Letter

Global pine tree invasions are linked to invasive root symbionts

Symbiotic soil microbes can facilitate plant invasions, yet it is unclear whether the invasive capacity of plants can be explained by the invasiveness of their microbial symbionts. After compiling a global dataset on associations between non-native invasive pine trees and ectomycorrhizal fungi (EMF), we found that the interaction with invasive EMF is an important predictor of pine invasion success that acts in concert with aboveground plant traits, questioning the way we currently predict plant invasions.

Introduction

Pine trees (species within the genus *Pinus*) are among the most invasive plants (Rejmanek & Richardson, 2013), yet we still do not fully understand the mechanisms behind their success outside their native range. Pines have invaded native habitats on all continents, with profound ecological, social, and economic impacts (Simberloff *et al.*, 2013; Nuñez *et al.*, 2017). Pine invasions have hindered native species conservation efforts (Franzese *et al.*, 2017; Nuñez *et al.*, 2017; García *et al.*, 2018), changed fire regimes (Taylor *et al.*, 2017), and negatively impacted tourism and local cultural identity (Bravo-Vargas *et al.*, 2019). National governments around the world have spent billions of dollars in invasive pine removal and restoration efforts over the past 20 yr (Nuñez *et al.*, 2017). Despite the magnitude and severity of the invasions and their extensive study (Richardson *et al.*, 2000, 2014; Simberloff *et al.*, 2010; Nuñez *et al.*, 2017; Castro-Díez *et al.*, 2019; Moyano *et al.*, 2019), the factors that determines pine invasiveness are unclear. Is pine invasiveness due to intrinsic biological characteristics of particular pine species, or is it better explained by external factors, such as their interactions with abiotic conditions or other organisms? Answering this question will help us understand pine invasions and better predict and manage them to reduce their impacts.

The invasiveness of plant species has historically been assessed using aboveground plant traits, yet evidence is accumulating that belowground ecology may be a key driver of pine invasion. Plant seed size, length of juvenile period, and frequency of high seed output generally correlate well with the number of places where an introduced plant species can successfully become naturalized (Richardson & Rejmanek, 2004; Rejmanek *et al.*, 2005). However, soil biota can facilitate plant species' invasion into non-native ranges (Reinhart & Callaway, 2006). Pines are obligate symbionts with EMF (Koele *et al.*, 2012), which increase plant access to nutrients and water, provide protection against pathogens (Smith & Read, 2008), and mediate interactions between plants and other soil microbes (Bonfante & Anca, 2009). If EMF are absent, pines fail to invade (Nuñez *et al.*, 2009). Moreover, highly invasive pine species are more dependent on EMF than non-invasive pine species (Moyano *et al.*, 2020) and often co-invade with non-native EMF (Dickie *et al.*, 2010; Nuñez *et al.*, 2013; Hayward *et al.*, 2015a; Gundale *et al.*, 2016). Recently, a subset of pine-associated EMF has been recognized as invasive (Dickie *et al.*, 2016; Policelli *et al.*, 2019). From all the non-native EMF that have been introduced (Vellinga *et al.*, 2009), some have never been reported outside nurseries or pine plantations, while some others have been able to disperse out of the initial points of introduction and co-invade (Dickie *et al.*, 2010; Hayward *et al.*, 2015a). Within the invasive EMF, some EMF species are reported only in mature pine invasions (dense invaded areas with adult pine trees), while some others are predominantly present in the invasion front (areas with disperse pine saplings) (Policelli *et al.*, 2019). While EMF at the invasion front are generally better at dispersing, forming a long-lasting spore bank, and exploring longer distances for roots, EMF in mature pine invasions require higher root density and have short-distance exploration types (Ashkannejhad & Horton, 2006; Peay *et al.*, 2011). Even when there is increasing evidence about this invasion pattern (Nuñez *et al.*, 2009; Dickie *et al.*, 2010; Hayward *et al.*, 2015a; Urcelay *et al.*, 2017; Policelli *et al.*, 2020), it is still unclear whether pine invasiveness is related to the invasion ecology of their obligate root symbionts.

Here, we explore whether invasive pine trees more frequently associate with invasive EMF than non-invasive EMF, and if so, whether this association explains the number of non-native sites in which each pine species has naturalized as a proxy of their invasion success. We hypothesized that: (1) pine species reported as invasive are more frequently associated with invasive EMF; and (2) the frequency of reported associations with invasive EMF better explains the invasion success of pines than aboveground plant traits.

Materials and Methods

To study the association between EMF and different pine host species, we performed a systematic review of the literature on EMF associations with non-native pine species world-wide. We used the Scopus database to search for papers that reported *Pinus* species presence in their non-native range, in which an association with EMF species was also reported. We built a dataset of every EMF species–pine species association reported across all papers (Supporting Information Table S1).

We classified each individual report into one of four EMF invasion categories, according to the spatial location from which the pine-associated non-native EMF were sampled: (1) 'Introduced' – EMF only reported to be found in nurseries, botanical

gardens, or isolated records such as local parks; (2) 'Plantation' – EMF reported from inside pine plantations in their non-native ranges; (3) 'Late-successional invasive' – EMF found in mature invasion stands with high pine density and adult pine trees present; and (4) 'Early-successional invasive' – EMF found far from the invasion sources, in areas with few isolated young pine trees, or no hosts (i.e. pine invasion front). Under these categories, all non-native EMF taxa are first placed in Category 1 and can progress to Category 4. This classification for the non-native EMF considers all those EMF species that were transported and introduced (Category 1), those that were able to establish a self-sustaining population that survives and reproduces (Category 2), and the subset that was able to spread away from the initial point of introduction and invade (Categories 3 and 4). We considered EMF species in both Categories 3 and 4 to be invasive ('late' and 'early'), as they all were able to disperse, survive, and reproduce at a distance from the pine plantation in at least one report (Blackburn *et al.*, 2011; Thakur *et al.*, 2019; Paap *et al.*, 2022).

We included data from 118 papers that met the criteria used (Table S1). With the information provided by those papers, we built a dataset with 695 pine–EMF interaction entries, including 194 different EMF taxa and 13 pine species. Each EMF species was assigned the highest invasion category reported for it (Table S1; Fig. S1). The total number of pine species included was conditioned by the number of available papers that addressed the ectomycorrhizal community associated with pine trees in the non-native range. Some pine species (e.g. *Pinus contorta*) were more studied than others based on their interest in forestry and in invasion ecology, biasing this dataset toward well-studied, invasive taxa. However, these 13 pine species are a good representation of a pine invasiveness gradient, with certain species considered to be some of the most invasive globally, and others that have been introduced, but have not invaded yet (Rejmanek & Richardson, 2013). For EMF, the range of invasiveness categories was also well-represented in the dataset, yet the taxonomic resolution of each EMF taxon was variable (Methods S1; Table S1), and there could be intraspecific variation in the invasion capacity and host specificity within one EMF species. From the total EMF taxa reported (194), 147 were reported at the species level, 35 at the genus level, seven at the family level, four at the order level, and one at the class level (Table S1). Most of the EMF taxa fell in the 'plantation' category (68), followed by those in the 'introduced' category (59). Within the group of EMF reported outside nurseries and plantations, we found more EMF taxa in mature pine invasions – category late-successional invasive – (43) than invasion fronts – category early-successional invasive (24) (Table S1; Fig. S1). Invasion is a population-level phenomenon, so we categorized a taxon as non-invasive when it had not been reported as invasive yet, which does not exclude the possibility of that taxon turning into invasive in the future. This approach is similar to the one taken for invasive plants, animals, and other organisms at the species level (Richardson *et al.*, 2000; Blackburn *et al.*, 2011).

For each pine species, we considered aboveground invasive traits using the *Z*-score, which is an extensively used discriminant function to predict woody plants' invasiveness (Rejmanek & Richardson, 1996; Rejmanek *et al.*, 2005). The *Z*-score was calculated based on mean seed mass, minimum juvenile period, and mean interval between large seed crops for each pine species, which was obtained from available bibliography (Grotkopp *et al.*, 2004; Krugman & Jenkinson, 2008; Mcgregor *et al.*, 2012).

To test the hypothesis that invasive pine species are more frequently associated with invasive EMF, we performed a principal coordinates analysis (PCoA), based on the dissimilarity among pine species in the frequency of association with each EMF species. To account for the phylogenetic non-independence of taxa, we explored the phylogenetic independence of EMF invasiveness before the PCoA, including 'invasive' and 'non-invasive' as a binary trait (Fig. S2; Methods S1). Invasiveness did not have significant phylogenetic structure (Brownian model P_{value} = 0.32; *D* model P_{value} = 0.063), so we used the nonphylogenetically corrected PCoA.

To test the hypothesis that association with invasive EMF is a key factor explaining the invasion success of pines, we ran a linear regression model using the number of naturalized occurrences of the pine species as the response variable (i.e. number of sites at a global scale where each pine species is reported as naturalized) (Perret *et al.*, 2018), which we use here as proxy for their invasiveness. Explanatory variables included the proportion of the total reported interactions with each of the four EMF invasiveness categories and the *Z*-score for the studied pine species. To account for the potential effect of the publication from which we extracted the pine–EMF interaction data, we included the reference as a random effect in our statistical models. As pine invasion may be influenced by climate and/or soil conditions where both plant and EMF species occur, we analyzed the influence of climatic and edaphic variables on our dataset by including 'mean altitude', 'soil nitrogen (N)', 'soil organic carbon (C)', 'soil pH', 'mean temperature', and 'mean precipitation' as explanatory variables in our model. We then used the second-order Akaike information criterion (AICc) to select the best model from all possible combinations. A detailed version of the methods used for the systematic search, dataset construction, and data analysis can be found in the Methods S1.

Results

We found a relationship between EMF invasiveness and pine invasiveness, where invasive EMF (both early-successional and late-successional) were more frequently reported with pine species that have higher numbers of naturalizations into non-native habitats (Fig. 1). Pine species with the greatest number of naturalizations such as *P. contorta*, *Pinus radiata*, or *Pinus sylvestris* grouped together and separated from those with a smaller number of naturalizations such as *Pinus pinea*, *Pinus caribaea*, or *Pinus virginiana* based on the frequency of their association with invasive EMF. These groups did not match the *Z*-score values calculated for each pine species: some pine species predicted to be invasive based on their *Z*-score grouped with plantation and introduced EMF, while some pine species predicted to be non-invasive based on their *Z*-score grouped with invasive EMF (both early- and late-successional) (Fig. 1). In accordance with our hypothesis, we also found that the association with invasive EMF better explained the

Fig. 1 Principal coordinates analysis (PCoA) of pine species according to their association with different ectomycorrhizal fungi (EMF) species. EMF species are coded by invasive category: green triangles, Introduced; gray crosses, Plantation only; light blue squares, Late-successional invasive; pink circles, Early-successional invasive. Pine species' names are colored according to their Z-score, with species in blue predicted to be less invasive and species in red predicted to be more invasive according to this index, based only on aboveground traits. The eigenvalues of each PCoA component are expressed in percentage next to the axis name.
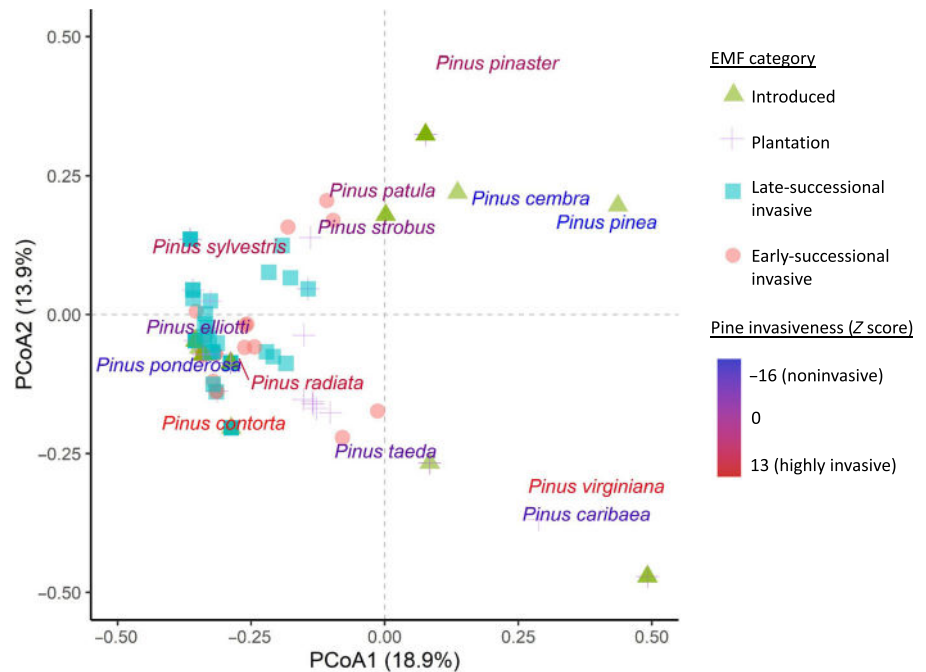

Fig. 2 Partial linear regression model showing the number of naturalized occurrences of pine species vs the proportion of the total ectomycorrhizal fungi (EMF)-reported interactions represented by late invasive EMF species. Pine species' names are colored according to their Z-score, with species in blue predicted to be less invasive and species in red predicted to be more invasive. The size of pine trees drawings next to each pine species' name is a scaled representation of the number of sites (from 77 sites to 0) in which that pine species is reported to be naturalized globally – as a proxy of its invasiveness. The green shaded area represents the 95% confidence interval of the regression model.
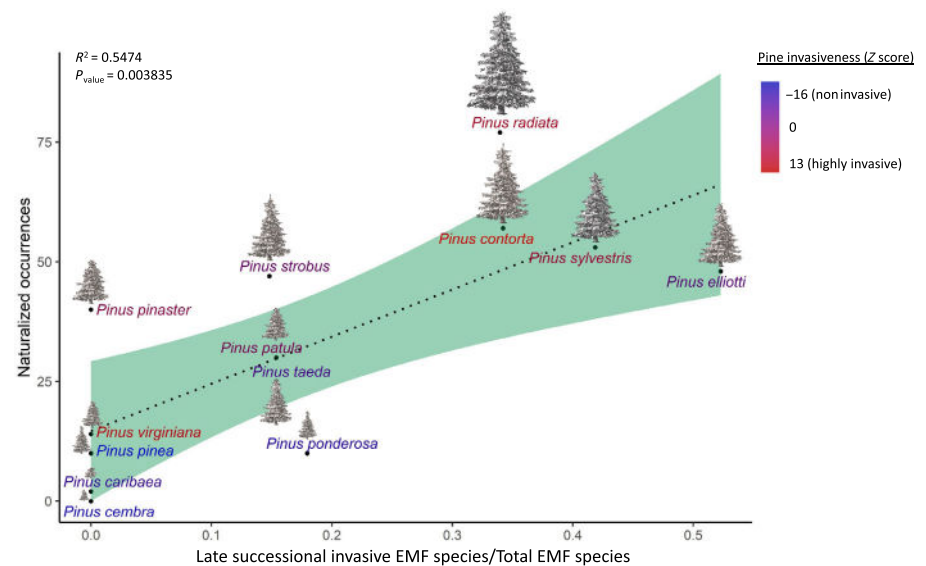
invasion success of pine species than pines' aboveground traits considered alone (Fig. 2; Table S2a). Pine invasion success was significantly related to the association with late-successional invasive EMF (Fig. 2, partial regression $R^2 = 0.5474$; $P = 0.003835$), but not with any other EMF category. The best model to explain pine invasion success included both association with late-successional invasive EMF and aboveground plant traits, collectively explaining more than 70% of the variance in the number of successful pine invasions (Table S2b) ($R^2 = 0.7034$; $P = 0.0006812$). When we included climatic and edaphic variables in the model, the proportion of late-successional invasive EMF still explained a significant portion of pine invasion success, as did Z-score, annual mean temperature, mean altitude, soil pH, and soil organic C content (Table S2c).

Discussion

Our results support the idea that certain plant species may be successful in new environments due to their interactions with soil microbes that exhibit invasive traits themselves (Rout & Callaway, 2009; Litchman, 2010; Policelli *et al.*, 2019). For pines in particular, which are among the most invasive plants, invasiveness has been historically described by a syndrome of aboveground traits mostly related to plant life history and ability to grow and reproduce (Rejmanek & Richardson, 1996; Richardson & Rejmanek, 2004). Co-invasion of pine trees and their belowground mutualists is one of the main mechanisms proposed to explain their success outside the native range (Dickie *et al.*, 2010); however, the main focus in general is on the invasive plant traits. Fungal

mycorrhizal traits (Chaudhary *et al.*, 2022) that determine their invasiveness are also expected to partially explain the co-invasion success. Here, we show, for the first time, that the most invasive pine species associate more frequently with the most invasive EMF species. Our results are consistent with recent findings showing that pine species that are more invasive depend more upon their EMF (Moyano *et al.*, 2020), a phenomenon that contradicts the ideal-weed hypothesis, which posits that invasive plant species depend less on mutualistic interactions (van der Putten *et al.*, 2007; Moyano *et al.*, 2020, 2021). Pinaceae species seem to be interesting exceptions to this idea (Dickie *et al.*, 2010; Nuñez & Dickie, 2014; Bogar *et al.*, 2015; Moyano *et al.*, 2020), being more successful when their EMF mutualists are also invasive. Lag times in invasions or invasion failures could be explained by lack of invasive mutualists, while encounters with invasive ectomycorrhizal symbionts could trigger an invasion (Nuñez *et al.*, 2016; Policelli *et al.*, 2019).

Associating with invasive EMF may enhance the host invasive capacity, but the relative importance of the different EMF species seems to change over time. Our results show that only the interaction with a subset of fungi – specifically, those that are associated with mature pine invasions (i.e. late-successional invasive EMF) – is related to the invasion success of pines. Previous evidence suggests that early-successional invasive EMF, dominated by suilloid fungi, have a key role as drivers of pine invasions (Policelli *et al.*, 2019). While early-successional fungi, and especially suilloid fungi, might be key to trigger a pine invasion and are more likely to naturalize outside their native range (Vlk *et al.*, 2020), late-successional fungi may have a substantial role in supporting the invasion. Early-successional invasive EMF seem to have a set of ecological traits that facilitate the establishment of pine hosts in invasion fronts (Hayward *et al.*, 2015b; Policelli *et al.*, 2020), such as the capacity to produce orders-of-magnitude more spores compared with other EMF species (Peay *et al.*, 2012; Horton, 2017). In turn, those spores are able to disperse further from the invasion source and form a long-lasting spore bank (Bruns *et al.*, 2009; Peay *et al.*, 2012; Hayward *et al.*, 2015a; Horton, 2017). Evidence also suggests that early-successional invasive EMF have the capacity to produce long-distance exploration structures (i.e. rhizomorphs or cords), which might increase the chances of better exploring the soil for nutrients and water and the chances of finding compatible plant hosts' roots (Lilleskov *et al.*, 2009; Pickles & Simard, 2017; Policelli *et al.*, 2019). Older trees might need late-successional fungi, such as *Amanita muscaria*, *Amanita rubescens*, *Boletus edulis*, *Inocybe curvipes*, *Paxillus involutus*, and *Scleroderma citrinum* (Nuñez *et al.*, 2009; Dickie *et al.*, 2010; Hynson *et al.*, 2013; Hayward *et al.*, 2015a), which benefit from the new soil conditions under dense pine invasion. These EMF species exhibit shorter exploration types, which may translate into a more efficient carbon allocation strategy in areas with higher root density (Peay *et al.*, 2011). Factors such as soil pH, soil nitrogen, and other soil nutrients, together with litter quality, surrounding vegetation, and the age of the Pinaceae hosts might also act as strong filters for this subset of EMF species. In turn, other EMF traits such as the capacity to mine organic matter to acquire nitrogen might be relevant as well for successful pine invasions (Talbot *et al.*, 2008; Zak *et al.*, 2019; Zanne *et al.*, 2020). Until now, we lacked a comprehensive list of pine-associated EMF species reported as invasive, so it was difficult to explore which EMF traits are mostly associated with invasiveness. We hope our dataset will be useful in further exploring these traits and identifying potential EMF species suitable for controlled experiments that address key questions related to pine invasion success. Still to be addressed is the extent to which our results can be extrapolated to other plant families or other species within Pinaceae.

Our results are in line with the idea that soil microbes might not be mere passengers in the process of plant invasions, but may interact in a biogeographically explicit way, triggering and maintaining the invasion (Rout & Callaway, 2009; Dawson & Schrama, 2016). Microbial symbionts' invasiveness, aboveground plant traits, and climate and soil variables likely act in concert to drive invasion success. Considering the invasiveness of symbiotic microbes to better predict the invasiveness of plants seems to be as important as taking into account aboveground plant traits and climatic and edaphic variables. In turn, we emphasize that paying attention to soil microbes associated with non-native plants that do not successfully invade will also increase our understanding of the importance of soil biota in plant invasions (Reinhart & Callaway, 2006). A better understanding of this dynamic could improve our ability to predict plant invasiveness and possibly to avoid future invasions.

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Author contributions

NP and JMB conceived the study. NP collected the data and led the data analysis and writing of the manuscript. NP, JDH, JM, RV, SV, and JMB participated in data interpretation and revised the manuscript.

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Data availability

The data that support the findings of this study are available in the Supporting Information of this article.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Number of papers reporting each ectomycorrhizal fungi in each of the four invasion categories.

Fig. S2 Phylogenetic tree of all ectomycorrhizal fungi taxa from this study, including invasiveness as a binary trait.

Methods S1 Detailed version of methods.

Table S1 Full dataset including all ectomycorrhizal fungi–pine interactions reported in the non-native range.

Table S2 Parameters of the regression models.

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