the native flora ($\chi^2 = 9.3$, $p = 0.002$). Data from the *Jepson Manual for the Higher Plants of California* (Hickman 1993). (b) A lower proportion of the naturalized flora of Great Britain are from nonmycorrhizal families compared to native flora ($\chi^2 = 10.7$, $p = 0.005$). Data from Fitter (2005).

Britain, where a greater proportion of the naturalized plant species are from plant families that do typically associate with AM fungi, as compared to the native flora (Fitter 2005). The difference in pattern suggests that mycorrhizal status plays a different role in plant invasions in different regions, a theme that we return to later.

2. *The growth response of the invading plant.* Plants can vary widely in their response to an association with a mycorrhizal fungus. In some cases plants require the association for their growth, development, and reproduction and cannot survive in the absence of a fungus. As discussed above, these plants are obligately mycorrhizal. Examples include the many orchids that cannot develop even to the seedling stage without an appropriate fungal partner; these species have tiny seeds and not enough C reserves to grow on their own (Smith & Read 2008). Many EM trees have also been shown to be obligately dependent on suitable mycorrhizal partners, particularly in the field. Although EM tree seedlings typically grow well in the absence of mycorrhizas under ideal laboratory conditions, their survival and growth is often greatly enhanced in the field when suitable fungi are present or have been added (Marx 1991). However, most plants, especially those that form AM associations, are facultatively mycorrhizal. They invariably do form mycorrhizal associations in the field, but they do not require the association to grow, develop, or reproduce. In the absence of mycorrhizal inoculum, the plants still grow. However, they may show responses to mycorrhizal inoculation (Janos 2007). It is not unusual to observe small stimulative effects, for example, a 5%–20% increase in plant biomass, in response to the addition of a mycorrhizal fungus. In many cases, the positive growth effects are larger, and the response can also be negative. The degree of a response is highly dependent on context, and factors influencing the growth response include the nutrient status of the soil environment, other environmental parameters (e.g., light), the plant genotype, and the fungal isolate(s) (Johnson et al. 1997, Klironomos 2003, Pringle & Bever 2008). Although most studies have been done in pots in the laboratory, similar results have been observed in the field (Pringle & Bever 2008).

Ecologists have a poor understanding of how the balance of costs and benefits differs among natal and novel habitats, as there are few data that record the benefits provided by mycorrhizal fungi in original and introduced ranges. However, there are patterns consistent with the suggestions of a reduced dependency of invasive species. For example, reanalysis of measures of mycorrhizal response of 96 plant species found in Kansas demonstrates that native plant species have a greater responsiveness to inoculation with mycorrhizal fungi than introduced plant species have, even

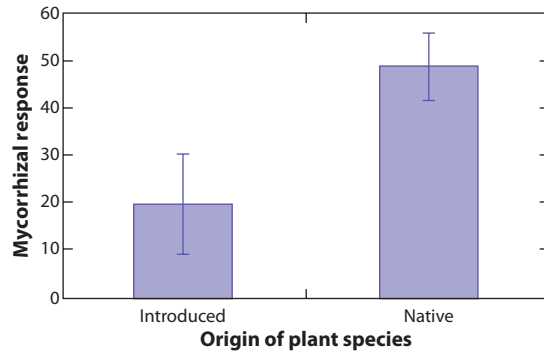


Figure 3

Reanalysis of data from Wilson & Hartnett (1998) demonstrates that plant species native to the Kansas prairie have greater mycorrhizal responses than introduced plant species ($F_{1,73} = 6.7$, $p = 0.01$). Mycorrhizal response was calculated as the difference in plant mass with and without mycorrhizal fungi relativized by mass with mycorrhizal fungi. Plant family (ns) and perenniality ($F_{1,73} = 13.1$, $p = 0.0005$) were also used as predictors. Ls means are presented with error bars representing standard errors.

after controlling for plant family and perenniality (**Figure 3**). In further work on a pair of these plant species, Hetrick & Wilson (1990) demonstrated that this difference was not dependent upon the origin of the mycorrhizal fungi, suggesting that the result was from a generalized difference in mycorrhizal responsiveness. Reduced responsiveness of introduced plant species relative to native plant species was also found for plants of southern California (J.D. Bever, unpublished manuscript).

A comparison of the mycorrhizal dependency of populations of St John's wort from its native Europe and its introduced range in North America suggests that there is selective pressure to evolve reduced dependency on mycorrhizal fungi during plant invasions (Seifert et al. 2009). North American populations of St. John's wort had a significantly reduced response to inoculation with AM fungi, and a correspondingly finer root system, as compared to populations from Europe. Although this pattern is consistent with the increase in the proportion of nonmycorrhizal species observed in invasive species in California but not Great Britain (**Figure 1**) and suggests an asymmetry in the importance of mycorrhizal fungi in the invasion of the North America relative to Europe, further work is required to confirm this pattern.

3. *The ability of the invading plant to associate with different fungi.* Many mycorrhizal plants can form associations with a diversity of fungal species, and when a plant is flexible and can associate with local species of fungi, invasion may be more likely. For example, most plant species that associate with AM fungi seem able to form associations with most AM fungal species, at least in the laboratory. In nature, a few mycorrhizal plant species may form highly specific mutualisms with one or a few AM fungal species (Helgason et al. 2002), but whether these kinds of specific associations are common is unknown.

The invasive *Centaurea maculosa* is an example of a plant associated in an apparently obligate mutualism with AM fungi that is able to form symbioses with a diversity of fungal species; because *C. maculosa* associates with local AM fungi the mutualism does not seem to be a constraint to invasion in western North America. In both its native and introduced ranges the plant is heavily colonized by AM fungi (Marler 1997). AM fungal symbioses are horizontally transmitted and established de novo as seeds germinate in soil; as seeds of *C. maculosa* have propagated, the plant species has been exposed to novel species of fungi. *C. maculosa* can associate with what appear to be local species of AM fungi, and the plant can even use these fungi to its advantage in competition with native grasses (Marler et al. 1999). In this case, the mutualism between an introduced grass

and endemic fungi has facilitated the plant's invasion. Other examples of plant species that can associate with a diversity of AM fungal species include the naturalized plant species of a North Carolina grassland that range from facultatively (*Anthoxanthum odoratum*) to obligately dependent (*Allium vineale*) on AM fungi (Bever et al. 1996). All of these plant species associate with a broad diversity of the resident AM fungi (Bever et al. 1996, 2001; Pringle & Bever 2008).

In contrast, the plants that form EM associations seem to vary more widely in the specificity of the symbiosis. Although some plant species associate with a diversity of fungi (for example, over 2000 species of fungi are recorded as associating with *Pseudotsuga menziesii*; Molina et al. 1992), other species are more specific and can associate with only one or a few genera or species. For example, species in the genus *Alnus* are highly specialized to a handful of species (Molina 1981). In this case mutualism may serve as a barrier to invasion, unless the plants are moved with associated fungi or needed fungi are independently introduced (see section 5 below).

4. *The benefit a plant provides to a mycorrhizal fungus and feedback dynamics in plant invasions.* The interaction of the invading plant and the native mycorrhizal fungi, and dynamics among communities of plants and fungi, can influence the trajectory and impact of a plant's invasion. An introduced plant may alter the density and/or composition of the mycorrhizal fungal community, which may cause positive or negative feedback on the spread of that plant species (Bever 2003; Bever et al. 1997, 2002). For example, the introduced, nonmycorrhizal garlic mustard inhibits native AM and EM fungal growth and thereby increases its competitive success against native species (Callaway et al. 2008, Stinson et al. 2006, Wolfe et al. 2008). Similarly, in California grasslands, the density of AM fungi is suppressed by the dominance of a mixed community of naturalized plant species, and the reduced density of AM fungi inhibits the growth of highly dependent native plant species (Vogelsang & Bever 2009). In both examples, the change in density of AM fungi generated a positive feedback that could push the community to an alternative stable state. The depression of AM fungal density may make the community more vulnerable to invasion by other naturalized plant species, promoting invasional meltdown (Simberloff & Von Holle 1999).

A change in the composition of a mycorrhizal fungal community may also inhibit plant invasion. For example, the naturalized facultative host, *Plantago lanceolata*, was found to grow well with the fungal species that accumulate with the native grass, *Panicum sphaerocarpon*, but is inhibited by the species of AM fungi that accumulate with itself (Bever 2002). In this case, negative feedback dynamics prevent *P. lanceolata* from completely replacing the native plant species.

Change in the composition of the AM fungal community may also reinforce invasion. This possibility is supported by suggestions of positive feedback through the mycorrhizal fungal community for several introduced plant species in Canada (Klironomos 2002). It also may be an important factor in the success of the invasive *C. maculosa*, as the composition of the AM fungal community in its roots is different from the composition of AM fungi in roots of native plant species (Mummey & Rillig 2006), and when grown together, roots of native plants with neighboring *Centaurea* have modified AM fungal community composition (Mummey et al. 2005). Similar changes have been observed in invasive grasses in the western United States and in African savanna (Hawkes et al. 2006, Van der Putten et al. 2007).

5. *The biogeography and dispersal biology of the fungi.* The distributions and biogeographies of all fungi are determined by the morphological features that limit dispersal, the ecological characters that determine whether or not a habitat is suitable, and the mating systems that dictate population establishment and persistence. Historically, it was hypothesized that microorganisms would possess cosmopolitan distributions: microorganisms would disperse across the globe, and environmental factors would limit the establishment of a species at a given location (Baas-Becking 1934). However, as biologists turned to molecular tools to delineate species and explore microbial distributions, it became clear that both bacteria and fungi have geographically organized

population structures and follow patterns of isolation by distance (see Martiny et al. 2006, Taylor et al. 2006 for reviews). Examples of fungal species with these kinds of biogeographies include both saprotrophic species, including *Pleurotus* spp. (Vilgalys & Sun 1994) and *Schizophyllum commune* (James et al. 2001), and EM species, for example, *Rhizopogon* spp. (Grubisha et al. 2007, Kretzer et al. 2005), *Russula brevipes* (Bergeman & Miller 2002), and *Tricholoma sculpturatum* (Carriconde et al. 2008). Furthermore, when multiple loci are sequenced from across the global distribution of saprotrophic species defined by morphology, the concordance of gene genealogies often suggests multiple, phylogenetically distinct species that share a similar appearance but are nonetheless distinct lineages [e.g., *Neurospora* (Dettman et al. 2003), *Saccharomyces paradoxus* (Kuehne et al. 2007)].

In fact, EM species previously defined according to morphology are also found to harbor multiple, phylogenetically distinct lineages, and these species also exhibit patterns of intercontinental divergence, probably the result of dispersal limitation. For example, results from a global survey of the false-truffle genus *Pisolithus* showed that what was formerly considered as a single morphological species, *P. tinctorius*, is a species complex encompassing 11 phylogenetic species (Martin et al. 2002). All of these possess restricted geographic distributions, for example, *P. tinctorius* is found only in the Northern hemisphere, and *P. marmoratus* is restricted to Australia. Similarly, molecular evidence from multiple loci of the EM *Amanita muscaria* show that what was formerly considered as a single, widespread, generalist species is actually comprised of eight distinct lineages, with two major clades showing geographic distributions restricted to North America (clade I) or Eurasia (clade II) (Geml et al. 2008).

In contrast to the free-living fungi, the biogeographies and population structures of the mycorrhizal fungi are also shaped by patterns of host specificity and the geographic distribution of compatible plant hosts (Halling 2001, Wilkinson 1998). For example, phylogeographic studies of the *Tricholoma matsutake* species complex suggest its present-day biogeographic patterns are a result of tracking by *T. matsutake* of the historic migratory routes taken by its coniferous hosts, westward across Beringia (Chapela & Garbelotto 2004). Within its geographic distribution in Australia, *P. marmoratus* is restricted to the host genus *Eucalyptus*, despite the co-occurrence of other EM trees with *Eucalyptus*. The pattern is hypothesized to have resulted from adaptation following the geographic isolation caused by the separation of Laurasia and Gondwana (Dunstan et al. 1998, Martin et al. 2002). Host specificity is a potential mechanism of ecological divergence leading to speciation in fungi (Giraud et al. 2008). For example, two closely related EM fungal species in the genus *Paxillus* (*P. involutus* and *P. filamentosus*) overlap in their geographic distributions but exhibit very different patterns of host associations, with *P. filamentosus* restricted nearly entirely to *Alnus*, whereas *P. involutus* associates with a wide range of host species (Jarosh & Bresinsky 1999). Patterns of host specificity may have played a role in the divergence of these two species.

Adaptations to particular environmental parameters or habitat types are also likely to be extremely important for determining the realized distribution patterns of genotypes and species of mycorrhizal fungi. Soil chemistry, including nitrogen concentrations (Avis et al. 2003, Lilleskov et al. 2002, Parrent et al. 2006) and the heavy metal concentrations associated with serpentine soils (Schechter & Bruns 2008) or human activities such as mining (Colpaert et al. 2004) affect the community composition of mycorrhizal fungi. Within the *A. muscaria* species complex, distribution patterns at smaller geographic distances—where dispersal is unlikely to be limiting—also provided evidence for habitat preference among species (Geml et al. 2008).

In summary, historical events over long temporal scales, for example, the formation of Gondwana and Laurasia, as well as dispersal limitation, host preference, and habitat specificity are all factors affecting the biogeographic patterns of mycorrhizal fungi. However, the number of studies that exist are few relative to the diversity and ecological importance of these organisms,



and global surveys of AM fungal species using multilocus sequence data are completely lacking. As ancient, apparently asexual, large-spored and seemingly generalist taxa, AM fungi are very different from EM fungi and would provide a valuable contrast, especially by giving insight into how variation among these traits influences the biogeographic patterns and population structures of symbiotic fungi. Ultimately, the goal would be to gain a comprehensive understanding of the role of plant distributions, edaphic factors, and geographic origins as determinants of mycorrhizal fungal distributions. Armed with a clearer understanding of the relative importance of these factors in determining mycorrhizal fungal distributions, it would be possible to predict more accurately the probability that a plant establishing into a novel location would find a compatible, beneficial mycorrhizal symbiont.

6. *Introductions of mycorrhizal fungi.* When fungi are independently introduced to a novel habitat, or when plants are moved with intact root systems, even highly specific symbioses will not be a barrier to spread. Fungi are rarely discussed as introduced or invasive species (Desprez-Loustau et al. 2007), although recent reviews have focused attention on the potential for mycorrhizal inocula to carry fungal species to novel habitats (Schwartz et al. 2006) and global patterns of EM fungal introductions (Vellinga et al. 2009).

Fungal individuals are typically hidden within soil or other substrates. When mushrooms appear they can be obvious and charismatic features of the landscape, and, for example, mushrooms of the deadly poisonous EM *Amanita phalloides* are now found in many different parts of the world (Pringle & Vellinga 2006). Although the species is native to Europe, it has been introduced to Australia, New Zealand, Africa, and North and South America; in California the species is invading coastal forests (Pringle et al. 2009). Mushrooms of the EM *A. muscaria* s.l. are also conspicuous and easily recognizable. These are the classic red and white-spotted mushrooms of fairy tales. Originally from the northern hemisphere, members of this species complex have also traveled to Australia, New Zealand, Africa, Hawaii, and South America (Birch 1937, Dunstan et al. 1998, Hemmes & Desjardin 2002, Singer 1953, Vellinga et al. 2009, Verwoerd 1929). In New Zealand and Australia, *A. muscaria* is invading native *Nothofagus* forests (Horak 1971, Johnston et al. 1998, Stevenson 1981, Vellinga et al. 2009, Young 2005).

An introduced plant that is obligately dependent on a specific fungus or type of mycorrhizal association may be able to invade after its symbionts are independently introduced. Although both *A. phalloides* and *A. muscaria* appear to be generalist species, a plant species that derives a particular benefit from association with these fungi may be more likely to invade after their introduction. The spread of an EM plant host in a landscape dominated by AM fungi may also be facilitated by the introduction of *A. phalloides* and *A. muscaria*. These fungi are invading native forests, and introduced plants may follow the fungi into the native forests. At least 200 species of EM fungi have been introduced to different parts of the world (Vellinga et al. 2009); all of these may influence the local spread of introduced plant species.

There is precedence for this kind of logic. Quite often, fungal introductions are mediated by the movements of soils, and soils were commonly shipped across Africa to aid in afforestation (Figure 4). These soils were obviously carrying many EM species to continents outside of their native ranges (Vellinga et al. 2009), and the plants were constrained from growing or spreading until the fungi were introduced. For example, *Pinus patula* could not be grown in Zambia until EM fungal symbionts were independently introduced. Once in the novel habitat, the fungus (or fungi) facilitated the tree's invasion (Richardson et al. 1994). A similar story can be told for pines in South Africa (Richardson et al. 1994).

Moreover, when plants are moved with intact root systems, even a highly specific symbiosis will not be a barrier to spread. Alder trees appear to form mycorrhizal associations with very few species of fungi (Molina 1981), but alders have been introduced to many parts of the world,



Figure 4

Records of soil moved into and across Africa to inoculate especially pine plantations, as documented by Mikola (1970). Soils housed communities of ectomycorrhizal fungi, and afforestation projects were generally unsuccessful until the ectomycorrhizal symbiosis was also introduced and established. There are very few data on which species were introduced and whether introduced fungal species subsequently formed novel associations with native flora (but see Vellinga et al. 2009). Blue shading marks countries that Mikola (1970) notes as having had introductions of soils of unknown origin. Arrows track the trajectories of soils of known origins. Arrows within a country mark when soils were widely distributed among a country's plant nurseries.

and since they have become established, we suggest that the trees were moved with mycorrhizal associations intact. Alternatively, the receptivity of alders toward novel fungal symbionts may be broader than has been observed.

7. *Community and ecosystem consequences.* Mycorrhizal fungi not only influence individual plant performance and the composition of plant communities; they are also integral components of ecosystems. They have known or putative influences on a broad variety of processes, including soil aggregation, nutrient cycling, primary production, and carbon storage (Rillig 2004). However, in most cases the relative contribution of mycorrhizas to a particular process rate is not known (van der Heijden et al. 2008). Mycorrhizas can influence ecosystem process rates through four different pathways (Rillig 2004), each of which could be affected by interactions with invasive plants: direct effects of the mycelium (e.g., soil aggregation), effects on the individual host plants scaled up to the ecosystem (e.g., nutrient cycling), effects on soil microbial communities, and effects on plant community composition (e.g., primary production). The different types of mycorrhizal associations (including nonmycorrhizal plants, AM and EM) are typically expected to array along various axes, for example, as delineated by longitudinal, altitudinal, or successional patterns in the availability

of mineralized nutrients, which mycorrhizal services are hypothesized to match (Read 1991). EM and AM have different nutrient cycling properties, with EM (and ericoid) mycorrhizal fungi able to access nutrients in organic forms, whereas AM dominate in systems with a predominance of mineralization (Aerts 2002). Thus it is useful to distinguish ecosystem effects of invasions taking place within the same mycorrhizal type from the invasion of one mycorrhizal type by another.

The first case is represented by invasions within the same mycorrhizal type, for example, when an AM plant or an AM fungus invades an ecosystem that is dominated by AM associations. Plant hosts tend to accumulate a subset of the resident AM community in their rhizospheres (e.g., Bever et al. 1996). In fact, Mummey & Rillig (2006) have shown that a grassland in Montana invaded by *C. maculosa* has an AM fungal community different from the communities in adjacent noninvaded sites. Invading plants can also alter the AM fungal composition in the roots of neighboring native plants (Hawkes et al. 2006, Mummey et al. 2005). These changes in fungal composition may provide feedback responses on plants that may be important for two reasons. As discussed in (4), the altered fungal community may be directly beneficial to the invader(s) as compared to the native plants (positive plant-fungal feedback). Second, there is also the possibility for indirect consequences through effects at the ecosystem level. The altered fungal community may contribute to changes in the abundance of nutrients, other physicochemical properties, or the soil microbial community, all of which may interact to promote further invasion. For example, altered AM fungal communities with increased abundance or functionality may more strongly deplete available nutrients in the soil, in effect altering the strength of competition among members of the local plant community. As another example, an altered AM fungal community may affect the aggregate structure, stability, and C storage of soil, which may then indirectly influence local plants, via altered water-holding capacity, cation exchange capacity, or different nutrient leaching losses. Altered AM fungal communities may also influence the abundance and composition of other soil microorganisms (e.g., P-solubilizers, pathogens) that may have functional consequences for nutrient cycling.

Invasion of a host of one mycorrhizal type into an ecosystem dominated by another could also result in ecosystem effects as described above, but likely with more dramatic consequences because mycorrhizal types are associated with different plant traits and ecosystem processes (Aerts 2002, Cornelissen et al. 2001, Read 1991). *Alliaria* invasions in North American maple forests are an example, where a nonmycorrhizal plant invades an AM-dominated forest (Callaway et al. 2008, Stinson et al. 2006). This invasion can lead to decreased services provided by AM fungi to germinating tree seedlings, but also would eliminate ecosystem functions mediated by AM fungi. The same plant also negatively affects EM fungal abundance (Wolfe et al. 2008). Thus (and as discussed in point 4), a tentative conclusion emerges that nonmycorrhizal weeds can tip a system into a more nonmycorrhizal state, which would be more conducive to further invasion by nonmycorrhizal (or less mycorrhizal-responsive) plants. Other examples include invasions of EM trees in grasslands dominated by AM fungi. Since EM fungi also have saprotrophic abilities, it is possible that organic forms of nutrients will be increasingly accessed, leading to a shortcut in the nutrient cycle (Schimel & Bennett 2004). Another important circumstance involves the potential invasion of new fungal taxa into resident fungal communities when commercial fungal inocula are used in agricultural or horticultural contexts; this is a widespread but poorly studied practice (Schwartz et al. 2006). The effects of invading fungal species on fungal community composition and functioning likely depend on the phylogenetic relatedness of invaders to members of the target community, as shown by Maherali & Klironomos (2007). In fact, Antunes et al. (2009) show that introducing the AM fungus, *Glomus intraradices*, to a resident AM fungal community that already contains this fungus has minimal impact. But with tools for tracking individual fungi in the environment becoming more accessible (Croll et al. 2008), the use of commercial inocula

needs further study, as many mycorrhizal fungi are commercially produced and are introduced and spread to novel habitats throughout the world.

This review has focused on the ecological consequences of mycorrhizal symbioses and plant invasions. However, there are also major economic consequences associated with these phenomena. We do not discuss these in detail here, except to provide a few examples. Murat et al. (2008) suggest that in Europe the Périgord black truffle (*Tuber melanosporum*), an EM fungal symbiont, may eventually be displaced by the closely related Chinese truffle, *Tuber indicum*; in addition to having an economic impact, there will be dire culinary consequences. In Madagascar, native species of EM fungi growing in native forests do not fruit in a quantity sufficient for commercial purposes. In contrast, in the introduced eucalypt forests that occupy over 70% of the total soil surface in large areas of the central plateau, edible mushrooms are harvested and sold in large quantities (Buyck 2008). These mushrooms are not native to the eucalypt forests of Australia and may be either species introduced from elsewhere or Malagasy species that are now growing with the new plant host. Whatever the source of the fungi, the novel associations are providing an important source of food and income to the people of Madagascar.

In conclusion, mycorrhizal symbioses are widespread, and mycorrhizal fungi commonly associate with the vast majority of plant species in terrestrial ecosystems. Several criteria are presented here that can determine the potential for mycorrhizal symbioses to constrain or facilitate the invasion process, particularly whether an introduced plant requires the mycorrhizal symbiosis, the plant's degree of flexibility in associating with a range of fungal species, and whether suitable fungi are transported with the plant or are independently introduced to a habitat. Following their successful establishment, invasive plants are influenced by (and can influence) their own (and neighboring) mycorrhizal symbioses, and these can further influence the trajectory of the invasion and have repercussions on the native community.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

We thank Tom Bruns and the Mycorrhizal Discussion Group of the University of California at Berkeley, Peter Alpert, Andrew Suarez, Jason Hoeksema, and Elizabeth Turner for advice on a previous version of the manuscript; and also Neil Hausmann for help with **Figure 1**. We are grateful for support from the National Science Foundation (DEB-0616891), California Department of Transportation, Région Midi-Pyrénées APPRT 2008, and Natural Sciences and Engineering Research Council of Canada.

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