Global patterns of ectomycorrhizal introductions

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Summary

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- Plants have often been moved across the globe with intact root systems. These roots are likely to have housed symbiotic ectomycorrhizal (EM) fungi and the movement of plants may have facilitated the introduction of EM fungi.
- Here, we report data compiled from a newly created database of EM fungal introductions. We estimate the magnitude of EM fungal introductions around the world and examine patterns associated with these introductions. We also use the data to develop a framework for understanding the invasion biology of EM fungi.
- At least 200 species of basidiomycete and ascomycete EM fungi have been moved from native ranges to novel habitats. The majority of recorded introductions are associated with *Pinus* or *Eucalyptus* plantations in the southern hemisphere. Most introduced species appear to be constrained from spreading in novel habitats and associate only with their introduced hosts. Aspects of life history, including host range, may influence the ability of EM species to establish or invade.
- Human-caused introductions of EM fungi are a common and global phenomenon. The mechanisms controlling EM fungi in novel habitats and potential impacts of EM fungal introductions are almost entirely unknown.

Introduction

Invasion biology is focused on animals and plants (Desprez-Loustau *et al.*, 2007; Pysek *et al.*, 2008), although humans may also move microbes to novel ranges. Previous work on microbial invasion biology has focused on pathogens (Wingfield *et al.*, 2001; Palm & Rossman, 2003; Anderson *et al.*, 2004; Loo, 2009; Rossman, 2009), probably because the effects of the pathogens in novel ranges are often obvious. However, there is evidence that microbial mutualists have also been introduced to areas outside their native ranges (Richardson *et al.*, 2000; Stepkowski *et al.*, 2005; Schwartz *et al.*, 2006; Desprez-Loustau *et al.*, 2007; Rodríguez-Echeverría *et al.*, 2007; van der Putten *et al.*, 2007). The dynamics associated with invasions of parasites and mutualists may be fundamentally different. For example, mutualists may have wider host ranges than antagonists (Borowicz & Juliano, 1991) and may therefore spread across broader geographic areas. Systematic surveys of the frequency of introductions or fate of microbial mutualists are rare.

Species of mutualists with the potential to be widely introduced include mycorrhizal fungi. As ubiquitous symbionts on the roots of most plant species, these fungi provide plants with nutrients from the soil in return for photosynthetically derived carbon (Jakobsen *et al.*, 2002; Leake *et al.*, 2004). Many plants depend on mycorrhizal fungi for growth and survival and mycorrhizal fungi are especially important in nutrient-poor ecosystems (Richardson *et al.*, 2000). Mycorrhizal associations may influence both biodiversity (Bever *et al.*, 2002; van der Heijden, 2002) and biogeochemistry (Hart & Klironomos, 2002; Hoffland *et al.*, 2004). Mycorrhizal fungi are also economically important as edible mushrooms (Yun & Hall, 2004) and as mutualists of trees planted for forestry (Marx *et al.*, 1992). The fungi forming these associations are not a monolithic entity; symbioses may involve any of three different phyla within the kingdom Fungi and the morphology and ecology of an association will vary when different species are involved. Two of the most common types of mycorrhizal fungi are the arbuscular mycorrhizal (AM) fungi (Glomeromycota) and the ectomycorrhizal (EM) fungi (Ascomycota and Basidiomycota). Mycorrhizal symbioses are assumed to be of benefit to both fungi and plants, and are discussed as mutualisms, although it is clear that the associations are dynamic and occasionally function as parasitisms (Johnson *et al.*, 1997; Egger & Hibbett, 2004).

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Thousands of plant species have been moved across the world and many plants have been moved as potted specimens with intact root systems in soil. Fungi are likely to have traveled in the roots and soil. For example, over 3800 genera of seed plants have been introduced to New Zealand (Duncan & Williams, 2002). Given that almost all of these plants associate with mycorrhizal fungi, it is likely that species of fungi were introduced to New Zealand with some of these specimens. Moreover, in New Zealand and other parts of the southern hemisphere, mycorrhizal fungi were intentionally introduced when *Pinus* spp., which are not native to this hemisphere, were inoculated with exotic EM fungal species (Richardson *et al.*, 2000). EM fungi have also been introduced to habitats without native EM hosts, for example the forests of Hawaii and fynbos of South Africa. Despite the apparently widespread movement of mycorrhizal fungi throughout the world, there have been no attempts to systematically characterize the extent of mycorrhizal introductions.

The movements of EM fungi may be poorly described, but it is not because of a lack of data. There are many records of EM fungal introductions, but reports are scattered in the unconventional or 'grey' literature, or as anecdotal information in formal checklists and floras. General patterns associated with plant or animal invasions have been observed (Hamilton *et al.*, 2005; Arim *et al.*, 2006; Cadotte *et al.*, 2006; Strauss *et al.*, 2006; Hayes & Barry, 2008), but invasions are often described as idiosyncratic phenomena controlled by the particular circumstances of any specific introduction (Lockwood *et al.*, 2007). Because the available literature has not been synthesized, it is difficult to infer any general patterns that may be associated with introductions of EM fungi.

Our goal is to use the literature to document the global distribution of introduced EM fungi, to give an overview of the scale of introductions and numbers of species involved and to use these data to discern general patterns. A previous review was explicitly focused on the potential consequences of inoculation by mycorrhizal 'fertilizers' in agriculture, and on arbuscular mycorrhizal fungi (Schwartz *et al.*, 2006). A second review encompassed both pathogenic and mutualist fungi and emphasized how rarely fungi are considered within invasion biology (Desprez-Loustau *et al.*, 2007). Our focus is on synthesizing the available literature to explore the biological process of mycorrhizal invasions. We focus only on EM fungi, as both morphological and phylogenetic species concepts and the genetics of EM species are well defined, in contrast to the arbuscular mycorrhizal fungi (but see Redecker & Raab, 2006; Hibbitt, 2007). This is crucial, as when a fungus is collected from a novel habitat its nomenclature and the species concept must be very well understood before that fungus can be called introduced (Pringle & Vellinga, 2006). What we have learned is that while there are a considerable amount of data from across the globe that can be used to address aspects of EM fungal introductions, including the numbers of introduced species and the host associations and genetic systems of introduced fungi, there is little understanding of the mechanisms controlling the spread of these species, and very little data on the impacts that EM fungi may have on local biota.

Materials and Methods

We compiled a database of introduced EM fungi using both targeted and random searches of the literature; both the database and its citations are provided in the Supporting Information. Originally, five sources with broad overviews of introduced taxa (Mikola, 1969; Garrido, 1986; Dunstan *et al.*, 1998; Montecchi & Sarasini, 2000; Díez, 2005) were used to create a database and make a list of relevant citations. Each species from every paper was given a single entry in the database, and each entry includes information on taxonomy, hosts and native and introduced ranges. Next, we initiated a search in ISI Web of Knowledge[SM] (http://images.isiknowledge.com/help/WOK/h_database.html) using the keywords 'introduced' and 'ectomycorrhiza' in association with any of various tree genera or species, including *Eucalyptus*, *Pinus radiata*, *Pseudotsuga menziesii*, and others. The search included the full span of Web of Knowledge records, dating from 1926 to 2007. An additional six journals in either Italian (*Rivista di Micologia*; *Bollettino del Gruppo Micologico G. Bresadola*), French (*Bulletin Trimestriel de la Féderation Mycologique de Dauphiné-Savoie*; *Bulletin de la Féderation des Assocations Mycologiques Méditerranéennes*), Danish (*Svampe*) or Dutch (*Coolia*) were searched for articles describing species new to a region; again, the entire span of each journal was used. Floras and checklists were also consulted. After the initial database was created additional literature on a subset of genera that appear to be commonly introduced was added (*Amanita*, *Descolea*, *Descomyces Hydnangium*, *Labyrinthomyces*, *Laccaria*, *Rhizopogon*, *Ruhlandiella*, *Setchelliogaster*, *Suillus*) using, for example, the Bibliography of Systematic Mycology database (CABI Bioscience Databases, 2008). Thirteen records gathered from seven websites were also added; these websites either focus on groups for which there is little other information, or focus on introduced species (see database citations).

Records that did not identify collections to species were excluded. We also excluded records with incorrect species' names, for example records that discuss *Pisolithus arrhizus* (syn. *Pisolithus tinctorius*) as associated with *Eucalyptus* (Martin *et al.*, 2002), because the species currently considered as *P. arrhizus* is a northern hemisphere fungus that does not associate with *Eucalyptus*. Approximately 10 records were excluded for these reasons, and most dealt with *P. tinctorius*.

Results

Overview of data sources and database

The database currently encompasses > 190 publications spanning 1839–2007, and includes 770 records. Each
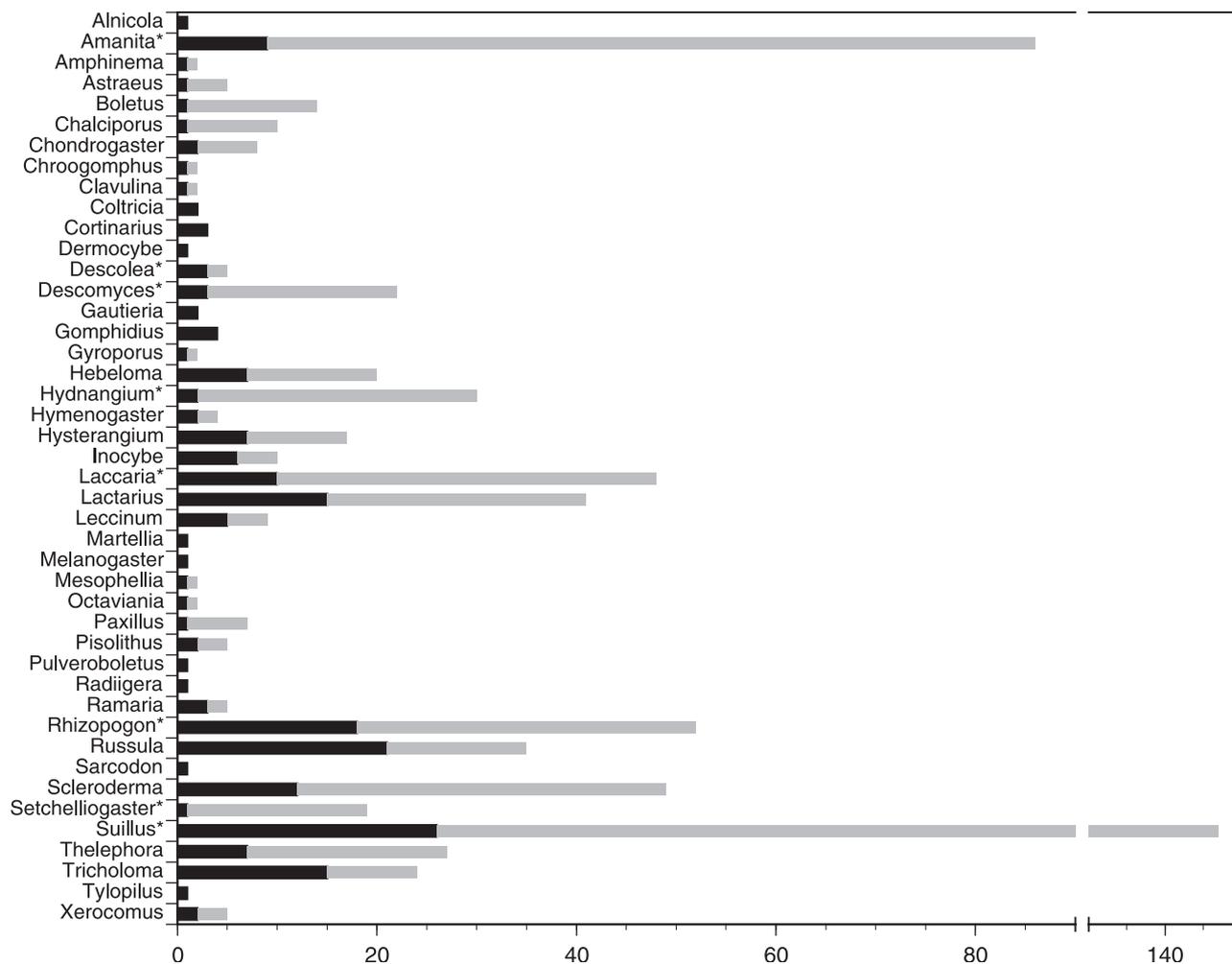
Fig. 1 The number of species reported as introduced (closed bars) and total number of introductions within 44 basidiomycete genera (tinted bars). The second metric reflects the number of times species within a genus are counted as introduced; because a single species may be reported as introduced to more than one location this number can be very large. Ascomycete genera reported as introduced include one species each of *Barssia*, *Elaphomyces*, *Genea*, *Geopora*, *Hydnotrya* and *Ruhlandiella*, two species in the genus *Labyrinthomyces*, and eight species in the genus *Tuber*. Genera with asterisks were a specific target of research (see the Materials and Methods section).

publication reports an average of four introductions, although a majority of publications record only one and the maximum number in any single publication is the 48 species reported from southern Brazil by Giachini *et al.* (2000). Publications typically focus on subsets of the globe and are rarely explicit in their classification of 'introduced' or 'established' species. The literature can be divided into three categories:
• articles focusing on the fungi associated with introduced tree species;
• articles describing species new to a region (either new to science or species described from elsewhere and found for the first time in a novel location);
• floras, monographs and checklists, which give an indication of whether species are established.

The phylogenetic breadth of introduced EM fungi

Introductions are common and encompass many different genera and species (Fig. 1). A total of 54 genera are reported as introduced outside of their native ranges. A few genera stand out as having greater numbers of species recorded as introduced, and greater numbers of introductions, although the number of *Rhizopogon* species (17) is questionable because the species are notoriously difficult to identify (Grubisha *et al.*, 2002). Rarely reported are species from the genus *Cortinarius*, which are also difficult to identify, and those that form inconspicuous fruiting structures, including genera in the Sebacinaceae and species of *Tomentella*. Introduced genera are scattered across the fungal tree of life (James *et al.*, 2006), and
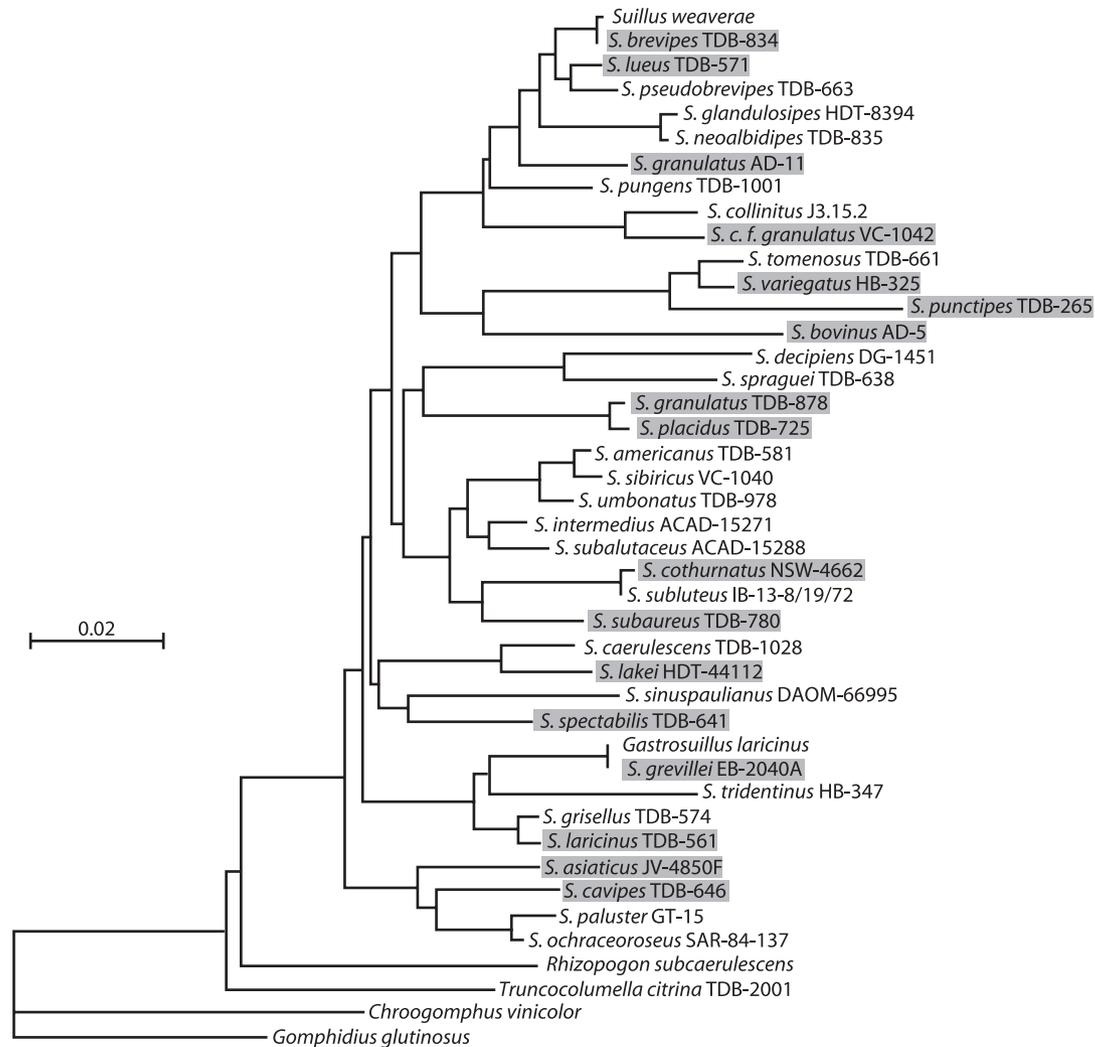
Fig. 2 Species reported as introduced (shaded) do not cluster within a phylogeny of the genus *Suillus*, suggesting that there is not a phylogenetic signal that would predict which species are likely to be detected as introductions. A similar result is found when introduced species are marked on a phylogeny of the genus *Amanita* (not shown). Note: not all species of *Suillus* reported in the database are shown in this phylogeny. Figure modified from Kretzer *et al*. (1996) and used with permission from *Mycologia*. © The Mycological Society of America.

even at finer phylogenetic scales there is no pattern associated with the species recorded as introduced (Fig. 2).

Of the nearly 800 records, 733 are of basidiomycete species. The lack of data on ascomycetes may reflect a real difference in what is introduced, or more likely, incomplete knowledge of which ascomycete species form EM associations (Egger, 2006) and the more conspicuous nature of basidiomycete fruiting bodies. The few documented ascomycete introductions include *Geopora sumneriana* and various edible truffle species. The star-shaped fruit bodies of the North African *G. sumneriana* have been recorded from a plantation in southern France, as well as from isolated trees in gardens throughout northern Europe (Daams, 1952; Fouchier & Neville, 1998; Montecchi & Sarasini, 2000). The European and North American black truffle *Tuber maculatum* is now grown in Australia, New Zealand and Argentina (Trappe & Cázares,

2000), and recently the Chinese *Tuber indicum* was reported from Europe (Murat *et al*., 2008).

The geography of introduced ectomycorrhizal fungi

Introductions are most commonly reported from Europe, South America, Australia and New Zealand; records from North America and especially Asia are rare. Although 15 papers discuss fungi in South Africa, and five target Morocco, only 20 papers cover the rest of Africa. Reports of introduced species are strongly correlated to the volume of papers published from each country ($r = 0.79$, $P < 0.01$). For example, one species is reported as introduced to Mexico and only one of the 199 papers includes information for Mexico, the same pattern holds for Canada; 83 species are reported as introduced to New Zealand and Australia and 46 papers target these

countries. The nominal number of studies on introduced EM fungi in North America is a striking contrast to the vast number of studies on introduced animals and plants in North America (Pysek *et al.*, 2008).

Although the literature is clearly biased to some parts of the world, with the data available it seems that introductions are disproportionately reported from the southern hemisphere (Fig. 3). The greatest numbers of introduced species are found in Brazil, New Zealand and South Africa. In addition to reflecting a publication bias, these data may correlate to the widespread development of plantations of northern hemisphere trees species, especially pines, in the southern hemisphere (Richardson & Higgins, 1998).

Fungi are normally dispersed at local scales as spores, but the introductions discussed in this manuscript are not likely to have involved spores and the distances traveled by introduced species are vast. Islands provide good examples. On the islands of Hawaii there are no native EM plants and so by definition an EM fungus discovered there is an introduction. The islands harbor a number of introduced EM fungal species including *Amanita marmorata*, found with *Eucalyptus* and *Casuarina*, *Suillus brevipes* with *Pinus radiata*; and *Suillus granulatus* and *Suillus salmonicolor* with *Pinus elliotii* (Hemmes & Desjardin, 2002). These species probably traveled the thousands of kilometers from a mainland to Hawaii in the roots and soil of introduced seedlings. As there are no native Hawaiian hosts the probability that these introduced fungi will establish or spread independently is minimal, although they can facilitate the invasion of the introduced tree species with which they associate. Other islands provide similar narratives; pines have been planted on Iceland, Greenland, and the Faeroe and the Falkland Islands, and all of these also harbor introduced *Suillus* species (Kallio & Heikkilä, 1992; Knudsen & Borgen, 1987; Jalink & Nauta, 1993; Petersen *et al.*, 1994).

The host associations of introduced EM fungi

Trees that have been introduced from one place to another and serve as hosts for EM fungi include species in the Pinaceae, Betulaceae, Casuarinaceae, Caesalpiniaceae, Dipterocarpaceae, Fagaceae, Myrtaceae and Salicaceae (Mikola, 1969, our database). *Pinus* and *Eucalyptus* species have been planted at very large scales outside of their normal species' ranges (del Lungo *et al.*, 2006), and not surprisingly these species most frequently serve as exotic hosts of introduced EM fungi (Fig. 4).

Discussion

The ectomycorrhizal invasion process: five potential outcomes

An introduced species has the potential to reach any of four stages: transport, establishment, spread, and impact (Lockwood

et al., 2007). A variety of parameters will influence the ability of a species to reach each stage, and the same species may reach a different stage at different geographic locations. We can use the framework provided by Lockwood *et al.* (2007) to group fungal examples from the literature into five different outcomes (Fig. 5): (1) EM fungi may be introduced but fail to establish; (2) introduced EM fungi may establish but be replaced by local fungi; (3) EM fungi may persist with introduced trees but fail to grow with local hosts; (4) EM fungi may persist with introduced trees and spread to local hosts; or (5) EM fungi may fail to persist with introduced trees but nonetheless spread to local hosts. We briefly discuss each of these outcomes and provide examples:

Failed introductions   To our knowledge, there are no carefully described examples of failed EM introductions. As is true for plants and animals, the lack of data is probably an artifact caused by the difficulty in detecting these phenomena and reflects a bias in what is recorded by humans, and does not prove that EM introductions always (or even commonly) establish. Because truffles are valuable, there is some knowledge of what causes crops of these fungi to succeed or fail. For example, in North America cultivated *Tuber* species can only establish in soils of appropriate pH (usually amended with lime) and when even moisture and good drainage are provided (O'Neill, 2007; Garland, 2008). Truffles are typically planted in association with introduced filbert (*Corylus*) or introduced or native oak (*Quercus*) species. Clearly, the right abiotic parameters and hosts are crucial to establishment.

Introduced EM fungi that are replaced by local species   Data taken from fungi introduced with forestry trees suggest that introduced EM species typically persist for short periods in the field (Molina *et al.*, 1992; Thomson *et al.*, 1996; Dell *et al.*, 2002), and because this is a problem for foresters (Dell *et al.*, 2002), the ability of EM fungi to establish at novel sites has become a focus for applied research. For example, Dell *et al.* (2002) monitored EM fungi used in association with introduced *Eucalyptus camaldulensis* and *E. urophylla* seedlings in China (Dell *et al.*, 2002). At planting, the seedlings were inoculated with Australian *Pisolithus* species, including *P. alba*. At one site, surprisingly (*Eucalyptus* is not native to China) a local, unidentified *Pisolithus* species was able to form mycorrhizae with the introduced Eucalypts, but it formed a poorly developed mantle around the tree roots and was not as beneficial to *Eucalyptus* growth as the Australian isolates. However, the Chinese species did fruit in the plots, beside the single Australian species that persisted within the site (Dell *et al.*, 2002). None of the other four introduced isolates, including *P. alba*, were recovered from the site, although Dell *et al.* (2002) point out that at least some of these may have persisted in some cryptic fashion (e.g. in soil but without fruiting). Another example involving *Eucalyptus* is given by Garbaye *et al.* (1988); a variety of exotic fungal species were
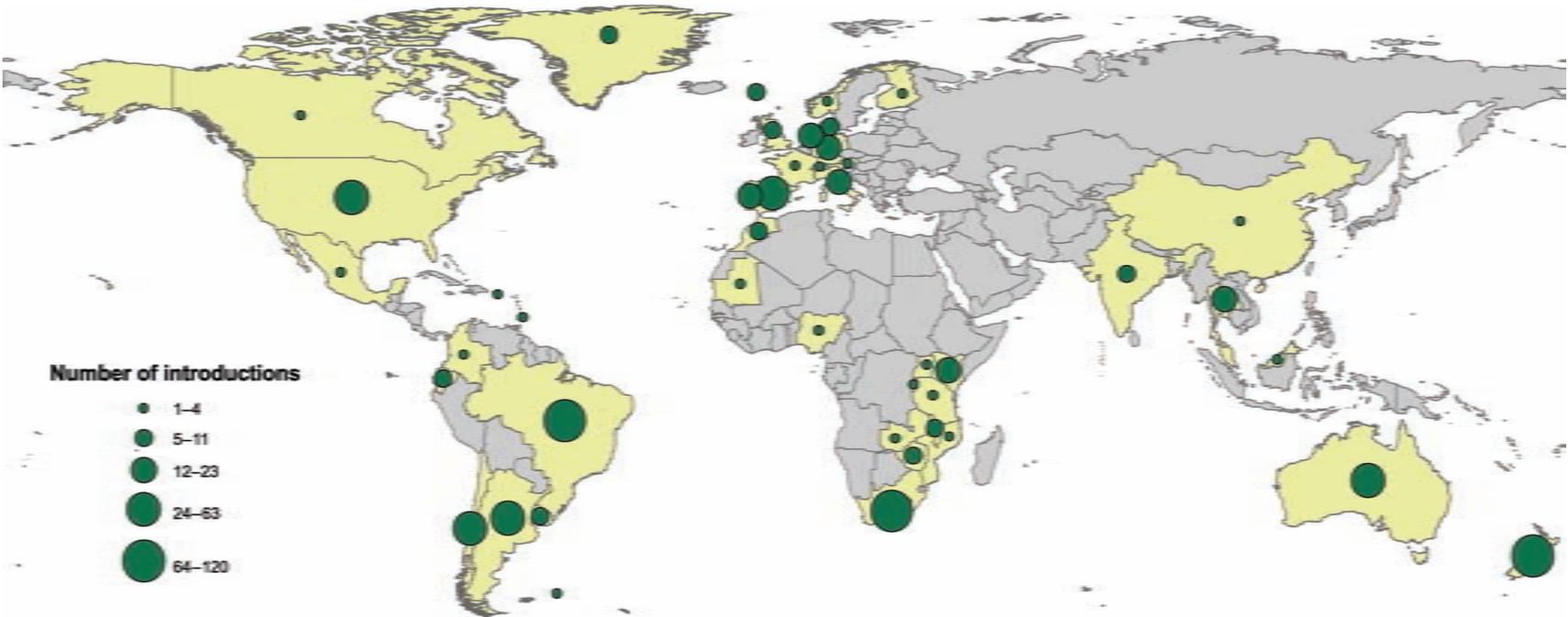
Fig. 3 The global distribution of ectomycorrhizal introductions. The numbers of introductions are strongly correlated to the numbers of publications from any given country (see text). Yellow indicates countries with at least one introduction, and circles are proportional to the number of species that have been reported as introduced.
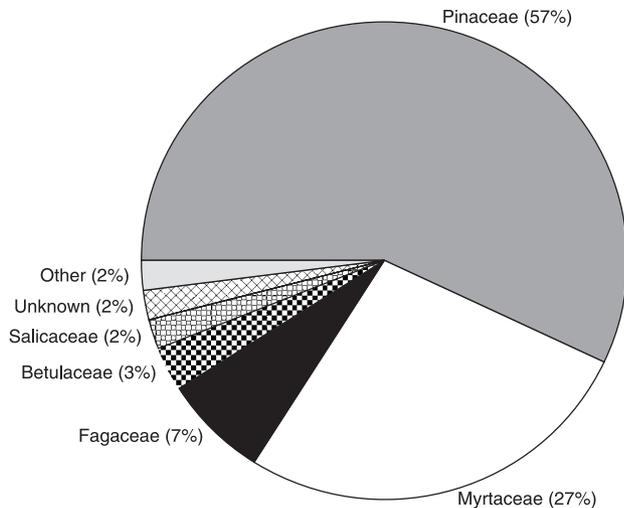
Fig. 4 Frequency of host plant families reported as hosts of exotic ectomycorrhizal fungi around the world. *Pinus* species in the Pinaceae and *Eucalyptus* species in the Myrtaceae make up the bulk of the reported hosts. Plant families in the 'Other' category include Casuarinaceae, Fabaceae, Cupressaceae, Malvaceae, Cistaceae, Rhamnaceae and Ulmaceae. The 'Unknown' category includes records where no host information was reported.

planted with hybrid *Eucalyptus* seedlings in the Congo but after 4 yr were replaced by local (unnamed) fungal species.

Introduced EM fungi that persist with introduced hosts, but do not spread to local hosts The most frequently recorded outcome of the introduction of EM fungi involves introduced EM fungi that persist on the exotic host plants but do not spread to native hosts. These fungi are typically associated with trees planted for forestry and have been the target of at least four major inventorying efforts (Garrido, 1986; Giachini *et al.*, 2000, 2004; Barroetaveña *et al.*, 2005, 2006; Díez, 2005). A majority of the examples provided in this manuscript are species restricted to introduced hosts (see for example the discussion of EM fungi on Hawaii, above).

Introduced EM fungi that persist with introduced hosts, and also spread to local hosts There are only a handful of cases in which an introduced fungus has invaded native forests to form mycorrhizas with local tree species. Perhaps EM fungi are rarely invasive or, equally likely, a lack of information about the past and current biodiversity of fungi at any particular site make definitive judgments on what is native or
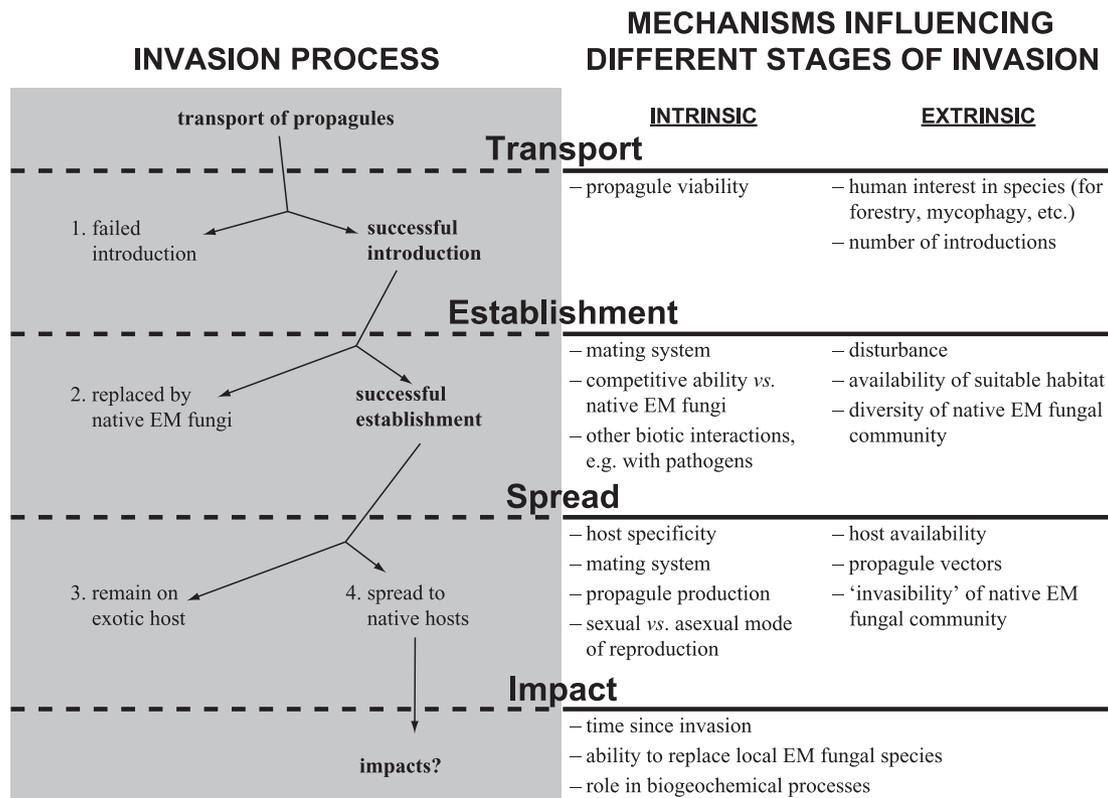
Fig. 5 Conceptual overview of the process and mechanisms involved in the invasion biology of ectomycorrhizal (EM) species. The left panel illustrates the various scenarios discussed in the text. The right panel highlights intrinsic and extrinsic mechanisms that may influence the major stages of the invasion process. Figure adapted from Lockwood *et al*. (2007).

invasive difficult. However, the rare examples of apparently invasive species have a global reach.

Members of the northern hemisphere species complex *Amanita muscaria* s.l. have traveled to Australia, New Zealand, different parts of Africa and South America, and Hawaii (Verwoerd, 1929; Birch, 1937; Singer, 1953; Garrido, 1986; Lundquist, 1986; Ryvarden *et al.*, 1994; Dunstan *et al.*, 1998; Johnston *et al.*, 1998; Giachini *et al.*, 2000; Hemmes & Desjardin, 2002; Sobestiansky, 2005). There are no native EM trees in many of these regions and, as was discussed for other EM fungi in Hawaii, in regions without EM trees *A. muscaria* s.l. cannot spread from its points of introduction. However, in New Zealand and Tasmania, the fungus has spread from the oaks, birches and pines with which it was introduced to the native *Nothofagus* species (Stevenson, 1962; Horak, 1971; Fuhrer, 1992; Johnston *et al.*, 1998). In New Zealand most sightings of *A. muscaria* s.l. with *Nothofagus* are at the edges of forests and where roads encroach on them (P.R. Johnston, pers. comm.), but the species has been classified as a regulated pest since 2001 (Ministry of Agriculture and Forest, New Zealand, 2008).

Laccaria fraterna has been introduced from Australia to many countries, including India and Japan, Brazil, the USA, Morocco, the UK and other European countries (Bakshi, 1966; Malençon, 1966; Mueller, 1992; Last & Watling, 1998; de Meijer, 2001; Díez, 2005). A caveat to these data concerns the species concept. Although *L. fraterna* is one of the few species in the genus with two spores per basidium, *Laccaria* species are notoriously difficult to identify. If morphological data are given in a paper then the species' description can be confirmed, otherwise the record must be treated with suspicion. As it stands, the species appears to have traveled widely. In Australia *L. fraterna* associates with eucalypts, but there are many records of it growing with other hosts in its novel habitats, for example with *Cistus* species in Spain (Díez, 2005) and with *Acacia*, *Eucalyptus*, *Pinus* and *Quercus* in Morocco (Malençon, 1966, described as *L. lateritia*). Even in its native Australia, *L. fraterna* has been found growing in exotic pine plantations (Dunstan *et al.*, 1998). In some countries it is clearly established on what appear to be native hosts, and Pegler & Rayner (1969) describe it as 'fairly frequent in wattle (*Acacia*) plantations, and elsewhere'. In New Zealand *L. fraterna* has been found in a nursery with the native tree species *Pomaderris kumeraho* (Rhamnaceae), and with *Leptospermum* (McNabb, 1972; the fungus is described as *L. ohiensis* in this publication).

Introduced EM fungi that do not persist with introduced hosts, but do spread to local hosts There is only a single (potential) example of an introduced EM fungus that appears to associate exclusively with native hosts, and not the host with which it was introduced. In New Zealand there are only two *Pisolithus* species, and these grow with *Kunzea ericoides* and *Leptospermum scoparium* in geothermal areas (Moyersoen

et al., 2003). Outside of New Zealand, *Pisolithus* species form mycorrhizas with *Eucalyptus* species. Moyersoen *et al.* (2003) assumed that long-distance dispersals from Australia caused the distribution pattern, but Orlovich & Cairney (2004) suggested that the *Pisolithus* species had been introduced with *Eucalyptus* species and jumped to the local tree species. The fungi have never been found growing with *Eucalyptus* in New Zealand.

Intrinsic and extrinsic controls on ectomycorrhizal invasions

Controls on the successful transport, establishment, and spread of EM fungal species include properties intrinsic to an EM fungus, for example, the ability to form mycorrhizas with a diversity of hosts, and extrinsic factors that are independent of the biology of a particular species, for example, the local availability of dispersal vectors (Fig. 5). Some of these mechanisms can be explored using the data available, and for others there is no information.

Host specificity Ectomycorrhizal fungi can have narrow, intermediate or broad host ranges (Molina & Trappe, 1982; Molina *et al.*, 1992; Newton & Haigh, 1998). Some genera, including members of the suilloid group (*Suillus*, *Rhizopogon*, *Truncocolumella*, *Gomphidius* and *Chroogomphus*), associate almost exclusively with hosts in the Pinaceae. Other groups, including the Russulaceae, are found with a diversity of plant families throughout the world.

If fungal species that can form mycorrhizas with a diversity of hosts are more likely to establish, there should be a relationship between the degree of host specificity within a genus and the number of species of that genus recorded as introduced. Data on host ranges are available for 20 of the genera in our database (Molina *et al.*, 1992). In our analyses, host specificity is measured as either the percentage of species within a genus specialized to a single genus of host (narrow host range) or the percentage of species within a genus that can form mycorrhizas with host species from different families, orders, or classes (broad host range; Molina *et al.*, 1992). When all of the genera are analysed together, there are no correlations between a narrow host range and the number of introduced species ($r = 0.06$, $P = 0.82$) or broad host range and the number of reported introductions ($r = 0.11$, $P = 0.66$). These patterns may be driven by one genus, *Suillus*, which can clearly be seen as an outlier in both datasets (Fig. 6). *Suillus* spp. specialize on *Pinus* spp. and because the most widely planted forestry trees are pines (Richardson & Higgins, 1998; del Lungo *et al.*, 2006), this relatively specialized group of EM fungi is disproportionately represented in terms of the total number of introduced species and number of reported introductions (Fig. 6). When the genus *Suillus* is excluded there is a weak negative correlation between narrow host ranges and number of introduced species ($r = -0.29$, $P = 0.26$). There is
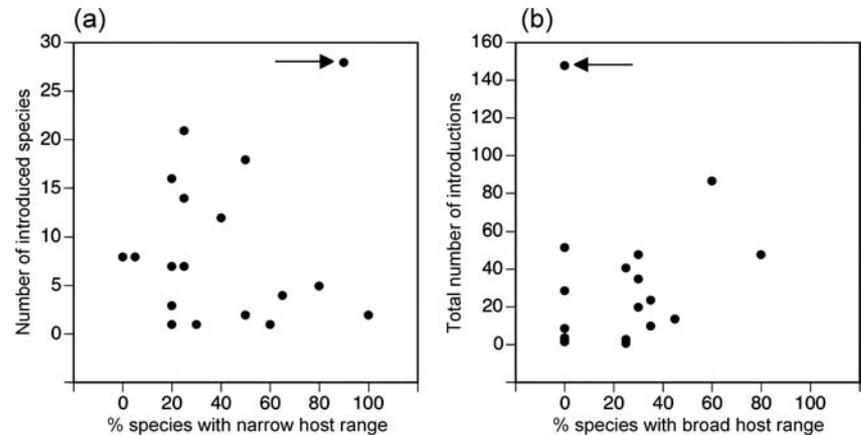
Fig. 6 Correlations between host range and the number of introduced species or number of introductions. Data of 20 genera of ectomycorrhizal (EM) fungi, arrows mark the genus *Suillus*. Per cent species with narrow or broad host ranges taken from Molina *et al.* (1992). When data for *Suillus* are excluded there is a significant correlation between broad host ranges and total number of introductions, see text for statistics and a discussion of the *Suillus* data.

a significant positive correlation between broad host ranges and total number of introductions ($r = 0.50$, $P = 0.04$).

In many cases, EM fungi experience range expansions that closely track a host's range expansion. In the southern hemisphere, pines are not native. The large-scale plantations encountered today are a product of the early post World War II years (Richardson, 1998). *Pinus radiata* is by far the most planted species and covered roughly 4 million ha by 1996 (Richardson, 1998). In its native California *P. radiata* is autochthonous to three small patches of land on the central coast (Vogl *et al.*, 1988); humans have facilitated a massive range expansion (Clapp, 1995) and these new forests now provide an additional 4 million ha of habitat to any fungus that can associate with *P. radiata*. At many sites where *P. radiata* is introduced a very limited number of symbionts have been recorded (e.g. only *Suillus luteus*, *Rhizopogon vulgaris* and *Thelephora terrestris* in the Ecuadorian highlands where the plantations replace the native paramo grasslands; Hedger, 1986; Chapela *et al.*, 2001). But these EM fungi appear wherever *P. radiata* is planted. The fungus *S. luteus* is native to Europe, and in this case an association that would never form in either species' native range is now commonly found across the globe.

Dispersal habits and propagule production Modes of dispersal appear to play a major role in the successful establishment and spread of invasive plant and animal species (Lockwood *et al.*, 2007). Introduced EM fungi may form either animal-dispersed (often hypogeous, or below ground) or wind dispersed (often epigeous, or above ground) fruit bodies and spores. Perhaps those fungi with fruit bodies that favor long-distance wind dispersal are more likely to be introduced. In our database 181 records are of species with hypogeous fruit bodies, and 585 records belong to species with epigeous fruit bodies. Although the greater number of species with epigeous reproductive structures may reflect actual differences in the frequencies of introduction, it may also reflect biases in the collection of these more obvious fungi. Within the Basidiomycota a wide variety of shapes of fruit bodies are introduced, including classic mushroom shapes as well as crusts, clubs and corals.

The gilled *A. muscaria*, the poroid *Boletus edulis*, false truffles in the genus *Rhizopogon*, secotioid *Setchelliogaster* species, coral fungi such as *Clavulina cristata* and *Ramaria toxica*, and the fan-shaped *Thelephora terrestris* offer examples of the wide variety of shapes that are moved. We conclude that neither dispersal habit nor morphology are barriers to introduction, and this is not surprising as it is humans who are moving the fungi across landscapes.

Studies of introduced plants and animals often suggest that introduced species that establish and spread should produce large numbers of viable propagules (Lockwood *et al.*, 2007). Estimates of propagule production for EM fungi are rare, but *Suillus bovinus*, which has successfully established on several continents, was estimated to produce between 110 000 000 and 1 280 000 000 spores per sporocarp in its native range (Dahlberg & Stenlid, 1994). As there is a paucity of data on the numbers of spores produced per individual for different EM fungal species, it is impossible to know if EM fungi that successfully spread once established are those that produce the most viable propagules. There is some evidence that sporocarp productivity increases for some EM species in novel habitats (Chapela *et al.*, 2001), but no careful comparisons of the reproductive biology of EM fungi in introduced and native ranges have been made.

Genetic systems The number of nuclei within an EM fungal spore may influence the ability of a species to establish when introduced, and spread once established. Although a single nucleus per spore is typical of basidiomycete fungi, several introduced species have multinucleate spores (Horton, 2006). Having multiple nuclei in a spore may facilitate colonization. For example, the species *Laccaria fraterna* seems capable of rapidly invading newly disturbed habitats (Tommerup *et al.*, 1991), and each spore houses four nuclei. These nuclei are of two different and compatible mating types (Tommerup *et al.*, 1991), and a single spore can form mushrooms on its own, without mating. The biology is analogous to self-fertilization in plants, and provides the spore with an ability to establish independently of other individuals (Jain, 1976). As a result,

the life cycle of *L. fraterna* is shortened, and in one experiment mushrooms formed within a record 3 months after inoculation of a *Eucalyptus* seedling (Tommerup *et al.*, 1991). *Amanita muscaria* s.l. also possesses an unusual nuclear structure. In this case each spore houses two nuclei (Horton, 2006). Although the nuclei appear to be genetically identical, the two nuclei may influence the metabolism of the germinating spore (Horton, 2006), perhaps allowing it to germinate more quickly than the uninucleate spores of other species.

Biases in discovering introduced EM fungi

Fungi are cryptic organisms and it is not surprising that biases pervade the literature. Most obviously, regions that have been intensively sampled using both morphological and molecular criteria have turned up the most numbers of introduced EM fungi. In Spain, 17 species of introduced fungi are recorded as growing with the genus *Eucalyptus*; extensive research on the mycota of this habitat has been done by, for example, Díez (2005) and Lago-Álvarez & Castro (2004). In the state of California (USA), where many species of *Eucalyptus* are widely planted, only 11 fungal species have been reported as introduced in association with any genus of tree (Arora, 1986; Castellano *et al.*, 1989).

Most EM fungi are only found after conspicuous fruiting bodies are discovered, although the mycelia of these species may have persisted for many years before fruit bodies were made; the biology of EM fungi may create a substantial lag between time of introduction and detection. For example, the EM hosts *Nothofagus antarctica*, *Nothofagus betuloides* and *Nothofagus pumilio* were imported from Tierra del Fuego (Argentina) to Denmark in the late 1970s, and in 1991 the Argentine fungus *Descolea antarctica* was found fruiting in a Danish arboretum (Petersen, 1992). Some of the same species were planted in the Faroe Islands, and in 1988/1989 *D. antarctica* was also found growing with these *Nothofagus* trees (Petersen *et al.*, 1994). In these examples the lag between planting (of hosts) and fruiting (of fungal symbionts) appears to be in the range of 15 yr. However, the autecology of most species of EM fungi is poorly known, and there is no way to know if 15 yr is a typical lag between infection and fruiting. Moreover, detection is dependent on humans watching for mushrooms, and many species fruiting in a novel location are likely to go unnoticed.

A final bias concerns the transition from introduction to established population. A fungus recorded as introduced may subsequently persist unnoticed in the novel location, and for this reason the literature cannot always be used to distinguish between a single occurrence and establishment. It is often more interesting to report a 'novelty', instead of the second find of a species. Species that are recorded as introductions may in fact establish but never again appear in the literature, while other species are almost certainly single occurrences (see Dring, 1980 for a nonmycorrhizal example).

Unanswered questions and future directions

What are the biogeographies of ectomycorrhizal fungi? The geographic ranges of most fungi are poorly documented and the lack of natural history data causes confusion over what is native or introduced (Pringle & Vellinga, 2006). In some cases even the species' native continent is unknown. For example, *Amanita inopinata* (whose mycorrhizal status is unknown) was formally described from a collection made in England, and in the species' description it is discussed as an introduction (Reid, 1987). Later, it was reported as an introduction to New Zealand (Ridley, 2000). Even as it spreads in these two novel regions (Bas, 2001; Uljé, 2001; Courtecuisse & Moreau, 2004; Kibby, 2005, 2006), its native range remains unknown.

To understand the magnitude of EM introductions it is imperative to develop global geospatial databases and catalog the ranges of both native and introduced EM fungal species. Australia has classified many EM fungi as either native or introduced, and monitors species' distributions (Fungimap, 2008). Similar mapping efforts have occurred in the UK (British Mycological Society, 2006). In North America, the highly successful USDA Plants Database (USDA NRCS, 2008) is used for invasive species research and an invasive species mapping tool is now available for some plants and animals (National Biological Information Infrastructure, 2008). Mapping tools are also available for plant pathogens (National Agricultural Pest Information System, 2008). No similar databases have been developed for mycorrhizal or saprophytic fungi.

Compiling exact information on species ranges is made more complicated by the changes in morphological species concepts caused by molecular data; more nuanced delineations of species can complicate efforts to track introductions. For example, the morphological species *P. arrhizus* appears to be a complex of at least 11 genetic species, each of which is specific to a different host (Martin *et al.*, 2002); *A. muscaria* includes at least three different 'ITS (internal transcribed spacer) types' (Oda *et al.*, 2004; Geml *et al.*, 2006). We do not know if the *A. muscaria* introduced to the Southern hemisphere comprises one or all three types; only one sample – from New Zealand – has been sequenced (Oda *et al.*, 2004). Neither do we know if the *A. muscaria* appearing with planted *P. radiata* in California is a native North American *A. muscaria*, or an introduced species. Although the phylogenetic species concept is emerging as an accepted standard within mycology, in the field identifications are based on morphological data, and often the sequence data needed to delineate phylogenetic species are not available.

What limits the spread of EM fungi? A variety of intrinsic and extrinsic factors may limit the spread of EM fungi, but as obligate symbionts the most likely control is an availability of potential hosts. In a novel environment there may be no local hosts, or the introduced fungi may have narrow host ranges

and be unable to form symbioses with local flora. Examples include the fungi introduced to Hawaii, where EM trees are not native, and in California the introduced fungus *Leccinum scabrum*, that grows exclusively with the genus *Betula* (Arora, 1986; E. C. Vellinga, pers. obs.). In some cases, fungi that appear to form mycorrhizas only with an introduced plant may be in a preliminary phase of the invasion process, and may yet spread. Abiotic parameters or the local diversity of fungi may also constrain introductions. However, biologists know very little about why a symbiotic fungus does or does not spread.

What are the effects of introduced EM fungi? Hundreds of EM fungal species have been moved across the world. Occasionally, these species associate with native hosts and invade local forests. Despite the widespread occurrence of introduced EM fungi, we know little about the potential effects of these introductions, either on the diversity of native communities or on ecosystem functioning (Schwartz *et al.*, 2006; Desprez-Loustau *et al.*, 2007).

Introduced EM fungi may displace native EM fungi, facilitate the invasion of introduced plant species, harm native plant species or alter nutrient cycles in soils. For example, the introduction of EM fungi allowed the invasion of exotic *Pinus* species into the African fynbos (Richardson *et al.*, 2000). The introduction of EM fungi to the paramo grasslands of Ecuador appeared to play a role in soil carbon depletion (Chapela *et al.*, 2001). In Tanzania *A. muscaria* s.l. is a health hazard as people confuse it with edible *Amanita* species from the native miombo vegetation (Härkönen *et al.*, 1994). To understand the potential effects of introduced EM fungi, several key questions need to be answered and these focus on the ecology of the introduced EM fungi. Questions include:

• When introduced EM fungi spread to native habitats or hosts, do they grow to be an abundant part of the local soil community? Do introduced fungi dominate as mycelia, root tips, or fruit bodies? Are they rare? Do introduced species outcompete local fungi, or fill empty niches?

• What characteristics allow EM fungi to spread and invade local communities? Do invasive EM fungi make more spores, grow faster, or possess allelochemicals? Are they parasites of local trees?

• How does the abundance of an introduced EM fungal species vary among different ranges, especially between native and introduced ranges (Hierro *et al.*, 2005)? Do these abundances relate to potential impacts?

A variety of tools are already available to assess potential impacts, including methods for measuring the mycelium of EM fungi in the soil (Wallander *et al.*, 2001), and high throughput molecular analyses of EM fungal diversity (Dickie & Fitzjohn, 2007). When combined with long-term field observations and experiments, these tools could be used to assess the potential changes in the structure and function of EM fungal communities as introduced fungi establish and spread.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Table S1 IntroducedEMF.mdb: a relational database of ectomycorrhizal introductions

Table S2 EMFIntroductions_CompleteDatabaseTables_PlusDocumentation.xls: a spreadsheet with information about the relational database. The first page describes the fields of the five database tables, and the next five pages are the five tables.

Table S3 EMFIntroductions_SingleTableView.xls: the same database presented as an Excel spreadsheet.

Text S1 IntroducedEMF_Database_Schema.pdf: a visual diagram of the relationships among the five database tables.

Text S2 IntroducedEMF_DatabaseReferences.doc: the database references.