

Research review

Suilloid fungi as global drivers of pine invasions

Author for correspondence:

Nahuel Policelli

Tel: +54 294 444 2676

Email: npolicelli@comahue-conicet.gob.ar

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Nahuel Policelli¹ , **Thomas D. Bruns²** , **Rytas Vilgalys³**  and **Martin A. Nuñez¹** ¹Grupo de Ecología de Invasiones, Instituto de Investigaciones en Biodiversidad y Medioambiente INIBIOMA, Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) – Universidad Nacional del Comahue (UNCo), Avenida de los Pioneros 2350, San Carlos de Bariloche, 8400 Río Negro, Argentina; ²Department of Plant and Microbial Biology, University of California at Berkeley, 111 Koshland Hall, Berkeley, CA 94720-3102, USA; ³Biology Department, Duke University, 130 Science Drive, Durham, NC 27708-0338, USA*New Phytologist* (2019) **222**: 714–725

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Key words: belowground biota, ectomycorrhizal fungi (EMF), invasive species, Pinaceae, plant–soil feedback, *Rhizopogon*, *Suillus*.**Summary**

Belowground biota can deeply influence plant invasion. The presence of appropriate soil mutualists can act as a driver to enable plants to colonize new ranges. We reviewed the species of ectomycorrhizal fungi (EMF) that facilitate pine establishment in both native and non-native ranges, and that are associated with their invasion into nonforest settings. We found that one particular group of EMF, suilloid fungi, uniquely drive pine invasion in the absence of other EMF. Although the association with other EMF is variable, suilloid EMF are always associated with invasive pines, particularly at early invasion, when invasive trees are most vulnerable. We identified five main ecological traits of suilloid fungi that may explain their key role at pine invasions: their long-distance dispersal capacity, the establishment of positive biotic interactions with mammals, their capacity to generate a resistant spore bank, their rapid colonization of roots and their long-distance exploration type. These results suggest that the identity of mycorrhizal fungi and their ecological interactions, rather than simply the presence of compatible fungi, are key to the understanding of plant invasion processes and their success or failure. Particularly for pines, their specific association with suilloid fungi determines their invasion success in previously uninvaded ecosystems.

Introduction

Biological invasions, the process by which human-introduced populations spread and maintain themselves without further human assistance (Blackburn *et al.*, 2011), are highly idiosyncratic and hence difficult to predict (Richardson *et al.*, 2000; Mitchell *et al.*, 2006; Bradley *et al.*, 2010). Perhaps one of the most unexplored aspects of plant invasions is the role of belowground biotic interactions in conditioning the success or failure of this process (Wardle *et al.*, 2004; Van Der Putten *et al.*, 2007; Simberloff *et al.*, 2013). The soil-inhabiting microbiota includes pathogens, herbivores and mutualists, and their negative or positive effects strongly influence the relative abundance and composition of plant species in a community (Klironomos, 2002; Wardle *et al.*, 2004), and can be crucial in determining the success or failure of invasive plants (Traveset & Richardson, 2014; Dickie *et al.*, 2017). The role of negative

plant–soil feedbacks has historically received greater attention as they can suppress plant recruitment, growth and survival, mediate successional trajectories and competitive processes, and help to maintain plant coexistence through Janzen–Connell effects (Kulmatiski *et al.*, 2008; Mordecai, 2011; Maron *et al.*, 2014). However, positive plant–soil feedbacks also occur and can facilitate the invasion of non-native plant species in the introduced range, increasing their invasiveness and impact (Simberloff & Von Holle, 1999; Simberloff, 2006). Although negative and positive interactions are not mutually exclusive and occur as part of the same invasion process (Dickie *et al.*, 2017), the positive effects of soil biota and their role in plant invasions have received less attention. Increasing evidence suggests that positive plant–soil feedbacks are at least as important as negative ones in mediating plant invasions (Reinhart & Callaway, 2006; Nuñez & Dickie, 2014; Traveset & Richardson, 2014) and, with respect to some invasive species

establishment, they can be even more important than interspecific competition in affecting the plant community assembly (Peay, 2018).

The symbiosis between plants and mycorrhizal fungi is a good example of a positive plant–soil feedback that can influence the trajectory of plant species invasion. Invasion success is strongly conditioned by the presence of suitable mycorrhizal fungi at the site at which the plant species are introduced (Pringle *et al.*, 2009). In the invaded range, non-native invasive plant species can establish novel associations with native, non-native or co-invasive mycorrhizal fungi (Nuñez & Dickie, 2014). Non-native invasive plant species can even disrupt existing native plant–fungal interactions, thus affecting native plant communities and having subsequent positive effects on the invasion (Callaway *et al.*, 2008).

A well-known example of the role of mycorrhizal fungi in plant invasions is the case of pines and their co-invading ectomycorrhizal fungi (EMF). Although both plants and fungi disperse independently, if EMF are absent in the novel habitat, pines are not able to establish and survive as a result of the obligate nature of this symbiosis (Briscoe, 1959; Nuñez *et al.*, 2009; Dickie *et al.*, 2010). Therefore, the co-introduction of competent fungi has been crucial in overcoming the barriers against establishment and has inadvertently led to several cases of pine invasions (Richardson *et al.*, 2000). Pine invasions constitute a major ecological and economic problem in the Southern Hemisphere. In New Zealand, for example, nearly 2 million hectares are invaded by pines, transforming previously opened habitats into dense monospecific forests with negative ecological and economic impacts (Nuñez *et al.*, 2017).

As mutualistic interactions are necessary for the success of invasive pines, our main question is about the identity of the mutualist. Can a specific belowground mutualistic interaction drive the invasion process of an invasive plant worldwide, or is the presence of any compatible fungus enough? To answer this, we reviewed all cases in which the role of EMF has been addressed for widely invasive and globally problematic pine species. We compared all available case studies of invasion in both native and non-native ranges, searching for common EMF species associated with invasive pines. Based on these studies, we tried to identify which traits of the mutualists might be involved in making them determinant in the invasion. Our hope was that, by studying the relationship between pine invasion and specific EMF, we could provide key insights that could predict and avoid future plant invasions, or could help us to understand cases of invasion failure.

Can a particular group of EMF fungi enable pine invasion globally?

We performed a global systematic review of the literature, gathering publications addressing the role of EMF on pine invasions. We used Scopus to search for the keywords ‘invas*’ and ‘mycor*’ and ‘Pinaceae’ in all fields (title, abstract, keywords and text body), yielding 351 documents. We repeated the search using Google Scholar to check for papers that could have been missed in the Scopus search. We considered cases of pine species invasion in both their native and non-native ranges, as well as evidence from

glasshouse bioassays, and field sampling. Papers that only evaluated EMF in plantations and did not evaluate invasion contexts were excluded, as were those that did not perform any molecular analysis to confirm fungal species identity and their effective association with plant roots, or only analyzed soil samples without examining roots. We restricted our search to the genus *Pinus* because it is the genus with by far the most case studies (92%). From the papers obtained, 12 were suitable according to the criteria used. These papers evaluated pine invasion in six different countries (Table 1).

All the reported evidence from pines in both native and non-native ranges showed that a particular group of EMF, suilloid fungi (and specifically the genera *Suillus* and *Rhizopogon*), is always associated with invasive pines and is crucial during the first stages of invasion (Table 1). *Suillus* and *Rhizopogon* species are always among the first fungi to occur in young nurseries and plantations (Chu-Chou & Grace, 1988; Menkis *et al.*, 2005), and are often critically important during early establishment by invading pines. Although many other ‘later’ stage EMF are also important as pines grow, these suilloid fungi are always associated with young, invasive pine seedlings, and play a key role in allowing their establishment and advance during the invasion (Hayward *et al.*, 2015a). Although the other co-invasive EMF species vary, all invasive pines are associated with at least one suilloid species (Table 1).

Suilloid fungi are the main group associated with pine invasion fronts (Fig. 1). In Patagonia, for example, Nuñez *et al.* (2009) showed how low levels of EMF inoculum retarded pine invasions. In that study, for two invasive pine species (*Pinus contorta* and *Pinus ponderosa*), suilloid fungi were the most abundant group of EMF associated far from the invasion source. In northwest Patagonia, *Rhizopogon* sp., as determined by root tip morphotyping, was reported as the most common EMF species colonizing pines at increasing distances from the invasion source, and was the only EMF capable of colonizing at 400 m from *Pinus ponderosa* plantation edges (Salgado Salomón *et al.*, 2011). *Suillus luteus* was found to be the only species present at > 750 m from the source of invasion in southern Patagonia and its presence was sufficient to enable the invasion of *Pinus contorta* (Hayward *et al.*, 2015b). In a recent study, suilloid fungi have also been found to be important drivers of pine invasions in high-altitude environments, with *Suillus granulatus* being the only EMF present associated with *Pinus elliotti* invading at 2200 m above sea level (asl) and > 6 km away from the closest pine plantation (Urcelay *et al.*, 2017).

Pines typically invade nonforested sites because of their shade intolerance, and, when they do, seedling establishment differs between mature invaded sites and invasion fronts in two main ways. First, in mature invaded areas, in which established trees already exist, there are also established mycelial networks with which new seedlings can interact. This means that EMF colonization of new seedling roots can occur efficiently without spores. By contrast, at the invasion front, EMF mycelial networks are absent; thus, the colonization of new seedlings must occur by spores. Second, habitat conditions are likely to be better for mycelial growth of EMF inside mature invaded areas, given the cooler, wetter soil environment and a higher density of roots (Peay *et al.*, 2011). These environmental conditions are also conducive for enhanced fruiting of a more diverse set of EMF, and this results in increased spore rain for such

Table 1 List of studies, ordered by publication year addressing the role of ectomycorrhizal fungi (EMF) in different *Pinus* species invasions around the world; considering different methodological approaches, suilloid fungi species (in bold) are always associated with pines, being particularly important at the invasion front and during the establishment of seedlings.

Citation	Invasion location	Invasive host	EMF present in invasion front	EMF present in mature stands	Type of study	Main findings
Collier & Bidartondo (2009)	Lowland heathlands, England	<i>Pinus sylvestris</i> (native invasive)	Rhizopogon luteolus , Suillus bovinus , Suillus variegatus	<i>Amanita rubescens</i> , Atheliaceae sp., <i>Cenococcum geophilum</i> , <i>Laccaria</i> spp., <i>Lactarius</i> spp., R. luteolus , <i>Russula emetica</i> , <i>Scleroderma citrinum</i> , S. bovinus , S. variegatus , <i>Thelephora terrestris</i> , <i>Tomentella</i> spp., <i>Xerocomus</i> sp.	Soil bioassay and <i>in situ</i> survey	Few keystone spore-dispersed EMF can mediate tree expansion
Núñez <i>et al.</i> (2009)	Isla Victoria, Patagonia, Argentina	<i>Pinus contorta</i>	<i>C. geophilum</i> , Cortinariaceae sp., Suillus luteus , <i>Hebeloma</i> sp., <i>Wilcoxina mikolae</i>	Atheliaceae sp., <i>Cadophora finlandica</i> , <i>C. geophilum</i> , Cortinariaceae sp., <i>Hebeloma</i> sp., <i>Lactarius quieticolor</i> , S. luteus , Thelephoraceae spp., <i>Wilcoxina</i> spp.	Soil bioassay and <i>in situ</i> survey	Low inoculum levels far from the plantations retard the invasion of pine species
Dickie <i>et al.</i> (2010)	Canterbury, New Zealand	<i>Pinus ponderosa</i>	S. luteus , <i>T. terrestris</i> , <i>W. mikolae</i>	Atheliaceae sp., Cortinariaceae sp., <i>Hebeloma</i> sp., <i>L. quieticolor</i> , Sebacinaceae sp., S. luteus , Thelephoraceae spp., <i>W. mikolae</i>	<i>In situ</i> survey	Co-invasion by mutualists rather than novel associations could explain how pines avoid or overcome the loss of mutualists
Kohout <i>et al.</i> (2011)	Elbe Sandstone Mountains, Czech Republic	<i>Pinus strobus</i>	Not assessed (9- to 20-yr-old self-established pines sampled)	Atheliaceae (cf <i>Tylospora</i>), <i>Amanita muscaria</i> , <i>Cantharellales</i> sp., <i>C. geophilum</i> , Suillus granulatus , S. luteus , <i>Tomentella</i> sp., <i>Tricholoma</i> sp., <i>Tylospora</i> sp.	Soil bioassay	Host plant species identity and surrounding vegetation may influence EMF assemblages in roots of establishing pine seedling
Salgado Salomón <i>et al.</i> (2011)	NW Patagonia, Argentina	<i>P. ponderosa</i>	Rhizopogon sp.	<i>C. geophilum</i> , <i>Inocybe</i> sp., <i>Meliniomyces bicolor</i> , R. luteolus , R. roseolus , Rhizopogon salebrosus , S. bovinus , S. granulatus , S. luteus , S. variegatus , <i>T. terrestris</i> , <i>W. mikolae</i>	Soil bioassay (species identity determined by morphotyping)	<i>Rhizopogon</i> sp. acts as a pioneering taxon regarding the colonization of seedlings, being the most persistent and frequent symbiont

Table 1 (Continued)

Citation	Invasion location	Invasive host	EMF present in invasion front	EMF present in mature stands	Type of study	Main findings
Hynson <i>et al.</i> (2013)	Maui and Hawaii, USA	<i>Pinus patula</i> , <i>Pinus pinaster</i> , <i>Pinus radiata</i> , <i>Pinus taeda</i> (<i>in situ</i> survey)	Atheliaceae sp. 1, <i>Cadophora</i> sp., <i>Suillus brevipes</i> , <i>S. luteus</i> (> 250 m far from plantation)	Atheliaceae spp., <i>Cadophora</i> sp., <i>Cortinarius</i> sp., Hyaloscyphaceae sp., <i>Inocybe</i> sp., <i>Laccaria</i> sp., <i>Meliniomyces</i> sp., <i>Pseudotomentella</i> sp., Pyronemataceae sp., <i>R. salebrosus</i> , <i>S. brevipes</i> , <i>S. luteus</i> , <i>Suillus pungens</i> , <i>Thelephora</i> sp., <i>Tuber</i> sp., <i>Wilcoxina</i> spp.	<i>In situ</i> survey and soil bioassay	A restricted suite of EMF are the common dominants with pine introductions
Núñez <i>et al.</i> (2013)	Isla Victoria, Patagonia, Argentina	<i>P. radiata</i> (soil bioassay)	<i>Rhizopogon rubescens</i> , <i>S. luteus</i> (1000 m far from plantation)	Atheliaceae sp. 1, <i>Descomyces</i> sp., <i>Laccaria</i> sp., Pyronemataceae sp., <i>R. rubescens</i> , <i>R. salebrosus</i> , Sebacinaceae sp., <i>S. brevipes</i> , <i>S. luteus</i> , <i>S. pungens</i> , <i>Thelephora</i> sp., <i>Tomentella</i> spp., <i>Tuber</i> sp., <i>Wilcoxina</i> spp.	Soil bioassay with fecal pellets of non-native mammals	Non-native mammals can be important dispersers of non-native EMF which, in turn, can promote pine invasion
Hayward <i>et al.</i> (2015a)	Isla Victoria, Patagonia, Argentina	<i>P. ponderosa</i> , <i>Pinus monticola</i> , <i>P. sylvestris</i> , <i>P. contorta</i>	<i>Amphinema</i> sp., <i>Hebeloma mesophaeum</i> , <i>Melanogaster</i> sp., <i>Rhizopogon cf arctostaphyli</i> , <i>R. cf rogersii</i> , <i>R. roseolus</i> , <i>S. luteus</i> , <i>Amphinema</i> sp., <i>Hebeloma</i> sp., <i>Inocybe</i> sp., <i>L. quieticolor</i> , <i>Leotiomyces</i> sp., <i>Rhizopogon</i> spp. , <i>Suillus lakei</i> , <i>S. luteus</i>	<i>Amphinema</i> sp., <i>Boletus edulis</i> , <i>Cortinarius</i> spp., <i>Hebeloma</i> spp., <i>Helotiales</i> sp. 1, <i>Inocybe</i> spp., <i>L. quieticolor</i> , <i>Leotiomyces</i> sp., <i>Melanogaster</i> sp., <i>Pseudotomentella tristis</i> , Pyronemataceae sp., <i>Rhizopogon</i> sp. , <i>Russula</i> sp., Sebacinaceae sp. 1, <i>S. lakei</i> , <i>S. luteus</i> , <i>T. terrestris</i> , <i>Tomentella</i> spp., <i>Tricholoma</i> sp.	<i>In situ</i> survey	Suilloid fungi possess notable potential to invade and to facilitate co-invasions by pine species
Hayward <i>et al.</i> (2015b)	Coyhaique, Chile	<i>P. contorta</i>	<i>S. luteus</i>	<i>H. mesophaeum</i> , Hydnaceae spp., <i>Tomentella cf Sublilacina</i>	<i>In situ</i> survey	Extremely depauperate fungal communities (even one species) may be sufficient to enable a pine invasion outside the native range

Table 1 (Continued)

Citation	Invasion location	Invasive host	EMF present in invasion front	EMF present in mature stands	Type of study	Main findings
Wood <i>et al.</i> (2015)	South Island of New Zealand	<i>P. contorta</i>	Rhizopogon spp., S. luteus (long distance dispersal by large mammals; only species effectively colonizing from fecal pellets)	No other effective colonizers from fecal pellets in spite of consumption evidence of <i>A. muscaria</i>	<i>In situ</i> survey Soil bioassay with fecal pellets of non-native mammals	Introduced mammals from Australia and Europe facilitate the co-invasion of invasive North American trees and Northern Hemisphere fungi in New Zealand, with no benefit for native trees or fungi Invading pines support different fungal communities in comparison with their places of origin. In environments with phylogenetically distant vegetation, <i>Pinus contorta</i> becomes associated with a unique fungal community that appears to have originated from multiple co-introduction events
Gundale <i>et al.</i> (2016)	Chile New Zealand	<i>P. contorta</i>	<i>Atheliales</i> sp., <i>Sistotrema</i> sp., S. luteus , <i>W. mikolae</i>	<i>A. muscaria</i> , <i>Atheliales</i> sp., <i>Cadophora finlandica</i> , Rhizopogon ochraceorubens , <i>Sistotrema</i> sp., S. luteus , <i>W. mikolae</i>	<i>In situ</i> survey	
Urceley <i>et al.</i> (2017)	Sierras Grandes mountain range, Córdoba, Argentina	<i>Pinus elliotii</i>	S. granulatus (EMF at high altitude: 2700 m above sea level, asl)	<i>A. muscaria</i> , <i>C. finlandica</i> , <i>Clavulina</i> sp., <i>Endogone lactiflua</i> , <i>Inocybe curvipes</i> , <i>Inocybe jacobii</i> , <i>Inocybe sindonia</i> , <i>Laccaria</i> sp., <i>M. bicolor</i> , <i>Paxillus involutus</i> , Rhizopogon pseudoroeseolus , <i>Russula</i> sp., <i>Scleroderma areolaum</i> , <i>Scleroderma</i> sp., <i>Sebacina</i> sp., <i>Sebacinaceae</i> sp., <i>Sistotrema</i> sp., S. granulatus , <i>Thelephoraceae</i> sp., <i>T. terrestris</i> , <i>Tomentella coerulea</i> , <i>Tomentella</i> sp., <i>Tuber</i> sp., <i>Tylospora</i> sp., <i>W. mikolae</i> , <i>Wilcoxina</i> sp. (EMF at lower altitudes: <2200 m asl)	Soil bioassay and <i>in situ</i> survey	The availability of suitable fungal symbionts might constrain, but not hinder, the expansion of a pine species over wide distances and altitudinal zones, even in areas with no native EMF

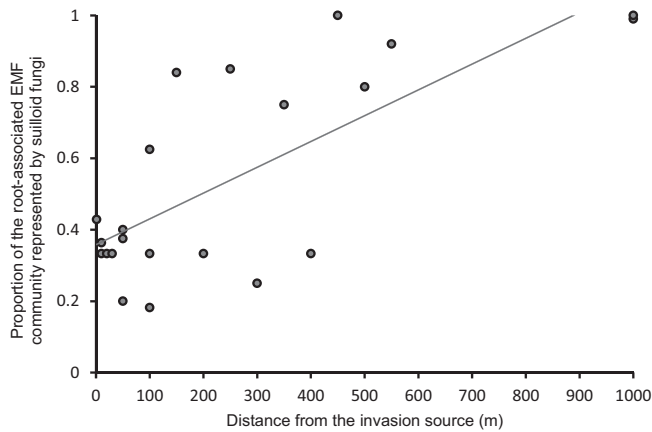


Fig. 1 The proportion of suilloid fungi associated with pine roots increases with distance from the invasion source; at 1000 m from the invasion source, the community is only represented by suilloid fungi ($R^2 = 0.546$). Data were extracted from papers that evaluated the community of root-associated ectomycorrhizal fungi (EMF) at different distances from the invasion source for pine seedlings (Nuñez *et al.*, 2009; Salgado Salomón *et al.*, 2011; Hynson *et al.*, 2013; Hayward *et al.*, 2015b). In cases in which a distance range was used, the proportion of the EMF community represented by suilloid fungi is given for the average distance of that range. Data were analyzed using 'Proportion of the community represented by suilloid fungi' as a response variable (number of suilloid fungi/total EMF species associated with the root). We assumed a binomial distribution using generalized linear mixed models (GLMM) based on a Laplace approximation and a logit link function (LME4 package, glmer function) (Bates *et al.*, 2015). Together with the explicative variable 'distance from the invasion source', we included an observation-level random effect for modeling overdispersion (Harrison, 2014). All analyses were performed with R 3.4.0 statistical software (R Core Team, 2018).

species within the forest (Peay *et al.*, 2012). The opposite happens in the invasion front, where only long-distance dispersed fungi, primarily *Suillus* spp., and those with resistant spores, *Suillus* and *Rhizopogon* spp., dominate the inoculum. In addition, fruiting is typically restricted to these same fungi on or near the invasion front (Ashkannejhad & Horton, 2006), with the addition of *Thelephora* spp. and *Laccaria* spp. in native settings (Peay *et al.*, 2007, 2012).

Suilloid fungi also act as pine expansion drivers in their native range (Table 1). For example, a few key suilloid fungal species are able to mediate the expansion of the native *Pinus sylvestris* into lowland heathland habitats in England (Collier & Bidartondo, 2009). Although fungal richness and colonization percentage decrease at increasing distance from the inoculum source, suilloid fungi are the only taxa found to colonize seedlings planted in soil from uninvaded areas (Collier & Bidartondo, 2009). In the Hawaiian islands, where there are no native pine species and no native ectomycorrhizal trees, suilloid fungi are also the dominant group colonizing invading pines (Hynson *et al.*, 2013). In Europe, several non-native pine species have been introduced together with their associated EMF, and many have become naturalized (Vellinga *et al.*, 2009; Richardson & Rejmánek, 2011; Nuñez *et al.*, 2017; Tedersoo, 2017). However, there are scarce records of pine invasions (Engelmark *et al.*, 2001) and less of the role of EMF in the process (Kohout *et al.*, 2011). Their limited expansion, in comparison with sites in the Southern Hemisphere, is probably the result of low introduction effort and phylogenetic closeness

between non-native and native trees and non-native and native EMF (Nuñez *et al.*, 2017).

In a noninvasive context, suilloid fungi often act as early-successional species able to colonize pine seedlings, and are later displaced by late-successional fungi (Peay *et al.*, 2011). As a result, in established pine forests, suilloid fungi are less frequent and less abundant relative to a diverse array of other EMF (Gardes & Bruns, 1996; Gehring *et al.*, 1998; Taylor & Bruns, 1999; Talbot *et al.*, 2014; Van Der Linde *et al.*, 2018). Suilloid fungi have been reported to constitute < 5% of the total mycorrhizas associated with noninvasive pine roots (Danielson, 1984; Gardes & Bruns, 1996). In native settings, suilloid fungi do become dominant after disturbance. *Rhizopogon* spp., for example, have been found to dominate EMF communities associated with native pine roots in post-fire settings (Horton *et al.*, 1998; Baar *et al.*, 1999; Buscardo *et al.*, 2010; Rincón *et al.*, 2014).

Several suilloid fungal species have been reported with invasive pines (Fig. 2). These EMF species were all introduced into non-native, Southern Hemisphere locations, in which they successfully established in the novel habitat with Northern Hemisphere pines, and were not replaced by local fungi (Vellinga *et al.*, 2009). Pine invasion success could be easily predicted if an already reported combination of one particular species of suilloid fungi is present in the invaded range together with a compatible pine host. From the set of all papers that have evaluated EMF interaction in a pine invasion context (Table 1), there are many examples of novel interactions between North American hosts and European EMF in the invasive context (Fig. 2). The most reported interaction is that between *Pinus contorta*, a North American pine, and *Suillus luteus*, a European fungus. *Suillus luteus* is also the suilloid fungus reported to interact with the greatest number of pine species (Fig. 2). The analysis of these common invaders reveals the range of species specificities within different invasions, and may account for a high context dependence of the ecological role of these fungal species. It is clear that North American pine species and European suilloid species are common associates in exotic settings, and a single suilloid–pine combination can be sufficient to drive an invasion, even when the combination is novel (e.g. *S. luteus* and *P. contorta*; Hayward *et al.*, 2015b). What is less clear is whether pines preferentially associate with their native suilloid species if the opportunity is available. There is some indication that preference for native suilloids may occur with exotic pines (McNabb, 1968; T. D. Bruns, pers. obs.), but the pattern is in need of more careful documentation.

Suilloid fungi also contribute to the invasion of other Pinaceae species. Douglas fir (*Pseudotsuga menziesii*), for example, is well documented as an invasive species spreading under forest gaps, as it is more shade tolerant than pines (Simberloff *et al.*, 2002; Nuñez *et al.*, 2009). *Rhizopogon* sp. was found to be the only EMF colonizing *P. menziesii* trees inoculated with soil far from the invasion source in a field experiment (Nuñez *et al.*, 2009), and also the only species effectively colonizing *P. menziesii* trees inoculated with fecal pellets of mammals (Wood *et al.*, 2015). *Suillus lakei* has also been reported as an invasion driver of Douglas fir in South America (Nuñez *et al.*, 2009; Hayward *et al.*, 2015a) and New Zealand (Moeller *et al.*, 2015).

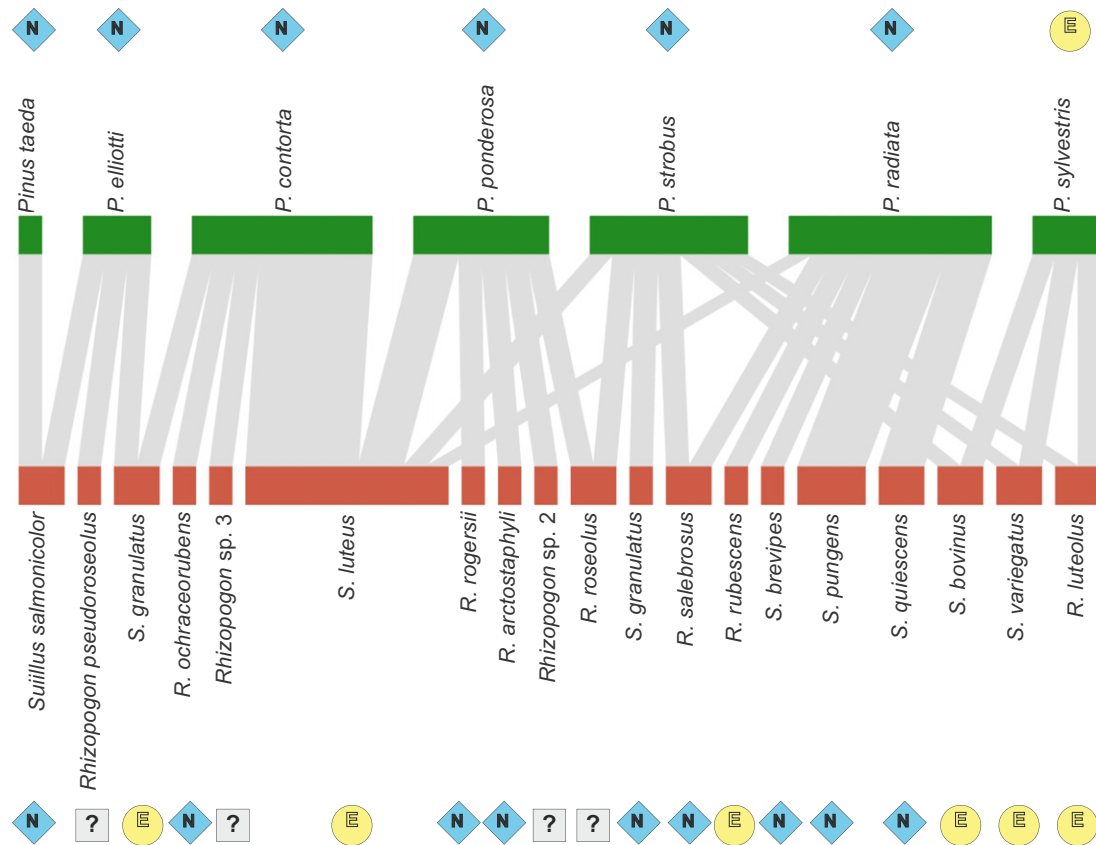


Fig. 2 Common invaders. A map of the reported interactions between suilloid fungi (red boxes) and pine host species (green boxes) in an invasion context. The size of the boxes and the width of the connections are proportional to the number of papers that found the interaction. The thickest connection (that between *Suillus luteus* and *Pinus contorta*) represents a total number of five studies. European (yellow circles with letter E) or North American (blue diamonds with letter N) origins are indicated for both pine and suilloid ectomycorrhizal fungi (EMF) species; gray squares with question marks symbolize an unknown origin. For *Suillus granulatus*, both North American (restricted to *Pinus strobus*) and European (reported with *P. elliotii* and *P. contorta*) species are indicated.

It is likely that other nonsuilloid EMF species will be able to colonize pines as the invasion process advances, and they may also be of special concern for global pine invasions (Nara, 2006; Bahram *et al.*, 2013). *Amanita muscaria*, for example, has been widely introduced in the Southern Hemisphere and is reported as highly invasive (Pringle *et al.*, 2009) in places such as Australia and New Zealand (Dickie *et al.*, 2010; Walbert *et al.*, 2010). *Amanita muscaria* is also capable of forming novel associations with different native tree species (Pringle *et al.*, 2009; Nuñez & Dickie, 2014), which could have severe implications in the displacement of native fungal partners (Orlovich & Cairney, 2004). By contrast with suilloid fungi, *A. muscaria* is considered as a later successional fungus (Peay *et al.*, 2011) and spreads into native habitats on a smaller scale and at a slower rate (Dickie *et al.*, 2016). Although it is possible that other EMF species may be required by pines at later life stages, current evidence shows that pines can invade with only suilloid partners.

What factors can explain the success of suilloid fungi?

We hypothesize that five characteristics of suilloid fungi are responsible for their success in colonizing young pine hosts and in facilitating the invasive behavior of these trees in both native and

non-native settings. In combination, these five factors ensure that seedlings become inoculated with these EMF fungi at a high frequency at the advancing front of invasion.

Abiotic long-distance dispersal

Suillus species are very effective at dispersing by air, and are quantitatively better at this than other fungi found at the margins of pine forest. This general trait can be seen as the consequence of numerous characteristics: the production of a large number of fruiting bodies at the edge of forests with young trees, together with the size, height and relative durability of these fruiting bodies (Peay *et al.*, 2012). At a fine scale, species with higher stem length and smaller spore size disperse further than species that produce fruiting bodies closer to the ground and have larger spores (Galante *et al.*, 2011). The presence of pores in *Suillus* allows for greater sporulation surface per unit area than that of a similar-sized gilled mushroom (Ingold, 1971), and the large biomass of a fruiting body makes it more resistant to desiccation and probably prolongs sporulation in drier climates. Although the majority of spores for any mushroom fall within a short distance of the cap and decrease with a leptokurtic function (Peay *et al.*, 2012; Horton, 2017), the total volume of spore production matters. This is evidenced by the

fact that very few fungal spores are able to wind disperse at a scale of kilometers from a forest edge, but *Suillus* is highly successful at this and is by far the most abundant EMF spore type in such settings (Peay *et al.*, 2012; Horton, 2017). *Suillus luteus*, for example, disperses spores at least 1000 m from the borders of pine plantations and at least 500 m from single pine trees outside plantations (Nuñez *et al.*, 2009; Hynson *et al.*, 2013). Similarly, in a native forest setting, *S. pungens* was found to be the only fungal species capable of colonizing pine seedlings at > 1 km away from native pine forests, and it exhibited an estimated spore production of 8×10^{12} spores km⁻² (Peay *et al.*, 2012). Other EMF in that system produced orders of magnitude fewer spores, resulting in dispersal at a more local scale (that is, less than a few meters from the fruiting body), and did not successfully colonize advancing pine seedlings.

Following long-distance dispersal, finding a compatible mating type is a major constraint to the successful establishment of EMF. The majority of EMF species can establish a functional mycorrhizal symbiosis only when a dikaryotic mycelium is formed, although some Basidiomycota can form functioning mycorrhizal roots even as monokaryons (Kropp & Fortin, 1988; Gardes *et al.*, 1990). As distance from fungal spore sources increases, the probability of encountering germinants of compatible strains and forming the dikaryon decreases (Horton, 2017). However, the chances of finding mating type-compatible spores distant from the inoculum source are higher for fungi with a bipolar mating system (e.g. *Rhizopogon rubescens*, Kawai *et al.*, 2008) compared with those fungi with a tetrapolar mating system (e.g. *Laccaria* spp., Kropp & Fortin, 1988; Horton, 2017). Also, secondary homothallism, a process of self-fertilization that produces binucleate spores (Horton, 2006), has been reported for some *Suillus* species as well as for other EMF (Horton, 2006, 2017). Those EMF with greater chances of finding a compatible mating type because of their mating system, or capable of producing dikaryotic spores by secondary homothallism, may be favored in invasive contexts. How EMF are able to prosper far from the inoculum source in terms of their mating system still needs to be elucidated further (Kawai *et al.*, 2008; Horton, 2017).

Biotic dispersal mediated by mammals

Mycophagy by mammals is a second key dispersal process of viable EMF propagules. Truffle-like fungi, such as *Rhizopogon*, rely almost exclusively on animal dispersion. No spores are actively shed to the wind; instead, mammals eat the fruiting bodies and a great mass of spores is ingested, transported and returned to the soil in feces (Johnson, 1996). Mammals also eat mushrooms, especially in seasonal abundance peaks (Piattoni *et al.*, 2012). Deer, for example, can effectively disperse *Suillus brevipes* through mycophagy in native habitats (Ashkannejhad & Horton, 2006). However, as discussed above, *Suillus* is also effectively dispersed through the air. In order to be effectively dispersed by animals, the fungal fruiting body needs to be attractive and nontoxic to the animal vector, and the spores must be resistant to the digestive system and remain viable in fecal pellets. Both *Suillus* and

Rhizopogon meet these criteria. Apart from being dispersed in feces, suilloid fungi are able to resist possible desiccation for at least 1 yr and remain viable (Ashkannejhad & Horton, 2006). Many other EMF fruiting bodies might be consumed by large mammals, but their spores may lack the ability to survive and rapidly colonize roots.

The ecological role of mammals in the dispersal of suilloid fungi in the non-native range can assemble novel three-way interactions. Non-native deer and wild boar eat fruiting bodies of non-native EMF, mainly *Rhizopogon* spp., and spores present in their feces are able to survive, germinate and colonize non-native pine seedlings, improving their growth and survival (Nuñez *et al.*, 2013). There is also experimental evidence of a similar three-way interaction in New Zealand, where non-native Australian possums disperse non-native European and North American suilloid fungi (species of *Rhizopogon* and *Suillus*), facilitating North American pine establishment (Wood *et al.*, 2015). Native EMF can also be consumed by non-native invasive mammals, but current evidence shows that they are not capable of readily colonizing either native or invasive tree species (Wood *et al.*, 2015). Interestingly, studies from South America show that native mammals (rodents and a native dwarf deer *Pudu pudu*) do not play a significant role in dispersing non-native fungi because of the scarce abundance of these animals (Nuñez *et al.*, 2013).

Resistant spore bank

Analogous to seed banks, fungal spore banks play a key role in terrestrial ecosystems as a source of fungal propagules. Not all fungal species are able to produce a long-lived spore bank, and so the species that remain viable in the soil can uniquely act as pioneers in colonization. More importantly, they can precondition a site to enable the growth of tree seedlings, thus facilitating establishment and, ultimately, invasion. Spore banks for some species, particularly *Rhizopogon* and *Suillus* species, are likely to be viable for decades (Bruns *et al.*, 2009; Nguyen *et al.*, 2012), enabling the colonization of plant hosts in the long term and preconditioning a site. By contrast with suilloid fungi, the spore longevity of most EMF is short and insufficient to accumulate effective numbers of viable spores at soil spore banks (Nara, 2009).

Both in their native and non-native ranges, suilloid fungi are the predominant group in the EMF spore bank for pines. In the native range, EMF spore banks are predominantly composed of species that produce truffles, within which *Rhizopogon* is the most common (Glassman *et al.*, 2015). The genus *Wilcoxina* can also be well represented in native pine spore banks, but, unlike the suilloids, *Wilcoxina* spores are not dispersed well by air or mammals. Most of the *Wilcoxina* propagules are chlamydospores that are produced on site within the soil and are dispersed through soil movement. Among the aboveground fruiting species, *Suillus* is the most common mushroom able to colonize *Pinus* spp. from spore bank propagules, if those species forming resupinate crusts are not considered (e.g. *Thelephora* spp., *Amphinema* spp., *Piloderma* sp., Marx & Ross, 1970; Glassman *et al.*, 2015). The fact that suilloid fungi last for years in the soil makes them particularly important in primary successional areas (Ashkannejhad & Horton, 2006) and

crucial in pine invasion fronts (Collier & Bidartondo, 2009). In an invasion context, having a resistant soil spore bank facilitates the introduction of suilloid fungi at any time at which soil is moved together with pine seedlings.

Several mechanisms could explain the high spore resistance of suilloid fungi. The deposition of a higher number of spores that remain deeper in the soil as the basidiome decomposes (Miller *et al.*, 1993) might be one of the main reasons that allows *Rhizopogon* to dominate spore banks. Moreover, the dependence of *Rhizopogon* on herbivore consumption of the fruiting bodies could partially explain its long-lived spore bank (Bruns *et al.*, 2009); as they must be well adapted to resist enzymatic and microbial degradation in the mammal gut, they may also have increased resistance to degradation by soil microbes. Mammal dispersal would also avoid loss of viability from UV irradiation or desiccation that would otherwise occur during aerial dispersal. Morphological and physiological traits that could be acting in spore resistance and longevity, such as spore wall thickness or biochemical traits, remain understudied.

Responsive, host-stimulated spores guarantee rapid colonization

Rapid colonization of pine seedling roots by suilloid spores is a critical feature of their biology that allows them to facilitate pine establishment (Ashkannejhad & Horton, 2006; Hayward *et al.*, 2015b). Although one might assume that most EMF should behave in this way, they do not. In fact, the reverse is true: spores from the overwhelming majority of EMF do not readily germinate and colonize seedlings under any conditions that can be reproduced in the laboratory, glasshouse or nature (Fries, 1987; Nara, 2009). Studies on fungal succession describe suilloid fungi as early-stage EMF that rapidly react to hosts (Ishida *et al.*, 2008; Peay *et al.*, 2011). By contrast with other EMF, basidiospores of most *Suillus* and *Rhizopogon* species will germinate readily, especially when stimulated by roots of compatible pine hosts (Fries, 1987; Liao *et al.*, 2016). Earlier colonization of roots can, in turn, provide a competitive advantage to suilloid fungi compared with late-successional EMF because of strong priority effects (Kennedy & Bruns, 2005). Spore quantity contributes to the predictability of the process in nature, as a fairly high spore density is needed to guarantee that all seedlings become colonized (Bruns *et al.*, 2009). However, the fact that specific, pine-derived chemical signals stimulate spore germination (Fries, 1987) is probably more important, because it means that suilloid spores can lie quiescently in soil until stimulated by an uncolonized pine root. This behavior, coupled with spore longevity, allows the density of the spore bank to increase over time and to remain responsive.

Long-distance exploration type

Suilloid fungi are an example of the long-distance exploration type (Agerer, 1994), characterized by the formation of long rhizomorphs able to colonize distant areas and to conduct nutrients efficiently. In a pine invasion context, long rhizomorphs may be able to better connect 'sink' seedlings into the existing hyphal network supported by the 'source' adult hosts

(Selosse *et al.*, 2006; F. Kuhar, pers. comm.). The formation of mycelial networks able to mediate long-range water and nutrient transfer between plants, and even mediate their interactions (Selosse *et al.*, 2006), could be fundamental for pines to prosper far from adult hosts (Teste & Simard, 2008). The formation of both long-distance and extensive vertically distributed mycelia also ensures that suilloid species have access to water sources during fruiting (Lilleskov *et al.*, 2009) and can be fundamental for pines to thrive under harsh conditions (Pickles & Simard, 2017). Whether resource and water subsidy as a result of these networks can explain pine invasion remains unsolved.

Suilloid fungi as drivers of pine invasions: open questions

Several aspects of the interaction between Pinaceae trees and suilloid symbionts remain completely unexplored or have evidence only from their native range. Here, we identify some gaps of knowledge in the current literature.

Causality

The literature shows that suilloid fungi are always present in pine invasions and occur on the invasion front. This strong pattern, coupled with the ecological traits outlined above, lead to our hypothesis that they are necessary components for successful pine invasion. However, direct experimental evidence for this hypothesis is not available and this represents a challenge for future research. There is still no reported cases in which suilloid species are present, but pines still fail to invade. Future experiments could address this topic by evaluating a certain range of circumstances under which suilloid fungi contribute to pine invasion, examining how this contribution may vary according to different soil types and climatic conditions.

Diversity

By contrast with the situation in the native range, an extremely depauperate community of fungal mutualists is present in the non-native range. The case of suilloid fungi as ecological drivers of global pine invasions is an example of how a low diversity of mutualists, in this case represented even by a single species, can drive an ecological process, such as the invasion of the tree host. In general terms, it seems intuitive to assume that greater numbers of EMF species are better for the host, but there is no strong evidence supporting this idea from either the native or non-native range. Instead, the pattern suggests that the identity of the EMF species and their ecological traits are more important than their diversity in invasive settings. In this context, one could take advantage of the relatively low number of EMF species in the non-native range, and use it to test the effects of different EMF species and different levels of EMF diversity on host growth and establishment. It might also be possible to establish pine plantations that have a low risk of invasion by selecting nonsuilloid EMF species for their EMF associates (Hayward *et al.*, 2015a).

Role of pathogens

Pathogen release is a common mechanism proposed to explain successful invasions, but whether reduced pathogen load in the invaded range interacts with EMF species and indirectly facilitates their host invasion is completely unknown. Certainly, the success of suilloid fungi in the non-native range could be partially increased by the absence of pathogens from their native range. For example, the absence of mycophagous insects (Hiol *et al.*, 1994) or mycoparasites (e.g. *Hypomyces*, members of the Gomphidiaceae family) might increase the numbers of fruiting bodies or extend their longevity, and thereby increase spore production. The escape from pathogens that could affect suilloid fungi during a non-reproductive stage may further represent an advantage in the invaded range compared with native settings.

The reduced load of pathogens on the host tree could also have indirect benefits to EMF. For example, mountain pine beetle (*Dendroctonus ponderosa*), which is currently absent from the Southern Hemisphere pine forests, has been found to affect both the proportion of EMF species and the hyphal length in the soil following an epidemic outbreak in western North America (Treu *et al.*, 2014). EMF that are highly specific, as in the case of *Suillus*, would be more strongly affected by host declines in comparison with EMF species that are capable of establishing symbiotic associations with other plant species. Richer EMF communities in the native range could also act as a protective mechanism against feeder root pathogens (Bennett *et al.*, 2017). However, trees such as *Pinus contorta* are aggressive colonizers of disturbed settings, even in their native range, where the presence of greater numbers of pathogens is typical.

Invasion failures and lag phase

As a result of their dispersal ability and the longevity of their spores, suilloid fungi are able to stay viable for long periods in areas in which hosts are absent and facilitate pine invasions. By contrast, does the absence of suitable fungal inocula and the low reactivity of spores during the first years post-introduction explain a lack of host establishment away from places in which they were initially introduced? Pines might not be invasive until the suilloid partner fungi arrive, or until they have built up a soil spore bank at the margins of the plantings, when the invasion could be triggered. This could explain the observed time lags (Hallett, 2006; Nuñez *et al.*, 2009) in pine invasions. Reported cases of EMF invasion failures are scarce (Vellinga *et al.*, 2009), but it would be useful to determine whether they coincide with pine invasion failures. In this aspect, the role of suilloid fungi in pine invasions is potentially testable. If small isolated pine plots with access only to noninvasive EMF are compared with pines in plots that have access to suilloid fungi, we would predict that only those pines with access to suilloid fungi will become invasive.

Legacy effects of pine invasions

Spores of suilloid fungi are likely to persist in the soil after removal of their hosts. Their high specificity, large quantities

and longevity may make lasting restoration difficult unless no pine propagules are present in the area. In turn, restoration chances in areas in which invasive pines have been removed could be hindered because of the presence of suilloid fungi that remain in the soil and allow the re-establishment of pines for a long time period (Dickie *et al.*, 2014). The possible management strategies for invasive EMF propagules that remain in the soil are increasingly being considered (Dickie *et al.*, 2016), together with an increasing recognition of some EMF as invasive species.

Concluding remarks

The study of belowground fungal ecology is increasing our understanding of aboveground ecological processes. Particularly for invasion ecology, an increasing number of studies have linked plant–fungal interactions as a mechanism to explain invasion success or failure. Here, we have reviewed the increasing evidence that shows that, within all co-invading EMF species, one particular group is key at driving pine invasions. All the evidence available from the native and the non-native ranges strongly suggests that, without suilloid fungi, pine invasion does not occur and that suilloid fungi are facilitating pine invasion worldwide. The set of key traits of suilloid fungi, related to effective and abundant dispersal and reactive spore banks, make them drivers of some of the most problematic invasive plants worldwide. Here, we provide an example of how the identity, rather than just the presence, of belowground mutualists can determine plant invasion success, and how the invasion of some plant species can be explained in part by the traits of their specific symbionts.





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Author contributions

NP and MAN conceived the study. NP collected the data and led the writing of the manuscript. NP, TDB, RV and MAN participated in data interpretation and revised the manuscript.

ORCID

Thomas D. Bruns  <https://orcid.org/0000-0002-2943-8669>
Martin A. Nuñez  <https://orcid.org/0000-0003-0324-5479>
Nahuel Policelli  <https://orcid.org/0000-0001-9708-5829>
Rytas Vilgalyš  <https://orcid.org/0000-0001-8299-3605>

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