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# Invasive belowground mutualists of woody plants

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**Abstract** Most plants require mutualistic associations to survive, which can be an important limitation on their ability to become invasive. There are four strategies that permit plants to become invasive without being limited by a lack of mutualists. One is to not be dependent on mutualists. The other three strategies are to form novel mutualisms, form associations with cosmopolitan species, or co-invade with mutualists from their native range. Historically there has been a bias to study mutualisms from a plant perspective, with little consideration of soil biota as invasive species in their own right. Here we address this by reviewing the literature on belowground invasive mutualists of woody plants. We focus on woody invaders as ecosystem-transforming plants that frequently have a high dependence on belowground mutualists. We found that co-invasions are common, with many ectomycorrhizal plant species and N-fixing species co-invading with their mutualists. Other groups, such as arbuscular mycorrhizal plants, tend to associate with cosmopolitan fungal species or to form novel associations in their exotic range. Only limited evidence exists of direct negative effects of co-invading mutualists on native mutualist communities, and effects on native plants appear to be largely driven by altered environmental conditions rather than direct interactions. Mutualists that introduce novel ecosystem functions have effects greater than would be predicted based solely on their biomass. Focusing on the belowground aspects of plant invasions provides novel insights into the impacts, processes and management of invasions of both soil organisms and woody plant species.

**Keywords** Biological invasions · Co-invasion · Cosmopolitan species · Co-xenic · Mutualism · Mycorrhiza · Novel interactions · Soil biota · Tree invasions

## Introduction

Biological invasions typically involve complex processes, frequently including the need for organisms to find mutualists (Richardson et al. 2000). Some exotic organisms are able to find local mutualists that can replace ones from their native range. Other exotics, perhaps with a higher degree of specialization, invade

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along with mutualists from their original range. For example, *Ficus* plants in Florida, USA, that have complex and specialized pollination systems, were able to invade only after their specific pollinator arrived (Ramirez and Montero 1988; McKey and Kaufmann 1991; Nadel et al. 1992). The need to find or co-invade with mutualists is particularly common for invasive woody species, which frequently need mycorrhizal fungi or nitrogen (N)-fixing symbionts in order to thrive and compete with native vegetation (e.g. Nuñez et al. 2009; Dickie et al. 2010; Rodriguez-Echeverria et al. 2012).

Historically there has been a bias to study mutualisms from a plant perspective. This has been driven, in part, by our own human epigeous bias and a common belief that soil microbial inoculum is ubiquitous in the environment (De Wit and Bouvier 2006; Peay et al. 2010). Nonetheless, the development of molecular tools has given rise to a greater appreciation that soil biotic communities are diverse and spatially structured, and that the presence or absence of belowground organisms can directly influence plant communities (Peay et al. 2008). The lack of focus on the belowground aspect of the invasion process means that basic questions still need to be answered regarding woody plant invasion and associated mutualisms. These questions include the description of general patterns of the invasion dynamic (e.g. how common are co-invasions, novel mutualisms or cosmopolitan associations?) and the impact of soil mutualists on native plant and fungal communities. We suggest that by addressing these questions, and considering invasive plant mutualisms from a belowground perspective, a more complete picture of the plant invasion processes can be achieved.

This paper reviews the literature on invasive mutualisms and suggests ways to further our understanding of mutualistic interactions in invasion. We considered invasive woody plants following Blackburn et al.'s (2011) definition, which excludes species that are introduced but never escape their introduction areas (like many crop species). Therefore, mutualist species described only in association with forestry plantations or other planted individual plants have not been included (Diez 2005; Barroetaveña et al. 2007; Vellinga et al. 2009). We consider a mutualist species invasive regardless of whether it is restricted to forming associations with invasive plants or also forms novel associations with native plants. This is a logical parallel treatment with plants, where a plant species is considered invasive regardless of whether it associates with native or co-invading mutualists. There is substantial work on native and non-native herbaceous plants and their associated soil biota (e.g. Klironomos 2003; Porter et al. 2011). However, we focus solely on woody species for our analyses as ecosystem-transforming species that tend to have a high dependency on belowground symbioses.

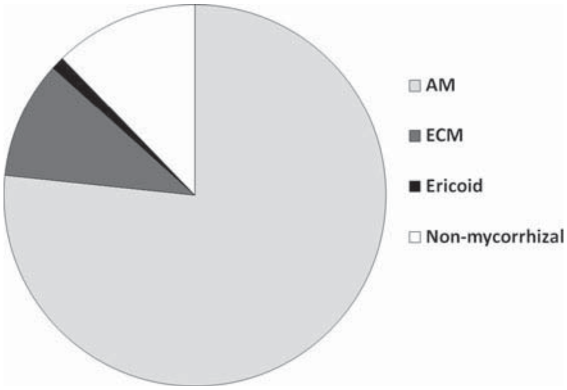

**Fig. 1** Proportion of families of woody plants with species found to be invasive (from Rejmánek and Richardson, 2013) that do or do not require mycorrhizal associations. Data from Brundrett (2009), Koele et al. (2012), Wang and Qiu (2006). The *white color* represents the number of families that do not require mycorrhizal fungi. We included as non-mycorrhizal families and species, those families that had at least some members that are non-mycorrhizal, to obtain a conservative estimate of the importance of mycorrhizal associations. For more details on these data see Online Resource 1. *AM* arbuscular mycorrhizal associations, *ECM* ectomycorrhizal associations

## Strategies for plant invasion with mutualists

There are four basic strategies that permit plants to become invasive without being limited by a lack of mutualists. One is simply to not be dependent on mutualisms. For example, while only about 6 % of angiosperm species are non-mycorrhizal (Brundrett 2009), many common invaders are non-mycorrhizal (Fig. 1, Online Resource 1), including the woody Proteaceae (Allsopp and Holmes 2001) and *Tamarix* (Beauchamp et al. 2005) as well as herbaceous garlic mustard and other Brassicaceae (Cipollini et al. 2012) and most *Polygonum* (Allsopp and Holmes 2001). Being non-mycorrhizal or having low dependence on mycorrhizas or other symbioses frees invasive plants from the need to establish symbioses, which might

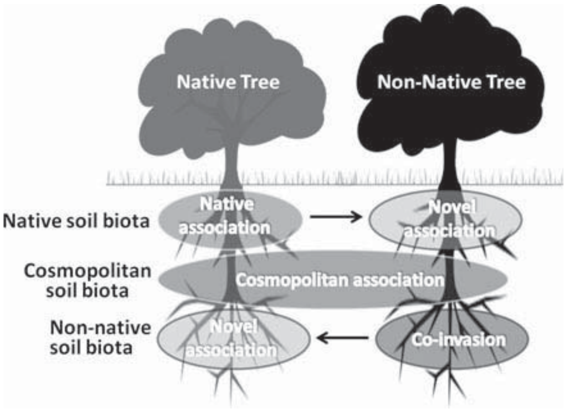

**Fig. 2** Interactions of native and non-native plants with native, cosmopolitan and non-native soil mutualists. The interactions analyzed in this study were those with at least one member (plant or soil mutualist) of a non-native origin. *Arrows* indicate potential host-switching by mutualistic soil biota. Novel associations can occur with non-native plant and native symbiont, native plant and non-native symbiont, or 'co-xenic novel associations' where both partners are non-native but do not co-occur in their respective native ranges

otherwise limit invasion. In high-nutrient sites, such as following disturbance, being non-symbiotic may not be a severe limitation for plant nutrient uptake (van der Putten et al. 2007). However, most invasive woody plants require one or more soil mutualists to thrive (Fig. 1, Online Resource 1). The exceptions may have alternative, non-symbiotic nutrient uptake strategies, such as cluster roots in the Proteaceae (Allsopp and Holmes 2001) or, in the case of *Tamarix*, may actively disrupt the mutualisms of competitors (Meinhardt and Gehring 2012), increasing their relative competitive ability (van der Putten et al. 2007).

For plants that require mutualists, Dickie et al. (2010) proposed three major strategies: novel mutualisms, cosmopolitan associations, and co-invasion (Fig. 2). Novel mutualisms can occur through three mechanisms. The first (Dickie et al. 2010), 'non-native plant and native symbiont', occurs when an invasive plant utilizes symbiotic organisms native to the invaded range. For example, some invasive plants in New Zealand recruit native, free-living *Bradyrhizobium* species into N-fixing mutualisms (Weir et al. 2004), and native fungi form ectomycorrhizal symbioses with planted *Eucalyptus* in the Seychelles (Tedersoo et al. 2007). Novel mutualisms can also occur when a non-native mutualist forms associations with native plants, such as in the invasive *Amanita muscaria* associating with native *Nothofagus* spp. trees in New Zealand (Orlovich and Cairney 2004). The third possible mechanism could be termed 'co-xenic novel associations' (from the Greek word *Xenos*, meaning stranger), where both plant and mutualist are non-native, but do not co-occur in their native ranges. This has been documented, for example, in pollination mutualisms between European bees and North American plant species invading in New Zealand (Hanley and Goulson 2003), and similarly in co-xenic pathogens on invasive plants (Sullivan 2013). We have also observed Northern-Hemisphere *A. muscaria* associating with planted Australian *Eucalyptus nitens* in New Zealand (I. A. Dickie, personal observation).

Cosmopolitan associations are defined as mutualisms between invasive plants and native species that are also native to the home-range of the invasive plant. Cosmopolitan associations appear common in some groups, where a few low-specificity cosmopolitan species are common on invasive plants (Benson and Dawson 2007; Moora et al. 2011; Knapp et al. 2012). Arbuscular mycorrhizal invasive plants, for example, associate with widespread, generalist mycorrhizal fungi (Moora et al. 2011).

Co-invasion, where a plant invades a novel range along with invasive mutualists, is the final possibility. Mutualists were frequently transported on potted plants (e.g. Herriott 1919) or, less commonly, intentionally introduced (Mikola 1970; Vellinga et al. 2009), and these mutualists can spread along with invasive plants. Co-invasion has been reported in ectomycorrhizal *Pinus* and actinorhizal *Casuarina* (Zimpfer et al. 1999; Benson and Dawson 2007). From our literature review we found that co-invasions seem to be as common as novel interactions (Table 1).

Some groups tend to co-invade more than others. For example, we found that the members of the Pinaceae family tend to co-invade with their symbionts. This has been the case in South America, New Zealand and Hawai'i. Based on sporocarp observations, it seems likely that North American Pinaceae may associate with European ectomycorrhizal fungi and vice versa in invasions. These would represent a type of invasive novel association (at least at the plant species level, if not at the genus or family level) in which neither partner was native. However, a lack of clear species concepts and documented native ranges for many fungi makes confirmation difficult (Pringle and Vellinga 2006). The observation that Pinaceae species tend to co-invade more than other groups

**Table 1** List of all recorded symbionts on (A) non-native plants and (B) native plants

| Class | Mutualist type | Interaction type | Soil mutualist | Invasion location | Phytosymbiont | Citation |
|---|---|---|---|---|---|---|
| *(A) Non-native plants* | | | | | | |
| Co-invasion | ECM | Exotic symbiont on exotic plant | *Amanita muscaria* | New Zealand | *Pinus contorta* | Dickie et al. (2010) |
| Co-invasion | ECM | Exotic symbiont on exotic plant | Atheliaceae (cf. *Tylospora*) | New Zealand | *Pinus contorta* | Dickie et al. (2010) |
| Co-invasion | ECM | Exotic symbiont on exotic plant | *Cadophora findlandica* | Argentina | *Pseudotsuga menziesii* | Nuñez et al. (2009) |
| Co-invasion | ECM | Exotic symbiont on exotic plant | Cantharellales sp. | New Zealand | *Pinus contorta* | Dickie et al. (2010) |
| Co-invasion | ECM | Exotic symbiont on exotic plant | *Hebeloma* sp. | Argentina | *Pinus contorta*, *P. ponderosa*, *Pseudotsuga menziesii* | Nuñez et al. (2009) |
| Co-invasion | ECM | Exotic symbiont on exotic plant | *Laccaria fraterna*, | Europe | *Eucalyptus globulus* | Diez (2005) |
| Co-invasion | ECM | Exotic symbiont on exotic plant | *Rhizopogon rubescens* group | Hawaii | *Pinus* sp. | Hynson et al. (2013) |
| Co-invasion | ECM | Exotic symbiont on exotic plant | *Rhizopogon* sp. | Argentina | *Pinus ponderosa* | Salgado Salomon et al. (2011) |
| Co-invasion | ECM | Exotic symbiont on exotic plant | *Rhizopogon sp.* | Argentina | *Pseudotsuga menziesii* | Nuñez et al. (2009) |
| Co-invasion | ECM | Exotic symbiont on exotic plant | *Suillus granulatus* | New Zealand | *Pinus contorta* | Dickie et al. (2010) |
| Co-invasion | ECM | Exotic symbiont on exotic plant | *Suillus lakei* | Argentina | *Pseudotsuga menziesii* | Nuñez et al. (2009) |
| Co-invasion | ECM | Exotic symbiont on exotic plant | *Suillus luteus* | Argentina, New Zealand | *Pinus contorta*, *P. ponderosa* | Nuñez et al. (2009), Dickie et al. (2010) |
| Co-invasion | ECM | Exotic symbiont on exotic plant | *Suillus pungens* | Hawaii | *Pinus* sp. | Hynson et al. (2013) |
| Co-invasion | ECM | Exotic symbiont on exotic plant | *Suillus subluteus* | Hawaii | *Pinus* sp. | Hynson et al. (2013) |
| Co-invasion | ECM | Exotic symbiont on exotic plant | *Thelephora terrestris* | Argentina | *Pinus contorta*, *Pinus ponderosa* | Nuñez et al. (2009) |
| Co-invasion | ECM | Exotic symbiont on exotic plant | *Tylospora* sp. | Argentina | *Pinus contorta* | Dickie et al. (2010) |

**Table 1** continued

| Class | Mutualist type | Interaction type | Soil mutualist | Invasion location | Phytosymbiont | Citation |
|---|---|---|---|---|---|---|
| Co-invasion | ECM | Exotic symbiont on exotic plant | *Wilcoxina* | Argentina, Hawaii | *Pinus ponderosa*, *P. contorta*, *Pinus* sp, *Pseudotsuga menziesii* | Nuñez et al. (2009), Salgado Salomon et al. (2011), Hynson et al. (2013) |
| Co-invasion | Endophytic fungus | Exotic symbiont on exotic plant | *Phialocephala fortinii* | New Zealand | *Pinus contorta* | Dickie et al. (2010) |
| Co-invasion | N-fixing | Exotic symbiont on exotic plant | *Bradyrhizobium canariense*, A110 strain | Europe | *Acacia longifolia*, *A. melanoxylon* | Rodriguez-Echeverria et al. (2012) |
| Co-invasion | N-fixing | Exotic symbiont on exotic plant | *Bradyrhizobium japonicum*, A120 strain (from Australia) | Europe | *Acacia longifolia*, *A. melanoxylon* | Rodriguez-Echeverria et al. (2012) |
| Co-invasion | N-fixing | Exotic symbiont on exotic plant | *Bradyrhizobium* spp. 15 different strains | Europe | *Acacia longifolia* | Rodriguez-Echeverria (2010) |
| Co-invasion | N-fixing | Exotic symbiont on exotic plant | *Bradyrhizobium yuanmingense*, U214 strain | Europe | *Acacia longifolia*, *A. melanoxylon* | Rodriguez-Echeverria et al. (2012) |
| Co-invasion | N-fixing | Exotic symbiont on exotic plant | *Cupriavidus* (two isolates) | Philippines | *Mimosa* spp. | Andrus et al. (2012) |
| Co-invasion | N-fixing | Exotic symbiont on exotic plant | *Frankia* | Hawaii | *Morella faya* | Vitousek et al. (1987) |
| Co-invasion | N-fixing | Exotic symbiont on exotic plant | *Frankia* sp. | Africa, America and Asia | *Casuarina. equisetifolia*, *C. cunninghamiana*, *C. glauca Allocasuarina torulosa*, *A. verticillata* | Simonet et al. (1999) |
| Co-invasion | N-fixing | Native symbiont on exotic tree | *Sinorhizobium* | China | *Robinia pseudoacacia* | Wei et al. (2009) |
| Cosmopolitan | AM | Cosmopolitan symbiont on exotic plant | Gigasporaceae | Europe | *Trachycarpus fortunei* | Moora et al. (2011) |
| Cosmopolitan | AM | Cosmopolitan symbiont on exotic plant | Glomeraceae (11 fungal taxa) | Europe | *Trachycarpus fortunei* | Moora et al. (2011) |
| Cosmopolitan | AM | Cosmopolitan symbiont on exotic plant | *Glomus fasciculatum* | Europe | *Trachycarpus fortunei* | Moora et al. (2011) |
| Cosmopolitan | AM | Cosmopolitan symbiont on exotic plant | *Glomus vesiculiferum* | Europe | *Trachycarpus fortunei* | Moora et al. (2011) |
| Cosmopolitan | AM | Cosmopolitan symbiont on exotic plant | *Scutellospora cerradensis* | Europe | *Trachycarpus fortunei* | Moora et al. (2011) |

**Table 1** continued

| Class | Mutualist type | Interaction type | Soil mutualist | Invasion location | Phytosymbiont | Citation |
|---|---|---|---|---|---|---|
| Cosmopolitan | N-fixing | Cosmopolitan symbiont on exotic plant | *Bradyrhizobium elkanii*, A12 strain | Europe | *Acacia longifolia*, *A. melanoxylon* | Rodriguez-Echeverria et al. (2012) |
| Cosmopolitan | N-fixing | Cosmopolitan symbiont on exotic plant | *Bradyrhizobium elkanii*, A12 strain | Europe | *Ulex europaeus*, *Cytisus grandiflorus* | Rodriguez-Echeverria et al. (2012) |
| Novel association | AM | Native symbiont on exotic plant | *Undescribed species* | USA | *Robinia pseudoacacia* | Callaway et al. (2011) |
| Novel association | Dark septate endophytes | Native symbiont on exotic tree | Dark septate endophytes (*Periconia*?) | Hungary | Tree of heaven, *Ailanthus altissima* | Knapp et al. (2012) |
| Novel association | ECM | Native symbiont on exotic plant | *Laccaria fraterna* | Europe | *Cistus ladanifer* | Diez (2005) |
| Novel association | N-fixing | Native symbiont on exotic plant | *Bradyrhizobium japonicum*, H32 strain | Europe | *Acacia longifolia* | Rodriguez-Echeverria et al. (2012) |
| Novel association | N-fixing | Native symbiont on exotic tree | *Bradyrhizobium* species | New Zealand | *Acacia* spp., *Cytisus scoparius* (broom), *Ulex europaeus* (gorse) | Weir et al. (2004) |
| Novel association | N-fixing | Native symbiont on exotic plant | *Bradyrhizobium yuanmingense*, UU22sfb strain | Europe | *Acacia longifolia* | Rodriguez-Echeverria et al. (2012) |
| Novel association | N-fixing | Native symbiont on exotic tree | *Burkholderia* | Australia | *Mimosa pigra* | Parker et al. (2007) |
| Novel association | N-fixing | Native symbiont on exotic tree | *Burkholderia* spp | China | *Mimosa* spp. | Liu et al. (2012) |
| Novel association | N-fixing | Native symbiont on exotic tree | *Mesorhizobium* | China | *Robinia pseudoacacia* | Wei et al. (2009) |
| (*B*) *Native plants* | | | | | | |
| Novel association | ECM | Exotic symbiont on native plant | *Amanita muscaria* | New Zealand | *Nothofagus* spp. | Dickie and Johnson (2009), Dunk et al. (2012) |
| Novel association | ECM | Exotic symbiont on native plant | *Amanita phalloides* | USA | Pines, *Picea*, *Abies*, *Cedrus*, *Fagus*, *Quercus* | Wolfe and Pringle (2012), Wolfe et al. (2010) |
| Novel association | ECM | Exotic symbiont on native plant | *Boletellus projectellus* | Europe | Not described | Motiejunaite et al. (2011) |
| Novel association | ECM | Exotic symbiont on native plant | *Tuber indicum* | Europe, USA | *Pinus taeda*, *Carya illinoinensis* and others | Murat et al. (2008), Bonito et al. (2011) |
| Novel association | N-fixing | Exotic symbiont on native plant | *Bradyrhizobium canariense*, A110 strain | Europe | *Ulex europaeus* | Rodriguez-Echeverria et al. (2012) |

**Table 1** continued

| Class | Mutualist type | Interaction type | Soil mutualist | Invasion location | Phytosymbiont | Citation |
|---|---|---|---|---|---|---|
| Novel association | N-fixing | Exotic symbiont on native plant | *Bradyrhizobium japonicum* A120 strain | Europe | *Ulex europaeus*, *Cytisus grandiflorus* | Rodriguez-Echeverria et al. (2012) |
| Novel association | N-fixing | Exotic symbiont on native plant | *Bradyrhizobium* spp. 10 different strains | Europe | *Ulex europaeus* | Rodriguez-Echeverria (2010) |
| Novel association | N-fixing | Exotic symbiont on native plant | *Bradyrhizobium* spp. 4 different strains | Europe | *Cytisus grandiflorus* | Rodriguez-Echeverria (2010) |
| Novel association | N-fixing | Exotic symbiont on native plant | *Bradyrhizobium yuanmingense*, U214 strain | Europe | *Ulex europaeus* | Rodriguez-Echeverria et al. (2012) |
| Novel association | N-fixing | Exotic symbiont on native plant | *Cupriavidus* spp. | China | *Mimosa* spp. | Liu et al. (2012) |

*ECM* ectomycorrhizal, *AM* arbuscular mycorrhizal

could be driven either by the high effort in introducing ectomycorrhizal symbionts of these commercially important species, differences in species biology, or biases in research effort (with more studies of Pinaceae than most other tree species).

Although co-invasion is most common, pines can also form novel associations. Neither Nuñez et al. (2009) nor Dickie et al. (2010) found any novel ectomycorrhizal symbioses of invasive *Pinus* with non-cosmopolitan fungi native to *Nothofagus* forests in the Southern Hemisphere. However, in Iranian pine plantations, it has been reported that pines form novel associations with fungi that typically associate with the distantly related genus *Fagus* (Bahram et al. 2012). It is unclear if these novel symbioses occur in invasive pines found outside of silvicultural plantations, but the possibility clearly exists. Bahram and colleagues suggest this might reflect evolutionary adaptation of the fungi to the overlapping ranges of the two plant families.

Other mutualistic species such as the ectomycorrhizal fungi *Tuber indicum*, *A. muscaria* and *Amanita phalloides* expand from their introduced hosts to form novel associations with native plants (Bagley and Orlovich 2004; Murat et al. 2008; Johnston 2010; Wolfe et al. 2010; Bonito et al. 2011; Dunk et al. 2012). *A. muscaria* and *A. phalloides* form showy mushrooms that can be toxic, and produce a relatively easily identified mushroom. *Tuber indicum* is a species with enormous economic importance since it is replacing the valuable tuber species that produces the famous Perigord black truffle (*T. melanosporum*). These species may therefore have been detected more readily than other invasive fungi. We suggest that many additional invasive mutualists on native plants may remain undetected, particularly those with less visible sporocarps or of less immediate economic importance (either in medical costs or in culinary use).

Many N-fixing plants are able to find mutualists in their new range (e.g. Rodriguez-Echeverria et al. 2009; Callaway et al. 2011), but there is evidence that they may perform better with symbionts from their native range. Rodriguez-Echevarria et al. (2012), using four plant species and five different N-fixing inocula from the *Bradyrhizobium* group, found that native and not-native plants had increased growth with the symbionts from their native range compared with symbionts from areas outside their native range. This suggests that these plants may require symbiotic co-invasion to become invasive.

For arbuscular mycorrhizal plant species, the current understanding is that they tend to be promiscuous in associations (Smith and Read 2008), so they can form novel symbioses in the exotic range without the need for co-invasion. However, Callaway et al. (2011) found *Robinia pseudoacacia* performs better with arbuscular mycorrhizal fungi from its native range, similar to the results of Rodriguez-Echevarria et al. (2012) for N-fixing bacteria. So it might be expected that there could be pressure for co-invasion, since some plants may need the optimal symbionts for their invasion. *Robinia pseudoacacia* seems to be able to invade despite having suboptimal arbuscular mycorrhizal symbionts, probably because of the benefit of losing pathogens that are common in their native range (Callaway et al. 2011). In general, ecosystems that completely lack arbuscular mycorrhizal plants are exceedingly rare. Hence, there are only a few cases where arbuscular mycorrhizal invasions of previously non-arbuscular mycorrhizal systems are well documented, such as *Hieracium lepidulum* invasion into pure *Nothofagus solandri* stands in New Zealand (Spence et al. 2011) but that study did not test whether the fungi were native.

## Are invasive soil mutualisms a distinctive subset of the ones introduced?

Across organismal groups, not all introduced species are able to invade (Rejmánek and Richardson 1996; Williamson and Fitter 1996). This is clearly the case for plants and animals (Zenni and Nuñez 2013). Propagule pressure (the size of the introduction effort) seems to play an important role, but still some plants and animals are more prone to invade than others. Is this also the case for invasive mutualistic soil biota? We see that the same species tends to invade multiple locations, for example the ectomycorrhizal fungus *Suillus luteus* is found in many *Pinus* spp. and *Pseudotsuga menzeisii* invasions in different parts of the southern hemisphere. *A. muscaria* is another species that tends to be highly invasive (Pringle et al. 2009a). This suggests some species are more prone to invade than others. For some other groups the definition of species makes distinguishing patterns more difficult. For example there are many species of arbuscular mycorrhizal fungi that appear in different continents (Moora et al. 2011), but it is not clear if these species are invasive or are just cosmopolitan. Similar results have been found for some N-fixing bacteria (Rodriguez-Echeverria et al. 2012). Indeed, for both fungi and bacteria there are real difficulties around species concepts, with species names inappropriately applied across continents (Pringle and Vellinga 2006), un-named species based on DNA sequences only (Dickie et al. 2010), and failure of molecular methods to effectively separate all species. More studies are needed to know if the patterns of invasions follow the patterns observed in other groups (a few species are highly invasive; most are not) or if the observed patterns are just a result of biases in the introduction efforts and non-native soil biota are mostly limited by their ability to find a suitable host in the new range.

## Mechanisms facilitating the invasion of non-indigenous mutualistic soil biota

There are several factors that could affect the dispersal and establishment of non-indigenous species of soil biota. Some species disperse easily with abiotic vectors (water, wind) or find local dispersal agents (e.g. native or exotic animals that disperse the fungi), produce high numbers of spores, can associate with a number of plant species, or are associated with a single but abundant plant species.

One factor that can promote invasion of some soil biota is a high investment in production of spores or propagules (Peay et al. 2012). Our results suggest that species with high production of sporocarps commonly invade (e.g. *Suillus* spp., *Amanita* spp.) while other species that are commonly found in areas of initial introduction (e.g. forestry plantations) are not common outside the areas of original introduction, suggesting dispersal limitations (e.g. Hynson et al. 2013). This pattern of invasion may be similar to the pattern observed in native areas after disturbances or in the colonization of remote areas (Ashkannejhad and Horton 2006; Peay et al. 2007).

Being associated with highly invasive host plants can also promote the invasion of soil biota. Host specificity of symbionts may not be a key issue limiting their spread, as previously assumed (e.g. Schwartz et al. 2006). As long as an invasive plant is successful, a new mutualist can also invade even if it is highly host-specific. This seems to be the case with some high-specificity Pinaceae-associated fungi, like *Rhizopogon* and *Suillus*. If soil mutualisms are associated with a highly invasive plant, there are more chances to invade than if they are associated with plants that do not invade. In some cases invasion of the soil mutualist can occur after the invasion of its plant symbiont, if the plants do not need them from invasions, as in the case of plants that are able to use native species as symbionts (e.g. arbuscular mycorrhizal species). For example, Vellinga et al. (2009)

**Table 2** Three ways of being novel (function, location, or magnitude) in invasive mutualisms, with selected examples

| Function | Location | Magnitude | Example |
|---|---|---|---|
| Novel | | | Ectomycorrhizal invasion of Hawai'i (Hynson et al. 2013). A novel function, as there are no native ectomycorrhizal plants in Hawai'i |
| Redundant | Novel | | Ectomycorrhizal/*Pinus* invasion above treeline in New Zealand (Ledgard 2001); *Morella* invasion on young soils in Hawai'i (Vitousek et al. 1987). Both symbioses occur in other habitats within these regions, but the invasion extends the function into novel locations |
| | Redundant | Novel | Displacement of N-fixing *Acacia* by *Cytisus* in Australia (Fogarty and Facelli 1999); greater N-fixation by invasive *Acacia* than native *Acacia* in South Africa (Tye and Drake 2012); increased arbuscular mycorrhizal infection and P uptake of invasive compared with native (Cuassolo et al. 2012). All of these represent functions already present in native flora, but the invasive symbiosis causes a quantitative change in the degree of function |
| | | Redundant | (Not novel) |

described in great detail fungal associations in the exotic range of many trees introduced for forestry. Many of these introduced trees are species that did not show abilities to spread outside of the original plantations, so soil symbionts would need to form novel associations with native hosts in order to invade.

Having low host-specificity may also promote invasion. For example Bonito et al. (2011) showed Asian truffles associated with native North American trees, Diez (2005) showed Australian fungi in European plants and Rodriguez-Echeverria (2010) found non-native N-fixing bacteria from Australia in European plants. There are several reports of *Amanita* spp. in numerous native hosts outside their native range (Bagley and Orlovich 2004; Pringle and Vellinga 2006; Wolfe et al. 2010; Dunk et al. 2012). So the ability to jump host and use native species can be seen as another important trait to facilitate the invasion of soil biotic species.

An important question for the future is whether similar ecological principles drive the invasion of aboveground and belowground partners in mutualisms. Some of the factors driving the invasion of belowground mutualists are similar to factors frequently noted for plants, such as propagule pressure. Symbiont-specificity also seems to be important as a potential limiting factor both for plant invasion (e.g. Zimpfer et al. 1999; Weir et al. 2004; Nuñez et al. 2009; Spence et al. 2011) and soil symbiont invasion (Diez 2005; Dickie et al. 2010). We have promoted parallel terminology for both parts of the symbiosis, including terming soil mutualists invasive regardless of whether they cross to native hosts, and using the term 'novel-associations' regardless of which partner is native. We hope that in using parallel terminology we highlight the potential for unified theoretical understanding of invasions. Nonetheless, one of the main differences between plant and belowground-mutualist invasions may be in the way that invasive mutualists modify ecosystem function. We address this in the next section.

## Impacts of invasive soil mutualists on ecosystem function

Soil mutualists can provide unique enzymatic pathways in ecosystem function. These novel functions include, for example, atmospheric di-nitrogen fixation (Vitousek et al. 1987) and uptake of nutrients from organic forms by ectomycorrhizal and ericoid mycorrhizal fungi. Species that change ecosystem function have ecosystem effects much greater than would be predicted based on biomass (Peltzer et al. 2009). The effects of invasive plants on ecosystem function have been previously reviewed primarily from the perspective of plant traits (Ehrenfeld 2010), while reviews of invasive soil mutualists have not extensively explored ecosystem effects of functional shifts (Schwartz et al. 2006; Pringle et al. 2009b).

Functional shifts can represent entirely novel ecosystem functions, novel habitats for an existing function, or changes in the magnitude of a function (Table 2). For example, the invasion of ectomycorrhizal trees in Hawai'i represents an entirely novel ecosystem function, as no native ectomycorrhizal trees are present in the archipelago (Hynson et al. 2013). In New Zealand, in contrast, ectomycorrhizal trees are present as natives but invasive pines are expanding the locations where ectomycorrhizal fungi occur by invading above the native treeline (Ledgard 2001). This then represents a novel location for ectomycorrhizal function. Other invasive mutualists are neither novel in function nor location but represent increased magnitudes of a particular function, such as the increased N-fixation by invasive *Acacia* in South Africa relative to native N-fixation rates (Tye and Drake 2012). Functional shifts may be particularly common in tree invasions, as forestry trees are disproportionately ectomycorrhizal and/or associated with N-fixing bacteria or *Frankia* (Richardson 1998; Richardson et al. 2000; Richardson and Rejmánek 2004).

## Impacts of nitrogen-fixing symbionts

The vast majority of biologically available nitrogen in ecosystems originates from symbiotic nitrogen fixation. Invasive N-fixing symbiotic bacteria can cause substantial increases in N-input (Vitousek et al. 1987; Rice et al. 2004), although direct measurement of increased N-input remains limited (Ehrenfeld 2010), and there are cases where invasive N-fixing symbioses do not increase total N (Hickey and Osborne 1998; Yelenik et al. 2007) or even decrease N availability (Wolf et al. 2004).

Increased N-mineralization and N-availability are frequently measured following invasion by plants with N-fixing symbioses (Von Holle et al. 2006; DeCant 2008). Increased N levels might be expected to have direct effects on other plant species, although Levine et al. (2004) found the evidence to be poorly demonstrated. Some studies clearly show that N-fixing invasives can cause large shifts in soil N that influence other plant species (Vitousek et al. 1987; Rice et al. 2004; Von Holle et al. 2006), but many other studies find little effect of N-fixing invasives on other plant species (Levine et al. 2004; Wolf et al. 2004; DeCant 2008; Van et al. 2009; Tsai et al. 2010) or on total ecosystem biomass (Asner et al. 2010). The inconsistency of demonstrated effects of N-fixing invasives on other plant species reflects several factors. First, plants with N-fixing symbioses tend to have multiple ecosystem effects, including competition for light, water and nutrients, which can make it difficult to demonstrate that N-fixation *per se* is driving associated changes in plant communities (Levine et al. 2004; DeCant 2008; Asner et al. 2010). Second, other soil nutrients, such as phosphorus (P), may be co-limiting, reducing the response of other plant species to increased N (Hickey and Osborne 1998; Haubensak and D'Antonio 2011). For example, Vitousek et al. (1987) found that mineral N-addition by invasive *Morella*-associated N-fixation increased other plant growth in young volcanic soils, but not in soils 1,000–2,000 years old, where other resources are likely to be more limiting. Finally, fixed N often remains relatively unavailable until after the death of the plant (Hickey and Osborne 1998). In contrast to invasives, native plants have been clearly demonstrated to facilitate the growth of other plant species by elevating soil N (St John et al. 2012) including facilitating invasive grass species (Maron and Connors 1996). The inconsistency of similar responses to invasive N-fixers (Levine et al. 2004; Tsai et al. 2010) could potentially reflect a lag-phase before ecosystem effects become apparent. Nonetheless, even studies looking at lag-effects have failed to find much response in either native or exotic species (Van et al. 2009).

The effects of N-fixing symbioses at an ecosystem scale are complex. While total soil N generally increases, concomitant increases in carbon (C) can result in little net change in the C:N ratio (Caldwell 2006). Plants with N-fixing associations tend to have high P demands (Haubensak and D'Antonio 2011), with these demands supplied by arbuscular mycorrhizal fungi (most Fabaceae, Elaeagnaceae), ectomycorrhizal fungi (e.g. *Acacia*, *Alnus*, *Casuarina*) or cluster roots (*Lupinus*). This can drive a decline in soil P (Caldwell 2006; Shaben and Myers 2010), although increased P availability has also been observed (Fogarty and Facelli 1999; Allison et al. 2006). A larger effect is seen in C:P ratios, driven by the high biomass of plants associated with N-fixing symbioses. In a similar fashion to plant responses, soil microbial responses depend heavily on the degree to which N is a limiting resource (DeCant 2008). Increased N-cycling associated with N fixation may result in a loss of soil organic layers, increasing the susceptibility of soils to nutrient loss via surface erosion (Tateno et al. 2007; Macdonald et al. 2009).

The effects of invasive N-fixing symbioses frequently extend beyond the invaded ecosystem. For example, litterfall from plants associated with N-fixing symbionts can result in elevated N in streams and in groundwater (Mineau et al. 2011), with effects on aquatic food webs (Atwood et al. 2010) and, in at least

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one case, the potential to increase groundwater nitrogen oxide levels above drinking water standards (Jovanovic et al. 2009). Under the highest levels of N-fixation, such as associated with kudzu (*Pueraria montana*) invasion, atmospheric nitric oxides can also be elevated, increasing local ozone pollution (Hickman et al. 2010).

Increased soil N availability following plant invasion can also be driven by the better litter quality (e.g. lower C:N ratio) of invasives (Rice et al. 2004; Gómez-Aparicio and Canham 2008; Rout and Callaway 2009). This may imply that some increased N availability following the invasion of plants associated with N-fixing symbionts could be due to plant foliar traits, rather than a direct consequence of bacterial N-fixation *per se*. Given the high correlation of these two traits it may be difficult to fully separate the two mechanisms, and indeed high-litter N recycling and the presence of N-fixing symbionts increasing total N input may have strongly interacting effects.

## Impacts of invasive ectomycorrhizal and ericoid mycorrhizal symbioses

While N-fixing symbioses are a major input of nutrients, ectomycorrhizal and ericoid mycorrhizal symbioses primarily change the availability of existing nutrients. Most C in terrestrial ecosystems is stored in soils (Guo and Gifford 2002). Ectomycorrhizal and ericoid mycorrhizal fungi have the potential to release at least some of this C by utilizing organic nutrient sources (Chen et al. 2008; Orwin et al. 2011). A loss of significant (~20 %) quantities of soil C has been observed following planting of pine (Chapela et al. 2001), although this could have been driven partially by planting-associated disturbance. More recently, Dickie et al. (2011) found a 30 % loss of soil C following *Pinus nigra* invasion by self-seeding into a conservation grassland, which can be unequivocally linked to tree invasion rather than planting-related disturbance. The utilization of organic nutrients results in major shifts in soil P pools under planted (Chen et al. 2008) and invasive (Dickie et al. 2011) ectomycorrhizal trees.

While the short-term effect of organic nutrient utilization is loss of soil C, a stoichiometric ecosystem model by Orwin et al. (2011) suggests that the long-term effect of organic nutrient utilization is an increase in soil C storage. This was partially driven by an increase in plant C fixation and subsequent increased belowground allocation and litter inputs, and by changing nutrient stoichiometry of the soil. In contrast to saprotrophic decomposition, mycorrhizal organic nutrient uptake is driven by N and P demand, while the fungus obtains its C from the host plant. The net result is that mycorrhizal organic nutrient uptake increases the residual C:N and C:P ratios of the soil and hence slows saprotrophic decomposition.

Invasive mutualists may also alter weathering rates of mineral nutrient sources. However, these processes appear to be slow relative to the other effects of invasive plants. On very young volcanic soils, increased N-fixation can result in large increases in extracellular acid phosphatase production by soil microbes, increasing weathering rates of P from mineral sources (Allison et al. 2006).

## Impacts of invading soil mutualists on native mutualists

The most obvious aboveground effects of plant invasions frequently include a substantial decline in local-scale diversity of the aboveground plant community, largely through competition. By analogy, we might expect that invasive mutualists would cause a loss of belowground diversity of native mutualists, as has been suggested by several authors as a possibility (Murat et al. 2008; Bonito et al. 2011). We find mixed evidence of whether this actually occurs. On native legumes co-occurring with invasive *Acacia* in Portugal, 95 % of *Bradyrhizobia* forming mutualisms were of Australian origin (Rodriguez-Echeverria 2010). While competitive displacement was not directly demonstrated, this finding is at least consistent with the view of competitive displacement. On the other hand, in a study of *Amanita phalloides* invading on native plants in North America, Wolfe et al. (2010) found no loss of ectomycorrhizal diversity in soil samples where *A. phalloides* was present, finding three species per soil core when *A. phalloides* was present, and two when it was absent. This finding is supported by preliminary data from New Zealand, where *A. muscaria* invading onto native *Nothofagus solandri* also causes no detectable loss of native fungal species richness (Salcedo-Watson and Dickie, unpublished data). This raises the intriguing possibility that more diverse communities (e.g. ectomycorrhizal fungal communities) are less susceptible to competitive displacement than lower diversity communities, such as *Rhizobium* (Thiele et al. 2010), but further research is needed to confirm or refute this possibility.

Concern has been raised about the China truffle *Tuber indicum* invading commercial Perigord truffle (*T. melanosporum*) producing plantations in Italy, where *T. melanosporum* is native (Murat et al. 2008), and in North America, where it is not (Bonito et al. 2011). Negative effects of *T. indicum* on *T. melanosporum* remain unproven, but seem likely given the reportedly uncompetitive nature of *T. melanosporum* (Murat et al. 2008).

### Ecosystem function legacies

Once invasive mutualists modify soil function, these changes can result in a significant legacy influencing future ecosystem trajectories (Malcolm et al. 2008; Grman and Suding 2010). Soil legacies persist after the removal of invasive plants and influence subsequent plant communities, including influencing subsequent restoration efforts and favoring the invasion of other species (Rook et al. 2011). These effects may be quite persistent, with Rook et al. (2011) reporting decreased native plant species richness and an increased invasive grass more than 10 years following *Cytisus scoparius* removal. Depending on environment, invasive N-fixing plants can also facilitate invasion by other species as well as native species by improving soil conditions (Carino and Daehler 2002; Von Holle et al. 2006). One of the interesting legacies of both N-fixing plants and ectomycorrhizal trees may be increased grass growth due to increased N (in N-fixing plants) or increased P availability (in ectomycorrhizal plants) (Carino and Daehler 2002; Levine et al. 2004; Malcolm et al. 2008; Dickie et al. 2011; Dickie unpublished data). Increasing in P availability appears to be driven both by plant roots and associated ectomycorrhizal fungal activity (Chen et al. 2008). In both cases, increased soil nutrients may favor aggressive grass growth over other species (Malcolm et al. 2008; Dickie et al. 2011).

In addition to abiotic legacies, invasive mutualists can cause long-term changes in soil biotic communities. Invasive plants accumulate soil pathogens over time, which can reduce local plant densities (Diez et al. 2010). By much the same process, invasive plants can accumulate mutualisms, potentially becoming more invasive with time (Diez 2005; Zhang et al. 2010) Sharing of mutualists among co-occurring species is common, hence prior invasion of one plant may favor subsequent invasion of other plants with the ability to share mutualists, although actual evidence of this remains scant. Spores of at least some mutualists can have considerable longevity in the soil (Bruns et al. 2009; Nguyen et al. 2012), suggesting that biotic legacies could be persistent.

### Direct impacts of invasive soil mutualists on native plants and animals

Most of the effects of soil mutualists are through changes in ecosystem function, as reviewed above. However, invasive soil mutualists can also directly influence native plants. Invasive Australian *Bradyrhizobium* spp., for example, have infected native plants in Europe and have much less beneficial effects than native *Bradyrhizobium* (Rodriguez-Echeverria 2010; Rodriguez-Echeverria et al. 2011). The ectomycorrhizal fungus *A. muscaria* has established on native *Nothofagus* in New Zealand and Australia (Bagley and Orlovich 2004; Johnston 2010; Dunk et al. 2012) but effects on plant hosts remain unknown.

Mycorrhizal fungi can also become a food source for native animals, including a large number of insects, but there is no evidence of how invasive fungi influence wildlife. On the other hand, human consumption of the invasive, highly-toxic *Amanita phalloides* has resulted in intensive medical emergencies in Australia and North America, with a lethal outcome rate of around 12 % of patients, even with treatment (Pinson et al. 1990; Trim et al. 1999; Ganzert et al. 2005).

## Conclusions

There are a number of ways in which soil biota can interact with non-native and native plants to form novel, cosmopolitan or co-invading mutualisms (Fig. 2). Co-invasion by plant and symbiont seems to be a relatively common phenomenon, especially for ectomycorrhizas and N-fixing symbioses. This can sometimes limit the spread potential of both partners, since both must co-invade and, in most cases, are dispersed independently (Nuñez et al. 2009). Co-evolution of the plants and their symbionts has been suggested to be especially important for ectomycorrhizal species where there could be population-level adaptations to local soil biota (e.g. Kranabetter et al. 2012). In other groups, such as arbuscular mycorrhizal fungi (the most important group for invasive plant species, Fig. 1), relatively low host-specificity (i.e. promiscuous associations) and wide fungal distributions allow novel and cosmopolitan associations, hence limitation by a lack of compatible mutualisms appears to be rare. One exception seems to be where arbuscular mycorrhizal fungi are completely absent, such as under monodominant ectomycorrhizal forest canopies (Spence et al. 2011). An intriguing theoretical possibility in novel associations is that 'enhanced mutualisms' may occur, where an invasive plant gains disproportionate benefit from the symbiosis (Reinhart and Callaway 2006).

Mycorrhizal and N-fixing associations can change from pathogenic to mutualistic depending on the species identity of the symbionts (Johnson et al. 1997; Denison and Kiers 2004; van der Putten et al. 2007). For example, in both N-fixing and arbuscular mycorrhizal symbionts, invasive plants can have higher fitness when inoculated by symbionts from their home range (Callaway et al. 2011; Rodriguez-Echevarria et al. 2012). Conversely, invasive soil mutualists can result in lower fitness of native plants, which can also further the invasion and impact of the exotic plants (Diez 2005; Rodriguez-Echeverria et al. 2012).

A deeper understanding of symbiotic interactions can be important to understanding plant invasions. For example, delayed invasions or 'lag times' (Crooks and Soule 1999; Crooks 2005), a common phenomenon in woody species invasion (Richardson and Higgins 1998; Simberloff et al. 2010), may be due to interactions with soil biota. If soil mutualists are not found in the invaded range, or if mutualists disperse poorly, this could delay invasion until the compatible symbionts establish or until the invasive plant forms novel symbioses with native species (e.g. via evolutionary processes by either the invasive plant or the native mutualists). Initial establishment of exotic symbionts may be slow due to a dependence on established hosts. However, once soil mutualists are established, removal could be difficult, especially where the mutualist can persist in an inactive form for long periods (Bruns et al. 2009; Nguyen et al. 2012).

The effects of invasive mutualists on an ecosystem seem highly context dependent. From a nutrient cycling perspective, we suggest that considering not only N but also C, P, and other limiting resources may help resolve inconsistencies across studies. Some of the impacts of invasive mutualists may be hard to control, especially if the mechanism is not identified early, as can be the case with many of these cryptic belowground invasions. Changes in belowground ecosystem properties may also result in significant, and difficult to remediate, post-removal legacies of invasive plants.

A recurrent problem identified in the papers that we reviewed is the uncertainty about the origins of the soil mutualist. Identifying the geographic origin of many symbionts is challenging, as many species have not been described from their native range or records can be confusing (e.g. multiple records from many distant locations) (Pringle and Vellinga 2006). Also, some current cosmopolitan species may have been the results of human-mediated dispersal, as has been suggested for the arbuscular mycorrhizal fungus *Glomus mosseae* (Rosendahl et al. 2009). There is a clear need for a better understanding of the biogeography of these soil mutualists in order to understand their native or non-native status, which has clear theoretical and conservation implications.

Our results show that the impact of invasive soil symbionts can be equally detrimental as other groups, such as plants or animals, which are more widely studied. Some of these impacts can extend well beyond the invaded site, such as the effects of N-fixation on streams and groundwater. To minimize potential impacts, care should be taken not to introduce non-native soil biota in native plantings. Even in exotic plantings (e.g. plantation or ornamental species) it may be possible to use native soil symbionts, or to minimize introductions of new, non-native symbionts. Selection of fungi that rarely produce spores, for example, could limit dispersal. It is important to control the spread of soil symbionts since management and restoration of areas invaded by soil symbionts may be a difficult task given their microscopic size, ability to persist for long periods, and their belowground habit.

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