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Mycorrhizal status helps explain invasion success of alien plant species

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Abstract. It is still debated whether alien plants benefit from being mycorrhizal, or if engaging in the symbiosis constrains their establishment and spread in new regions. We analyzed the association between mycorrhizal status of alien plant species in Germany and their invasion success. We compared whether the representation of species with different mycorrhizal status (obligate, facultative, or non-mycorrhizal) differed at several stages of the invasion process. We used generalized linear models to explain the occupied geographical range of alien plants, incorporating interactions of mycorrhizal status with plant traits related to morphology, reproduction, and life-history. Non-naturalized aliens did not differ from naturalized aliens in the relative frequency of different mycorrhizal status categories. Mycorrhizal status significantly explained the occupied range of alien plants; with facultative mycorrhizal species inhabiting a larger range than non-mycorrhizal aliens and obligate mycorrhizal plant species taking an intermediate position. Aliens with storage organs, shoot metamorphoses, or specialized structures promoting vegetative dispersal occupied a larger range when being facultative mycorrhizal. We conclude that being mycorrhizal is important for the persistence of aliens in Germany and constitutes an advantage compared to being non-mycorrhizal. Being facultative mycorrhizal seems to be especially advantageous for successful spread, as the flexibility of this mycorrhizal status may enable plants to use a broader set of ecological strategies.

Key words: alien plants; biological invasion; Central Europe; functional traits; invasion stage; MycoFlor; mycorrhizal status; neophytes; trait interactions.

Introduction

With increasing concern about the effects of invasive alien plants on native plant species, communities and ecosystems, as well as the economic consequences of plant invasion (Vilà et al. 2010, 2011, Simberloff et al. 2013), there has been growing interest in studying the processes and mechanisms underlying successful invasion, including the role of species traits. Besides a set of functional plant traits known to promote invasion (Küster et al. 2010, van Kleunen et al. 2010, Knapp and Kühn 2012, Pyšek et al. 2015), an interest in mutualistic interactions and their influence on invasion success has emerged (Richardson et al. 2000*a*, Traveset and Richardson 2014). Next to pollination (Pyšek et al. 2011, Bezemer et al. 2014), the mycorrhizal symbiosis is the mutualistic interaction that attracted the attention of invasion ecologists (Reinhart and Callaway 2006, Pringle et al. 2009, Shah et al. 2009*a*, Bunn et al. 2015). Nevertheless, analyses using mycorrhizal traits to characterize plant species (Moora 2014) are still rare. Whereas experimental studies, which are mostly local in scale, report the majority of alien plant species to be mycorrhizal (Štajerová et al. 2009, Dickie et al. 2010, Moora et al. 2011, Nuñez and Dickie 2014), studies based on greater numbers of plant species report ambiguous results. Fitter (2005) found that alien plant species were more likely to belong to families that typically associate with mycorrhizal fungi, compared to the native flora of Great Britain. Pringle et al. (2009) reported an opposite pattern for alien plant species in California. Hempel et al. (2013) showed that neophyte plant species of Germany (i.e., those aliens species introduced after the year 1500; Pyšek et al. 2004) are more frequently obligate mycorrhizal compared to archaeophytes (introduced before the year 1500) and native species. Therefore, it is still debated

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whether alien plant species benefit from being mycorrhizal, or whether engaging in the symbiosis constrains their establishment and geographical spread in the new environment and region. A few case studies report positive impacts of the mycorrhizal symbiosis on the growth and development of alien plant species, resulting in a competitive advantage over native species (Fumanal et al. 2006, Sun and He 2010, Chmura and Gucwa-Przepiora 2012). In a meta-analysis conducted by Bunn et al. (2015), the authors did not find a positive correlation between arbuscular mycorrhizal (AM) colonization and growth response in invasive plants, but invasives were more colonized by mycorrhizal fungi, when grown in direct competition with natives. Additionally, the spread of alien plants may be inhibited if required specific fungal partners are not co-introduced (Pringle et al. 2009).

Relationships with mycorrhizal fungi are of great importance in shaping the ecology of plant species and communities (Hartnett and Wilson 2002, van der Heijden et al. 2003, Klironomos et al. 2011), including those invaded by alien species (Callaway et al. 2004, Hawkes et al. 2006). Incorporating plant mycorrhizal status and other mycorrhiza-related plant functional traits may thus help to provide further understanding of the establishment of alien plant species and their invasion success. Three groups of plant species can be distinguished according to their mycorrhizal status: (1) obligate mycorrhizal (OM) plant species that are always colonized by mycorrhizal fungi, (2) facultative mycorrhizal (FM) plant species that are colonized under some conditions but not others, and (3) non-mycorrhizal (NM) plant species that are never found to be colonized by mycorrhizal fungi (Smith and Read 2008, Moora 2014). It is important to note that plant mycorrhizal status and plant mycorrhizal dependency (or responsiveness) are distinct plant traits, not to be confused (Moora 2014). While mycorrhizal dependency depicts plant species growth responses under given conditions, mycorrhizal status does not give direct information about the functional significance of mycorrhizal colonization for plant individuals. It rather refers to the mere presence/absence of fungal colonization, and can be used as a proxy for estimating the potential importance of mycorrhizal symbiosis for plants at species level.

The mycorrhizal symbiosis potentially affects the nutrient uptake and C economy of plant species (van der Heijden et al. 2015). Depending on mycorrhizal type, mycorrhizal fungi can supply up to 90% of plant P uptake (Smith and Smith 2011) as well as a significant amount of plant N uptake (Hobbie and Hobbie 2008), and can consume up to 50% of a plant's net primary production (Hobbie and Hobbie 2008). Therefore, we expect trade-offs between mycorrhizal status and the expression of other plant traits, which require further plant investment, such as the development of morphological structures for storage, dispersal, or vegetative or sexual propagation (Onipchenko and Zobel 2000, Philip et al. 2001, Varga 2010). Küster et al. (2008) demonstrated that trait interactions help explain the invasion success of alien plants in Germany. However, these authors did not include mycorrhizal plant traits. Here we test for interactions between mycorrhizal status and other functional traits on neophyte invasion success in order to improve our understanding of potential ecological strategies involving the symbiosis.

Although Hempel et al. (2013) found that neophytes in the flora of Germany are more frequently OM in comparison with archaeophyte and native plant species, this cannot be used to make inferences about the role of mycorrhizal status in invasion success, as the importance of being mycorrhizal may change during the different stages of invasion (Shah et al. 2009*a*, Blackburn et al. 2011). In the present study, we aim to answer the following questions: (1) Does the relative frequency of different mycorrhizal statuses (OM, FM, NM) differ between groups of neophyte plant species at different stages of invasion in the German flora, i.e., (a) casual (non-naturalized) species, (b) species naturalized only in human-made habitats, and (c) species also naturalized in habitats with (semi)natural vegetation? (2) Do these groups of neophytes differ from archaeophyte and native plant species in the relative frequency of different mycorrhizal status categories? (3) Do certain combinations of mycorrhizal status and other functional plant traits underlie invasion success?

METHODS

Plant species distribution data were obtained from the 2003 version of FLORKART, a database of the German Network for Phytodiversity, provided by the German Federal Agency for Nature Conservation (*available online*[11]). For our analysis, we used a grid where the total area of Germany is divided into cells of 10′ longitude × 6′ latitude (arcminutes, i.e., ~130 km²) size, resulting in 2,995 grid cells. We used the number of occupied grid cells as a proxy for the invasion success of each particular neophyte. Therefore, this measure potentially ranges from 1 to 2,995 occupied grid cells.

Information on species status with respect to immigration time (i.e., native, archaeophyte, neophyte) and stage of invasion, i.e., (1) casual species that are not a permanent component of the flora and depend on the repeated supply of propagules by humans for their occurrence in the wild (Richardson et al. 2000*b*), (2) species naturalized only in human-made habitats, and (3) species also naturalized in habitats with (semi) natural vegetation, were obtained from BiolFlor (Klotz et al. 2002), as was information on plant functional traits (Table 1). In addition to the traits in BiolFlor, we used N fixation ability as a supplemental trait, since this trait also constitutes an important mutualistic symbiosis besides the formation of

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[11] http://www.floraweb.de

mycorrhizas. We assigned a “yes, N fixing” to all plant species of the *Fabaceae* family and genus *Alnus* and a “no, not N fixing” to all other plant species (Table 1). Plant functional traits were selected according to their potential to impose an energy cost, in terms of C and nutrients, on the plant species, which might be ameliorated (in the case of N or P) or exacerbated (in the case of C) by the symbiosis.

Information on mycorrhizal status for each plant species—OM, FM, or NM—was taken from the MycoFlor database (Hempel et al. 2013). In total, we analyzed the invasion success of 266 neophytes in the German flora: 64 plant species were casual, 112 naturalized only in human-made habitats, and 90 also naturalized in habitats with (semi)natural vegetation. Of the total number of neophytes considered, 180 were OM, 48 FM, and 38 NM. In turn, of the total number of mycorrhizal neophytes (OM and FM), 211 were arbuscular mycorrhizal, seven ectomycorrhizal, four ericoid mycorrhizal, and six were arbuscular and ectomycorrhizal. Besides mycorrhizal status, the availability of trait information differed among species for the other selected traits (Table 1). We did not analyze very rare attributes (trait values), which are those with <10 species per group. This resulted in different numbers of species per plant trait (Table 1).

Four questions were tested using *G* tests of goodness of fit with expected extrinsic frequencies (Sokal and Rohlf 1995): whether or not (1) neophyte plant species at different stages of invasion differ from neophytes collectively in terms of the relative frequency of different mycorrhizal status categories represented; (2) casual neophytes differ from neophytes naturalized in human-made and/or (semi)natural habitats; (3) casual neophytes differ from archaeophyte and native plant species; and (4) neophytes naturalized in human-made habitats and/or (semi) natural habitats differ from archaeophyte and native plant species.

As a second step, the number of grid cells occupied was used as response variable in models of neophyte invasion success, with plant mycorrhizal status and the additional selected plant traits as predictors. We used generalized linear models with a negative binomial error distribution to account for overdispersion and established a model for each of the functional plant traits, i.e., including the main effects of the functional trait and mycorrhizal status, along with their interaction. Due to their common evolutionary history, phylogenetically closely related species are more likely to be functionally similar compared to more distantly related species (Felsenstein 1985, Harvey and Pagel 1991). We took into account the phylogenetic relatedness of plant species using the phylogenetic tree DaPhnE provided by Durka and Michalski (2012). A modification of the approach of Bini et al. (2009), originally proposed to account for spatial dependencies, was used to incorporate phylogenetic relatedness within the generalized linear models. The triangular phylogenetic distance matrix was subjected to a principal coordinates analysis. The resulting eigenvectors that jointly explained at least 99% of the phylogenetic distance were regressed on the residuals of the models. Significant eigenvectors (i.e., phylogenetic filters) were then added as covariates to each particular model. Moreover, the distribution of alien plants is correlated with residence time: the longer a species is present in a region, the more propagules are spread and the probability of establishment and successful spread increases (Pyšek and Jarošík 2006, Williamson et al. 2009, Pyšek et al. 2015). To assure that our analysis was not confounded by the residence times of neophytes, we regressed species introduction time on their occupied geographical range. Information on the time of introduction was available for 130 of the 266

TABLE 1. Summary of selected plant functional traits for modeling invasion success in interaction with plant mycorrhizal status.

Functional trait	Value	No. species
Growth form	woody; non-woody	266
Storage organ (existence)	yes; no	266
Storage organ	none; pleiocorm; rhizome; runner; variable	239
Root metamorphoses (existence)	yes; no	266
Root metamorphoses	none; root shoot; primary storage root	262
Shoot metamorphoses (existence)	yes; no	266
Shoot metamorphoses	none; pleiocorm; rhizome; runner	238
Vegetative propagation and dispersal (existence)	yes; no	266
Vegetative propagation and dispersal	none; rhizome; runner; variable	226
Reproduction strategy	predominantly via seeds; seeds and vegetative; predominantly vegetative	266
Life span	annual; perennial; variable	260
Leaf persistence	summer green; overwintering green; persistent green	243
N fixation ability	yes; no	266

Notes: For details on traits (except N fixation ability) see Klotz et al. (2002). Pleiocorm: system of compact, perennial shoots occurring at the proximal end of the persistent primary root. Rhizome: transformed shoot growing subterraneously or close to the soil surface, mostly thickened with short internodes with adventitious roots. Runner: usually lateral shoots with long, thin internodes and adventitious roots; severance from the mother plant causes the formation of individual ramets. Traits referring to storage organs and shoot metamorphoses share most of their trait values but do not necessarily need to be the same, e.g., rhizomes can be shoots and storage organs but not every rhizome is a storage organ (see Appendix S1 for trait correlations).

species from BiolFlor (Klotz et al. 2002). Residence time did not significantly explain the number of grid cells occupied (Appendix S2). Differences in the mean number of occupied grid cells in Germany among the three mycorrhizal statuses within each attribute of the functional plant traits were tested with Tukey's honestly significant differences post hoc test (Tukey HSD). Furthermore, we conducted an outlier analysis using Cook's distance (Cook and Weisberg 1982) to see whether the model results changed if the plant species with the highest influence on the particular model outcomes were excluded from each particular analysis. We calculated Cook's distance for each of the established trait-interaction models and excluded all plant species with a Cook's distance greater than one while rerunning the particular model without them. Successive changes in significance levels are reported.

All statistical analyses were performed using the statistical software R (version 3.0.2, R Development Core Team 2013), in particular the packages ape (Paradis et al. 2004), lsmeans (Lenth 2016), MASS (Venables and Ripley 2002), and multcomp (Hothorn et al. 2008). Interaction plots were made with the help of ggplot2 (Wickham 2009).

RESULTS

Neophyte plant species at different stages of invasion did not differ from neophytes collectively in the relative frequency of different mycorrhizal statuses ($G = 2.5$, df = 6, $P = 0.87$, Appendix S3: Fig. S1); neither did casual neophytes differ from naturalized neophytes in this respect ($G = 1.44$, df = 2, $P = 0.49$, Appendix S3: Fig. S1). However, casual neophytes significantly differed in this respect from archaeophytes ($G = 7.24$, df = 2, $P = 0.03$, Appendix S3: Fig. S2) and native species ($G = 6.45$, df = 2, $P = 0.04$, Appendix S3: Fig. S2), in both cases by being more frequently OM and less frequently FM. Naturalized neophytes significantly differed from archaeophytes ($G = 13.9$, df = 2, $P < 0.01$, Appendix S3: Fig. S3) and native species ($G = 28.02$, df = 2, $P < 0.001$, Appendix S3: Fig. S3) by being more frequently OM and less frequently FM.

In a phylogenetically informed generalized linear model containing all 266 species, mycorrhizal status had a significant effect on the number of occupied grid cells (df = 2, deviance = 7.4, $P = 0.02$; Appendix S4). The subsequent post-hoc test revealed that FM neophytes occupied a significantly greater number of grid cells than NM neophytes ($P < 0.01$). Similarly, OM neophytes tended to occupy a greater number of grid cells than NM neophytes ($P = 0.08$), whereas FM and OM species did not differ in this respect ($P = 0.19$). Apart from growth form (df = 1, deviance = 7.7, $P < 0.01$), with grasses and herbs occupying a significantly greater number of grid cells than shrubs and trees, none of the functional plant traits significantly explained the number of occupied grid cells in a single-trait model (Appendix S4). However, we found significant interactions between mycorrhizal status and 9 out of 13 additional traits (Table 2).

The results of Tukey HSD post-hoc analysis revealed that neophytes with storage organs, shoot metamorphoses, or specialized structures promoting vegetative dispersal and propagation, occupied more grid cells if being FM (Fig. 1 and Table 3). In particular, rhizomatous FM species exhibited a positive association with the number of grid cells occupied. Among perennial and non-woody (i.e., herb and grass) species, FM plants were more successful. For woody species (shrubs and trees) and plant species with variable life span, OM neophytes occupied the highest number of grid cells. The same was true for neophytes with primary storage root as type of root metamorphoses (Fig. 1 and Table 3).

DISCUSSION

Our results indicate that being mycorrhizal promotes the invasion success of neophyte plant species in Germany. This is supported by FM neophytes showing a significantly higher invasion success than NM plant species, and OM neophytes tending toward higher invasion success compared to NM species. Moreover, our study is one of the first to demonstrate the significance of interactions between mycorrhizal status and plant functional traits related to morphology, reproduction and life history, in explaining invasion success. We found significant interactions between neophyte mycorrhizal status and 9 out of 13 functional plant traits. This emphasizes the importance of mycorrhizal status in understanding alien plant invasion. Although neophytes are more likely OM than natives and archaeophytes in Germany (Hempel et al. 2013), this mycorrhizal status does not particularly promote invasion success. OM and FM neophytes did not differ in terms of occupied geographical range. However, in interaction with other functional traits, being FM appears to promote invasion success (Table 3). We conclude that being mycorrhizal (OM or FM) is important for the establishment and persistence of neophytes in a new environment and constitutes a competitive advantage compared to NM plants, especially in the early stage of invasion. Being FM seems to be advantageous for persistence and allowing successful spread across a large geographical range, as the flexibility of FM plants may enable a broader set of ecological strategies. This is supported by our finding that the relative frequency of different mycorrhizal statuses did not differ among neophytes at different stages of invasion (casuals against naturalized neophytes, Appendix S3: Fig. S2), but did differ between neophytes and both archaeophytes and natives, which both showed higher proportions of FM plant species (Appendix S3: Fig. S2).

Seedling establishment is promoted by the presence of mycorrhizal fungal symbionts (van der Heijden 2004, Wurst et al. 2011, Koorem et al. 2012). Following establishment, alien plants that are mycorrhizal potentially have immediate access to common mycorrhizal

TABLE 2. Results of phylogenetically informed generalized linear models explaining the number of occupied grid cells as a proxy for invasion success.

Variable	df	Deviance	P	P*
Growth form				
Growth form	**1**	**5.9**	**0.01**	<0.001
Mycorrhizal status	**2**	**7.5**	**0.02**	0.006
Growth form × mycorrhizal status	**2**	**6.8**	**0.03**	0.008
Storage organ (existence)				
Storage organ (existence)	1	0.4	ns	ns
Mycorrhizal status	**2**	**7.8**	**0.02**	0.001
Storage organ (existence) × mycorrhizal status	**2**	**9.8**	**0.007**	<0.001
Storage organ				
Storage organ	4	5.8	ns	ns
Mycorrhizal status	**2**	**10.1**	**0.006**	0.01
Storage organ × mycorrhizal status	**8**	**17.5**	**0.03**	ns
Root metamorphoses (existence)				
Root metamorphoses (existence)	1	0.2	ns	ns
Mycorrhizal status	**2**	**7.4**	**0.02**	0.02
Root metamorphoses (existence) × mycorrhizal status	2	0.9	ns	ns
Root metamorphoses				
Root metamorphoses	2	0.5	ns	ns
Mycorrhizal status	2	5.5	ns	ns
Root metamorphoses × mycorrhizal status	**4**	**9.8**	**0.04**	ns
Shoot metamorphoses (existence)				
Shoot metamorphoses (existence)	1	0.2	ns	ns
Mycorrhizal status	**2**	**7.8**	**0.02**	0.002
Shoot metamorphoses (existence) × mycorrhizal status	**2**	**12.5**	**0.002**	<0.001
Shoot metamorphoses				
Shoot metamorphoses	3	0.8	ns	ns
Mycorrhizal status	**2**	**8.6**	**0.01**	0.01
Shoot metamorphoses × mycorrhizal status	**6**	**13.5**	**0.04**	0.02
Vegetative dispersal (existence)				
Vegetative dispersal (existence)	1	0.3	ns	ns
Mycorrhizal status	**2**	**7.6**	**0.02**	<0.001
Vegetative dispersal (existence) × mycorrhizal status	**2**	**9.5**	**0.009**	<0.001
Vegetative dispersal				
Vegetative dispersal	3	2.9	ns	ns
Mycorrhizal status	**2**	**7**	**0.03**	0.02
Vegetative dispersal × mycorrhizal status	**6**	**19.2**	**0.004**	0.004
Reproduction strategy				
Reproduction strategy	2	1.2	ns	ns
Mycorrhizal status	**2**	**7.6**	**0.02**	0.002
Reproduction strategy × mycorrhizal status	4	9.3	ns	0.02
Life span				
Life span	2	1.2	ns	ns
Mycorrhizal status	**2**	**7**	**0.03**	0.02
Life span × mycorrhizal status	**4**	**15.4**	**0.004**	<0.001
Leaf persistence				
Leaf persistence	2	4.7	ns	ns
Mycorrhizal status	**2**	**6.9**	**0.03**	ns
Leaf persistence × mycorrhizal status	4	2.5	ns	ns
N fixation ability				
N fixation ability	1	0	ns	ns
Mycorrhizal status	**2**	**7.4**	**0.02**	0.002
N fixation ability × mycorrhizal status	2	1.6	ns	ns

Note: Error probabilities are displayed (P, with, P*, without outliers identified using Cook's distance [Cook and Weisberg 1982]) for the main effect of mycorrhizal status, the main effect of the corresponding additional selected plant trait, and their interaction for each trait–interaction model. Rows in boldface type highlight an error probability $P \leq 0.05$; ns, not significant.

networks (Barto et al. 2012). They may profit from additional nutrient (Koide 1991) and water availability (Augé 2001) at relatively low energy cost compared to non-mycorrhizal seedlings. Hence, mycorrhizal alien plant species may obtain a competitive advantage compared to non-mycorrhizal alien plant species. By mediating seedling survival of introduced species, mycorrhizal fungi have the potential to determine whether an alien plant species persists until a second factor occurs (e.g., disturbance) that weakens the competitive strength of natives (Hobbs and Huenneke 1992) and may allow successful spread.

FM neophytes show a significantly higher invasion success compared to NM and OM neophytes when the comparison is made between species with additional morphological structures for storage, propagation and dispersal as well as rhizomatous species or species with longer life span (Fig. 1 and Table 3). This suggests that

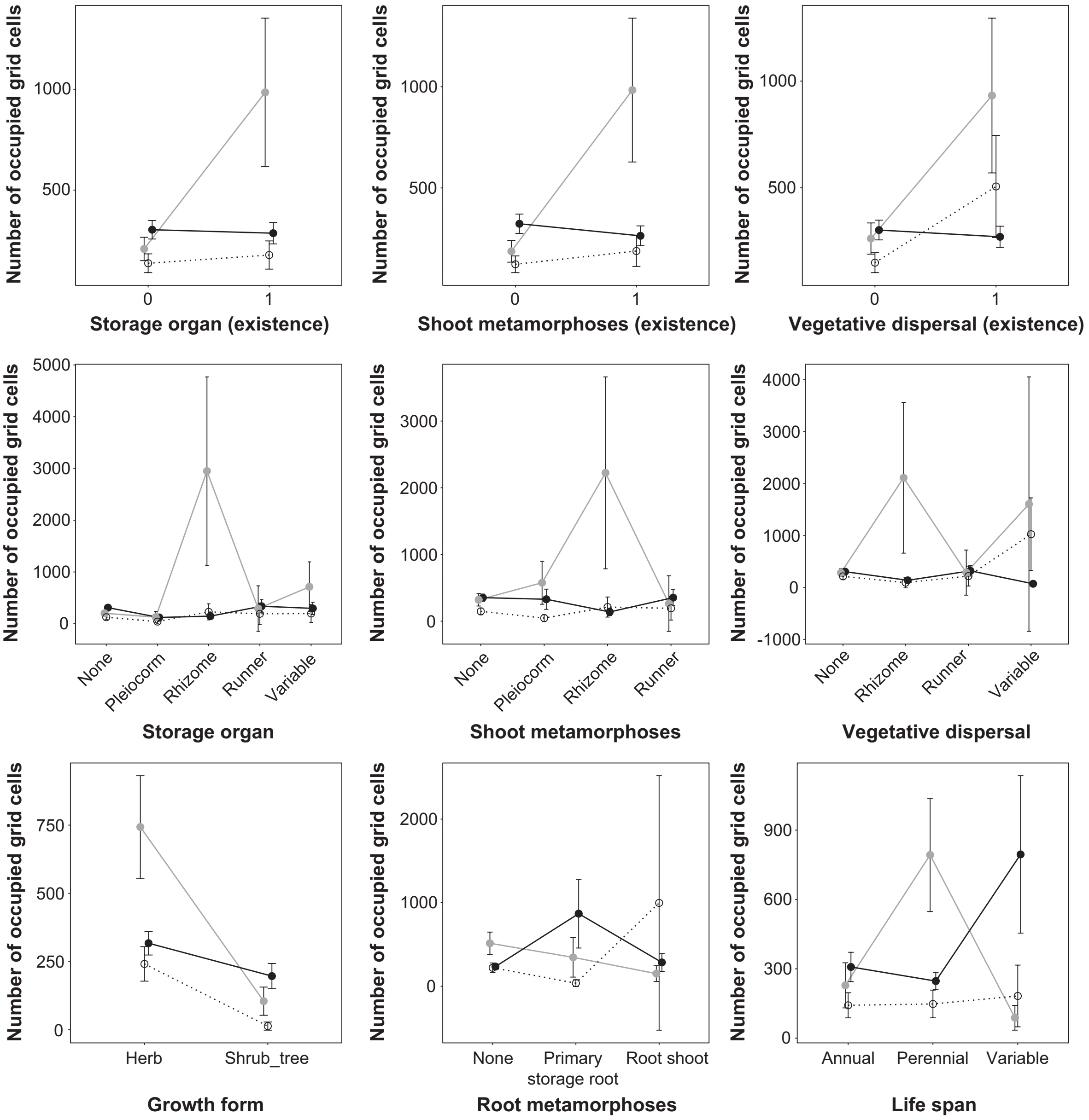

FIG. 1. Interaction plots for significant two-way interactions between mycorrhizal status and the shown plant functional traits (Table 2); obligate mycorrhizal (OM) plant species, solid black line and black circles; facultative mycorrhizal (FM) plant species, solid gray line and gray circles; non-mycorrhizal (NM) plant species, dotted line and open circles. Displayed are the least-squares means (±SE) per each trait value interaction. Traits referring to storage organs and shoot metamorphoses share most of their trait values but do not necessarily need to be the same, e.g., rhizomes can be shoots and storage organs but not every rhizome is a storage organ (see Appendix S1 for trait correlations).

Table 3. Results of the Tukey post hoc test following the generalized linear models explaining the number of occupied grid cells; only plant functional traits that showed significant interaction effects with mycorrhizal status are displayed (Table 2).

Traits	Mycorrhizal status		
	OM	FM	NM
Growth form			
Non-woody	−	+	−
Woody	+	NS	−
Storage organ (existence)			
Yes	−	+	−
No	NS	NS	NS
Storage organ			
None	NS	NS	NS
Pleiocorm	NS	NS	NS
Rhizome	−	+	−
Runner	NS	NS	NS
Variable	NS	NS	NS
Root metamorphoses			
None	−	+	NS
Primary storage root	+	−	NS
Root shoot	NS	NS	NS
Shoot metamorphoses (existence)			
Yes	−	+	−
No	NS	NS	NS
Shoot metamorphoses			
None	NS	NS	NS
Pleiocorm	NS	NS	NS
Rhizome	−	+	−
Runner	NS	NS	NS
Vegetative propagation and dispersal (existence)			
Yes	−	+	NS
No	NS	NS	NS
Vegetative propagation and dispersal			
None	NS	NS	NS
Rhizome	−	+	−
Runner	NS	NS	NS
Variable	−	NS	+
Life span			
Annual	NS	NS	NS
Perennial	−	+	−
Variable	+	−	NS
Number of positive associations	3	9	1

Notes: OM, obligate mycorrhizal; FM, facultative mycorrhizal; NM, non-mycorrhizal. A plus sign indicates a significantly higher, and a minus sign a significantly lower, number of occupied grid cells between categories of mycorrhizal status within each row of the table (Freeman Tukey test; $P < 0.05$). NS marks nonsignificant differences, i.e., no significant differences were found to any of the other mycorrhizal statuses. The last row gives the sum of the positive associations in terms of occupied grid cells for all 27 mycorrhizal status × plant trait level combinations. Pleiocorm: system of compact, perennial shoots occurring at the proximal end of the persistent primary root. Rhizome: transformed shoot growing subterraneously or close to the soil surface, mostly thickened with short internodes with adventitious roots. Runner: usually lateral shoots with long, thin internodes and adventitious roots; severance from the mother plant causes the formation of individual ramets. Traits referring to storage organs and shoot metamorphoses share most of their trait values but do not necessarily need to be the same, e.g., rhizomes can be shoots and storage organs but not every rhizome is a storage organ (see Appendix S1 for trait correlations).

flexibility of C investments can be a crucial advantage for FM neophytes that exhibit these high energy cost characteristics. Assuming that FM plant species are able to regulate their mycorrhizal association with changing abiotic or biotic conditions (Grman 2012, Grman et al. 2012), for example, such that mycorrhiza is reduced if C is limiting, this may allow plants to pursue different strategies depending on the prevailing conditions. Hence, FM neophytes are more likely than NM or OM neophytes to possess a versatile range of ecological strategies, as OM and NM neophytes lack flexibility in their mycorrhizal association. Additionally, this potentially explains the results of Hempel et al. (2013), who demonstrated that FM species in general show wider ecological amplitudes and occupy larger geographical ranges. However, the (nutritional or other) benefits gained from the symbiosis seem to exceed the (C) costs, as our results indicate that OM neophytes occupy a larger geographical range than NM neophytes. Nevertheless, further investigation is needed to understand the physiological mechanisms underlying the trade-offs as well as the ability of FM plant species to modify their mycorrhizal association depending on local abiotic and biotic conditions.

The great majority of mycorrhizal neophytes in our analysis are involved in an AM relationship (93%), indicating that mycorrhizal type may also influence the establishment of neophyte plant species. The AM symbiosis is relatively non-specific in terms of both plant and fungal partners (Moora et al. 2011) and taxa of AM fungi are known to be globally distributed (Davison et al. 2015). Contrary to ectomycorrhizal plants, for which the lack of symbionts is believed to act as a barrier (Richardson et al. 2000*a*, Nuñez et al. 2009), the availability of a fungal partner should not constrain the establishment in new environments of alien plants engaged in an arbuscular mycorrhiza. Nevertheless, the numbers of ectomycorrhizal and ericoid plant species considered here were too few to conduct an additional analysis to gain insights into differences between neophytes associated with different mycorrhizal types.

Further insights may be obtained by investigating neophytes that belong to the *Arum* or *Paris* structural type of the AM symbiosis (Smith and Smith 1997, Dickson et al. 2007). Alien plants that are AM are more often from the *Arum* than the *Paris* type (Shah et al. 2009*b*, Majewska et al. 2015). Ahulu et al. (2005) reported a higher proportion of plants with the former rather than the latter type in early successional stages, which indicates functional differences among the two types. Nevertheless, these differences are little understood, especially concerning nutrient transfer, and data on AM structural type is still patchy and mostly available at the family level only (Dickson et al. 2007). However, if data availability increases, future analyses incorporating AM structural type will deepen our knowledge of the interplay between mycorrhizal status and other plant functional traits in explaining the invasion success of alien plants.

Mycorrhizal symbioses are known to function along a mutualism–parasitism continuum (Johnson et al. 1997), and Klironomos (2003) even demonstrated that the plant response to AM fungi varies with the geographic match of plant and fungal species. Nevertheless, studies addressing the continuum typically investigated single plant and fungal individuals. At the plant community level and under natural conditions it is most likely that plants interact mainly with mycorrhizal fungi that optimize their fitness (Bever et al. 2009, Kiers et al. 2011), as reflected in the higher number of occupied grid cells by OM and FM compared to NM species (Fig. 1). However, the fact that FM species are more successful in terms of geographic spread compared to OM species, indicates that in conditions where the benefits of the symbiosis are slight (e.g., in high soil nutrient concentrations), the obligate costs imposed on OM species might shift the symbiosis into the direction of parasitism (Johnson et al. 1997). Additionally, the invasion success of alien plant species can be influenced by the neighboring plants' functional group identity (Bunn et al. 2015) as well as the neighboring plants' species identity (Callaway et al. 2001, 2003). Some authors even suggest that invasion by alien plants is contingent upon neighbor identity (Shah et al. 2008). However, at our chosen scale with a grid cell size of ~130 km², it is impossible to disentangle which plants grow in the immediate neighborhood of the selected neophytes and this fact made it impossible to incorporate the existence of any neighboring effects.

Our findings appear transferable to other regions in Europe, as Fitter (2005) found that alien plant species disproportionally represented plant families that typically associate with mycorrhizal fungi, compared to the native flora of Great Britain, which is similar to the starting point of our analysis. The contrasting conclusions of Pringle et al. (2009) concerning alien plants in California might reflect the different evolutionary histories of the respective alien floras, and especially the strong and long-term exposure of aliens of European origin to intensive agriculture (i.e., North American aliens; La Sorte and Pyšek 2009, Seifert et al. 2009). However, the different conclusions may also reflect aspects of the data and analysis (including the availability of mycorrhizal trait information) that differed between this study and that of Pringle et al. (2009). Thus, it remains to be fully established whether or not the findings of our study apply to this and other geographical regions. Moreover, additional investigation is needed to disentangle why many more neophytes in Germany are OM and not FM (Hempel et al. 2013), although they do not significantly differ in their invasion success. A qualitative difference in mycorrhizal responsiveness between OM and FM species, especially in the stage of seedling establishment, may be one possible explanation. Additionally, the trait models would certainly benefit from accounting for the abundance of plant species. Using presence/absence data, rare species disproportionally influence the models. Unfortunately, such abundance data are not available, although FLORKART (provided by the German Federal Agency for Nature Conservation) is one of the best documented databases of regional plant distributions.

Although the mycorrhizal symbiosis has long been a focus for invasion biologists (Richardson et al. 2000*a*, Reinhart and Callaway 2006, Pringle et al. 2009, Shah et al. 2009*a*, Bunn et al. 2015), we do not know of any study combining plant mycorrhizal status with other plant functional traits. Therefore, we encourage the consideration of mycorrhizal status and related mycorrhizal plant traits in future analyses of alien plant invasion success. Such analyses would further benefit if root traits are included (Maherali 2014, Yang et al. 2015), the traits of mycorrhizal fungi are conceptualized (Öpik and Moora 2012, Aguilar-Trigueros et al. 2014, 2015, Koide et al. 2014) and interactions with other factors such as above- and belowground herbivory are taken into account (Barto and Rillig 2010, Kempel et al. 2013). This will enhance our functional understanding of alien plant invasion and will provide a fruitful context for understanding the role of the mycorrhizal symbiosis.

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