



Alien ectomycorrhizal plants differ in their ability to interact with co-introduced and native ectomycorrhizal fungi in novel sites

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Abstract

Alien plants represent a potential threat to environment and society. Understanding the process of alien plants naturalization is therefore of primary importance. In alien plants, successful establishment can be constrained by the absence of suitable fungal partners. Here, we used 42 independent datasets of ectomycorrhizal fungal (EcMF) communities associated with alien Pinaceae and *Eucalyptus* spp., as the most commonly introduced tree species worldwide, to explore the strategies these plant groups utilize to establish symbioses with EcMF in the areas of introduction. We have also determined the differences in composition of EcMF communities associated with alien ectomycorrhizal plants in different regions. While alien Pinaceae introduced to new regions rely upon association with co-introduced EcMF, alien *Eucalyptus* often form novel interactions with EcMF species native to the region where the plant was introduced. The region of origin primarily determines species composition of EcMF communities associated with alien Pinaceae in new areas, which may largely affect invasion potential of the alien plants. Our study shows that alien ectomycorrhizal plants largely differ in their ability to interact with co-introduced and native ectomycorrhizal fungi in sites of introduction, which may potentially affect their invasive potential.

Introduction

Introductions of alien species into new areas may strongly affect the structure and functioning of ecosystems and

communities of native organisms [1–3]. Human migrations and global trade have tremendously increased introductions of non-native species to novel regions [4], causing huge economic costs worldwide [5, 6]. Success of alien species establishing in new areas is determined by numerous factors, such as the pathway of introduction, amount of propagules introduced to a site, climate match between the native and invaded range, probability of encountering suitable habitats, and species traits that manifest in biotic interactions [7–10]. Beyond their native distribution range, alien species can benefit from the escape from pathogens, predators, or competitors as predicted by the enemy release hypothesis [11]. By contrast, alien species' establishment in new environments can be constrained by the absence of suitable mutualists [7, 12]. Recent studies indicate that the role of mutualistic interactions is as important for the establishment of alien species as the escape from the effects of more commonly studied enemies, such as herbivores or pathogens [13–16].

The role of mutualistic interactions may be particularly important for introductions of plants with obligate symbiosis. Woody plants forming ectomycorrhizal (EcM) symbiosis with soil fungi represent an example of plants which cannot complete their life cycle without the

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mycobionts [12]. EcM fungi (EcMF) provide plants with mineral nutrients, water, or defense against pathogens, whereas plants supply EcMF with energy-rich carbon compounds in return [17]. To establish in plantations or successfully naturalize in new areas, EcM plants may either: (i) interact with EcMF co-introduced from the plant's native range (co-introduction), (ii) associate with EcMF, which naturally occur in both native and introduced range of the host plant (familiar association), or (iii) form novel associations with EcMF species native to the region where the plant was introduced (novel association) [18, 19].

Co-introductions of alien EcMF species together with their alien host trees were documented for introductions of pines (Pinaceae family) to the Southern Hemisphere [20]. Various EcMF were also co-introduced around the world with other plant groups, such as *Alnus* spp. or *Coccoloba* spp. [21–23]. Although *Eucalyptus* spp. were shown to be able to establish in new areas with the aid of novel associations with local EcMF [24], many EcMF were also co-introduced with eucalypts to new areas (e.g., [22, 25]). Therefore it is nowadays widely assumed, that co-introductions of EcMF represent the prevailing strategy of alien EcM plants to successfully establish in new areas [12].

In their native range, EcM plants usually host highly diverse EcMF communities on their root system [26, 27]. However, introductions to the new areas often lead to substantial reduction of EcMF species richness, with an extreme example of a single co-introduced EcMF species on roots of successfully established seedlings of *Pinus contorta* [28]. It remains questionable whether the successful introductions of EcM plants, other than pines, can also be associated with a few distinctive EcMF species [29] or rather associated with broad spectra of EcMF species. This might have important consequences for management of EcM plant and fungal invasions [30].

Understanding of the process of EcM plant naturalization in new areas is an issue of primary importance, because EcM plants form a disproportionately high share of alien trees globally, and many of them are regarded as the most severe invaders [31–34]. Although the global share of EcM plants is estimated between 1.7 and 2.4% of higher plant species [35], 21% of the 90 most hazardous alien plants are EcM [36]. The majority of introduced EcM plants belong to the families Pinaceae (represented particularly by pines) and Myrtaceae (represented by eucalypts), due to their massive planting in the last century [37, 38], commonly in areas with native vegetation of mostly different mycorrhizal type [14, 39]. Members of Pinaceae and Myrtaceae also belong to the 90 most hazardous alien plants, namely: *Pinus patula*, *P. pinaster*, and *P. radiata*, *Eucalyptus camaldulensis* and *E. globulus* [36]. In many regions these introductions resulted in invasive spreading of the alien trees [40]. Pine invasions are recognized as important ecological

phenomenon and threat to local diversity, especially in the Southern Hemisphere [41]. The importance of the their EcM mycobionts in the invasion dynamics is nowadays widely recognized [16, 28]. Compared with Pinaceae, less species of *Eucalyptus* have become invasive [32, 42], but these numbers are likely to grow in the future [38, 43].

This paper aims to determine the share of mycorrhizal strategies (co-introduction vs. familiar association vs. novel association) among EcMF associated with alien Pinaceae and *Eucalyptus* on a global scale. These two groups were selected because they represent the most frequently introduced and cultivated woody plants worldwide [31, 44] and in numerous cases became invasive with detrimental effect on native ecosystems [37, 45, 46]. Particularly we aimed to find out if the share of mycorrhizal strategies differs between the two groups of alien plants or among geographical regions to which the alien plants were introduced. In addition, we sought to determine differences in composition of EcMF communities associated with alien EcM plants in different regions to which they were introduced. These objectives were achieved by using a metastudy and synthesis approach based on fungal sequences deposited in public databases and our own unpublished results.

Materials and methods

Data sources

This global-scale data synthesis is based on data from individual studies that focused on molecular identification of EcMF communities associated with alien plants sampled from habitats in their introduced range. The list of studies was compiled from the Web of Science and Google Scholar (5 November 2018) by searching for combination of terms ‘non-native’, ‘alien*’, ‘invasion*’ and ‘introduction*’ with ‘ectomycorrhiza*’, yielding over 200 results. The final selection included studies in which at least one alien EcM plant species belonged to Pinaceae (e.g., *Pinus* spp., *Abies* spp., *Pseudotsuga* spp.) or Myrtaceae (*Eucalyptus* spp.) and where root-associated EcMF were identified using sequencing of the ITS region of rDNA. The ITS region was chosen, because it represents the most commonly used barcoding region for fungi [47]. Studies with experimentally manipulated soil treatments were excluded. Besides that, we also searched for sequences of EcM mycobionts associated with alien EcM plants in public sequence repositories, such as UNITE [48] or INSDC (International Nucleotide Sequence Database Collaboration; <http://www.insdc.org>). The final dataset (17 published studies) was complemented with our unpublished data, which met the criteria listed above. Altogether our study was based on 42 independent datasets (Table 1; Supplementary Table S1).

Table 1 List of datasets of EcMF associated with exotic Pinaceae and *Eucalyptus* spp. trees, included in this study.

ID ^a	Country	Region	Host plant	GPS coordinates	Reference ^b
1	Iran	Eurasia	<i>Pinus sylvestris</i>	36.066667N, 53.150000E	Bahram et al. [26]
2	Argentina	South America	<i>Pinus ponderosa</i>	43.170055S, 71.509176W	Barroetaveña et al. 2010
3	Pakistan	Eurasia	<i>Eucalyptus</i> sp.	31.3333N, 74.0833E	Bashir et al. [97]
4	Spain	Eurasia	<i>Eucalyptus globulus</i>	42.333333N, 8.550000W	Calviño-Cancela (unpublished)
5	Spain	Eurasia	<i>Eucalyptus globulus</i>	42.233333N, 8.350000W	Calviño-Cancela (unpublished)
6	Spain	Eurasia	<i>Eucalyptus globulus</i>	42.283053N, 8.767100W	Calviño-Cancela (unpublished)
7	New Zealand	Oceania	<i>Pinus contorta</i>	Not available	Dickie and Bolstridge (unpublished)
8	South Africa	Africa	<i>Pinus patula</i>	24.590507S, 30.190191E	Hawley et al. [74]
9	Argentina	South America	Pinaceae	40.983546S, 71.513335W	Hayward et al. [28]
10	Argentina	South America	<i>Pinus</i> sp.	40.983546S, 71.513335W	Hayward et al. [28]
11	Argentina	South America	<i>Pseudotsuga</i> sp.	40.983546S, 71.513335W	Hayward et al. [28]
12	Chile	South America	<i>Pinus contorta</i>	45.500556S, 71.704167W	Hayward et al. [76]
13	Japan	Eurasia	<i>Pinus strobus</i>	36.104166N, 138.233841E	Hirose (unpublished)
14	Hawaii	Oceania	<i>Pinus</i> sp.	20.769167N, 156.241111W	Hynson et al. [73]
15	Kenya	Africa	<i>Eucalyptus</i> sp.	0.17073S, 35.59617E	Kluthé et al. 2016
16	Czech Republic	Eurasia	<i>Pinus strobus</i>	50.870000N, 14.381667E	Kohout et al. [82]
17	China	Eurasia	<i>Pinus elliotii</i>	28.102491N, 113.034989E	Ning (unpublished)
18	Argentina	South America	<i>Pseudotsuga menziesii</i>	40.950415S, 71.537314W	Nuñez et al. [13]
19	Argentina	South America	<i>Pinus ponderosa</i>	40.983546S, 71.513335W	Nuñez et al. [75]
20	Argentina	South America	<i>Pseudotsuga menziesii</i>	40.983546S, 71.513335W	Nuñez et al. [75]
21	Ireland	Eurasia	<i>Picea sitchensis</i>	52.883333N, 7.366667W	O'Hanlon et al. 2012
22	China	Eurasia	<i>Eucalyptus grandis</i>	Not available	Pan et al. (unpublished)
23	UK	Eurasia	<i>Eucalyptus nitens</i>	51.479800N, 0.296500W	Pennington et al. [94]
24	UK	Eurasia	<i>Eucalyptus gunnii</i>	51.479800N, 0.296500W	Pennington et al. [94]
25	Poland	Eurasia	<i>Abies alba</i>	54.2152N, 17.9860E	Rudawska et al. 2016
26	Reunion	Africa	<i>Eucalyptus camaldulensis</i>	Not available	Sené et al. (unpublished)
27	Senegal	Africa	<i>Eucalyptus camaldulensis</i>	Not available	Sené et al. (unpublished)
28	Seychelles	Africa	<i>Eucalyptus</i> sp.	4.623930S, 55.433089E	Tedersoo et al. [24]
29	Seychelles	Africa	<i>Pinus caribaea</i>	4.623930S, 55.433089E	Tedersoo et al. [24]
30	Madagascar	Africa	<i>Eucalyptus</i> sp.	24.966711S, 46.99986E	Tedersoo et al. [24]
31	Zambia	Africa	<i>Eucalyptus camaldulensis</i>	13.316667S, 24.500000E	Tedersoo et al. [77]
32	Cameroon	Africa	<i>Eucalyptus grandis</i>	5.016667S, 8.800000E	Tedersoo et al. [77]
33	Zambia	Africa	<i>Eucalyptus grandis</i>	13.316667S, 24.500000E	Tedersoo et al. [77]
34	Madagascar	Africa	<i>Eucalyptus robusta</i>	24.966711S, 46.99986E	Tedersoo et al. [77]
35	Zambia	Africa	<i>Pinus kesiya</i>	13.316667S, 24.500000E	Tedersoo et al. [77]
36	Cameroon	Africa	<i>Pinus</i> sp.	5.016667S, 8.800000E	Tedersoo et al. [77]
37	New Zealand	Oceania	<i>Pinus radiata</i>	44.245800S, 176.24000W	Walbert et al. [77]
38	Czech Republic	Eurasia	<i>Pinus strobus</i>	50.870000N, 14.430000E	This study
39	Madeira	Africa	<i>Cedrus deodara</i>	Not available	This study
40	Madeira	Africa	<i>Eucalyptus globulus</i>	Not available	This study
41	Madeira	Africa	<i>Pinus pinaster</i>	Not available	This study
42	Estonia	Eurasia	<i>Abies sachalinensis</i>	58.686316N, 26.582143E	This study

Where available, we provide GPS information obtained from the original publications or public databases.

^aID numbers are used as identifiers of individual datasets in Figs. 1 and 2.

^bFull references are provided in Supplementary Table 2.

For each dataset, metadata on geographic (latitude, longitude), host plant species and environmental variables were

retrieved from the original publications or public databases, if available.

Morphotyping of EcM root tips with subsequent Sanger sequencing of the ITS rDNA region was applied for mycobiont identification in all of the analysed studies as high-throughput sequencing (HTS) studies on this topic were unavailable. All sequences from the selected studies were downloaded in FASTA format from INSD or obtained directly from the individual studies, in cases where the sequences were provided in supplementary materials. The obtained sequences were individually checked and only those without ambiguous bases and covering full length of at least one of the variable regions of the ITS were used for subsequent analysis. These sequences were then assigned to existing units corresponding to fungal Species Hypothesis [49] (referred to as SH from here on) based on BLASTn [50] search on 98.5% sequence similarity level. Detected SHs were assigned to existing EcM lineages based on previous studies [51, 52]. Non-EcM SHs were excluded from analysis.

To determine putative native ranges of EcM fungal SHs, we used (i) SH's distribution maps implemented in UNITE [49] (19 November 2018), after excluding all sequences associated with non-native EcM vegetation and (ii) a newly developed database of fungal HTS studies [53]. Only studies reporting fungal community composition in natural vegetation without any non-native EcM plants were included in the HTS database. Combining these two independent sources enabled us to determine the putative native ranges of EcMF SHs from Sanger sequencing as well as HTS-based studies, yielding probably the most comprehensive overview of global distribution of EcMF so far.

Based on putative native distributions of the SHs, we assigned them to three biogeographic categories. The assignment was done independently for each dataset. The three biogeographic categories were based on the simplified framework of Dickie et al. [18, 19]. This framework is so far the only one which conceptualized plant–fungal invasions from the perspective of plant and fungal origin. Specifically, we assigned all EcMF SHs to: (i) co-introduction: introduction to a new region of an alien SH with an alien plant, either concurrently or asynchronously, (ii) familiar association: an alien plant associates with an SH native to the plant's both native and novel ranges, and (iii) novel association: interaction between alien plant and SH native to the plant's new range. The biogeographic categories were not defined for SHs with a low number of records in UNITE or HTS database (less than five records) as previously described in Vik et al. [54]. Biogeographical regions were determined according to Morrone [55].

Statistical analyses

To determine the differences in community composition of EcMF associated with alien trees among biogeographic

regions, we performed permutational ANOVA (PERMANOVA) as implemented in the *adonis* function of the VEGAN package in R [56]. First, we transformed all datasets into binary format, because many datasets did not provide quantitative information about EcM morphotypes or species. The Sørensen dissimilarity metric was then used to calculate the distance matrix of the EcMF communities. To assess whether differences in fungal communities among biogeographic regions were statistically significant, 999 permutations were used. Adjusted R^2 were calculated based on the Adonis results in order to check for model quality. Pairwise PERMANOVA with 99,999 permutations was performed to test differences in composition of EcMF communities between geographical regions. Bonferroni correction was used to calculate the corrected P value determined by the pairwise PERMANOVA analysis. The Sørensen dissimilarity of the EcMF communities was used for nonmetric multidimensional scaling (NMDS) analyses in the ECODIST package [57]. Only samples with sufficient species overlap were included in the NMDS analysis. We also analyzed the response of EcMF composition variation to biogeographic regions. Composition variation was defined following [58] as variation β -diversity, which is the variance calculated for the different samples per a biogeographic region. For statistical comparison, the composition variation was calculated using the functions *betadisper* and *permutest.betadisper* in the VEGAN package of R software.

To test whether there are differences in the strategies that alien EcM plants adopt to establish in the new areas among geographic regions, their counts were analysed by row \times column contingency tables, using generalized linear models with the log-link function and a Poisson distribution of errors [59]. For the models that significantly explained the effects, adjusted standardized residuals of G -tests were then compared with critical values of the normal distribution to ascertain for which species groups the counts are lower or higher than expected by chance [60]; see e.g., [61]. To test whether alien Pinaceae and *Eucalyptus* adopt different strategies to associate with suitable EcMF in the new areas, nonparametric Mann–Whitney–Wilcoxon test was applied. All calculations were done in R 3.5.0 software [62].

Results

Description of the dataset

Our data synthesis is based on 42 independent datasets (28 published and 14 unpublished) of EcMF communities associated with alien woody plants worldwide. Most datasets were obtained from Africa (16), Europe (10), South America (8), Oceania (3), and Asia (5). EcM fungal communities associated with alien Pinaceae (e.g., *Abies alba*,

Pinus strobus, *P. contorta*, *P. elliottii*, *Pseudotsuga menziesii*) and the genus *Eucalyptus* were represented by 25 and 17 datasets, respectively.

In total, 1167 fungal ITS sequences were obtained from roots of alien EcM plants (ranging from 1 to 77 sequences per dataset). After filtering steps, 401 sequences were retained and further assigned to 273 fungal SHs (based on 98.5% sequence similarity thresholds) with EcM lifestyle. Natural distribution area was determined based on our criteria for almost 270 SHs and these SHs were subsequently assigned to one of the three biogeographic categories (number of records per category: 209 co-introductions; 100 native to both areas; 76 novel interactions) in each dataset separately (Supplementary Table S2). Overall, alien *Eucalyptus* spp. tended to enter novel association (in 11 of 17 studies) with native EcMF in new areas more often than alien Pinaceae spp. (in 10 of 25 studies; Mann–Whitney–Wilcoxon test; $p = 0.021$). Association with familiar or co-introduced EcMF did not differ between the two groups of alien plants.

EcMF associated with alien Pinaceae species

EcMF associated with alien plant species from the Pinaceae family were represented by 25 datasets (South America—8, Eurasia—8, Africa—6, and Oceania—3). *Tomentella*, *Suillus*, and *Russula* were the most species-rich EcM fungal genera associated alien Pinaceae species, represented by 22, 20, and 15 SHs, respectively. The share of strategies that Pinaceae species adopted to establish EcM partnership in new regions differed profoundly among biogeographic regions (Fig. 1a). While alien Pinaceae almost exclusively associated with co-introduced EcMF in regions with no native Pinaceae spp. (such as South America, Africa, and Oceania), familiar or novel associations with native EcMF prevailed among alien Pinaceae introduced to regions where other members of the Pinaceae family naturally occur (Table 2). Although co-introduced EcMF dominated on roots of the Pinaceae species in the Southern Hemisphere (mostly Argentina), the alien plants were in some cases (~25%) also able to form novel interactions with native EcMF, such as *Ruhlandiella* sp. (SH207800.07FU), *Sebacina* sp. (SH214642.07FU), or Thelephoraceae sp. (SH010118.07FU). Only nine EcMF species associated with alien Pinaceae trees in regions where other members of the Pinaceae family naturally occur can be considered as putative alien species (Supplementary Table S2).

The composition of EcMF communities associated with alien Pinaceae showed distinct patterns among geographic regions. Alien Pinaceae species tend to associate with distinct EcMF communities in regions with and without native Pinaceae spp. (PERMANOVA, $n = 21$; $df = 1$; $F = 1.93$; $p < 0.01$; $R^2 = 0.1$). While in the regions without native Pinaceae

spp., EcMF communities associated with Pinaceae trees were dominated by *Hebeloma mesophaeum* (SH218845.07FU), *Suillus pseudobrevipes* (SH176742.07FU) and Thelephoraceae sp. 1 (SH189355.07FU), *Cenococcum geophilum* (SH214459.07FU) and *Tylospora* sp. (SH192265.07FU) were commonly found on roots of alien Pinaceae species in the regions with native Pinaceae spp. (Fig. 2). Interestingly, the composition of EcMF communities also differed among the regions without native Pinaceae spp. (PERMANOVA, $n = 13$; $df = 2$; $F = 1.96$; $p < 0.01$; $R^2 = 0.28$). While EcMF community composition did not differ between alien Pinaceae in South America and Oceania, it differed between alien Pinaceae from these two regions and Africa (Fig. 2).

EcM fungal communities associated with alien Pinaceae also differed in composition overlap between the regions with and without native Pinaceae spp. While only 13% of SHs were detected in at least two samples in the regions with native Pinaceae spp., 63% of SHs were shared among two or more sites in the regions without native Pinaceae spp.

EcMF associated with alien *Eucalyptus* species

EcMF associated with alien eucalypts were represented by 17 datasets (Africa—10 and Eurasia—7). Predominantly co-introduced EcMF and novel associations with local EcMF were recorded while familiar associations were almost absent (Fig. 1b). *Laccaria*, *Clavulina*, and *Tomentella* were the most species-rich EcM fungal genera associated with alien *Eucalyptus* species. All reported datasets were obtained in regions without natural distribution of *Eucalyptus* spp. or any other EcM members of the Myrtaceae family.

Species composition of EcMF communities associated with alien eucalypts showed very little overlap among the datasets (for more details see Supplementary Table S3). More than 80% of all EcMF associated with alien eucalypts were recorded only once. Therefore, we were not able to statistically analyse differences in the composition of eucalypt-associated EcMF communities among regions. *Scleroderma albidum* (SH179810.07FU) and *Scleroderma* sp. (SH179808.07FU) were the most frequently detected EcMF associated with alien eucalypts. These two putatively co-introduced EcMF species were both recorded in five datasets.

Discussion

EcM plant species form a disproportionately high share of alien trees globally, and many of them are regarded as the most severe invaders [31–34]. Recently, Moyano et al. [63] provided evidence that alien EcM plants that rely more on EcMF are more prone to become invasive in introduced

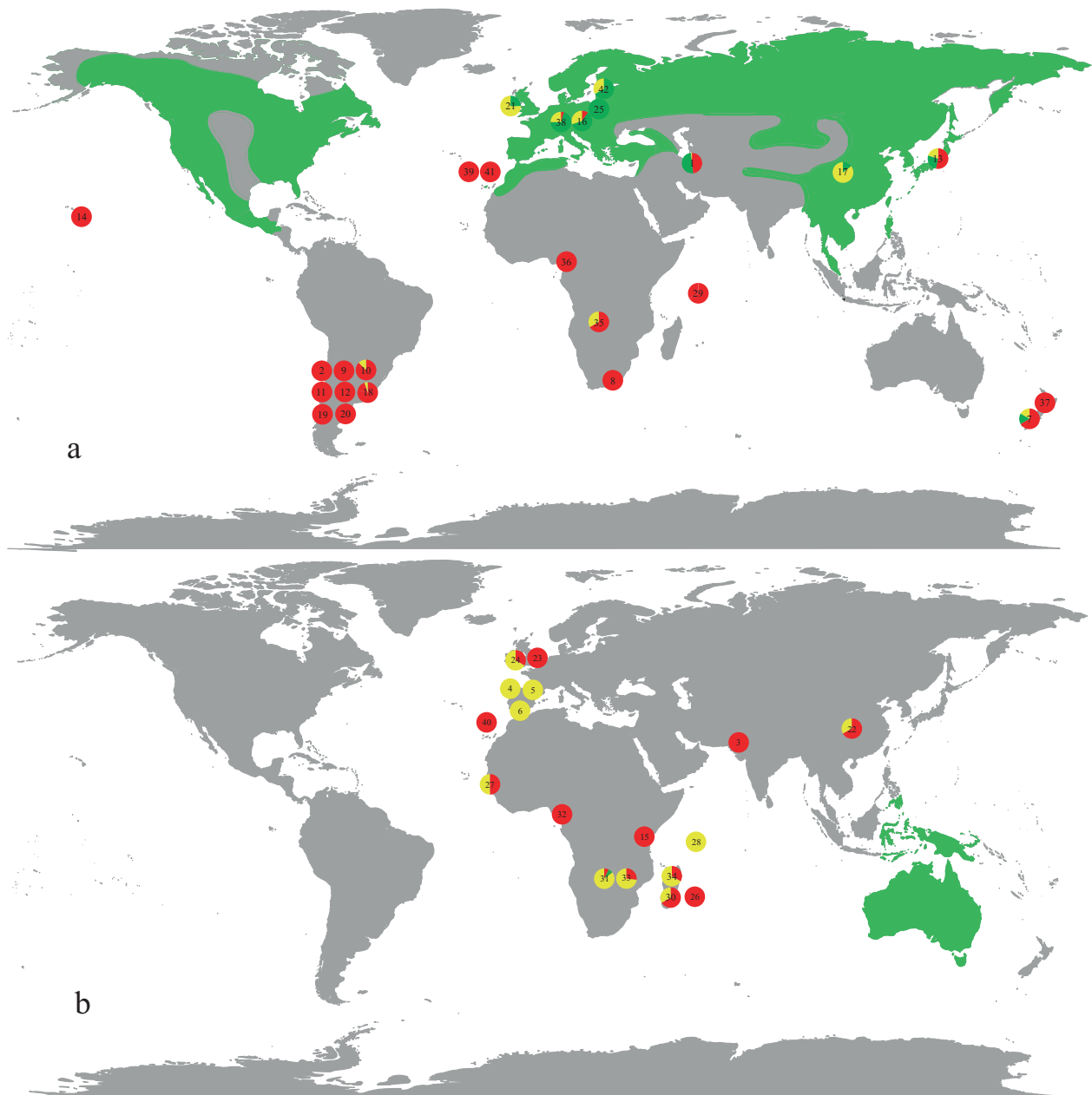


Fig. 1 Global distribution of analysed datasets of EcMF communities associated with alien Pinaceae and alien eucalypts. Global distribution of analysed datasets of EcMF communities (pie charts) associated with (a) alien Pinaceae and (b) alien eucalypts. Colors of the pie charts indicate share of the three strategies that alien EcM plants adapted to establish in new areas: interaction with co-introduced EcMF from their native range (red), association with EcMF which

naturally occur in both native as well as introduced regions of the host plant (green), and establishment of novel associations with native EcMF species (yellow; based on Dickie et al. [18] and Dickie et al. [19]). Native distribution ranges of Pinaceae and eucalypts are highlighted by green color based on Stevens et al. [99]. Numbers in the pie charts correspond to the ID of individual EcMF datasets (Table 1).

regions. Therefore, our study, which provides the most comprehensive overview of strategies that alien EcM plants adopted to establish a mycorrhizal partnership in regions to which they were introduced, represents a substantial step forward in understanding the mechanisms of EcM plant naturalization. The 42 analysed datasets of EcMF communities associated with alien EcM plants concern species of

the Pinaceae family and *Eucalyptus*. Yet, our study is of general interest not only due to its nearly global coverage, but also because these two groups represent the most widely introduced EcM plants worldwide [31, 44] including many highly invasive species [64].

The lack of mutualists represents one of the main hypotheses explaining failure of introduced tree species

Table 2 Distribution of strategies that alien Pinaceae adopt to associate with suitable EcMF in regions with no native Pinaceae spp.

EcM strategy	Regions without native Pinaceae	Regions with native Pinaceae
Co-introduction	125 ⁺	44 ⁻
Native to both areas	1 ⁻	98 ⁺
Novel interaction	4	24

Strategies that are significantly over- or under- represented in regions with or without native Pinaceae species compare with the proportion expected by chance (*G*-test, *p* value < 0.001) are marked by ⁺ indicating over- or under- representation within the group.

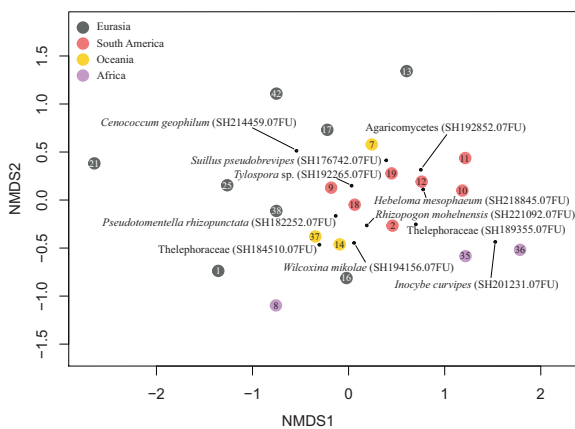


Fig. 2 Nonmetric multidimensional scaling (NMDS) plot of community composition of EcMF associated with alien Pinaceae. Symbols with numbers correspond to the individual datasets. Colors of the symbols indicate different geographical regions of origin. Black dots indicate positions of the most common EcMF in the ordination space. Stress value = 0.21. Numbers in the sample points correspond to the ID of individual EcMF datasets (Table 1).

[65, 66]. To overcome the barrier of obligatory symbiotic lifestyle, alien EcM plants are believed to rely on association with co-introduced EcMF from their native distribution range [15]. Although this mechanism was suggested by studies on alien EcM plant species from various regions (e.g., [12, 18, 21, 22]), we provide the first comprehensive test of this hypothesis on a global scale. We found that the occurrence of co-introduced EcMF on roots of alien EcM plants as well as their ability to form novel interactions with native EcMF differed among biogeographical regions as well as between the two studied plant groups. While Pinaceae introduced to sites without other native Pinaceae spp. relied upon interaction with co-introduced EcMF, native EcMF dominated on roots of alien Pinaceae on sites where other Pinaceae spp. naturally occur. Compared with the alien Pinaceae, the alien *Eucalyptus* spp. more often formed novel associations with native EcMF on sites of introduction. These observed patterns can be potentially explained by different level of specificity of EcMF communities of Pinaceae spp. (gymnosperms) and *Eucalyptus* spp. (angiosperms). While some

Pinaceae species are known to evince certain level of specificity by interacting with specific groups of EcMF [67–69], *Eucalyptus* spp. usually associate with more generalist EcMF communities [70]. Although previous case studies indicated that plant hosts with specialized and generalized EcMF communities rely upon association with co-introduced EcMF [21, 24], our global comparison of alien Pinaceae and *Eucalyptus* may indicate distinct pattern. However, to generalize our conclusions to all alien EcM plants, more data are needed particularly for alien EcM plants from other angiosperm families.

Although our study represents so far the most comprehensive comparison of EcMF associated with alien woody plants on a large spatial scale, many geographical regions are still largely undersampled. Numerous European Pinaceae spp. [71] as well as other EcM plants [40, 72] have been historically planted in North America. Similarly, *Eucalyptus* spp. were introduced to South America [25, 34], where they often spread into native vegetation [38]. Unfortunately, we lack information about EcMF communities associating with the above-mentioned alien plants from these regions. Similarly, more studies reporting EcMF communities from native vegetation from various biogeographical regions will largely increase precision of the native ranges of EcMF species.

EcMF associated with alien Pinaceae

Co-introduced EcMF dominated on alien Pinaceae roots in case the host plants were introduced into areas without any native Pinaceae species (e.g., Africa, Oceania and South America). Not surprisingly, this pattern was strongest in regions with no native EcM vegetation, such as Madeira (this study) and Hawaii [73] islands or South African fynbos vegetation [74]. Co-introduced EcMF also prevailed on roots of alien Pinaceae when the host plants were introduced to areas with native EcM vegetation formed by other than Pinaceae species. These cases were represented by introductions of Pinaceae spp. to Patagonia where natural vegetation is dominated by EcM *Nothofagus* spp. (e.g., [75, 76]), to Zambia, where large areas are still covered with EcM miombo forests [77] or to New Zealand with several native EcM tree species (e.g., [78]). Therefore, our study, in accordance with previous works (e.g., [12, 18]), shows comprehensive evidence that Pinaceae introduced to regions without naturally occurring Pinaceae associate almost exclusively with co-introduced EcMF.

EcMF communities associated with alien Pinaceae introduced to sites with and without native Pinaceae species showed only a limited overlap. Although these results are based on relatively small number of samples, we identified similarities among EcMF communities from South America and Oceania with only limited overlap with communities in

Africa. This pattern may be explained by differences in biogeographical origins of the alien Pinaceae species introduced to these regions. While all studied alien Pinaceae in South America and Oceania originated from the west coast of North America (*Pinus ponderosa*, *P. contorta*, *P. radiata*, and *Pseudotsuga menziesii*), the analysed alien Pinaceae in Africa were introduced from Mexico (*P. patula*) or Southeast Asia (*P. kesiya*). Therefore, we assume that the original distribution range represents the best predictor of EcMF communities associated with alien Pinaceae. Similar comigration patterns of host plant and mycorrhizal fungi were previously reported for postglacial expansion of *Tuber melanosporum* and oaks and hazelnuts [79], ancient migration patterns of *Alnus* spp. and associated EcMF [80] and comigration of Ericaceae spp. and their mycobionts from the Sebacilanes order [81].

Only very few co-introduced EcMF associated with alien Pinaceae on sites where other Pinaceae species naturally occur (e.g., Europe and Asia). In our dataset, *Rhizopogon salebrosus* represented the only known co-introduced EcMF species associated with roots of alien Pinaceae in Europe [82]. *R. salebrosus* was recently also found on roots of *P. strobus* and *P. menziesii* in Poland [83]. In case of introduction of North American *P. elliotii* into continental Asia, we did not find any associated co-introduced EcMF at all (Ning, unpublished). Clearly, alien species of Pinaceae introduced to the sites where other Pinaceae species naturally occur rather associated with native EcMF. Although the association between EcMF and certain Pinaceae spp. shows some specificity, the specificity at the plant species level is relatively low [67–69]. Therefore, the presence of distantly related plants from the Pinaceae family and their EcMF symbionts probably enables alien members of this family to enter novel associations in the regions of introduction. This observation corresponds to previously formulated hypothesis that phylogenetic distance between the alien plant and the native species in the community facilitates its integration into the community—phylogenetically closer aliens have to overcome weaker barriers to successful establishment [84, 85]. Similarly, alien species with traits similar to native species are more likely to successfully naturalize than those that are different [86]. The only exception from this general pattern represents dataset from Japan. There, we identified several co-introductions of EcMF associated with North American *P. strobus* (Hirose, unpublished). We speculate that this discrepancy can be explained by island biogeography, because it is generally assumed that islands are more prone to introductions of alien species [87].

EcMF communities associated with alien Pinaceae on sites where other Pinaceae species naturally occur were characterized by presence of the globally distributed *Cenococcum geophilum* complex [88] and differed from EcMF communities associated with Pinaceae from sites without any native Pinaceae. The only exception represented EcMF

community associated with alien *Pinus strobus* in Czechia [82]. In this particular case, EcMF community rather resembled those associated with Pinaceae introduced to sites without native Pinaceae vegetation. Importantly, the Czech dataset was obtained from a pot experiment, where seedlings of *P. strobus* were cultivated in forest soil from *P. strobus* dominated sites. Therefore, EcMF from soil spore bank dominated the *P. strobus* associated EcMF community developing in pot microcosms. The overlap of EcMF communities from the Southern Hemisphere with this particular dataset indicate that EcMF with stronger potential to regrowth from the soil spore bank prevail on roots of alien Pinaceae on sites without native Pinaceae species, as previously indicated [76].

Altogether, our study documented several factors which can influence the composition of EcMF communities associated with alien EcM plants on a large spatial scale. The information on the composition of EcMF communities associated with alien Pinaceae species is particularly important for prediction of the invasive potential of this important group of tree invaders. For example, Policelli et al. [16] recently indicated that one particular group of EcMF, the suilloid fungi, may trigger plant invasion. Besides that, composition of EcMF communities may largely affect ecosystem processes, such as carbon [89] or nutrient [90, 91] cycling.

EcMF associated with alien *Eucalyptus*

All studies focused on EcMF associated with alien *Eucalyptus* included in our metastudy were conducted in regions without native *Eucalyptus* spp. or any other EcM Myrta-ceae. When introduced to regions with native vegetation dominated by EcM plant species, such as miombo forest vegetation in Zambia [92], Madagascar, and Seychelles with several native EcM plant families [93], or temperate EcM forests in UK [94], the alien eucalypts were able to establish EcM symbiosis with native mycobionts. These observations indicate an ability of eucalypts to enter novel associations in various vegetation types. Eucalypts from commercial plantations in Spain were observed to associate exclusively with native EcMF and never with co-introduced EcMF (Calviño-Cancela, unpublished). This contradicts previous reports of alien EcMF (*Laccaria fraterna*, *Pisolithus albus*, and *P. microcarpus*) originating from Australia and previously described from eucalypt plantations in Spain [22]. Such discrepancy between results based on fruiting body survey and analysis of EcMF community composition on host roots is well known [95]. We assume that in our case the missing co-introduced EcMF on roots of alien eucalypts can be explained by low sampling effort of the root-associated EcMF communities. However, it might also indicate that the association with native EcMF is more

favorable for the establishment of the alien eucalypts than association with co-introduced mycobionts. The simultaneous association of eucalypts with both co-introduced and native EcMF was detected in several other datasets. It remains unknown how the association with co-introduced or native EcMF affects host plant physiology and establishment. The locally adapted native EcMF may be more mutualistic in the site-specific environmental conditions [96], while the co-introduced mycobionts may have more favorable effect on the host plants because of their long co-evolutionary history. Relative role of the native and co-introduced EcMF in the establishment of alien EcM plants remains an open but important question for future research.

The EcMF communities associated with alien *Eucalyptus* spp. showed very low overlap in species composition among the analysed datasets. Basically, almost no fungal species was found twice on roots of *Eucalyptus* spp. in our final dataset. The only exceptions are co-introduced *Scleroderma* spp., which were detected on roots of alien eucalypts in several independent studies [77, 94, 97]. The low overlap of the EcMF communities indicates random selection of mycobionts by alien *Eucalyptus* spp. from local species pools, whose compositions may largely differ among biogeographical regions [98]. This observation can be again explained by ability of some *Eucalyptus* spp. to interact with more generalist EcMF communities compared with the alien Pinaceae [70]. We assume that establishment and potential spread of alien *Eucalyptus* is less constrained by the lack of compatible mutualistic fungi than in case of alien Pinaceae.

Conclusions

To conclude, alien EcM plants from the Pinaceae family and the genus *Eucalyptus* differ in the probability of finding suitable mycorrhizal partners in new areas. While alien Pinaceae introduced to new regions rely upon association with co-introduced EcMF, alien *Eucalyptus* often form novel interactions with EcMF species native to the region where the plant was introduced. The region of origin primarily determines species composition of EcMF communities associated with alien Pinaceae in a new area, which may largely affect invasion potential of the alien plants.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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