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Research

Widely distributed native and alien plant species differ in arbuscular mycorrhizal associations and related functional trait interactions

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It is debated whether alien plants in new environments benefit from being mycorrhizal and whether widely distributed natives and aliens differ in their associations with mycorrhizal fungi. Here, we compared whether species differing in their origin status, i.e. natives, archaeophytes (alien species introduced before the year 1500) and neophytes (introduced after the year 1500), and arbuscular mycorrhizal (AM) status (obligate, facultative, non-mycorrhizal) differ in their area of occupancy in Germany (i.e. number of occupied grid cells, each ~130 km²). We used generalized linear models, incorporating main effects and up to three-way interactions combining AM status, origin status and plant functional traits. The latter were chosen to describe the possible trade-off in carbon allocation either towards the symbiosis or to other plant structures, such as storage organs (significant interactions involving traits were assumed to indicate the existence of such trade-offs). AM status significantly explained the area of occupancy of natives and neophytes – with facultative mycorrhizal species occupying the largest area in both groups – but was less pronounced among archaeophytes. Archaeophytes may have reduced dependency on AM fungi, as they are generally agricultural weeds and the symbiosis potentially becomes obsolete for plants growing in habitats providing a steady provision of nutrients. Trait interactions between AM status and other functional traits were almost exclusively detected for neophytes. While facultative mycorrhizal neophytes benefit from trade-offs with other traits related to high C cost in terms of area of occupancy, such trade-offs were almost absent among natives. This indicates that natives and neophytes benefit differently from the symbiosis and suggests that native AM fungal partners might be less important for neophytic than for native plant species or that more time is required to establish similar relationships between neophytes and native fungal symbionts.

Keywords: alien plants, arbuscular mycorrhiza, central Europe, MycoFlor, mycorrhizal status, origin status, trait interactions



Introduction

Numbers of alien plant species have been increasing in floras around the world (van Kleunen et al. 2015), and interest in the processes and mechanisms underlying the successful establishment and spread of aliens in new environments has emerged in parallel (Richardson and Pyšek 2012). The invasion success of alien plant species depends, amongst other things, on their functional traits (i.e. invasiveness; Küster et al. 2008, Pyšek et al. 2009) and the susceptibility of ecosystems (invasibility; Chytrý et al. 2008a, b). There is now increasing interest in including biotic interactions (Mitchell et al. 2006), particularly mutualistic associations (Richardson et al. 2000, Traveset and Richardson 2014), into frameworks assessing alien plant invasions, as they help bridge the invasibility (facilitated or inhibited by mutualists of the receiving habitat, e.g. mycorrhizal fungi) and invasiveness (exerted by introduced mutualists, e.g. alien plants) features. The great majority of terrestrial plant species are associated with arbuscular mycorrhizal (AM) fungi (Smith and Read 2008, Brundrett 2009), and these appear to be important in shaping the ecology of plant species and communities (van der Heijden et al. 2003, Callaway et al. 2004, Klironomos et al. 2011). The role of the AM symbiosis during the alien plant invasion process has consequently gained increasing attention (Fitter 2005, Pringle et al. 2009, Shah et al. 2009, Bunn et al. 2015, Menzel et al. 2017, Reinhart et al. 2017). Investigating these links has been facilitated by the publication of comprehensive data sets compiling information on plant mycorrhizal associations (Wang and Qiu 2006, Akhmetzhanova et al. 2012, Hempel et al. 2013) and the recognition of plant mycorrhizal traits, including mycorrhizal status (Moora 2014).

Three categories of plant species can be distinguished according to the frequency of occurrence of AM symbiosis among individuals of each species, i.e. their AM status: 1) obligate mycorrhizal (OM) plant species that are consistently mycorrhizal in all documented instances, 2) facultative mycorrhizal (FM) plant species that are found to be colonized under some conditions but not others, and 3) non-mycorrhizal (NM) plant species that are never found to be colonized by mycorrhizal fungi (Trappe 1987, Smith and Read 2008, Moora 2014). It is important to note that plant mycorrhizal status and plant mycorrhizal dependency (or responsiveness) are distinct traits (Moora 2014). While mycorrhizal responsiveness describes plant species growth responses under given conditions, mycorrhizal status does not provide any indication about the functional significance of mycorrhizal colonization for individual plants. Rather, plant mycorrhizal status simply indicates the presence or absence of fungal colonization, and can provide an indication of plant reliance on the mycorrhizal symbiosis, with reliance presumed to be low among NM plants, intermediate among FM plants and high among OM plants. This measure (at plant species level) has been used to estimate the importance of the mycorrhizal symbiosis along environmental gradients at intermediate and larger scales (Peat and Fitter 1993, Hempel et al. 2013,

Menzel et al. 2016). Large scale patterns of plant mycorrhizal status might similarly be used to identify conditions that mediate the importance of the mycorrhizal symbiosis for plant invasion success.

It remains debated whether alien plants benefit from being mycorrhizal, or whether engaging in the symbiosis constrains their establishment and spread in new environments (Fitter 2005, Pringle et al. 2009, Shah et al. 2009, Bunn et al. 2015, Menzel et al. 2017, Reinhart et al. 2017). Hempel et al. (2013) demonstrated that neophytes (i.e. those alien species introduced after the year 1500, Pyšek et al. 2004) in the German flora are more frequently OM compared with archaeophytes (introduced before the year 1500) and native species. Using the same data set, Menzel et al. (2017) found that mycorrhizal status explained the invasion success of neophyte species in terms of area of occupancy in Germany, with the results indicating that being mycorrhizal (OM or FM) is important for the establishment of neophytes.

The AM symbiosis potentially affects nutrient uptake and the carbon (C) economy of plant species. AM fungi can supply up to 90% of plant phosphorus (P) uptake, up to 20% of nitrogen (N) uptake, and consume a significant fraction of plant net primary production (van der Heijden et al. 2015). Hence, despite the benefits plants gain from the symbiosis, there is a potential cost in terms of C provided to the fungal partner, and trade-offs between retention of the mycorrhizal symbiosis and the development of other C-costly plant properties have been predicted (Peat and Fitter 1993, Reinhart et al. 2012). Grman (2012) suggested that storage organs and retention of the mycorrhizal symbiosis may represent competing carbon sinks and therefore different ecological strategies, in which FM (and potentially OM) plants hold an advantage in possessing the ability to choose the strategy or property they invest in. Following this, Menzel et al. (2017) analyzed the interactive effect of neophyte species mycorrhizal status and the occurrence of storage organs and other plant structures on their invasion success. They reported a variety of trade-offs and demonstrated that being FM is especially beneficial for the successful spread and persistence of neophytes.

We aimed to gain deeper insights into the trade-offs between plant retention of the mycorrhizal symbiosis and allocation of C to the development of other plant structures. We compared alien species (i.e. neophytes and archaeophytes) with native species and investigated whether these groups differ in the effects of trade-offs (those identified by Menzel et al. 2017 as well as interactions with additional traits; Table 1) on species area of occupancy in Germany.

We specifically address the hypothesis that successful invaders exhibit trade-offs between mycorrhizal status and potentially costly functional traits, meaning that FM plant species probably possess more costly structures, compared with OM and NM species. Second, we hypothesize that this trade-off differs between natives, archaeophytes and neophytes. This hypothesis relates to the general debate whether invasive, i.e. rapidly spreading and hence often widely

Table 1. Summary of the plant functional traits selected in addition to those included in Menzel et al. (2017) to gain deeper insights into the trade-offs between plant retention of the mycorrhizal symbiosis and allocation of C to the development of other plant properties. The second column provides the reasoning for selection of the particular traits. See Table 2 for further information on trait attributes, the percentage of missing information, primary data sources and retention of traits for analysis.

Trait	Reasoning for trait selection
Functional group identity	– functional group identity influences plant–soil feedbacks and invasion trajectories (Meisner et al. 2014, Bunn et al. 2015)
Root type	– plant species with thick and slow-growing roots and/or less root-hair are more responsive to mycorrhizal fungi than plants with fine, fast-growing and/or abundant root-hair (Hetrick et al. 1992, Peat and Fitter 1993, McCormack et al. 2014)
Tap root persistence	– plant species with tap root architecture are more responsive to mycorrhizal fungi than plants with fibrous root systems (Marler et al. 1999, Yang et al. 2015), potentially indicating that investment into highly branched roots and the mycorrhizal symbiosis are alternative strategies for absorbing nutrients (Wilson and Hartnett 1998)
Rooting depth	
Seed dry mass	– mycorrhizal plants produce heavier seeds compared to non-mycorrhizal species (Peat and Fitter 1993), potentially indicating nutritional benefits gained through the symbiosis
Existence of seed appendages	– both traits represent plant investment into nutrient reserves
Seedling vigor	
Specific leaf area (SLA)	– both traits are associated with high performance in terms of physiology and fitness and have been shown to be characteristics of invasive alien plants (van Kleunen et al. 2010, Pyšek et al. 2015)
Plant growth rate	
Ability of chemical self-defense	– AM fungal colonization can alter plant C and nutrient balance towards increased allocation to C-based defense mechanisms (Gange and West 1994) – plant individuals benefit from mycorrhizal extraradical hyphae due to an increased efficacy of allelochemicals (Barto et al. 2012)

distributed alien plant species, differ in their characteristics from widely distributed native species or are functionally similar (van Kleunen et al. 2010, Davis et al. 2011, Simberloff 2011, Knapp and Kühn 2012). There are two possible scenarios concerning AM status and related trait interactions with respect to plant invasions.

1) Trait interactions are characteristic of successful neophytes occupying a large area and this may explain the differences in composition of mycorrhizal status between natives, archaeophytes and neophytes in Germany, i.e. why neophytes are more frequently OM (Hempel et al. 2013).

2) Trait interactions are consistent across all plant species, independent of their origin status, and depict a general pattern. This is supported by the observation that FM species show the largest area of occupancy in neophytes (Menzel et al. 2017) as well as across all plant species in Germany for which their mycorrhizal status is known (Hempel et al. 2013).

While neophyte invasion success has been investigated in this way (Menzel et al. 2017), to the best of our knowledge, the corresponding relationships for native and archaeophyte species have not been distinguished, in Germany or elsewhere.

Material and 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 (<www.floraweb.de>). The database records plant distribution in cells of 10' longitude × 6' latitude (arcminutes) size, which are roughly 130 km² in Germany, depending on the geographical position. For our

analysis we used this grid system, in which the total area of Germany is divided into 2995 grid cells and the measure therefore ranges from 1 to 2995 occupied grid cells per plant species. We used the number of occupied grid cells (i.e. area of occupancy) as a proxy for invasion success, as it is the best information available to date and has been effectively established in the scientific literature (Küster et al. 2008, Knapp and Kühn 2012, Pyšek et al. 2012). Since larger scaled biotic and abiotic conditions (e.g. temperature, precipitation, geology, land use, forest coverage; Menzel et al. 2016) vary between grid cells and cover the full range of conditions in Germany, a higher number of occupied grid cells consequently indicates a higher niche breadth of the respective species.

Information on mycorrhizal status for each plant species – OM, FM or NM – was taken from the MycoFlor database (Hempel et al. 2013). Although MycoFlor contains information on a range of mycorrhizal associations, we restricted the analysis to AM plants, as they are by far the most widespread and largest group represented in the database. Furthermore, neophyte species in Germany are predominantly AM (Menzel et al. 2017). Therefore, restricting the analysis to plant species forming the AM symbiosis allowed us to avoid confounding effects, while comparing species with different origin status. We assigned the NM status to strictly non-mycorrhizal plant species, i.e. non-AM species that may form symbiotic relationships with other mycorrhiza types (e.g. ecto- or ericoid mycorrhiza) were excluded. Information on species origin status, i.e. whether native, archaeophyte or neophyte, was obtained from BiolFlor (Klotz et al. 2002). Overall, we analyzed the area of occupancy of 1462 plant species, of which 1084 were natives, 129 were archaeophytes, and 249 were neophytes.

Table 2. Summary of functional plant traits: n – number of species for which trait information is available (rare trait values, i.e. trait values occurring less than ten times are not excluded here); NAT – native species; A – archaeophyte species; NE – neophyte species; the last column ‘selected’ indicates whether the functional trait was selected for modeling the area of occupancy in three-way and two-way interactions with plant mycorrhizal status and origin or whether it was excluded due to a lack of information. Traits referring to storage organs and shoot metamorphoses are partially, but not completely, confounded, e.g. rhizomes can be shoots and storage organs but not every rhizome is a storage organ (see Supplementary material Appendix 1 Fig. A1 for trait correlations)

Functional trait	Values	Unit	n	Percentage of missing information			References	Selected (yes/no)
				NAT	A	NE		
Growth form	non-woody; woody	–	1462	0	0	0	BiolFlor (Klotz et al. 2002)	yes
Functional group	fern; forb; grass; rush; sedge; shrub/tree	–	1462	0	0	0	–	yes
Storage organ (existence)	yes; no	–	1462	0	0	0	BiolFlor (Klotz et al. 2002)	yes
Storage organ	bulb; none; pleiocorm ¹ ; primary storage root; rhizome ² ; root tuber; runner ³ ; tuft; variable	–	1462	0	0	0	BiolFlor (Klotz et al. 2002)	yes
Root metamorphoses (existence)	yes; no	–	1462	0	0	0	BiolFlor (Klotz et al. 2002)	yes
Root metamorphoses	none; primary storage root; root shoot; root tuber	–	1462	0	0	0	BiolFlor (Klotz et al. 2002)	yes
Shoot metamorphoses (existence)	yes; no	–	1462	0	0	0	BiolFlor (Klotz et al. 2002)	yes
Shoot metamorphoses	bulb; none; pleiocorm ¹ ; rhizome ² ; runner ³ ; variable	–	1462	0	0	0	BiolFlor (Klotz et al. 2002)	yes
Vegetative propagation and dispersal (existence)	yes; no	–	1462	0	0	0	BiolFlor (Klotz et al. 2002)	yes
Vegetative propagation and dispersal	bulb; none; pleiocorm ¹ ; rhizome ² ; root shoot; runner ³ ; tuft; variable	–	1462	0	0	0	BiolFlor (Klotz et al. 2002)	yes
Reproduction strategy	predominantly via seeds; seeds and vegetative; predominantly vegetative	–	1462	0	0	0	BiolFlor (Klotz et al. 2002)	yes
Life span	annual; perennial; variable	–	1434	0	0	0	BiolFlor (Klotz et al. 2002)	yes
Leaf persistence	summer green; overwintering green; persistent green	–	1359	5	2	6	BiolFlor (Klotz et al. 2002)	yes
Nitrogen fixation ability	yes; no	–	1462	0	0	0	–	yes
Plant defense: chemical	yes; no	–	359	78	63	70	USDA Plants (Green 2009)	no
Root type	adventitious; fibrous; tap root; variable	–	265	81	81	85	EcoFlora (Fitter and Peat 1994)	no
Tap root persistence ⁴	yes; no	–	1095	23	11	41	CLO-PLA (Klimešová and de Bello 2009)	yes
Seedling vigor	low; medium; high	–	281	88	88	74	USDA Plants (Green 2009)	no
Rooting depth	0–50; > 50	cm	161	87	84	98	EcoFlora (Fitter and Peat 1994)	no
Plant growth rate	continuous	mm	587	63	40	59	The xylem database (Schweingruber and Landolt 2005)	yes
Seed dry mass	continuous	mg	1206	30	6	20	KEW seed information database (< http://data.kew.org/sid/ >)	yes
Specific leaf area (SLA)	continuous	mm ² mg ⁻¹	1061	25	17	43	LEDA (Kleyer et al. 2008)	yes
Seed morphology: existence of appendages	yes; no; both	–	1005	31	12	40	LEDA (Kleyer et al. 2008)	yes

¹Pleiocorm: system of compact, perennial shoots occurring at the proximal end of the persistent primary root.

²Rhizome: transformed shoot growing subterraneously or close to the soil surface, mostly thickened with short internodes with adventitious roots.

³Runner: usually lateral shoots with long, thin internodes and adventitious roots; severance from the mother plant causes the formation of individual ramets.

⁴Tap root persistence: this trait describes whether the primary root survives over the entire life span or not or whether both cases are reported.

Information on other plant functional traits was obtained from TRY, a compilation of worldwide trait databases (Kattge et al. 2011). We aimed to select trait information originating from Europe, as it should be sufficiently representative of the German flora (Pyšek et al. 2009; Table 2, including primary source data). Furthermore, we did not merge trait information from different data sources, as presence in TRY does not guarantee similar trait concepts (Garnier et al. 2017) and protocols of trait measurement across databases (Kattge et al. 2011). We preferentially selected those databases that contained information about the largest number of plant species included in MycoFlor, i.e. the most information per particular trait. Prior to analysis we assessed the availability of information for each functional trait and each origin status and selected traits to include in the analysis based on the availability of trait information. Due to a limited availability of information, we did not include the following functional traits: root type, rooting depth, seedling vigor, and availability of chemical plant defense (Table 2). We did not analyze very rare attributes (i.e. trait values) with fewer than ten species in each group of plants with different origin status. This resulted in different numbers of species per plant trait included in the respective analyses (Table 2).

Plant traits are not independent of each other, but co-vary jointly due to environmental conditions, evolutionary history, and trade-offs (i.e. biophysical constraints) in the allocation of matter and energy (Laughlin 2014, Díaz et al. 2016). In this light, trait interactions in regression models have been shown to provide indications of underlying ecological strategies (Küster et al. 2008). Throughout this text we use the term ‘trait interactions’ to refer to this statistical relationship, i.e. if two or more predictor variables significantly interact in a regression analysis, the relationships of individual predictor variables with the response variable are conditional on other interacting variables. We use the term ‘trade-off’ to describe and discuss potential (eco)physiological mechanisms.

We used the number of occupied grid cells in Germany as a response variable to model the area of occupancy and used generalized linear models with negative binomial error distributions to account for overdispersion. We established a model for each of the plant functional traits, including as predictor variables the particular trait, AM status and origin status, along with all possible two-way interactions and the three-way interaction. Each model was reduced to the minimum adequate model using a backwards stepwise model selection procedure in which predictors were removed based on error probabilities (type I error probabilities ($p < 0.05$)), but retained when a significant higher-order trait interaction was present. In parallel, we split the data set by plant origin status and analyzed the resulting three data sets separately, as the unbalanced number of native, archaeophyte, and neophyte species may superimpose significant interaction terms in each group. These models included the two-way interaction of AM status and the particular plant trait. For each of the three separated data sets, differences in the mean number of occupied grid cells among the three mycorrhizal statuses

within each categorical functional trait attribute were tested using Tukey’s honest significant difference post-hoc procedure (Tukey HSD).

Due to their common evolutionary history, phylogenetically closely related species are more likely to be functionally similar, compared with more distantly related species (Felsenstein 1985, Harvey and Pagel 1991). We accounted for the phylogenetic relatedness of plant species by using the phylogenetic tree DaPhnE provided by Durka and Michalski (2012). A modified phylogenetic eigenvector approach, originally proposed to account for spatial dependencies by Bini et al. (2009), was used to incorporate phylogenetic relatedness within each generalized linear model. The phylogenetic distance matrix was subjected to a principal coordinates analysis (PCoA). The resulting eigenvectors that jointly explained at least 99% of the phylogenetic distance were regressed on the residuals of the trait \times mycorrhizal status models. Significant eigenvectors (i.e. phylogenetic filters) were then added as covariates to each particular model. All statistical analyses were performed using the statistical software R (ver. 3.0.2, R Development Core Team), in particular the packages ‘ape’ (Paradis et al. 2004), ‘lsmeans’ (Lenth 2016), ‘MASS’ (Venables and Ripley 2002) and ‘multcomp’ (Hothorn et al. 2008).

Results

Mycorrhizal status had a significant effect on plant species area of occupancy in Germany in phylogenetically informed generalized linear models describing all 1462 plant species ($df=2$, deviance=55.7, $p < 0.001$), 1084 natives ($df=2$, deviance=36.0, $p < 0.001$), and 249 neophyte species ($df=2$, deviance=8.4, $p=0.02$); but did not have a significant effect in the model describing 129 archaeophytes ($df=2$, deviance=3.1, $p=0.21$). For each of the significant models, subsequent post-hoc analysis revealed that FM species occupied a significantly greater number of grid cells than NM (all species: $p < 0.001$, natives: $p=0.01$, neophytes: $p < 0.001$; Fig. 1) and OM ($p < 0.001$, $p < 0.001$, $p=0.02$, respectively; Fig. 1) species.

We found significant three-way interactions involving AM status, origin status and the following plant functional traits: functional group, mode of shoot metamorphoses, the existence and mode of vegetative propagation and dispersal as well as the existence of seed appendages (Supplementary material Appendix 1 Table A1).

We found significant two-way interactions between mycorrhizal status and 13 out of 19 additional traits for neophytes, and one trait interaction for both archaeophytes and natives (Table 3). 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 they were FM (Table 3). In particular, rhizomatous FM neophytes had large areas of occupancy. FM neophytes were most widespread in

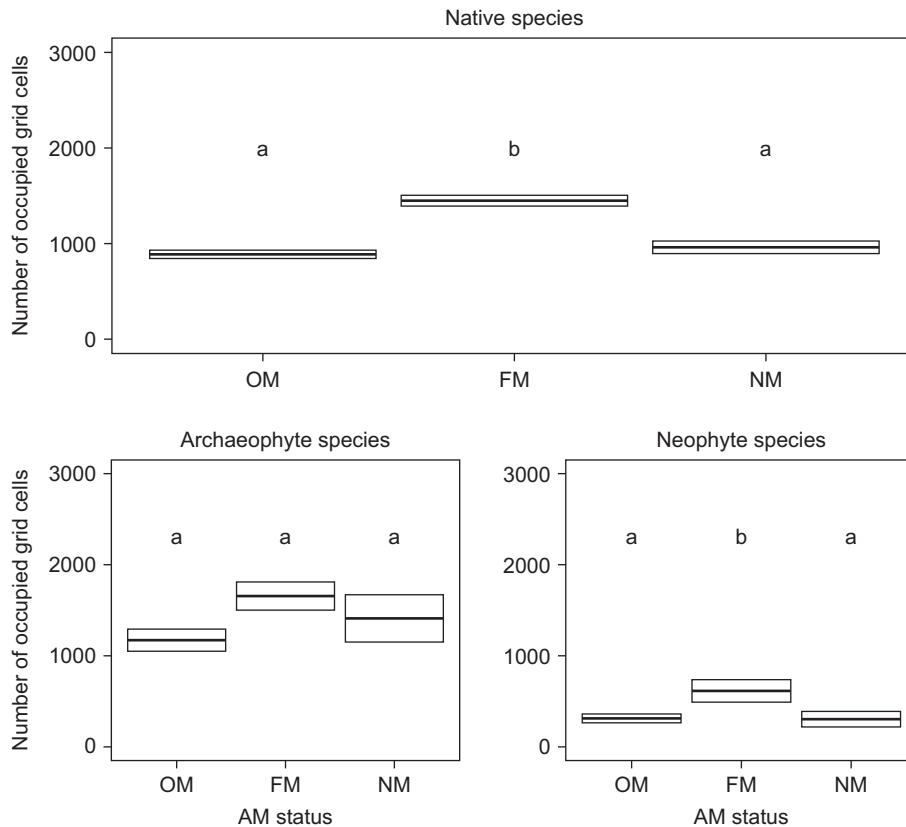


Figure 1. Area of occupancy in Germany for plants of different AM status (OM, FM, and NM). Area of occupancy is measured as the number of occupied grid cells (each ~130 km² in size) and is presented separately for 1) natives (n = 1084), 2) archaeophytes (n = 129), and 3) neophytes (n = 249). Horizontal bars show mean values; boxes show standard errors. Different letters above bars indicate significant differences according to Tukey HSD tests ($p < 0.05$).

Germany among perennial and non-woody as well as forb species. OM neophytes were most widespread when not developing storage organs and structures promoting vegetative dispersal and propagation, as well as having variable life spans (Table 3).

Discussion

Our analysis reveals that plant AM status has a significant effect on the area of occupancy, i.e. indicating the breadth of their habitat niches, of native and neophyte species in Germany, but a much less pronounced effect on archaeophytes. In both groups for which significant effects were found, FM species showed the largest area of occupancy. However, interactions between AM status and other plant functional traits related to C allocation are almost exclusively present in neophytes but absent from natives; corroborating the importance of considering trait interactions in the analysis of plant invasiveness (Küster et al. 2008). This result suggests differences in the AM association and related C allocation strategies between neophytes and native species. The detected trade-offs may be an important characteristic determining invasion success for a particular subset of neophyte species, but could

also reflect a time-lag in the development of AM interactions between neophyte plants and native fungal symbionts.

Native AM fungal partners are less important for neophyte than for native plant species

AM fungi are generally not considered to be barriers to alien plant invasion, as it has been shown that many AM fungal taxa are ubiquitous generalists (Davison et al. 2015) while the AM symbiosis is relatively non-specific in terms of plant and fungal partners (Smith and Read 2008, Moora et al. 2011). Nevertheless, even if the global diversity of AM fungi is relatively low, the local diversity of AM fungi communities can be high. For instance, Oehl et al. (2010) found up to 30 AM fungi species interacting with 50 plant species at low land-use intensity field sites. Differences are also apparent in the AM fungal communities occurring in different ecosystems (Öpik et al. 2006, 2010, Davison et al. 2015, Vályi et al. 2016). Therefore, it has been suggested that alien plants differ from natives in their responses to local AM fungi communities (Klironomos 2002) and that aliens are less responsive to native fungal species (Klironomos 2003, Pringle et al. 2009). Our study adds additional nuance to this previous work and suggests that trade-offs in C allocation strategies affect the area

Table 3. Results of Tukey post-hoc tests following generalized linear models explaining the number of occupied grid cells. The plant functional traits that showed significant interactive effects with mycorrhizal status are displayed. Plus and minus signs respectively indicate significantly higher and significantly lower numbers of occupied grid cells within each row of the table (Tukey HSD: $p < 0.05$) Non-significant plant functional trait interactions are indicated in brackets after NS. The table is split into three parts, separating the results for each origin status.

Traits	Mycorrhizal status		
	OM	FM	NM
Natives			
vegetative propagation and dispersal (NS: pleiocorm; rhizome; root shoot)			
none	–	+	+
runner	–	+	–
variable	–	+	–
number of positive interactions	0	3	1
Archaeophytes			
seed dry mass	+	–	+
number of positive interactions	1	0	1
Neophytes			
growth form (NS: woody)			
non-woody	–	+	–
functional group (NS: grass; shrub/tree)			
forb	–	+	–
storage organ (existence) (NS: no)			
yes	–	+	–
storage organ (NS: pleiocorm; runner; variable)			
none	+	NS	–
rhizome	–	+	–
root metamorphoses (NS: root shoot)			
none	–	+	–
primary storage root	+	–	NS
shoot metamorphoses (existence)			
yes	–	+	–
no	+	NS	–
shoot metamorphoses (NS: pleiocorm; runner)			
none	+	NS	–
rhizome	–	+	–
vegetative propagation and dispersal (existence)			
yes	–	+	–
no	+	NS	–
vegetative propagation and dispersal (NS: none; runner)			
rhizome	–	+	–
variable	–	NS	+
reproduction strategy (NS: seeds and vegetative)			
predominantly via seeds	NS	+	–
predominantly vegetative	–	+	NS
life span (NS: annual)			
perennial	–	+	NS
variable	+	–	NS
specific leaf area	+	–	NS
seed morphology: appendages (NS: yes; both)			
no	–	+	NS
number of positive interactions	7	13	1

The final row in each part shows the sum of the positive associations in terms of occupied grid cells for all 27 mycorrhizal status \times plant trait level combinations per origin status. Traits referring to storage organs and shoot metamorphoses are partially, but not completely, confounded, e.g. rhizomes can be shoots and storage organs but not every rhizome is a storage organ (see Supplementary material Appendix 1 Fig. A1 for trait correlations).

of occupancy of neophytes, but not of natives, in Germany. FM neophytes (i.e. flexible species with respect to their AM association) occur in the largest number of occupied grid cells, especially when they additionally exhibit C-costly plant properties such as storage organs or rhizomes to disperse

vegetatively (Table 3). These traits in turn positively affect the area of occupancy by potentially supporting establishment or competitive ability once a plant has reached a new locality. In contrast, OM neophyte species (i.e. species requiring AM associations) show the largest area of occupancy in Germany

if they do not develop additional properties (Table 3). Therefore, neophytes appear especially successful in their new environment if they are flexible in their AM association, i.e. they can survive without retention of the symbiosis.

The majority of neophyte species in Germany are OM (Hempel et al. 2013), despite this characteristic seeming to inhibit the development of other C-costly plant properties (Table 3). Therefore, it is important to note that the AM symbiosis provides additional functions to plants that are independent of nutrient availability. It has been shown that AM fungi offer pathogen protection (Newsham et al. 1995, Veresoglou and Rillig 2012), protection against heavy metals (Hildebrandt et al. 2007), and provide stabilization of soil structure (Rillig et al. 2015). Unfortunately, these features could not be assessed in the present analysis.

AM associations between neophytes and their native fungal partners may establish slowly

Some alien plant species have been shown to respond differently to AM fungi in an invaded range compared to their native range (Seifert et al. 2009, Waller et al. 2016). However, such a relationship should not necessarily be expected to persist as alien species become well established in new ranges. The discrepancy in responses toward native and alien mutualists could rather be temporary and could diminish as alien plants encounter the most useful mutualistic partners and adapt to native fungal communities. An analogous phenomenon has already been suggested for the interactions of alien plants with native pollinators (Pyšek et al. 2012) and with native pathogens (Mitchell et al. 2010). Additionally, native plant species may profit to a larger degree from the non-nutritional benefits of the AM symbiosis due to the longer joint history with native fungal communities. This might mask or preclude the existence of C allocation trade-offs indicated by significant trait interactions in statistical models. However, empirical evidence is needed to test this hypothesis.

The geographical range of archaeophytes is not affected by their AM status

Archaeophytes show a similar mycorrhizal status composition compared to natives (Hempel et al. 2013), but the effect of their AM status on their area of occupancy in Germany is much less pronounced. Alien species generally differ from native species in their ecological adaption to the environment of the recipient range for two reasons: 1) most were introduced by humans for special purposes, such as cultivation (Pyšek et al. 2005, Lambdon et al. 2008) and 2) they evolved under biotic and abiotic conditions differing from those in the area in which they were introduced (Pyšek et al. 2005, Seifert et al. 2009). Among alien species, neophyte and archaeophyte species not only differ in residence time, but also in their introduction pathways and habitat associations. Whereas the entry points of neophytes are typically urban or industrial areas, archaeophytes are mostly associated with agricultural habitats (Pyšek et al. 2005, Pyšek and Jarošik

2006). Therefore, archaeophytes represent an ecologically distinct group compared with both natives and neophytes. They are mostly weeds of arable land, differing from neophytes in life form and habitat requirements (Pyšek et al. 2004, 2005, Pyšek and Jarošik 2006, Chytrý et al. 2008a), and are recruited from less diverse places of origin (Pyšek et al. 2012). Overall, they form a functionally homogenous group of plant species, which is reflected by the similarity in trait values in our analysis. Additionally, archaeophytes show weak or no responsiveness towards AM fungi, which contrasts with the responses of native and neophyte species. This may be explained by their close association with agricultural habitats, as management practices such as tillage (Jansa et al. 2002), grazing (Eom et al. 2001) or fertilization (Johnson 1993, Oehl et al. 2003) are known to inhibit or disrupt existing mycorrhizal networks and associations. Therefore, plant retention of the symbiosis in agricultural habitats with steady supplies of N and P potentially becomes less beneficial. Consequently, archaeophyte species may have evolved a lower AM dependence overall or were already adapted in this way (cf. Seifert et al. 2009). As such, they may not serve as a missing link to elucidate the process by which AM interactions are established between alien plant species and native fungal taxa.

Understanding the effect of the AM symbiosis on alien plants by using plant functional traits

Approaching the effect of AM symbiosis on the invasion success of alien plant species using plant functional traits facilitates an understanding of the invasion process as well as the ecology of the symbiosis. Nevertheless, we were unable to include root traits in our analysis, due to a lack of information. At present, even large trait databases like TRY have relatively poor coverage of root traits (Table 2), even though the plant-root interface is the major link between mycorrhizal fungi and plant individuals and is recognized to be highly relevant for plant species responses to their abiotic and biotic environment (Valverde-Barrantes et al. 2013, McCormack et al. 2014). Comprehensive measurements of traits like specific root length, root diameter, root hair length or root hair density would improve our understanding of both the belowground physiology of plants and symbiotic mycorrhizal interactions (McCormack et al. 2014, Yang et al. 2015, Laliberté 2017). Different metrics of root traits and root architecture may be combined to reflect a spectrum of root system functioning (Maherali 2014) and would considerably augment our understanding of plant–fungi relationships.

Conclusions

Our study suggests that alien (i.e. archaeophytes and neophytes) and native plant species differ in their relationship with the AM symbiosis and related trade-offs regarding C allocation, and that these differences affect the distribution of those species groups. However, although we are confident that our database is a good representation of the central

European flora, extrapolation of our findings to other, especially non-European areas, should be done with caution.

Future studies are required to establish whether recorded differences are due to functional disparities or due to the time needed to establish the symbiosis. Therefore, studying differences in non-nutritional benefits provided by the symbiosis as well as the introduction pathways and reasons for introduction of neophyte plant species (e.g. seed contaminants, escaped crop or ornamental plants) can clarify their natural environments of origin and ultimately shed light on the underlying mechanisms.

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Supplementary material (Appendix ECOG-03367 at < www.ecography.org/appendix/ecog-03367 >). Appendix 1.