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Research

Patterns of plant naturalization show that facultative mycorrhizal plants are more likely to succeed outside their native Eurasian ranges

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The naturalization of an introduced species is a key stage during the invasion process. Therefore, identifying the traits that favor the naturalization of non-native species can help understand why some species are more successful when introduced to new regions. The ability and the requirement of a plant species to form a mutualism with mycorrhizal fungi, together with the types of associations formed may play a central role in the naturalization success of different plant species. To test the relationship between plant naturalization success and their mycorrhizal associations we analysed a database composed of mycorrhizal status and type for 1981 species, covering 155 families and 822 genera of plants from Europe and Asia, and matched it with the most comprehensive database of naturalized alien species across the world (GloNAF). In mainland regions, we found that the number of naturalized regions was highest for facultative mycorrhizal, followed by obligate mycorrhizal and lowest for non-mycorrhizal plants, suggesting that the ability of forming mycorrhizas is an advantage for introduced plants. We considered the following mycorrhizal types: arbuscular, ectomycorrhizal, ericoid and orchid mycorrhizal plants. Further, dual mycorrhizal species were those that included observations of arbuscular mycorrhizas as well as observations of ectomycorrhizas. Naturalization success (based on the number of naturalized regions) was highest for arbuscular mycorrhizal and dual mycorrhizal plants, which may be related to the low host specificity of arbuscular mycorrhizal fungi and the consequent high availability of arbuscular mycorrhizal fungal partners. However, these patterns of naturalization success were erased in islands, suggesting that the ability to form mycorrhizas may not be an advantage for establishing self-sustaining populations in isolated regions. Taken together our results show that mycorrhizal status and type play a central role in the naturalization process of introduced plants in many regions, but that their effect is modulated by other factors.

Keywords: fungi, invasive plants, mutualism, mycorrhizal status, mycorrhizal type, plant establishment

Introduction

Understanding why some plant species are able to naturalize and become invasive while others fail is a fundamental question in ecology (van Kleunen et al. 2015). Of the total number of plant species introduced to a new region a small fraction becomes naturalized, and of these a small fraction becomes invasive (Williamson and Fitter 1996, Caley et al. 2008). Hence, the naturalization of a non-native species (i.e. when it establishes a self-sustainable population) is the first major filter in the invasion process of a species that has been introduced (Richardson et al. 2000a, b, Blackburn et al. 2011). Identifying the traits that favor naturalization success is key to understand why some plant species become invasive (Richardson and Pyšek 2012). It has been proposed that species that rely on mutualisms, such as on animal pollinators, are less likely to establish in new environments (Baker 1965, Baker 1974, Burns et al. 2011, Rodger et al. 2013, Razanajatovo et al. 2016). Another mutualism that could be vital during the naturalization stage of non-native plants is the mutualistic interaction between plants and mycorrhizal fungi (Smith and Read 2008, Richardson and Pyšek 2012, Dickie et al. 2017, Brundrett and Tedersoo 2018).

Plants vary widely in their associations with mycorrhizal fungi (i.e. the mycorrhizal status of a plant). Non-mycorrhizal plants do not associate with mycorrhizal fungi and, therefore, are completely independent of this mutualism. In contrast, functionally-obligate (hereafter 'obligate') mycorrhizal plants require associations with appropriate fungal partners to survive in natural ecosystems. Finally, facultative mycorrhizal plants form mycorrhizas but may, under some conditions, survive without mycorrhizas (Smith and Read 2008, Brundrett and Tedersoo 2018). Further, there are different types of mycorrhizas (i.e. mycorrhizal types): arbuscular mycorrhizas, ectomycorrhizas, orchid mycorrhizas and ericoid mycorrhizas (Brundrett 2009, Moora et al. 2011, van der Heijden et al. 2015, Brundrett and Tedersoo 2018). In addition, dual mycorrhizal plants are those that include individuals that associate with arbuscular mycorrhizal fungi, individuals that associate with ectomycorrhizal fungi, and individuals that associate with both (Harley and Smith 1983, Chilvers et al. 1987, Adjoud-Sadadou and Halli-Hargas 2017, Teste et al. 2019). When a plant species is introduced to a new region, its mycorrhizal type may affect the probability of finding suitable fungal partners (Nuñez and Dickie 2014).

Plants can naturalize in an introduced region without being limited by a lack of mycorrhizal fungi through different pathways (Nuñez and Dickie 2014). First, a plant may not depend on mycorrhizas by being a non-mycorrhizal or facultative mycorrhizal plant species (15% of all terrestrial plants) (Brundrett and Tedersoo 2018). Not depending on mycorrhizas makes it possible for these species to succeed in environments where they cannot find fungal partners (Nuñez and Dickie 2014). It has been proposed that in most situations mycorrhizal fungi are available and non-mycorrhizal plants are in disadvantage compared with mycorrhizal species (Richardson et al. 2000a, b). However, in some contexts these mutualistic interacions may be disrupted by the lack of symbionts (Dickie et al. 2017), for example in isolated islands (Carlquist 1974, Trøjelsgaard et al. 2015). Further, non-mycorrhizal plants may have a competitive advantage in highly disturbed locations (Delavaux et al. 2019). On the other hand, facultative mycorrhizal plants can succeed both in the absence of mycorrhizal fungi and also when these symbionts are available (Smith and Read 2008), which may enable facultative mycorrhizal species to take advantage in a broader context. Plants can also form novel associations with mycorrhizal fungi, either native or non-native symbionts (Dickie et al. 2010), although this may be difficult to assess because the native distribution of most fungi is poorly known (Pringle and Vellinga 2006). Novel associations have been found for ectomycorrhizal *Eucalyptus* (Tedersoo et al. 2007), and for ectomycorrhizal Pinaceae (Bahram et al. 2013, Moeller et al. 2015). Forming novel associations may also be possible for arbuscular mycorrhizal plants, as their fungal partners are mainly not host-specific (van der Heijden et al. 2015).

Non-native plants may also form associations with familiar (cosmopolitan) symbionts. For example, more than 40% of arbuscular mycorrhizal fungi have been suggested to have such cross-continental distribution (Moora et al. 2011, Stürmer et al. 2018, but see Bruns and Taylor 2016). In addition, plants can co-invade with the mycorrhizal fungi from its native range (Dickie et al. 2010). Co-invasion seems the most likely for ectomycorrhizal and orchid mycorrhizal plants, whose fungal partners can be host-specific (van der Heijden et al. 2015, Dickie et al. 2017). The dispersal ability of fungi, which is highly variable among fungal species (Peay et al. 2012), is particularly important for the co-invasion pathway because plants will only establish in locations where their fungal partners have dispersed. In this regard, it may be that many ectomycorrhizal fungal species disperse more readily than arbuscular mycorrhizal fungi because they produce fruiting bodies (sporocarps) which enhance fungal spore dispersal (Tedersoo et al. 2010), especially when these sporocarps are eaten by biotic dispersers (Nuñez et al. 2013, Wood et al. 2015). The number of possibilities available to different plant species varies according to their mycorrhizal status and type. In this regard, plants that rely more on mycorrhizas and that form specific mutualistic interactions with their fungal partners may be more limited when introduced to a new region and probably less likely to naturalize (Nuñez and Dickie 2014).

In this study we test the relationship between plant naturalization success and mycorrhizal status and type. Specifically, we build and analyse a database on mycorrhizal status (non-mycorrhizal, obligate mycorrhizal and facultative mycorrhizal) and type (arbuscular mycorrhizal, ectomycorrhizal, ericoid mycorrhizal, orchid mycorrhizal and dual mycorrhizal) for 1981 vascular plant species (covering 155 families and 822 genera) and match this record with data

on the most comprehensive database on naturalized alien plants (GloNAF) (van Kleunen et al. 2019). Since facultative mycorrhizal plants can succeed both in the absence of mycorrhizal fungi and also when these are available, we expect them to have higher naturalization success than obligate mycorrhizal and non-mycorrhizal species. Additionally, we ask whether mycorrhizal host specificity favors or hinders plant naturalization success. We predict that arbuscular mycorrhizal species, which are less host-specific (van der Heijden et al. 2015), have naturalized more than the other mycorrhizal types. Further, to assess the influence of land type on patterns of naturalization success we analyse our data for mainland regions and for island regions separately. We expect that on islands mycorrhizal plants will no longer have an advantage over non-mycorrhizal plants, due to the lower abundance of mycorrhizal plants and the lower availability of mycorrhizal fungi. Therefore, we expect that non-mycorrhizal plants will show higher naturalization success on islands.

Material and methods

Database

We compiled information on mycorrhizal status and mycorrhizal type from different sources: a database on mycorrhizal occurrence on vascular plant species across eastern Europe and north Asia (Akhmetzhanova et al. 2012), a database on mycorrhizal associations for plant species in central Europe (Hempel et al. 2013), a database on mycorrhizal associations for plants across Europe (Bueno et al. 2017) and a database on mycorrhizal occurrence on vascular plants from Europe and north Asia (Correia et al. 2018). We checked entries in several databases and their cited references to minimize errors. We included three mycorrhizal statuses: non-mycorrhizal, obligate mycorrhizal and facultative mycorrhizal. We classified each plant species into one mycorrhizal status according to observations of mycorrhizal associations (or the absence of mycorrhizal associations) directly on plant roots, at the individual plant level, following an approach repeatedly used in previous studies (Hempel et al. 2013, Bueno et al. 2017, Menzel et al. 2017, Correia et al. 2018). Non-mycorrhizal species were those that included only observations (on individual plants) of absence of mycorrhizal associations, and obligate mycorrhizal species were those that included only observations of mycorrhizal associations. Facultative species were those that included observations of mycorrhizal associations (either with arbuscular mycorrhizal or ectomycorrhizal fungi) as well as observations of absence of mycorrhizal associations. We considered a minimum of two independent observations for each mycorrhizal status (mycorrhizal associations and absence of mycorrhizal associations) to classify a species as facultative mycorrhizal in order to reduce the influence of observer errors. The number of species with observations of facultative ericoid mycorrhizal associations or facultative orchid mycorrhizal associations was too low to consider them in our analyses. It is important to note that these three mycorrhizal categories only indicate observed root colonization status and do not include information about functionality, such as mycorrhizal dependence. There were some cases of conflicting databases, which were caused by Correia et al. (2018) not including facultative ectomycorrhizal and dual mycorrhizal categories. In this regard, Correia et al. (2018) considered as obligate ectomycorrhizal plants those with observations of this mycorrhizal type, without any regard on facultative ectomycorrhizal species (ectomycorrhizal–non-mycorrhizal) or dual mycorrhizal species (arbuscular–ectomycorrhizal). Therefore, we checked every plant species classified as obligate ectomycorrhizal according to Correia et al. (2018) in their original data source and in other mycorrhizal databases to evaluate if any plant species was originally classified as facultative ectomycorrhizal or as dual mycorrhizal.

We considered five mycorrhizal types within the obligate mycorrhizal status: arbuscular mycorrhizal, ectomycorrhizal, ericoid mycorrhizal, orchid mycorrhizal and dual mycorrhizal (Smith and Read 2008, Moora 2014, Correia et al. 2018). Dual mycorrhizal species were those that included observations of arbuscular mycorrhizas as well as observations of ectomycorrhizas (at least two independent observations of each mycorrhizal type). The number of plant species with observations of dual mycorrhizal associations involving either ericoid or orchid mycorrhizal types was too low to consider them in our analyses. We standardized species names according to The Plant List (<www.theplantlist.org>) using the TPL function from the 'taxonstand' package (Cayuela et al. 2012) (Supplementary material Appendix 1 Table A1).

We use data on naturalization of vascular plant species from the GloNAF database ver. 1.2 (van Kleunen et al. 2019). The GloNAF database is the most comprehensive data source on naturalized vascular alien plant species. This database includes information of 13 939 taxa and 1029 regions, based on 210 data sources (van Kleunen et al. 2019). A region is defined here as the smallest geographic area for which a list of alien plant species is available. From the total number of regions a subset of 648 are considered as mainland regions and a subset of 381 as island regions. Both mainland and island regions vary widely in their surface area. Species names in the GloNAF database are already standardized according to The Plant List. We merged our database on mycorrhizal status and type with the GloNAF database. From the 3719 species in our mycorrhizal database 1981 were recorded as naturalized in at least one region according to the GloNAF database. For these 1981 species we calculated naturalization success as the number of regions where each species is reported to be naturalized. This would be an indicator of the tendency to spread, or invasiveness, of a plant species belonging to a particular group. We also calculated naturalization success as the area where each species is naturalized (adding up the areas of all the regions where the species is reported to be naturalized) to evaluate if we obtained the same patterns of naturalization success.

Statistical analyses

To test the relationship between plant naturalization success, and plant mycorrhizal status and type we used phylogenetic linear models. We fitted phylogenetic linear regressions using the 'phylolm' package (Ho and Ane 2014). Using phylogenetic regressions, we can run analyses accounting for phylogenetic relatedness between species to separate the effect of phylogeny from the effect of other predictive variables. To evaluate if patterns of naturalization success (as the number of naturalized regions) were affected by surface area differences among regions we repeated our analyses using the surface area where the species is naturalized. As predictive variables we used either mycorrhizal status or mycorrhizal type. We also included the number of references for each mycorrhizal status and type as a predictive variable to account for a possible bias in mycorrhizal databases. To evaluate if patterns of naturalization success differed between land types we repeated our analyses only considering mainland regions and only considering island regions. Finally, to test the effect of mycorrhizal status accounting for mycorrhizal type we used three different subsets of data: 1) arbuscular mycorrhizal plants, 2) ectomycorrhizal plants and 3) dual mycorrhizal plants. Within each subset we compared the naturalization success of obligate versus facultative mycorrhizal plants. In other words, we compared naturalization success (as the number of naturalized regions) of: 1) obligate arbuscular mycorrhizal plants versus facultative arbuscular mycorrhizal plants, 2) obligate ectomycorrhizal plants versus facultative ectomycorrhizal plants and 3) obligate dual mycorrhizal plants versus facultative dual mycorrhizal plants.

To fit these phylogenetic regressions we built a phylogenetic tree including the 1981 plant species included in both our mycorrhizal database and GloNAF database using a supertree for vascular plants constructed by Zanne et al. (2014), which was corrected and extended by Qian and Jin (2016). To build the phylogenetic tree we used the function 'S.PhyloMaker' implemented for the 'phytools' package (Revell 2012, Qian and Jin 2016). We tested for model assumptions and these were valid in all cases. We log transformed our response variable (either number of naturalized regions or naturalized area) to achieve normality, as recommended by Mundry (2014). We evaluated the homogeneity of variance for each model, checking that there was no clear pattern between model residuals and fitted values (Quinn and Keough 2002). In addition, none of the plant species in our dataset showed a Cook's distance over 1, which indicates the absence of influential cases (Cook and Weisberg 1982).

Mycorrhizal status datasets include errors at a rate estimated near 10% (Brundrett and Tedersoo 2018), which can have important implications for the results obtained from analyses based on such databases (Dickie et al. 2007). Of particular importance are biased sources of errors because these can have a strong influence on the results. One biased source of errors affecting classification of plant mycorrhizal status is the number of observations per plant species: plant species with more observations are more likely to be classified

as facultative mycorrhizal (Dickie et al. 2017). Facultative mycorrhizal plants can only be identified when the same plant species includes both observations of obligate mycorrhizal status and observations of non-mycorrhizal status (Smith and Read 2008). Therefore, plants with only one observation can only be obligate or non-mycorrhizal. On the other hand, plants with many observations are likely to be considered facultative mycorrhizal due to observation errors (Dickie et al. 2017). For example, an arbuscular mycorrhizal plant may be classified erroneously as non-mycorrhizal by a new observer and the probability of these errors increases with the number of observations.

Previous studies have either not corrected for errors, or have tested for sensitivity to errors by adding random noise to the final status assignment (Bueno et al. 2017). This approach fails to account for biases driven by increasing observation numbers. We suggest that directly including the number of references in statistical models is a robust approach to dealing with two sources of bias. To evaluate the presence of bias due to different number of observations per plant species in our database we fitted logistic regressions. We used the number of references (as proxy for number of observations) for each plant species as a predictive variable and the probability of being classified as facultative mycorrhizal as response variable. If the number of references increased the probability of being facultative we would have a biased source of errors. Moreover, plant species that have spread widely outside their native range would be more likely to be found in surveys and therefore would have more references. As a result, plant species that have spread more widely would be more likely to be classified as facultative mycorrhizal. To evaluate the effect of the number of references in the naturalization success (either the number of naturalized regions or the naturalized area) of plant species we directly included the number of references as a predictive variable in our phylogenetic linear regressions. Therefore, if we found that the number of references was a source of bias and that it affected the naturalization success of plants we could approach this issue by including the number of references as a predictive variable in our models. Then, the number of references for each plant species and the mycorrhizal status and type were the predictive variables, while the naturalization success was the response variable in our models. In this way we could evaluate the effect of mycorrhizal status and type, while accounting for the effect of number of references. We performed all analyses using R software ver. 3.5.1 (R Core Team).

Results

In our database the great majority of plant species formed mycorrhizas (80%), including 631 plant species (17%) classified as facultative mycorrhizal and 2358 plant species (63%) classified as obligate mycorrhizal. We classified 730 plant species (20%) as non-mycorrhizal (Supplementary material Appendix 1 Fig. A1a). The obligate mycorrhizal status included 1926 arbuscular mycorrhizal (82%), 250

ectomycorrhizal (11%), 92 orchid mycorrhizal (3%), 45 ericoid mycorrhizal (2%) and 45 dual mycorrhizal (2%) plant species (Supplementary material Appendix 1 Fig. A1b). The proportion of naturalized species that belong to each mycorrhizal status showed high variability among regions, from cases of 100% facultative mycorrhizal, to 100% obligate mycorrhizal and even a few cases where the only naturalized species were non-mycorrhizal (Fig. 1).

The proportion of plant species that have naturalized outside their native range varied greatly between different mycorrhizal statuses and types (Fig. 2). Regarding mycorrhizal status, 76% of facultative mycorrhizal, 52% of obligate mycorrhizal and 39% of non-mycorrhizal plants have become naturalized in at least one region (Fig. 2a). Regarding mycorrhizal type, 69% of dual mycorrhizal, 54% of arbuscular mycorrhizal, 45% of ectomycorrhizal, 38% of ericoid mycorrhizal and 16% of orchid mycorrhizal plants have become naturalized outside their native range (Fig. 2b). When considering mycorrhizal types within the facultative mycorrhizal status, 81% of facultative dual mycorrhizal species, 76% of facultative arbuscular mycorrhizal species and 64% of facultative ectomycorrhizal species have naturalized outside their native range (Fig. 2c).

According to the phylogenetic linear regressions (including the number of references per species as a predictive variable), the number of naturalized regions was highest for facultative mycorrhizal plants, 41% lower for obligate mycorrhizal plants (p = 0.0001) and 45% lower for non-mycorrhizal plants (p < 0.0001; Fig. 3a). When considering only mainland regions this pattern of naturalization success according to mycorrhizal status remained (Fig. 3b). However, when considering only island regions the differences between mycorrhizal statuses were reduced and only non-mycorrhizal plants showed lower naturalization success than facultative mycorrhizal plants (Fig. 3c). Regarding mycorrhizal type, the number of naturalized regions was highest for arbuscular mycorrhizal and dual mycorrhizal, and progressively lower for ectomycorrhizal, orchid mycorrhizal and finally ericoid mycorrhizal, in order (Fig. 4a). When considering only mainland regions this pattern of naturalization success according to mycorrhizal type remained (Fig. 4b). However, when considering only island regions we found no difference in the number of naturalized regions among mycorrhizal types (Fig. 4c). The probability that a plant species was classified as facultative mycorrhizal increased with the number of references per species (p < 0.0001). Furthermore, a higher number of references per species was correlated with higher number of naturalized regions (p = 0.0024; Table 1). Therefore, to account for both sources of bias we included the number of references per plant species in our regression models.

When comparing the naturalization success of obligate arbuscular mycorrhizal plants versus facultative arbuscular mycorrhizal plants, obligate ectomycorrhizal plants versus facultative ectomycorrhizal plants, and obligate dual mycorrhizal plants versus facultative dual mycorrhizal plants we found the following results: the number of naturalized regions was 37% higher for facultative arbuscular mycorrhizal than for obligate arbuscular mycorrhizal plants (p < 0.0001; Supplementary material Appendix 1 Fig. A2a), 56% higher for facultative ectomycorrhizal than for obligate ectomycorrhizal plants (p = 0.0238; Supplementary material Appendix 1 Fig. A2b) and we found no difference between facultative dual mycorrhizal and obligate dual mycorrhizal plants (p = 0.6364; Supplementary material Appendix 1 Fig. A2c). When considering only mainland regions these patterns of naturalization success (as the number of naturalized regions) remained constant. However, when considering only island regions we only found differences between facultative arbuscular mycorrhizal and obligate arbuscular mycorrhizal plants. We performed all the previous analyses using the naturalized area per plant species (calculated as the sum of the areas of the regions where the plant species was reported as naturalized) as response variable in our models and we found the same results as before (Supplementary material Appendix 1 Fig. A6–A8). Therefore, we can assume that the differences in the area of each region in our database is not introducing any bias into our results.

Discussion

Our results on this study show that plant naturalization success was affected by plant mycorrhizal status and type on mainland regions around the globe. Facultative mycorrhizal plants, which can grow without mycorrhizas but can also take advantage of this mutualism when their fungal partners are present (Smith and Read 2008, Moora 2014), were more successful outside their native range than both obligate mycorrhizal and non-mycorrhizal plant species. When compared within mycorrhizal types facultative mycorrhizal plants also showed higher naturalization success than obligate mycorrhizal plants (although not when comparing facultative dual with obligate dual mycorrhizal plants). Non-mycorrhizal plants showed the lowest naturalization success, which suggests that the ability of forming mycorrhizas is an advantage for introduced plants. However, other aspects of non-mycorrhizal plants, such as narrower ecological niches (Correia et al. 2018, Gerz et al. 2018), may be driving these results. Considering mycorrhizal types, naturalization success was highest for arbuscular mycorrhizal and dual mycorrhizal plants, as expected due to the lower host specificity of arbuscular mycorrhizal fungi (Smith and Read 2008, van der Heijden et al. 2015). On the other hand, these patterns of naturalization success were much less clear on island regions. A possible explanation is that isolated oceanic islands may lack mycorrhizal fungi due to dispersal limitations (Peay et al. 2012). Therefore, without their fungal partners, mycorrhizal plants may not have an advantage over non-mycorrhizal plants. Oceanic islands are also sites of high nutrient inputs via sea birds, which may reduce plant reliance on mycorrhizas (Otero et al. 2018).

Facultative mycorrhizal plants, that do not require mycorrhizal fungi, but have the capacity to form mycorrhizas
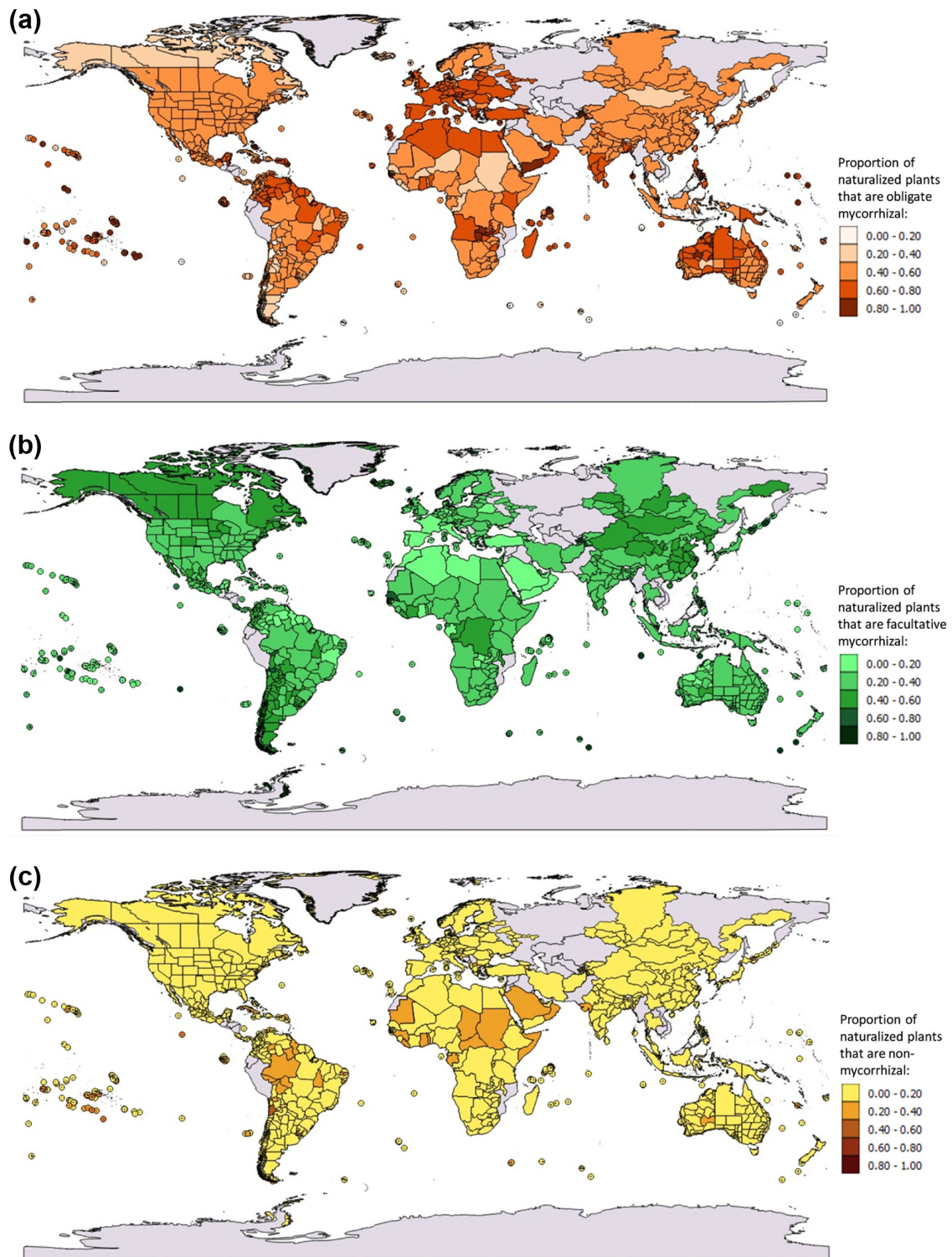
Figure 1. World map showing the proportion of naturalized species that are (a) obligate mycorrhizal, (b) facultative mycorrhizal and (c) non-mycorrhizal for all the regions included in our study. We colored each region according to a graded scale. In the case of small islands we used colored dots. Regions without data are grey.
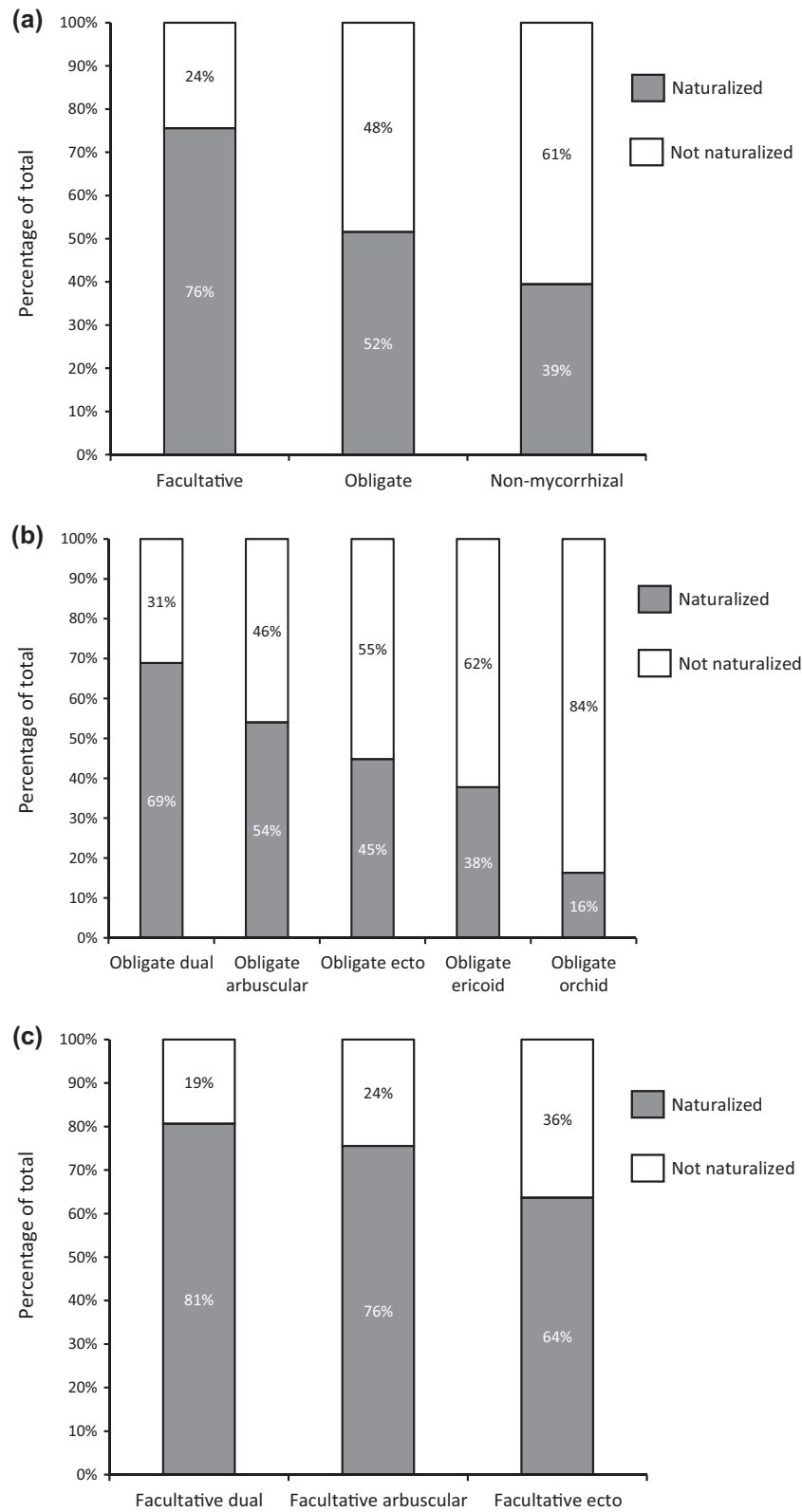
Figure 2. Percentage of species that have naturalized outside their native range and species that have not for each (a) mycorrhizal status: facultative mycorrhizal (n = 631), obligate mycorrhizal (n = 2358) and non-mycorrhizal (n = 730); (b) mycorrhizal types within the obligate mycorrhizal status: dual mycorrhizal (n = 45), arbuscular mycorrhizal (n = 1926), ectomycorrhizal (250), ericoid mycorrhizal (n = 45), orchid mycorrhizal (n = 92); and (c) mycorrhizal types within the facultative mycorrhizal status: dual mycorrhizal (n = 31), arbuscular mycorrhizal (n = 589) and ectomycorrhizal (n = 11).
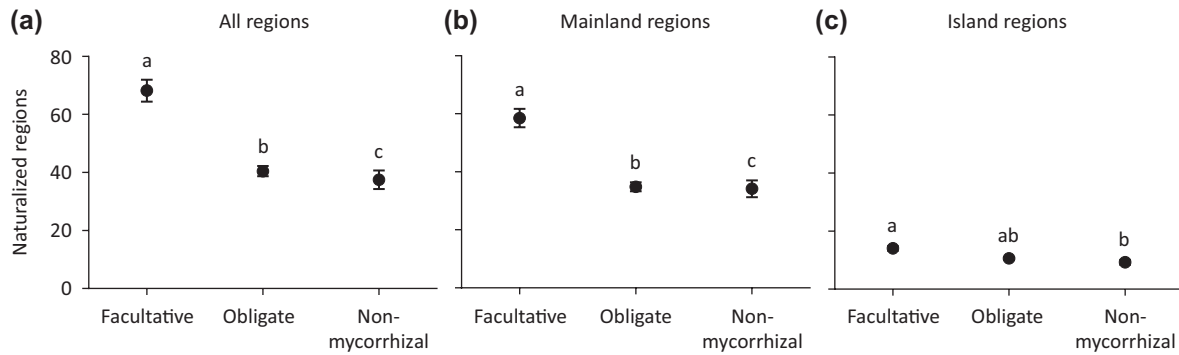
Figure 3. Mean number (±SE) of naturalized regions for plant species of different mycorrhizal status: facultative mycorrhizal, obligate mycorrhizal and non-mycorrhizal including (a) all regions, (b) mainland regions and (c) island regions. The letters indicate the results of comparisons using phylogenetic linear regressions. Same letters indicate values that are not significantly different after accounting for phylogenetic relatedness, the number of naturalized regions and the number of references for each species. Regression estimates (±95% CI) from our phylogenetic linear models including mycorrhizal status as predictive variable are given in Supplementary material Appendix 1 Fig. A3.

(Smith and Read 2008, Moora 2014), were the most successful outside their native range for both mainland and island regions. The wide geographic and ecological range of facultative mycorrhizal plants when compared with other mycorrhizal statuses (Hempel et al. 2013, Gerz et al. 2018) might explain why plants belonging to this mycorrhizal status are so successful. Indeed a wide native range size is a plant trait that has been frequently associated with plant naturalization success (Hanspach et al. 2008, Bucharova and van Kleunen 2009, McGregor et al. 2012, Procheş et al. 2012, Moodley et al. 2013, Maurel et al. 2016, Razanajatovo et al. 2016). Our results are in accordance with a recent study that found that facultative mycorrhizal plants are the most successful invaders in Germany, when compared with other mycorrhizal statuses (Menzel et al. 2017). Facultative mycorrhizal plants may have the capacity to establish sustainable

populations (naturalization) in new regions without their fungal partners (Smith and Read 2008). Further research on population dynamics with or without mycorrhizal fungi is needed to evaluate the mechanisms behind the success of facultative mycorrhizal plants outside their native range.

The mycorrhizal status with lowest naturalization success in mainland regions was non-mycorrhizal plants. Prior studies, reviewed by Pringle et al. (2009), have shown that a high proportion of naturalized plants are non-mycorrhizal. However, at a global level mycorrhizal plants represent the majority (60%) of naturalized species in mainland regions (Delavaux et al. 2019). Accordingly, we found that mycorrhizal plants, both facultative and obligate, were more successful than non-mycorrhizal plants on mainland regions. The mutualism with mycorrhizal fungi brings important benefits to the host plants: better access to water (Augé 2001),
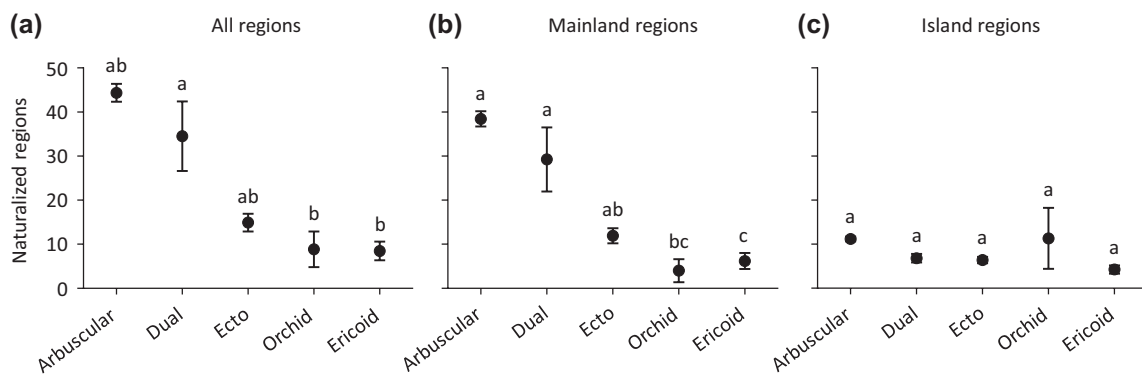

Figure 4. Mean number (±SE) of naturalized regions for plant species of different mycorrhizal types: arbuscular mycorrhizal, dual mycorrhizal, ectomycorrhizal, orchid mycorrhizal, ericoid mycorrhizal and orchid mycorrhizal including (a) all regions, (b) mainland regions and (c) island regions. The letters indicate the results of comparisons using phylogenetic linear regressions. Same letters indicate values that are not significantly different after accounting for phylogenetic relatedness, the number of naturalized regions and the number of references for each species. There are no significant differences between ericoid mycorrhizal plants and the other mycorrhizal types because ericoid mycorrhizal species all belong to the same family. For groups of low genetic variability, such as ericoid mycorrhizal plants, our phylogenetic model is not able to separate the effect of mycorrhizal type from the effect of phylogenetic relatedness. Something similar happens with orchid mycorrhizal plants, which include only two plant families. Regression estimates (±95% CI) from our phylogenetic linear models including mycorrhizal status as predictive variable are given in Supplementary material Appendix 1 Fig. A4.

Table 1. Parameters of the phylogenetic linear regression for number of naturalized regions according to mycorrhizal status (facultative, obligate and non-mycorrhizal), number of references and their interaction. Significant effects (p<0.05) are shown in bold letters. For the predictive variable mycorrhizal status, which has three levels, the reference level is facultative mycorrhizal (and is included in the intercept of the model). The effect of the other two levels (obligate and non-mycorrhizal) are shown on the table.

Predictive variables	Estimate	SE	t	p
References	0.0294	0.0097	3.0366	**0.0024**
Status_Obligate	−0.4662	0.1213	−3.8438	**0.0001**
Status_Non-mycorrhizal	−1.1186	0.1881	−5.9463	**< 0.0001**
References×Status_Obligate	0.0015	0.0116	0.1278	0.8983
References×Status_Non-mycorrhizal	0.2018	0.0798	2.5287	**0.0115**

nutrients (Smith and Read 2008, Delavaux et al. 2017) and protection from pathogens (Veresoglou and Rillig 2012, Delavaux et al. 2017). In this regard, the ability to form mycorrhizal associations can expand the realized niche of the host plants (Bruno et al. 2003, Rodriguez-Cabal et al. 2012, Hempel et al. 2013, Gerz et al. 2018) which helps mycorrhizal plants to thrive and dominate in many different habitat types around the world (Brundrett and Tedersoo 2018). Accordingly, non-mycorrhizal plants have narrower ecological niches than mycorrhizal plants (Correia et al. 2018, Gerz et al. 2018) and are successful in limited habitat types, particularly aquatic, dry, cold, saline, nutrient poor or disturbed habitats (Peat and Fitter 1993, Miller 2005, Brundrett 2009, Lambers and Teste 2013, Gerz et al. 2016, Swaty et al. 2016, Soudzilovskaia et al. 2017). On the other hand, previous studies have found a lower proportion of native plants that are mycorrhizal in island regions (Koske et al. 1992, Hemmes and Desjardin 2008, Delavaux et al. 2019) suggesting a mycorrhizal filter produced by geographic isolation (Delavaux et al. 2019). However, regarding naturalized plant species on islands at a global scale, more than 65% are mycorrhizal, suggesting that the human induced increase of mycorrhizal fungi dispersal has removed this mycorrhizal filter on islands (Delavaux et al. 2019). In accordance, we found that, on islands, facultative mycorrhizal plants were more successful than non-mycorrhizal plants.

Obligate arbuscular mycorrhizal plants were less successful than facultative arbuscular mycorrhizal plants outside their native range, on both mainland and island regions. The advantage of facultative arbuscular mycorrhizal plants over obligate arbuscular mycorrhizal plants is that the first can succeed in the absence of mycorrhizal fungi (Smith and Read 2008). However, given the low endemism of arbuscular mycorrhizal fungi (Davison et al. 2015, but see Bruns and Taylor 2016) and their low host specificity (van der Heijden et al. 2015) we expected that introduced obligate arbuscular mycorrhizal plants would be as successful as facultative arbuscular mycorrhizal plants. Our results suggest that introduced facultative arbuscular mycorrhizal plants have higher naturalization success (as the number of naturalized regions) than obligate arbuscular mycorrhizal plants. This would contradict the idea that introduced obligate arbuscular mycorrhizal plants are not limited by their fungal partners because most arbuscular mycorrhizal fungi have a cosmopolitan distribution and low host specificity (Richardson et al. 2000a, b, Pringle et al. 2009, Davison et al. 2015). A possible explanation for this pattern is that although there is no evidence of host specificity for arbuscular mycorrhizal fungi, there are many reports on arbuscular mycorrhizal fungi host preference and host selectivity (Sanders and Fitter 1992, Helgason et al. 1998, van der Heijden et al. 1998, Kiers et al. 2000, Klironomos 2000, Vandenkoornhuyse et al. 2003, Torrecillas et al. 2012) and many arbuscular mycorrhizal fungal species have restricted distributions (Bruns and Taylor 2016, Stürmer et al. 2018). We acknowledge that other traits, not considered in this study, are influencing the naturalization success of facultative and obligate arbuscular mycorrhizal plants (van Kleunen et al. 2007, Pyšek et al. 2015, Razanajatovo et al. 2016). Interestingly, we found no difference in the number of naturalized regions between facultative dual and obligate dual mycorrhizal plants. It may be that the flexibility of association with both arbuscular and ectomycorrhizal fungi gives dual mycorrhizal plants a significant advantage and the additional advantage of being facultative mycorrhizal has lower importance. For example, dual mycorrhizal plants can have higher nutrient uptake, and higher survival and growth when compared with obligate arbuscular or obligate ectomycorrhizal plants (Teste et al. 2019). Further, dual mycorrhizal plants may acquire the benefits from one mycorrhizal type in regions where fungal inoculum of the other mycorrhizal type is missing (Teste et al. 2019).

Dual mycorrhizal and arbuscular mycorrhizal plants were among the most successful mycorrhizal types in establishing across multiple ranges in mainland regions, but we found no evidence that they were more successful than ectomycorrhizal plants after correcting for phylogenetic independence. We would have expected that the lower host-specificity and wider geographical distribution of arbuscular mycorrhizal fungi (Pringle et al. 2009, Tedersoo et al. 2012, Davison et al. 2015, but see Bruns and Taylor 2016) would favor their naturalization success (as the number of naturalized regions) over that of ectomycorrhizal species. However, the naturalization success of ectomycorrhizal plants was not significantly lower, according to our models. One possibility is that the high dispersal ability of ectomycorrhizal fungi (Peay et al. 2012) compensates for the possible limitations of their higher host specificity (van der Heijden et al. 2015). Another possibility is that the wider ecological niche of ectomycorrhizal species favors their naturalization success (Gerz et al. 2018). Further, it could be that there are differences in naturalization success which are accounted for by plant traits related to phylogeny. For example, the great majority of ectomycorrhizal plants are

woody species. The lack of differences in naturalization success between mycorrhizal types in island regions may reflect that the presence of mycorrhizal fungi is unreliable on isolated regions. Therefore, without their fungal partners, arbuscular and dual mycorrhizal plants may not have an advantage over other mycorrhizal types.

Ericoid and orchid mycorrhizal plants were always in the lowest end of naturalization success outside their native range in mainland regions. One possible explanation is that these mycorrhizal associations are less geographically distributed than ectomycorrhizal associations (Soudzilovskaia et al. 2017). As a consequence, the availability of appropriate fungal partners for ericoid and orchid mycorrhizal associations may be more restricted geographically. Another possibility is that a higher specificity in the associations between orchid mycorrhizal plants and their fungal partners limits their establishment in new environments (Pyšek 1998, Dickie et al. 2017). Further, both ericoid and orchid mycorrhizal plants may have not been introduced to new regions with the same intensity and at such large scales as arbuscular or ectomycorrhizal plants. This lower introduction effort would inevitably reduce their probability of naturalization (Lockwood et al. 2005). Nonetheless, as each of these types is phylogenetically constrained to a single group, we cannot rule out non-mycorrhizal explanations linked to phylogeny.

Our results show that in mainland regions the facultative mycorrhizal status is positively associated with naturalization success. Indeed, facultative mycorrhizal plants, which can live in the absence of their fungal partners but also have the ability to take advantage of these symbionts were the most successful in mainland regions outside their native range. However, on island regions differences in naturalization success of plants with different mycorrhizal status or mycorrhizal type were eroded, possibly because of the unreliable presence of mycorrhizal fungi on isolated islands. The patterns of naturalization success that we show here can help understand why some plant species become naturalized outside their native range while others fail.

Data availability statement

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.hdr7sqvdg> (Moyano et al. 2020).

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Supplementary material (available online as Appendix ecog-04877 at <www.ecography.org/appendix/ecog-04877>). Appendix 1.