Novel Hosts

In addition to providing habitat, many invasive plants serve as a food source for native species. A survey of California butterflies found that over one-third of native species use introduced plants, and many native butterflies currently have no native host plants. In some cases, this has been the result of evolution of native species, such as the checkerspot butterfly, to take advantage of abundant invasive weeds as hosts. Similarly, invasive pollinators now serve as primary pollinators for native plants in areas where native pollinators have declined in abundance.

Release from Enemies

When introduced species preferentially consume particular native species, they potentially indirectly benefit the competitors or prey of the native species they consume. For example, island endemic skunks increased when golden eagles were introduced, because the eagles preferentially consumed foxes, the main competitors of skunks on the island.

The reciprocal effects of natives on invasive species are rarely measured, so it is often unknown whether these interactions are mutualisms. In some cases it is clear that the introduced species is unaffected, or at least does not benefit, so these are not true mutualisms. In other cases, the interactions may be mutually beneficial (as in the example of the zebra mussel and the snail).

Mutualism between natives, between introduced species, and between natives and introduced species are all common and important interactions in determining invasion success. The lack of an appropriate mutualist only rarely seems to limit invasion, because most interactions are facultative, and native species can be recruited to perform mutualistic services for introduced species.

SEE ALSO THE FOLLOWING ARTICLES

Disturbance / Enemy Release Hypothesis / Invasional Meltdown / Mycorrhizae / Pollination / Transformers

FURTHER READING

Bruno, J.F., J.D. Fridley, K.F. Bromberg, and M.D. Bertness. 2005. Insights into biotic interactions from studies of species invasions (13–40). In D.F. Sax, J.J. Stachowicz, and S.D. Gaines, eds. *Species Invasions: Insights into Ecology, Evolution and Biogeography.* Sunderland, MA: Sinauer Press.

Olyarnik S.V., M.E.S. Bracken, J.E. Byrnes, A.R. Hughes, K.M. Hultgren, and J.J. Stachowicz. 2008. Ecological factors affecting community invasibility (215–238). In G. Rilov and J.A. Crooks, eds. *Biological Invasions of Marine Ecosystems: Ecological, Management, and Geographic Perspectives.* Heidelberg: Springer.

Ricciardi, A. 2005. Facilitation and synergistic interactions among introduced aquatic species (162–178). In H.A. Mooney, R.N. Mack, J. McNeely, L.E. Neville, P.J. Schei, and J.K. Waage, eds. *Invasive Alien Species: A New Synthesis.* Washington, DC: Island Press.

Richardson, D.M., N. Alsopp, C.M. D'Antonio, S.J. Milton, and M. Rejmánek. 2000. Plant invasions: The role of mutualisms. *Biological Reviews* 75: 65–93.

Rodriguez, L.F. 2006. Can invasive species facilitate native species? Evidence of how, when and why these impacts occur. *Biological Invasions* 8: 927–939.

MYCORRHIZAE

ANNE PRINGLE AND BENJAMIN WOLFE

Harvard University, Cambridge, Massachusetts

ELSE VELLINGA

University of California, Berkeley

Symbioses between mycorrhizal fungi and plant roots are referred to as mycorrhizae. Mycorrhizal fungi play three critical roles in biological invasions (Fig. 1). First, the mycorrhizal fungi can themselves invade novel habitats, either with introduced plants, or after association with native plants. Second, introduced mycorrhizal fungi can facilitate the invasion of introduced plants. Third, native mycorrhizal fungi will respond to invasions by other exotic species, for example by associating and spreading with introduced plants, or by declining after introduced insects or pathogens attack native host plants.

THE BIOLOGY OF MYCORRHIZAE

Mycorrhizal symbioses are ubiquitous. In these symbioses, the fungal mycelia scavenge through soil for resources (often phosphorus or nitrogen) and give these resources to plants in exchange for carbon. The associations are mutualisms but can sometimes function as parasitisms. Mycorrhizal associations may involve any of four different fungal phyla and a broad range of plants including mosses and liverworts, ferns, and seed plants. The mycorrhizal status of many plants is unknown, but for the 6,507 species that have been examined, only 18 percent do not form mycorrhizal associations. 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 and the structures formed in or around plant roots. In addition to AM and EM symbioses, mycorrhizal associations include arbutoid, monotropoid, ericoid, and orchid forms. This entry focuses on AM and EM symbioses, because there is more information about these

From Daniel Simberloff and Marcel Rejmánek, editors, *Encyclopedia of Biological Invasions*, Berkeley and Los Angeles: University of California Press, 2011.

mycorrhizal types and because it is increasingly clear that other forms involve the same fungal species as associate in EM symbioses.

MYCORRHIZAL SPECIES INVADE

Mycorrhizal symbioses are obligate; although many fungi and plants can be grown alone in the greenhouse or laboratory, in nature most species require the symbiosis. For this reason, mycorrhizal fungi have been introduced to novel ranges when plants are managed for commercial purposes; species are moved to facilitate agriculture, forestry, and horticulture. For example, in the southern hemisphere, pine forests did not grow until soils with mycorrhizal fungi were imported and mixed with the native soils around planted pine seedlings. Moreover, the potted plants sold by nurseries are often associated with mycorrhizal fungi, and fungi are introduced to novel ranges when potted plants are moved and replanted in local soils. Although specificity is a feature of some associations, and, for example, the fungal genus *Suillus* is specific to the plant genus *Pinus*, other mycorrhizal fungi are generalists, and these species may jump to new hosts in novel habitats.

Introductions of AM fungi are difficult to track because the diagnostic features of different species appear in soil and may be complicated to isolate or identify. However, all of the world's major crop plants associate with AM fungi, and because commercial mixes of the fungi are sold as alternatives to phosphorus fertilizers, species have probably been carried by humans to new ranges. But an understanding of how often fungal species are introduced, whether introduced species typically establish, if they establish whether they associate with native hosts, and if and how introduced AM fungi impact the local biodiversity of plants or fungi is prevented by an almost total lack of basic knowledge about species numbers and native ranges. Although the global diversity of AM fungi appears to be low (fewer than 200 described species), estimates of species richness are hindered by the potential for many species to remain undescribed. For example, intensive sampling in one North Carolina field demonstrated that more than one-third of the species described from this single 1 ha site were novel. Nor do biologists have a clear understanding of the native ranges of AM fungi. For example, the morphological species *Glomus mosseae* is assumed to have a global distribution, but recent data suggest a cryptic genetic diversity that may translate to distinct genetic species. If a morphological species concept is used, an introduction of *G. mosseae* from Europe

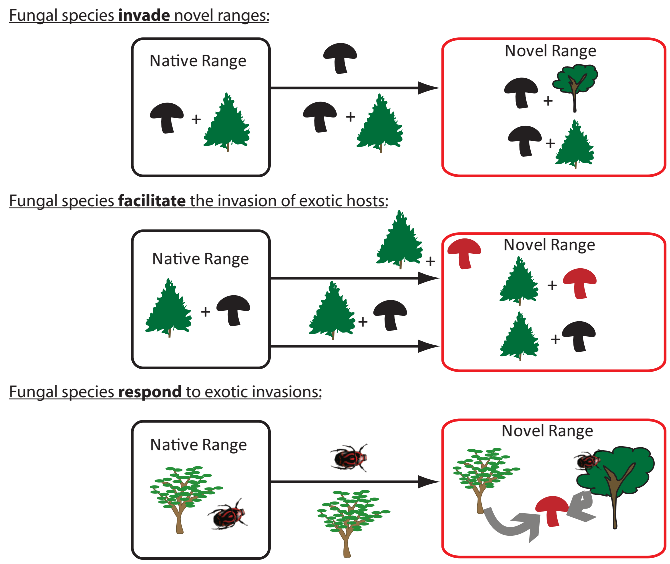

FIGURE 1 The roles of mycorrhizal fungi in biological invasions.

to North America is the movement of a species within its native range. Using a genetic species concept, this kind of introduction would be the movement of a species outside of its native range. Even apparently endemic species, for example the novel species of the North Carolina field, are considered as endemic only because of limited sampling from other sites. Until the biology, taxonomy, and biogeography of AM fungi are understood, introductions of AM fungi will be difficult to define or identify.

More is known about EM fungal introductions because many of these fungi form obvious, macroscopic reproductive structures: mushrooms (Fig. 2). At least 200 species from a diverse group of over 50 genera have been moved among different continents and islands (Fig. 3). As discussed above, EM fungi are likely to have been moved in the soil associated with plants used for forestry or horticulture. More is known about the biogeography of EM fungal species, although historical records of species presence or absence are sometimes incorrect. Inaccuracies are caused by the use of European names for native species; for example, early sources often list European species as found in North America, although in many cases the species being listed is a North American species misidentified with a European name. Most introduced EM fungal species appear not to spread and seem constrained to grow with the tree species on which they were introduced—for example, the species found with Australian eucalyptus in Spain. Exceptions include *Amanita phalloides*, invasive on the West Coast of North America and associated with the endemic *Quercus agrifolia*, and *Amanita muscaria*, invasive in Australia and

New Zealand and associated with native *Nothofagus* spp. Mechanisms facilitating the spread of *A. phalloides* and *A. muscaria* are poorly understood but may involve an ability to establish symbioses with local trees or competitive dominance over local mycorrhizal species. A limited diversity of native *Amanita* species may also provide niche space for *A. phalloides* in California, but this hypothesis remains untested.

MYCORRHIZAL FUNGI INFLUENCE PLANT INVASIONS

Mycorrhizal associations may also facilitate or limit the spread of introduced plants, although symbiotic constraints on the spread of introduced species are poorly understood. As discussed above, it is clear that *Pinus* species introduced to the southern hemisphere did not grow until associated mycorrhizal fungi were deliberately introduced. *Pinus* trees require introduced EM fungi either because the native trees don't associate with EM fungi or because they associate with a different set of EM fungal species that cannot associate with *Pinus*. Other trees may also rely on introduced mycorrhizal associates to spread, for example, eucalypts introduced to Spain. Mycorrhizal fungi also play a role in natural range expansions, and native birch expanding into the lowland heathlands of England grow better at sites where mycorrhizal fungi have also dispersed. And native fungi may also facilitate the

FIGURE 2 Mycorrhizal fungi are rarely discussed as introduced or invasive species. Fungal individuals are typically hidden within soil or other substrates, but when mushrooms appear, they can be obvious and charismatic features of the landscape. Pictured in A–C are the introduced species *Hydnangium carneum, Amanita muscaria, and Suillus luteus*. These are examples of commonly introduced ectomycorrhizal species (Vellinga et al., 2009). (A) *Hydnangium carneum* is a *Eucalyptus* associate from Australia, first described when it was found in Europe growing with potted plants. It forms subterranean fruit bodies. The species has also been recorded from North Africa, North and Central America, New Zealand, and more recently China. In New Zealand, it can form ectomycorrhizae with the native *Nothofagus* species, although reports of the species occurring in native forests are rare. (Photograph courtesy of Celestino Gelpi Pena.) (B) *Amanita muscaria* s.l. is a very conspicuous and easily recognizable mushroom, the classic red-and-white spotted mushroom of fairy tales. Originally from the northern hemisphere, members of this species complex have traveled to Australia, New Zealand, Africa, Hawaii, and South America. In Tanzania the species is a health hazard, as the local people confuse it with edible, equally orange- to red-colored *Amanita* species from the native miombo vegetation. As of this writing, the species appears to be confined to plantations within Tanzania, but in Australia and New Zealand, the species appears to be invading native *Nothofagus* forests. It also associates with introduced *Eucalyptus* in Uruguay. (Photograph courtesy of Tom May.) Two *Suillus* species, *S. luteus* and *S. granulatus*, have also been moved across the planet. (C) *Suillus luteus* is a Eurasian native, and *S. granulatus* is native to northern temperate *Pinus* forests. *Suillus luteus* was taken to North America with *Pinus sylvestris*. It is now grown with the California endemic *P. radiata* all over the world, even though it does not associate with *P. radiata* in its native habitat. Thus, the species is being taken to novel places in association with a host it would not normally find, and the two species travel together. The fungus now grows in Africa, South America, Australia, New Zealand, and in other places where pines have been introduced. *Suillus granulatus* has been recorded from Africa, South America and the Falkland Islands, Australia, New Zealand, and Hawaii. (Photograph courtesy of Dimitar Bojantchev.)

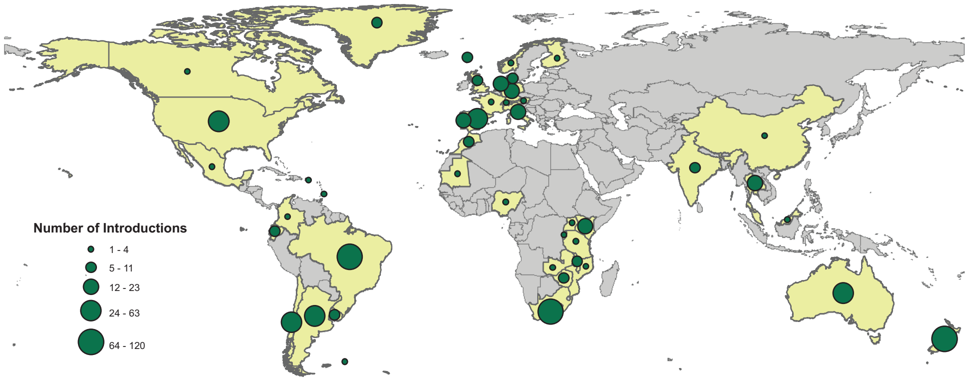

FIGURE 3 The global distribution of ectomycorrhizal introductions. Numbers of introductions are strongly correlated with the number of publications from any given country; for many countries there are no data. Colors and circles are proportional to the number of species that have been reported as introduced. (Reprinted from Vellinga et al., 2009.)

spread of introduced plants, as AM fungi appear to have done for *Centaurea maculosa* in North America.

NATIVE MYCORRHIZAL FUNGI ARE AFFECTED BY INTRODUCTIONS OF OTHER SPECIES

Exotic plants, pathogens, and insects may cause direct or cascading effects on native mycorrhizal communities, although data on these phenomena are rare. Introductions can clearly cause damage; for example, the introduced plant *Alliaria petiolata* (garlic mustard) kills local communities of both AM and EM fungi in North America. But introduced plants that associate with local fungal species may also facilitate the growth of these native species in new habitats. Introduced pathogens or insects impact native fungal communities by attacking the trees that host mycorrhizal fungi; *Phytophthora ramorum* (sudden oak death) is one example of an introduced pathogen that kills a diversity of tree species. As it kills the trees that host mycorrhizal communities, the mycorrhizal fungi are also likely to die.

SEE ALSO THE FOLLOWING ARTICLES

Agriculture / Belowground Phenomena / Eucalypts / Forestry and Agroforestry / Fungi / Hemlock Woolly Adelgid / Horticulture / Mutualism

FURTHER READING

Bever, J. D., P. A. Schultz, A. Pringle, and J. B. Morton. 2001. Arbuscular mycorrhizal fungi: More diverse than meets the eye, and the ecological tale of why. *BioScience* 51: 923–931.

Collier, F. A., and M. I. Bidartondo. 2009. Waiting for fungi: The ectomycorrhizal invasion of lowland heathlands. *Journal of Ecology* doi 10.1111/j.1365-2745.2009.01544.x.

Díez, J. 2005. Invasion biology of Australian ectomycorrhizal fungi introduced with eucalypt plantations into the Iberian Peninsula. *Biological Invasions* 7: 3–15.

Marler, M. J., C. A. Zabinski, and R. M. Callaway. 1999. Mycorrhizae indirectly enhance competitive effects of an invasive forb on a native bunchgrass. *Ecology* 80: 1180–1186.

Mikola, P. 1970. Mycorrhizal inoculation in afforestation. *International Review of Forestry Research* 3: 123–196.

Nuñez, M. A., T. R. Horton, and D. Simberloff. 2009. Lack of belowground mutualisms hinders Pinaceae invasions. *Ecology* 90: 2352–2359.

Pringle, A., R. I. Adams, H. B. Cross, and T. D. Bruns. 2009. The ectomycorrhizal fungus *Amanita phalloides* was introduced and is expanding its range on the West Coast of North America. *Molecular Ecology* 18: 817–833.

Pringle, A., J. D. Bever, M. Gardes, J. L. Parrent, M. C. Rillig, and J. N. Klironomos. 2009. Mycorrhizal symbioses and plant invasions. *Annual Review of Ecology, Evolution and Systematics* 40: 699–715.

Pringle, A., and E. C. Vellinga. 2006. Last chance to know? Using literature to explore the biogeography and invasion biology of the death cap mushroom *Amanita phalloides* (Vaill. Ex Fr.: Fr.) Link. *Biological Invasions* 8: 1131–1144.

Richardson, D. M., N. Allsopp, C. M. D'Antonio, S. J. Milton, and M. Rejmánek. 2000. Plant invasions: The role of mutualisms. *Biological Reviews* 75: 65–93.

Schwartz, M., J. Hoeksema, C. Gehring, N. Johnson, J. Klironomos, L. Abbott, and A. Pringle. 2006. The promise and potential consequences of the global transport of mycorrhizal fungal inoculum. *Ecology Letters* 9: 601–616.

Smith, S. E., and D. J. Read. 2008. *Mycorrhizal Symbiosis*, 3rd ed. San Diego, CA: Academic Press.

Stinson, K. A., S. A. Campbell, J. R. Powell, B. E. Wolfe, R. M. Callaway, G. C. Thelen, S. G. Hallett, D. Prati, and J. Klironomos. 2006. Invasive plant suppresses the growth of native tree seedlings by disrupting belowground mutualisms. *PLoS Biology* 4: 727–731.

Vellinga, E. C., B. E. Wolfe, and A. Pringle. 2009. Global patterns of ectomycorrhizal introductions. *New Phytologist* 181: 960–973.

Wolfe B. E., V. L. Rodgers, K. A. Stinson, and A. Pringle. 2008. The invasive plant *Alliaria petiolata* (garlic mustard) inhibits ectomycorrhizal fungi in its introduced range. *Journal of Ecology* 96: 777–783.