Effects of the mycorrhizal symbiosis on plant distributions and alien plant invasions at a large spatial scale

Dissertation
zur Erlangung des Doktorgrades der Naturwissenschaften
(Dr. rer. nat)

der

Naturwissenschaftlichen Fakultät I - Biowissenschaften -
der Martin-Luther-Universität Halle-Wittenberg,

vorgelegt

von Herrn **Andreas Menzel (Dipl.-Biol.)**
geboren am 03.02.1987 in Jena

Halle (Saale), den 23.03.2016

Referees

Prof. Dr. Ingolf Kühn (Martin Luther University Halle-Wittenberg and Helmholtz Centre for Environmental Research - UFZ, Germany)
Prof. Dr. Isabell Hensen (Martin Luther University Halle-Wittenberg, Germany)
Dr. Maarja Öpik (University of Tartu, Estonia)

Thesis defence

20.09.2016

Copyright notice

TABLE OF CONTENTS

SUMMARY

Mycorrhizas are of crucial importance for the organisation of terrestrial plants across all hierarchical levels. The intimate interaction between plant roots and fungal hyphae is mainly based on nutrient exchange. Plants predominantly gain phosphorus and nitrogen from fungi and fungi gain photosynthates from plants. The great majority of described plant species of almost all biomes is mycorrhizal and mycorrhizal fungi are considered as the most abundant plant mutualists. Despite this close and ubiquitous relationship, the symbiosis is rarely considered in plant ecology, which is partly based on experimental limitations in jointly assessing both partners in controlled and especially under field conditions. Hence, mycorrhizal ecology has experienced a strong focus on pot experiments and molecular approaches. Due to the fields' dominantly reductionist character, deepening our knowledge of the co-variation of plants and their symbionts at larger scales remains difficult and associated studies are rare. However, the availability of information regarding mycorrhizal associations of a large number of plant species has increased recently. This is accompanied by conceptualising plant mycorrhizal traits including plant mycorrhizal status. Three groups of plant species can be distinguished according to their mycorrhizal status: (1) obligate mycorrhizal plant species that are always found to be colonised by mycorrhizal fungi, (2) facultative mycorrhizal plant species that are colonised under some environmental conditions, but not colonised under others, and (3) non-mycorrhizal plant species, which are never found to be colonised by mycorrhizal fungi. By utilising this differentiation, the present thesis aims to investigate the effects of the mycorrhizal symbiosis on plant distributions and alien plant invasions. For this purpose, I used macroecological frameworks by linking a large spatial scale (the German country scale) with large numbers of plant species represented by their mycorrhizal status as well as other plant functional traits. First, I investigated whether plant species assemblages are composed of different proportions of species regarding their mycorrhizal status. Furthermore, I analysed if the variation of these proportions is linked to the geographical variation of ecological and environmental conditions at the chosen spatial scale. Secondly, I analysed whether the invasion success of alien plant species of the German flora is influenced by their mycorrhizal status and whether certain trade-offs between plants' mycorrhizal status and other functional plant traits related to morphology, reproduction, dispersal and life-history are underlying the invasion success. Subsequently, I examined whether alien plant species differ from native plant species regarding their mycorrhizal associations and these potential trade-offs.

To the best of my knowledge the thesis provides the first evidence of spatial patterns of plant assemblages differing in their proportions of obligate, facultative, and non-mycorrhizal plant species at the chosen scale. The identified patterns resemble general parts of the German topography, which emphasises the importance of including plant mycorrhizal status into macroecological analyses of plant distributions at large spatial

scales. Moreover, the associated model shows that the assemblages of plants differing in their mycorrhizal status can be linked to gradients of climate, geological parent material, and land use. Large shares of obligatory mycorrhizal plant species are associated with regions of high temperature and precipitation ranges, high mean temperatures, large limestone and urban areas as well as small areas of mixed and coniferous forest. Contrastingly, large non-mycorrhizal shares are associated with regions of low temperature range and low values of mean precipitation. Furthermore, the thesis provides evidence that plant mycorrhizal status helps explain the invasion success of alien plant species. Being mycorrhizal promotes the invasion success of alien plants in Germany, with facultative mycorrhizal species being the most wide-spread aliens. The results indicate that facultative mycorrhizal species benefit from the ability to flexibly choose the potential plant property to invest, e.g., carbon allocation to perpetuate the mycorrhizal symbiosis or to develop storage organs or root and shoot metamorphoses. This implies that the mycorrhizal flexibility acts as a competitive advantage compared to non-flexible plant species. In native plant species, facultative mycorrhizal plants are the most wide-spread species as well. Nevertheless, the detected trade-offs are only present in alien plant species suggesting a different association with mycorrhizal fungi among both plant groups. This suggests that native and alien plant species benefit differently from the symbiosis and that the benefits of natives are independent of carbon allocation strategies. This adds an important perspective to the ongoing debate in invasion ecology, as it is still discussed whether being mycorrhizal is beneficial for the invasion success of alien plant species.

The thesis demonstrates that using plants' mycorrhizal status is a reasonable and valuable tool to incorporate the symbiosis to analyses of plant distribution and alien plant invasions at large spatial scales. It shows that the mycorrhizal status is a useful extension to the current set of typically used plant traits in plant ecology. Incorporating mycorrhizal status accounts for the ubiquity of the symbiosis and creates a surplus in understanding plant distributions, alien plant invasions, and plant community ecology in general. The thesis' macroscopic view enhances our knowledge of the co-variation of plants and their mycorrhizal symbionts and complements the reductionist approaches in plant mycorrhizal ecology. As small-scale studies are suitable to disentangle mycorrhizal effects on plant physiology at the level of plant individuals, studies addressing larger scales aim at relating the symbiosis to plant community and ecosystem functioning. Therefore, studying higher hierarchical levels of plant organisations at large spatial scales increases the likelihood that observations have greater relevance for answering questions to uncover general principles of mycorrhizal functioning in the context of plant ecology. Consequently, the present thesis encourages the use of plant mycorrhizal status (and potentially related mycorrhizal traits) as straightforward and simple functional trait to incorporate the mycorrhizal symbiosis to analyses of the abiotic and biotic processes shaping large-scale plant distributions and compositions of plant communities.

ZUSAMMENFASSUNG

Als Mykorrhiza bezeichnet man die zumeist symbiotische Verbindung von Pflanzenwurzeln und Pilzhyphen. Die überwiegende Mehrheit aller beschriebenen Pflanzenarten nahezu aller Biome geht eine solche Verbindung ein und Mykorrhizapilze gelten als weltweit häufigste Pflanzenmutualisten. Die Mykorrhizierung ist daher von großer Bedeutung für alle hierarchischen Ebenen der Organisation terrestrischer Pflanzen. Die enge Verbindung zwischen beiden Partnern basiert zu großen Teilen auf dem Austausch von Nährstoffen. Pflanzen erhalten im Besonderen Phosphor und Stickstoff, während sie im Austausch Photosyntheseassimilate an Mykorrhizapilze abgeben. Innerhalb der Pflanzenökologie findet die Symbiose, ungeachtet ihrer Allgegenwärtigkeit, bisher nur geringe Beachtung. Die Gründe hierfür liegen zum Teil in experimentellen Beschränkungen, wenn beide Partner gemeinsam unter kontrollierten und insbesondere unter natürlichen Bedingungen untersucht werden. Daraus resultiert eine starke Fokussierung auf Gewächshausstudien und molekulare Untersuchungen innerhalb mykorrhiza-ökologischer Forschung. Aufgrund dieses vorherrschenden Reduktionismus ist das allgemeine Verständnis von großskaligen Mustern und Prozessen hinsichtlich der Mykorrhizierung von Pflanzen limitiert und entsprechende Studien sind selten. Die Verfügbarkeit von Daten bezüglich des Mykorrhizierungsverhaltens vieler Pflanzenarten hat sich innerhalb der letzten zehn Jahre allerdings stark erhöht. Dies geht einher mit der Konzeption einer Pflanzenklassifizierung anhand ihres Mykorrhizierungsverhaltens, beispielsweise ihres Mykorrhizierungstatus. Drei Gruppen von Pflanzenarten können nach diesem unterschieden werden: (1) obligat mykorrhizierte Arten, die permanent von Mykorrhizapilzen kolonisiert sind, (2) fakultativ mykorrhizierte Arten, die unter bestimmten abiotischen und biotischen Bedingungen kolonisiert sind, und (3) nicht mykorrhizierte Arten, die nie von Mykorrhizapilzen kolonisiert sind. Das Ziel der vorliegenden Arbeit ist die Untersuchung des Einflusses der Symbiose auf die Verbreitung von Pflanzen und die Invasion gebietsfremder Pflanzenarten basierend auf dieser Einteilung. Zu diesem Zweck verknüpfe ich eine große räumliche Skala (die der politischen Grenzen Deutschlands) mit einer großen Anzahl von Pflanzenarten, die durch ihren Mykorrhizierungsstatus und andere funktionelle Eigenschaften repräsentiert werden. Zunächst untersuche ich, ob sich die Zusammensetzung von Pflanzengemeinschaften aus verschiedenen Anteilen von Pflanzenarten mit unterschiedlichem Mykorrhizierungsstatus verändert und ob dies mit sich ändernden Umweltbedingungen und ökologischen Gegebenheiten innerhalb der gewählten Skala korrespondiert. Darüber hinaus betrachte ich die Abhängigkeit des Invasionserfolges gebietsfremder Pflanzenarten von ihrem Mykorrhizierungsstatus und inwiefern Trade-offs zwischen Ausprägung des Mykorrhizierungsstatus und anderen funktionellen Pflanzenmerkmalen hinsichtlich Morphologie, Ausbreitung und Lebensstrategien dabei eine Rolle spielen. Abschließend analysiere ich inwieweit diese potentiellen Trade-offs typische Eigenschaften gebietsfremder Pflanzenarten sind oder auch bei einheimischen Arten auftreten.

Die vorliegende Arbeit erbringt auf der Skala von Deutschland den Beweis für ausgeprägte räumliche Muster der Zusammensetzung von Pflanzengemeinschaften hinsichtlich des Mykorrhizierungsstatus der einzelnen Arten. Die identifizierten Muster geben dabei die Topographie Deutschlands wieder und unterstreichen so die generelle Bedeutung des Mykorrhizierungsstatus in makroökologischen Analysen von großskaligen Pflanzenverbreitungen. Das zugehörige statistische Modell zeigt, dass die Zusammensetzung von Pflanzengemeinschaften hinsichtlich Arten mit verschiedenem Mykorrhizierungsstatus selbst innerhalb dieser Skala durch Klima-, Geologie- und Landnutzungsgradienten maßgeblich erklärt werden kann. Hohe Anteile von obligat mykorrhizierten Arten finden sich überwiegend in Regionen, die durch größere Unterschiede im Jahresgang bezüglich Temperatur und Niederschlag, hohe mittlere Jahrestemperatur, einen großen Anteil an Misch- und Nadelwäldern, sowie durch einen hohen Anteil an Kalk als Ausgangsgestein charakterisiert sind. Hohe Anteile von nicht mykorrhizierten Arten finden sich dagegen in Regionen mit geringerem Jahresniederschlag und gemäßigten Temperaturunterschieden im Jahresgang. Dies erweitert das allgemeine Verständnis der Verbreitung beider Symbionten sowie der Verbindung von Mykorrhizierung und Umweltparametern innerhalb dieser Skala. Darüber hinaus macht die Dissertation die große Bedeutung des Mykorrhizierungsstatus für den Invasionserfolg gebietsfremder Pflanzenarten deutlich. Insgesamt haben mykorrhizierte Arten einen größeren Invasionserfolg als nicht-mykorrhizierte, wobei dieser bei fakultativ mykorrhizierten Arten am größten ist. Die Flexibilität in Bezug auf Mykorrhizierung ist dabei ein Konkurrenzvorteil gegenüber unflexiblen Pflanzenarten. Fakultativ mykorrhizierte, gebietsfremde Arten profitieren davon, situativ Photosyntheseassimilate an die Aufrechterhaltung der Mykorrhizierung oder in andere Pflanzenorgane wie Speicherorgane oder Spross- und Wurzelmetamorphosen allozieren zu können. Auch bei einheimischen Arten sind die fakultativ mykorrhizierten Pflanzenarten diejenigen, die über das größte Areal innerhalb Deutschlands verbreitet sind. Allerdings findet man die beschriebenen Trade-offs tatsächlich nur bei gebietsfremden, nicht aber bei einheimischen Arten. Dies deutet zum einen darauf hin, dass sich beide Pflanzengruppen in ihrer Verbindung mit Mykorrhizapilzen unterscheiden und zum anderen, dass einheimische Arten in einer Weise von Mykorrhizierung profitieren, die unabhängig von solchen Verteilungsstrategien ist. Dies ist ein wichtiger Beitrag zum aktuellen Forschungsstand, da noch immer zur Diskussion steht, ob gebietsfremde Pflanzenarten in anderer Weise mit Mykorrhizapilzen verbunden sind als einheimische oder nicht.

Die vorliegende Dissertation zeigt zusammenfassend, dass die Einführung des Mykorrhizierungsstatus von Pflanzen in großskalige Studien mit einer großen Anzahl von Arten einen begründeten und wichtigen Zugewinn für das Verständnis von Pflanzenverbreitungen und dem Invasionserfolg gebietsfremder Arten bietet. Dies gilt auch im Hinblick auf die aktuell überwiegend genutzten funktionellen Pflanzeneigenschaften, zu denen der Mykorrhizierungsstatus eine sinnvolle Ergänzung darstellt. So kann zukünftig die Allgegenwärtigkeit der Symbiose und ihr Einfluss auf die Zusammensetzung von Pflanzengemeinschaften in merkmalsbasierten Analysen berücksichtigt werden. Der makroskopische Blickwinkel der vorliegenden Arbeit ist ein wichtiger Beitrag zur Erweiterung des Verständnisses der gegenseitigen Beeinflussung der Symbionten und ergänzt die vorherrschenden reduktionistischen Ansätze in mykorrhiza-ökologischen Studien. Während kleinskalige Untersuchungen geeignet sind um die Effekte von Mykorrhizierung auf die Physiologie einzelner Pflanzenindividuen zu ergründen, sind Untersuchungen großer Skalen besser dazu geeignet, die Symbiose mit ganzheitlichen Ökosystemfunktionen zu verknüpfen. Mit der Betrachtung von solch größeren Skalen und höheren Ebenen der Pflanzenorganisation ergibt sich somit die Möglichkeit, generelle Grundsätze bezüglich der Rolle von Mykorrhizierung für die Ökologie von Pflanzen aufzudecken. Die vorliegende Arbeit hebt dabei den Mykorrhizierungsstatus als wichtige Charakteristik der Symbiose zwischen Pflanzen und Mykorrhizapilzen hervor und zeigt somit eine Möglichkeit auf, diese Symbiose als Pflanzeneigenschaft in derartige Analysen aufzunehmen.

CHAPTER 1

GENERAL INTRODUCTION

CHAPTER 1: General Introduction

The importance of mycorrhizal symbioses in plant ecology

Mycorrhizas are of crucial importance for the organisation of terrestrial plants across all hierarchical levels, finally affecting ecosystems as a whole (Read, 1991; Smith and Read, 2008). The symbiosis is predominantly based on the mutual exchange of nutrients. While fungi gain carbon from plants, nutrients transferred from fungi to plants via external hyphae mainly include soil-derived phosphorus and nitrogen (but also trace elements; Smith and Smith, 2011a; van der Heijden et al., 2015). The symbiotic relationship between terrestrial plant roots and mycorrhizal fungi (MF) is of ancient origin and co-evolved in continuous interaction with their abiotic and biotic environment over at least 450 million years (Simon et al., 1993; Redecker et al., 2000). MF are considered as the most abundant plant mutualists and have been highlighted as keystone symbionts (O'Neill et al., 1991). Being mycorrhizal is the condition of the large majority of vascular plants under most ecological conditions on earth (Brundrett, 2009); being non-mycorrhizal is the exception. The unique position of the mycorrhizal symbiosis has been perfectly emphasised by the committee of the International Bank of Glomeromycota (1993): "The study of plants without mycorrhiza is a study of artefacts; the majority of plants, strictly speaking, do not have roots - they have mycorrhizas."

Several types of mycorrhizas are distinguished (Table 1). While arbuscular mycorrhizas are formed by plant species across all phyla and biomes (Treseder and Cross, 2006; Smith and Read, 2008) and dominate phosphorus-limited vegetation on mineral soils at lower latitudes, ectomycorrhizas are mainly developed by trees in temperate and boreal regions with low concentrations of inorganic nitrogen in the soil (Aerts, 2002). Additionally, there are two types of mycorrhizas that are specialised to a greater extent: ericoid mycorrhizas are the dominant type in most heathland ecosystems, while orchid mycorrhizas are formed by the highly diverse plant family *Orchidaceae*. All members of this plant family share the nature of being depend on the provision of nutrients by MF during early seedling development (Smith and Read, 2008). Roughly 10% of plant species are described as non-mycorrhizal, a condition that presumably evolved several times and which occurs among mosses, ferns as well as distantly related families of angiosperms, predominantly *Brassicaceae*, *Caryophyllaceae*, and *Cyperaceae*. Several factors may have led to the loss of mycorrhizal dependency: adaptation to aquatic habitats, or growth in nutrient rich, extremely nutrient poor or disturbed environments (Smith and Read, 2008). Non-mycorrhizal plant species are still most abundant in habitats with these characteristics (Lambers and Teste, 2013) and utilise alternative nutritional strategies such as parasitism, carnivory or the formation of cluster roots (Brundrett, 2009).

Table 1: Types of mycorrhizas with estimated numbers of associated plant and fungal species (modified from van der Heijden et al., 2015).

Mycorrhizal type	Major group of plant symbionts	Number of plant species hosting mycorrhizal fungi	Fungal identity	Estimated number of fungal taxa
Arbuscular mycorrhiza	Most herbs, grasses, and many trees, many hornworts, and liverworts	200000	*Glomeromycota*	250-350[a]
Ectomycorrhiza	*Pinaceae* and primarily angiosperms (mostly shrubs and trees) of temperate regions, some liverworts	6000	*Basidiomycota* and *Ascomycota*	20000
Orchid mycorrhiza	Orchids	20000-35000	*Basidiomycota*	25000
Ericoid mycorrhiza	Members of the *Ericaceae*, some liverworts	3900	Mainly *Ascomycota*, some *Basidiomycota*	>150
Non-mycorrhizal plant species	*Brassicaceae*, *Caryophyllaceae*, *Crassulaceae*, *Cyperaceae*, *Orobanchaceae*, etc.	51500	-	-

[a] See Kivlin et al. (2011) for alternative estimates of numbers of arbuscular mycorrhizal fungal taxa (up to ~1400 species).

The arbuscular mycorrhizal symbiosis holds an exceptional position within the different types of mycorrhiza. Arbuscular mycorrhizal fungi (AMF) are assumed to have the longest possible joint history with terrestrial plants, as they supposedly enabled vascular plants to conquer terrestrial habitats (Pirozynski and Malloch, 1975; Brundrett, 2002; Wang and Qiu, 2006). Today about 80% of all described plant species are potential hosts for a comparatively low number of ca. 250 morphospecies (Redecker et al., 2013; Schüßler, 2016) and 350 identified molecular species of AMF (Öpik et al., 2013). All of these species are assigned to the phylum *Glomeromycota* (Schüßler et al., 2001) and show a low degree of endemism even across continents (Davison et al., 2015). Even if we consider the biological species concept to be inappropriate for classification of the clonal and asexual AMF (Smith and Read, 2008), the number of species will not reach the magnitude of the number of plant species, suggesting a low specificity of the symbiosis and high functional redundancy of AMF (Klironomos et al., 2000). Generally, AMF have relatively limited and ineffective dispersal mechanisms (Smith and Read, 2008) and therefore benefit from such a low specificity towards plant hosts, enabling them to access photosynthates from a wide range of host species. Overall, the pronounced intimate character of the AMF-plant-relationship advances the interest on arbuscular mycorrhizas in plant ecology. Therefore, the arbuscular mycorrhizal symbiosis is a focal point in studies investigating mycorrhizal ecology and will also be the main focus of the present thesis. From a plant's perspective, the arbuscular mycorrhizal symbiosis has been shown to increase water availability (Augé, 2001; Jayne and Quigley, 2014), to enhance biomass productivity (Klironomos et al., 2000; Lekberg and Koide, 2005), to provide soil health by regulating soil conditions (Rillig and Mummey, 2006; Bender et al., 2015), and to offer pathogen protection (Newsham et al., 1995; Veresoglou and Rillig, 2012) as well as protection against heavy metals (Hildebrandt et al., 2007). Besides the relationship of AMF to individual plants, several studies demonstrated their influence on plant communities (van der Heijden et al., 1998; Hartnett and Wilson, 2002; Klironomos et al., 2011), plant populations (Koide and Dickie, 2002), and whole ecosystems (Kivlin et al., 2011; Johnson et al., 2012; Yang et al., 2014).

Despite the dependence of plants on MF has been reported for more than one century (Frank and Trappe, 2005), soil processes in general as well as the mycorrhizal symbiosis in particular are still rarely considered in plant ecology (Fitter, 2005; Öpik et al., 2014). This is partly caused by the disconnected history of soil sciences and plant ecology, but is also induced by several other obstacles when studying mycorrhizas: (1) While plants are easily counted and measured under field conditions, measurements of fungal communities are laborious (Bever et al., 2001). AMF are rather cryptic organisms that are hard to detect (Krüger et al., 2012). They complete their life-cycle belowground and as obligate symbionts this is closely linked to plant hosts, which makes solitarily cultivation of AMF rather difficult (Hildebrandt et al., 2002; Smith and Read, 2008). Moreover, natural communities of AMF are mostly composed of uncultured taxa (Ohsowski et al., 2014) and it remains unknown whether these fungi functionally differ from cultivated ones (van der Heijden et al., 2015). (2) Studying both symbionts together is as elusive as studying them separately and particularly complex under field conditions (Klironomos et al., 2011). Although the global diversity of AMF species may be low, local species richness can be comparatively high, e.g., Oehl et al. (2010) found up to 30 fungal species together with 50 plant species at field sites of minor land-use intensity. Due to the widespread occurrence of mycorrhizas, non-mycorrhizal control sites are rare under field conditions but necessary to satisfy sound experimental designs. As yet, no completely satisfactory 'fungal-free' control treatments could be established in field experiments, as commonly applied fungicides are not MF-specific (Hartnett and Wilson, 2002). Consequently, these experiments cannot differentiate between the effects of MF reduction and other susceptible groups, such as plant pathogens or saprotrophs (Smith and Read, 2008). Furthermore, dual symbioses are possible (Smith and Read, 2008) and plant individuals (even of different species) may be connected via common mycelial networks (Barto et al. 2012). Additionally, it is suggested that mycorrhizas are not solely mutualistic but rather form a continuum from mutualism to parasitism (Johnson et al., 1997; Klironomos, 2003). Overall, the two symbiotic partners do not only mutually influence each other but are rather linked to a broad spectrum of interacting biotic and abiotic factors. All this lead to a strong focus on molecular studies paired with a rapid enhancement of molecular techniques (Martin et al., 2008, 2011; Lindahl et al., 2013; Oldroyd, 2013; Plett et al., 2014) as well as the common utilisation of pot and microcosm experiments (Read, 2002). These approaches undoubtedly promoted the knowledge on mycorrhizal ecology so far, still it remains uncertain whether they reassemble natural conditions. As (controlled) field experiments are limited and a disentanglement of the manifold drivers of the symbiosis is complex, studies of the co-variation of plants and their associated MF (and thereby variation of importance of the mycorrhizal symbiosis) are challenging, particularly when focussing on the variation at larger scales.

Macroecology of the mycorrhizal symbiosis

Although researchers are conducting macroecological studies for a long time (e.g., Lutz 1921; Preston 1948; MacArthur 1972) the term itself was just coined in 1989 (Brown and Maurer, 1989). Since then, macroecology has become an established subdiscipline of ecology. It aims at uncovering general patterns and mechanisms of 'ecological particles' (Brown, 1995) that emerge with large sample sizes, usually (but not exclusively) at large spatial or temporal scales. Typically, these 'ecological particles' are species but can also include populations, traits or other kinds of genetic or ecophysiological information. Macroecology is a rather method-based and non-experimental discipline with a main focus on ecological questions concerning the richness, abundance, and diversity of its study objects. The rapid establishment of macroecology as an independent discipline was therefore highly promoted by the availability of larger data sets (species distribution data, e.g., Atlas of European Breeding Birds - Hagemeijer and Blair, 1997, Atlas Florae Europaeae - Lahti and Lampinen, 1999; trait data, e.g., TRY - Kattge et al., 2011; climate data, e.g., CliMond - Kriticos et al., 2012; biodiversity data, e.g., GBIF, 2016) and strong advancements in computer technology and statistical methods (Blackburn, 2004; Dormann et al., 2007; Chave, 2013). Additionally, the societal and scientific interest in understanding patterns and processes at larger scales (up to global scales) fundamentally increased during the past decades, as more and more processes like climate and land-use change, habitat fragmentation, urbanisation, and the loss of biodiversity were found to (inter)act at these scales (Sala et al., 2000; Ellis and Ramankutty, 2008; IPCC, 2013). Certainly, macroecology has by far extended its original scope of dealing with “the division of food and space among species on continents” (Brown and Maurer, 1989) as well as exclusively describing patterns (Kühn et al., 2008; Smith et al., 2008; Beck et al., 2012). Macroecological frameworks developed general theories that for example emphasise the importance of metabolism in driving processes from cells to the entire biosphere (Metabolic Scaling Theory; West et al. 1997; Brown et al. 2004) or explain the assembly of ecological communities as a stochastic process involving species of the same trophic levels that are similar in their rates of dispersal, speciation, death, and birth (The Unified Neutral Theory of Biodiversity and Biogeography; Hubbell, 2001).

Brown (1995) saw the development of macroecology as a holistic counterbalance to the reductionist approaches increasingly used in plant ecology during the 1990s. He also emphasised the benefits of analyses of large-scale patterns as an important and fruitful extension to field and lab experiments on smaller scales. A macroecology of the mycorrhizal symbiosis, which might ignore fine-scaled details, may similarly help to overcome some of the experimental restrictions of field studies, especially across landscapes and geographical ranges. Certainly, macroecological and reductionist approaches are both valuable and can jointly increase the understanding of the symbiosis’ ecology, combining a small-scale ’bottom-up’ and a large-scale ’top-down’ approach (Blackburn and Gaston, 2003). Even though there has been a growing scientific interest in the macroecology of MF themselves (Treseder and Cross, 2006; Öpik et al., 2006, 2010, 2013; Davison et al., 2015), our understanding of the co-variation of plants and their associated MF at larger scales remains limited, leaving the potential of MF in determining plant distribution lie idle (Moora et al., 2011). Over the last ten years, comprehensive data sets of plants and whether they form mycorrhizal associations have been published (Wang and Qiu, 2006; Akhmetzhanova et al., 2012; Hempel et al., 2013). At the same time, distributions of plant species are relatively well studied and this provides an opportunity to study the co-variation of the mycorrhizal symbionts in macroecological frameworks. The present thesis aims at initiating such a plant mycorrhizal macroecology by crossing information on mycorrhizal associations of Central European plant species (Hempel et al., 2013) with information on their distribution at the German country scale obtained from FLORKART (provided by the German Federal Agency for Nature Conservation; http://www.floraweb.de), probably representing one of the best-studied regional floras worldwide.

Mycorrhizal traits in functional plant ecology

Plant ecologists classified plants by their characteristics early on (Schimper, 1903; Grime, 1974). However, with the beginning of this century, community ecology has experienced a so far lasting shift from focussing on species identities to focussing on species traits. Thereby, community ecologists aim at generality and predictability in explaining processes of community composition and ecosystem functioning (Lavorel and Garnier, 2002; McGill et al., 2006; Westoby and Wright, 2006). *Traits* are defined as “any morphological, physiological or phenological feature measurable at the individual level, from the cell to the whole-organism level, without reference to the environment or any other level of organisation” (Violle et al., 2007, p. 882). Furthermore, a *functional trait* is “any trait which impacts fitness indirectly via its effects on growth, reproduction, and survival” (Violle et al., 2007, p. 882). The functional trait approach has been extensively developed in plant ecology and benefited from the establishment of standardised protocols and methodologies (Cornelissen et al., 2003; Pérez-Harguindeguy et al., 2013). One of the advantages of using traits as entities of interest is the progress of moving from the idea of a community as filtered set of a species pool, to studying the actual filtering processes (Shipley et al., 2006; Knapp and Kühn, 2012; Laughlin et al., 2012). Next to addressing the functional composition and assembly of plant communities, trait information can be incorporated into models to describe species distributions in terms of environmental gradients (Bernhardt-Römermann et al., 2008; Dray and Legendre, 2008; Jamil et al., 2013). Facing global changes, this has led to a call for using functional traits at even larger scales to study, understand, and possibly predict changes in plant communities (and higher organisational levels) as well as their ecosystem functioning (Díaz et al., 2004; Violle et al., 2014).

Only a few plant mycorrhizal traits have been described so far, but have mostly been neglected in plant ecology (Moora, 2014). After establishing the manifold effects of mycorrhizas onto plants, these traits are certainly all covered by the definition of functional traits. Therefore, they are a promising tool for synthetic approaches studying the mycorrhizal symbiosis, which potentially identify relationships between mycorrhizal traits and life-history traits, habitat preferences, and distribution patterns of plant species (Moora, 2014). Plant mycorrhizal traits can be distinguished as follows (Moora, 2014): (1) *mycorrhizal type* - plant species are classified according to the mycorrhizal symbiosis they are part of (cf. Table 1), (2) *mycorrhizal dependency* - describes plant species’ growth response under mycorrhizal colonisation, (3) *mycorrhizal flexibility* - depicts the ability of plant species to grow either (a) with or without mycorrhiza (mycorrhizal status OM or

NM, see below) or (b) can flexibly do both (status FM, see below). (4) The basis of each analysis in this thesis will be the *mycorrhizal status* of plant species in Germany obtained from the MycoFlor data base (Hempel et al. 2013). Three groups of plant species can be distinguished according to their mycorrhizal status: (a) obligate plant species (OM) that are always found to be colonised by MF, (b) facultative plant species (FM) that are colonised under some environmental conditions, but not colonised under others, and (c) non-mycorrhizal plant species (NM), which are never found to be colonised by MF (Smith and Read, 2008; Moora, 2014). It is important to note that the plant mycorrhizal status does not give direct information on the functional significance of mycorrhizal colonisation of a given species' individuals at a specific location. It rather refers to the mere presence/absence of fungal colonisation and can be used as a proxy for the potential importance of mycorrhizal symbiosis for plants at species level. It hence is a functional trait of a plant species rather than depicting the fungal characteristics.

The reasons for sporadic mycorrhizal colonisation, i.e., mycorrhizal flexibility and the underlying regulatory processes in FM plant species are poorly understood. Plants usually have reduced levels of root colonisation in highly fertile soils or in environments of low light intensities and low carbon availability, which demonstrates that certain plant species are able to regulate the symbiosis under varying conditions (van der Heijden et al., 2015). This is especially true in arbuscular mycorrhizas, as AMF are obligatory dependent on their plant hosts. As the symbiotic partners exchange goods, the symbiosis has been described as a biological market (Selosse and Rousset, 2011). However, considering the existence of common mycelial networks (Barto et al., 2012), as well as the described mutualism-parasitism continuum (Johnson et al., 1997), this description may be inappropriate to model the symbiosis (Grman et al., 2012). Nevertheless, if species differ in their ability to grow with and without MF and to reduce their allocation to non-beneficial AMF, these differences may affect the distribution and abundance of plants (Grman, 2012). This may finally affect the set of traits characterising FM plant species. In fact, plant traits are not independent of each other, but vary and correlate jointly due to environmental conditions, evolutionary history, and biophysical constraints or trade-offs in the allocation of matter and energy (Figure 1; Reich et al. 2003; Westoby and Wright 2006; Díaz et al. 2016). Following that, trait interactions have been shown to allow implications of underlying ecological strategies (Küster et al., 2008). As already presented, the mycorrhizal symbiosis potentially affects the nutrient uptake and carbon economy of plant species (van der Heijden et al., 2015). Depending on mycorrhizal type, up to 90% of the plant's phosphorus as well as a significant amount of its nitrogen uptake can be attributed to MF (Hobbie and Hobbie, 2008; Smith and Smith, 2011a). In turn, they consume up to 50% of a plant's net primary production (Hobbie and Hobbie, 2008). Thus, trade-offs between mycorrhizal status and the expression of other plant traits, particularly those that require further plant investment, can be expected (Peat and Fitter, 1993; Reinhart et al., 2012). Grman (2012) suggests that storage organs and retention of the mycorrhizal symbiosis may represent competing carbon sinks and therefore different ecological strategies, in which FM plants hold the advantage of the ability to choose the strategy or property they invest in. Plant species were shown to be colonised by AMF at a lower rate, if they acquire patchily distributed nutrients via clonal growth instead of mycorrhizal colonisation (Onipchenko and Zobel, 2000). Moreover, it has been suggested that vegetative and reproductive characteristics of plants change with AMF association (Philip et al., 2001; Varga, 2010); with non-mycorrhizal species producing smaller seeds (Peat and Fitter, 1993). Further, plant species with thick and slow-growing roots, which are abundantly covered by root hair, are known to rely considerably more on MF than plants with fine, and fast-growing ones, covered by less root hair (Baylis, 1970; Hetrick et al., 1992; Peat and Fitter, 1993; McCormack et al., 2014). Moreover, plant species with tap root architecture were reported to be more dependent on the symbiosis than plants with fibrous root systems (Yang et al., 2015). This indicates that highly branched roots and retention of the symbiosis may be alternative strategies for absorbing nutrients (Wilson and Hartnett, 1998).

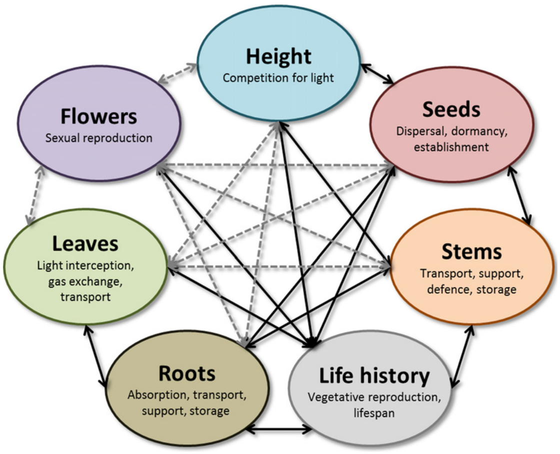


Figure 1: Scheme of plant organs or whole plant properties and their interrelations. Known verified relationships between circles are illustrated by black solid arrows; weaker relationships are shown as grey dashed arrows. The importance of the mycorrhizal symbiosis is insistently emphasised, if we are aware of the fact that roots of the great majority of described plant species are affected by MF, and therefore substitute 'Roots' with 'Mycorrhizas' in this scheme (modified from Laughlin, 2014).

Mycorrhizas and alien plant invasion

Due to the current process of globalisation, species easily surmount biogeographical barriers that prevented them from extending their natural distribution ranges in the past (Mack et al., 2000; Pyšek et al., 2010; van Kleunen et al., 2015). Undoubtedly, species experience a much faster pace of spread along transit pathways of global markets and travel than they have ever had historically (Hulme, 2009; Pyšek et al., 2010; Seebens et al., 2015). Due to the anthropogenic interferences on a global scale, species (no matter if native or unintentionally or intentionally introduced) are now co-occurring, which would have not been the case without these interferences (Mack et al., 2000; Hobbs et al., 2006). Although research on biological invasions has a long tradition (Darwin, 1859; Elton, 1958), the threats that the introduction of alien and invasive species bear for global biodiversity have not been identified much before the 1990s (Drake et al., 1989; Sala et al., 2000). With increasing concern about invasive alien plant species' effects on native plant species, communities, ecosystems as well as their economic consequences (Vilà et al., 2010, 2011; Simberloff et al., 2013), the common interest in studying processes underlying successful invasion has highly increased. Although a large body of theories has been developed and general principles have been established (Catford et al., 2009; Jeschke et al., 2012), the overall understanding of processes driving biological invasions is still limited (Richardson and Pyšek, 2012; Kueffer et al., 2013). Invasion ecology still lacks explanations for underlying mechanisms (Levine et al., 2003) and struggles with strong context dependency in biological invasions (Heger et al., 2013).

There are several ways to classify alien plant species while studying their impact and characteristics: (1) *by residence time*: The discovery of the Americas marks a profound break in the history of alien species, due to a strong increase in global species interchange, mostly unidirectional from Europe to the Americas (di Castri, 1989). Hence, the distinction between archaeophytes, i.e., the species introduced to Europe before 1500, and neophytes, i.e., the ones introduced after 1500, is common practice (Pyšek et al., 2004). Both groups of alien plant species have been shown to respond differently to environmental conditions (Pyšek et al., 2005) and to differ in association with habitat and trait characteristics (Pyšek et al., 2005; Knapp and Kühn, 2012). (2) *By invasion stage*: Plant invasions are dynamic processes and represent a sequence of different stages (Richardson et al., 2000a; Milbau and Stout, 2008; Blackburn et al., 2011). First, the plant or its propagules get transported to the new environment and the alien species occurs either only in cultivation or casually in the wild. Second, the species (or rather some individuals) successfully survives in the new habitat, overcomes certain abiotic and biotic filters and establishes first self-reproducing populations; the species gets naturalised. At a third stage, the alien plant species starts to spread and establish stable populations across large distances; the species' range expands, it becomes invasive. As different processes can affect the different stages, it has been suggested to discriminate species according to their stages of invasion while analysing invasion success (Pyšek et al., 2008, 2009). With regard to the mycorrhizal symbiosis, it has been proposed that the functional importance of colonisation by MF may change with the respective invasion stages of the host plant (Shah et al., 2009). Usually seedlings benefit more from the symbiosis than adult plants (Jones and Smith, 2004), providing large effects on seedling establishment (van der Heijden and Horton, 2009; Wurst et al., 2011; Koorem et al., 2012).

Next to the susceptibility of an ecosystem (invasibility), the invasion success of alien plant species depends on their trait characteristics (invasiveness; Lonsdale 1999). Therefore, functional traits got into the focus of interest, as they represent the characteristics of alien and invasive species and have been identified as a useful tool to overcome context dependency irrespective of species identity. A set of functional plant traits known to promote plant invasion has been already identified (e.g., Küster et al. 2010; van Kleunen et al. 2010; Pyšek et al. 2012, 2015). However, an interest in mutualistic interactions and their impact on plant invasion success has emerged (Richardson et al., 2000b; Traveset and Richardson, 2014), as they bring together the concepts of invasibility (facilitated by mutualists of the receiving habitat) and invasiveness (exerted by introduced mutualists). The mycorrhizal symbiosis is one of the mutualistic interactions that attracted the attention of invasion ecologists (Reinhart and Callaway, 2006; Pringle et al., 2009; Shah et al., 2009; Bunn et al., 2015). On a world-wide basis, phosphorus and nitrogen are crucial limiting resources for plants and it has been established that soil nutrient levels play an important role in determining the invasibility of a certain habitat or community (Davis et al., 2000; Blumenthal, 2005). Although the mycorrhizal symbiosis strongly affects the availability of these nutrients, the consideration of mycorrhizal traits in invasion ecology of alien plant species is still in its infancy. It is an ongoing debate whether alien plants benefit from being mycorrhizal, or if it constrains their establishment and spread in new regions. The importance of MF for plant invasion success may be identified by studying the mycorrhizal status or mycorrhizal dependency of alien plant species as well as their ability to alter the MF community in the new environment (Lekberg et al., 2013). Accordingly, several possible hypotheses have been identified (Pringle et al., 2009; Shah et al., 2009): (1) Non-mycorrhizal invaders reduce the fungal abundance which in turn negatively affects mycotrophic native plants ('Degraded mutualism hypothesis'; Vogelsang and Bever 2009; Johnson et al. 2013). This scenario is possible, if native plants are more dependent on the mycorrhizal symbiosis than alien plants, and/or when alien species directly alter mycorrhizal communities in the new environment (Hawkes et al., 2006; Mummey and Rillig, 2006). (2) Invasiveness is enhanced due to an encounter of better mutualists in the exotic than the native range ('Enhanced mutualism hypothesis'; Reinhart and Callaway 2006; Sun and He 2010). (3) Invasions are inhibited due to the absence of specific fungal partners (Nuñez et al., 2009; Dickie et al., 2010). Therefore, alien plants have most likely been suggested to be arbuscular mycorrhizal due to the low specificity of this mycorrhizal type, whereas the lack of symbionts is proposed to be a major barrier for ectomycorrhizal plants (Richardson et al. 2000b; but see Bogar et al. 2015). Nevertheless, due to the increasing joint transport of soil and soil mutualists, several other scenarios become possible (Figure 2).

A few case studies report positive impacts of the mycorrhizal symbiosis on the growth and the development of alien plant species, resulting in a competitive advantage over native species (Fumanal et al., 2006; Chmura and Gucwa-Przepióra, 2012; Sun and He, 2010). In a meta-analysis conducted by Bunn et al. (2015), the authors found no positive correlation between arbuscular mycorrhizal colonisation and the growth response of alien plants. However, their colonisation by MF was increased when growing in direct competition with natives. Whereas experimental, mostly small-scale studies report the majority of alien plant species to be mycorrhizal (Štajerová et al., 2009; Moora et al., 2011; Nuñez and Dickie, 2014), studies comparing large numbers of plant species report contradictory results. In comparison to the native flora of Great Britain, Fitter (2005) found alien plant species to be more likely from families that typically associate with MF. Pringle et al. (2009) reported the opposite pattern for alien plant species in California and Hempel et al. (2013) showed that neophytes in Germany are more frequently obligatorily associated with MF compared to archaeophytes and native plant species. Still, there is a lack of studies which investigated the mycorrhizal status of alien plants in relation to their stages of invasion. Alike, research on ecological strategies involving the interaction of mycorrhizal status and other plant functional traits is still missing. This thesis aims to fill these gaps.

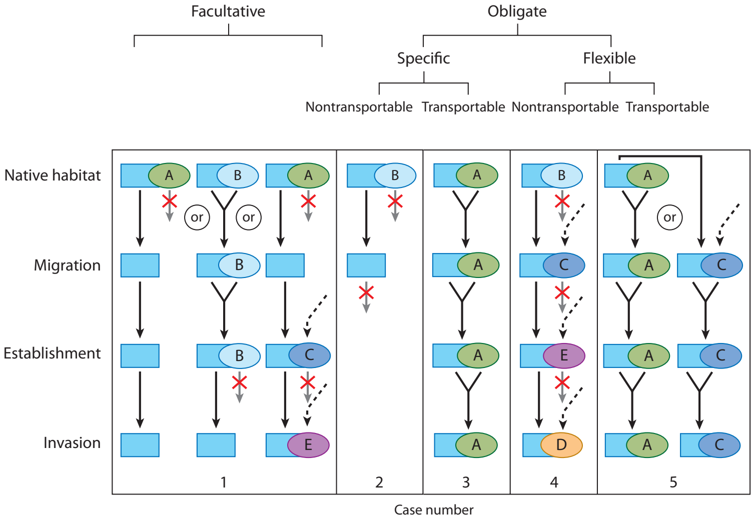


Figure 2: Possible scenarios in plant invasions with respect to mycorrhizas. Squares depict a plant and ovals depict an associated root fungus. Colours and numbers designate different species. For example, the facultative case depicts a plant species that can grow without symbionts or associates with a variety of MF; it emigrates alone or is planted in a novel habitat as a seedling with or without its symbiont, and may subsequently establish and spread without fungal associates, or with the original, or a third or fourth mycorrhizal species (Case 1). In contrast, when a plant associated in an obligate, specific, and non-transportable mycorrhizal association is introduced to a novel habitat without its mycorrhizal fungus, it cannot establish or spread (Case 2). Plants associated in obligate symbioses but moved with mycorrhizal associations intact may more easily spread because the symbiosis is transportable (Case 3). Plant species that are generalists and flexible in their mycorrhizal partner will associate with a diversity of MF and may also spread (Case 4). Obligate and flexible plant species may be moved with intact symbioses but will also spread with local fungal symbionts (Case 5). Note that ’flexible’ in this case does not mean flexibility in their mycorrhizal status, but their mycorrhizal partner (modified from Pringle et al., 2009).

Objectives and thesis outline

As presented so far, the upmost importance of mycorrhizas for plant ecology is well known and has already been studied for more than a century. Nevertheless, studies addressing plant mycorrhizal ecology at larger scales remain rare and mycorrhizal traits are often neglected in analyses of plant distributions as well as plant community assembly. A plant mycorrhizal macroecology is an essential approach to deepen our understanding of the co-variation of plants and their fungal symbionts and will give insights from a position unlike the reductionist approaches dominating the field. Likewise, studying large numbers of alien plant species with (now) known mycorrhizal associations and in relation to other plant functional traits, as well as in combination with already established plant distribution data, may broaden our knowledge of the role of mycorrhizas during plant invasions. Nevertheless, at this point it is important to note that the approach presented in this thesis is a plant-centric generalisation, which does not aim to reveal (ecophysiological) mechanisms affecting individual plants and fungi in detail, but rather plant ecological strategies involving the symbiosis.

In **chapter 2** I present results from an analysis regarding the spatial distribution patterns of plants' arbuscular mycorrhizal status at the German country scale. At this scale, I investigated whether plant species assemblages are composed of different proportions of species differing in their arbuscular mycorrhizal status, and whether the variation of these proportions can be explained by the geographical variation of ecological and environmental predictors related to climate, land use, and geology.

Based on the finding that neophyte plant species are more frequently obligate mycorrhizal compared to archaeophytes and native plants (Hempel et al., 2013), I analysed in **chapter 3** whether the representation of plant species with different mycorrhizal status differs at several stages of the invasion process. Furthermore, I used generalised linear models to explain the occupied geographical range of these neophyte species in Germany by incorporating interactions of mycorrhizal status and other functional plant traits. Subsequently, I investigated potential trade-offs and ecological strategies relating the mycorrhizal status to traits of morphology, reproduction, and life history.

The study presented in **chapter 4** builds on the previous analyses of chapter 3. Here, I investigated whether the detected trade-offs involving neophyte plants' mycorrhizal status are likewise present in archaeophytes and native plants, although they differ in their composition of proportions of mycorrhizal status (Hempel et al., 2013).

CHAPTER 2

Distribution Patterns of Arbuscular Mycorrhizal and Non-Mycorrhizal Plant Species in Germany

Andreas Menzel, Stefan Hempel, Ameur M. Manceur,
Lars Götzenberger, Mari Moora, Matthias C. Rillig,
Martin Zobel, and Ingolf Kühn

Perspectives in Plant Ecology, Evolution, and Systematics 21: 78-88 (2016)

CHAPTER 2: Distribution Patterns of Arbuscular Mycorrhizal and Non-Mycorrhizal Plant Species in Germany

Abstract

We analysed the spatial distribution patterns of plant arbuscular mycorrhizal status across an intermediate geographical scale (i.e., the country of Germany) and related this distribution of plant species arbuscular mycorrhizal status to environmental drivers. Three levels of arbuscular mycorrhizal status of plant species could be defined: (1) obligate arbuscular mycorrhizal species that are always colonised by mycorrhizal fungi, (2) facultative arbuscular mycorrhizal species that are colonised under some conditions but not colonised under others, and (3) non-mycorrhizal species that are never found to be colonised by arbuscular mycorrhizal fungi. We aimed to investigate whether plant species assemblages at the studied grid cell scale are composed of different proportions of species regarding their arbuscular mycorrhizal status, and whether the variation of these proportions can be linked to the geographical variation of ecological and environmental factors. We fitted a vector generalised additive model (VGAM) for log-ratios of proportions of plant species' arbuscular mycorrhizal status per grid cell (2859 grid cells, each c. 130 km^2). The spatially explicit plant arbuscular mycorrhizal status distribution model was based on environmental predictors related to climate, geology, and land use. The spatial distribution of plant arbuscular mycorrhizal status can be explained as a function of nine environmental predictors (D^2=0.54). Proportion of obligate arbuscular mycorrhizal plant species per grid cell increased with increasing temperature range, mean annual temperature, urban area, and area of lime as geological parent material and decreased with increasing area of mixed forest and coniferous forest. Annual temperature range was by far the most important predictor. These results extend the comparative context of former studies that established relationships between arbuscular mycorrhizal status and other plant characteristics at species level, including those describing species ecological requirements, to a context at the level of assemblages and species distributions. We encourage integrating plant mycorrhizal status as a functional trait in future macroecological analyses.

Keywords: arbuscular mycorrhiza, Central Europe, distribution model, MycoFlor, mycorrhizal status, vector generalised additive model

Introduction

Mutualistic associations formed by arbuscular mycorrhizal fungi (AMF) and terrestrial plants are ancient and probably have existed since vascular plants colonised terrestrial habitats (Pirozynski and Malloch, 1975; Brundrett, 2002). AMF are widely distributed across most terrestrial ecosystems (Öpik et al., 2006, 2013; Smith and Read, 2008; Davison et al., 2015) and potentially establish a symbiosis with approximately 75% of all vascular plant species (Smith and Read, 2008; Brundrett, 2009). Mycorrhizas are known to affect plant nutrition (Koide, 1991), to improve and regulate plant water status (Augé, 2001), to offer protection from pathogens (Veresoglou and Rillig, 2012), and to possibly enhance biomass productivity (Klironomos et al., 2000). Whereas the symbiosis is obligate for AMF, some terrestrial plant species and families have partly or entirely lost their ability to form mycorrhizal relationships (Fitter and Moyersoen, 1996; Brundrett, 2002). In principle, there are three levels of plant mycorrhizal status: (1) obligate arbuscular mycorrhizal plant species (OM) that are always colonised by AMF, (2) facultative arbuscular mycorrhizal plant species (FM) that are colonised under some conditions but not colonised under others and (3) non-mycorrhizal plant species (NM) that are never found to be colonised by AMF (Smith and Read, 2008; Moora, 2014). Thereby, OM and NM plant species are specialised regarding their mycorrhizal strategy, whereas FM plant species are generalists and show great differences in life-history trait characteristics compared with OM and NM species (Hempel et al., 2013).

Plant mycorrhizal status and plant mycorrhizal dependency (or responsiveness) are distinct plant traits not to be confused (Moora, 2014). A plant species' mycorrhizal status does not give direct information about functional significance of mycorrhizal colonisation of individuals of this species, but rather on the mere presence/absence of fungal colonisation among individuals of plant species. Thereby, it offers a coarse proxy for estimating the importance of the mycorrhizal symbiosis for a plant at species level. AMF-plant interactions are potentially of great importance in shaping the ecology of the partners and whole communities (van der Heijden et al., 2003; Klironomos et al., 2011). Although there are a few biogeographic studies of AMF on global scale (Treseder and Cross, 2006; Öpik et al., 2010, 2013; Kivlin et al., 2011; Davison et al., 2015), our understanding of the co-variation of plants and their associated mycorrhizal fungi (and thereby variation of importance of the mycorrhizal symbiosis) at larger scales remains quite limited. At the same time, distributions of plant species are relatively well studied and this provides an opportunity to study environmental drivers of the mycorrhizal symbiosis using plant mycorrhizal traits (e.g., mycorrhizal status) as a response variable in macroecological frameworks.

The recently published MycoFlor data base (Hempel et al., 2013) compiles information on plant mycorrhizal status for about half the species of the German flora (i.e., 1752 species; thus a major part of the Central European flora). It is publicly available and allows investigating whether plant species assemblages are composed of different proportions of plant species regarding their AM status, using available plant species distribution data. Hempel et al. (2013) showed that plant species with different mycorrhizal status are associated with different ecological requirements (i.e., species attributes). For example, using ecological indicator values of Ellenberg et al. (1992), they found that OM species tend to be associated with warmer, drier, and more alkaline habitats, whereas NM species are species of wet and disturbed habitats. Following these associations, we predict to find different spatial patterns of plant species assemblages composed of species with different arbuscular mycorrhizal status, which are based on the geographical variation of these ecological and environmental conditions. While Hempel et al. (2013) analysed species attributes (functional traits and species realised preference, i.e., having species as replicates), the aim of the present study was to test whether actual spatial distributions of proportions of OM, FM, and NM plant species exist (i.e., having spatial replicates). We used available literature information, including the findings reported by Hempel et al. (2013), to formulate predictions concerning the relationship between the distribution of plant species with different mycorrhizal status and actual environmental predictors (Table 1: environmental drivers; Table 2: ecological predictions) to extend the knowledge on this relationship in a spatial context. To test these predictions, we based a distribution model across ordnance survey maps at the German country scale (i.e., grid cells with a size of 10' (arc minutes) longitude × 6' latitude; circa 130km^2 each) on a set of environmental predictors. We aim to unravel whether the rather locally acting plant-AMF interactions have an impact on plant species distributions across a larger, intermediate geographical scale. Thereby, we aim to detect the underlying environmental drivers of different AM plant strategies. This will not only help to understand the macroecology of plant-fungi relationships, but will contribute to establish plants' mycorrhizal status as a functional trait in analyses related to plant assemblages.

Materials and Methods

Data sources

Plant species distribution data were compiled from FLORKART, a database of the German Network for Phytodiversity, provided by the German Federal Agency for Nature Conservation (http://www.floraweb.de). The spatial resolution is defined by grid cells with a size of 10' longitude × 6' latitude (arcminutes, i.e., c. 130km^2) resulting in 2995 cells for Germany. The database was assembled with the help of thousands of volunteer helpers, organised at a regional level. Therefore, mapping quality is heterogeneous across grid cells. To this end, we followed a procedure suggested by Kühn et al. (2006) by using 50 'control plant species' (which are considered to be ubiquitous) to characterise grid cells according to their data quality. Only grid cells containing at least 45 of these 50 species were considered during the analysis, finally resulting in 2859 cells.

We used the MycoFlor database (Hempel et al., 2013) to obtain information on mycorrhizal status per plant species. Although MycoFlor contains information on a range of mycorrhizal associations, we restricted the analysis to symbioses involving AMF, as they are the most cosmopolitan and largest group represented in MycoFlor. We then distinguished between OM, FM, and NM plant species. Information on plant mycorrhizal status within MycoFlor was verified and quality controlled. Successive citations were traced back and primary studies were counted to obtain information about data reliability. To assure appropriate data quality the authors recorded, whether the source of information originated from a journal listed in Web of Science, EBSCO, SCOPUS, CABI, or a book/book chapter from an international publisher as a proxy for data quality. In that case, they assumed the publications passed through a peer review process or similar robust quality assessment (Hempel et al., 2013). They furthermore used a reduced 'core data set', only including plant species with at least two primary literature references reporting their mycorrhizal status and fulfilling their criteria for data quality. Using this core data set, AM status information was available for a total of 1019 plant species (i.e., 39% of the plant species with distributional information in Germany according to FLORKART as a reference); 438 were OM, 485 FM, and 96 NM plant species. We assigned the NM status to strictly non-mycorrhizal plant species, i.e., non-arbuscular mycorrhizal species that may form dual symbiotic relationships with other mycorrhiza types (e.g., ecto- or ericoid mycorrhiza) were excluded to avoid confounding the analysis by incorporating other types of mycorrhizal interaction. By amending plant compositional data with AM status information, each grid cell was characterised by compositional data of three proportions - p(OM), p(FM), p(NM) - that sum up to 1.

For each cell we compiled data on climate, land use, and geology. Geological and pedological data were obtained from the Geological Survey Map of Germany (Bundesanstalt für Geowissenschaften und Rohstoffe, 1993). We used the covered area of geological substrate classes such as lime, sand, clay, and loess per grid cell. Land-use data were taken from CORINE land cover data sets (Statistisches Bundesamt, 1997). We included area of rivers, area of agricultural fields, urban area (sum of continuous and non-continuous urban areas classified by CORINE) as well as the area of deciduous (i.e., broad-leaved trees), mixed and coniferous forest stands as environmental predictors in the distribution model. We used mean annual temperature and mean annual within-year temperature range (1901-2000) as well as the mean annual precipitation and its range (1901-2000), provided by the European Union ALARM project (Fronzek et al., 2012; cf. Table 1). Each environmental predictor was centred by subtracting its mean and scaled by dividing the centred value by the standard deviation to ensure comparable effect sizes of the final distribution model. We assessed the collinearity of the selected environmental predictors prior to the analysis (Fig. S1) and only used predictors with τ<0.7 (Dormann et al., 2013).

Table 1: Summary of selected environmental predictors, their abbreviations, units (per grid cell), mean, standard deviation (sd), maximum values (max), minimum values (min), and data sources, i.e., CORINE Land Cover (CLC; Statistisches Bundesamt, 1997), EU project ALARM (ALA; Fronzek et al., 2012), and Geological Survey Map of Germany (GEO; Bundesanstalt für Geowissenschaften und Rohstoffe, 1993)

environmental predictor	abbreviation	source	unit	mean	sd	min	max
area of stream courses	stream area	CLC	km^2	0.2	0.7	0	7
area of deciduous forest stands	deciduous forest area	CLC	km^2	7	10	0	87
area of mixed forest stands	mixed forest area	CLC	km^2	7	10	0	97
area of coniferous forest stands	coniferous forest area	CLC	km^2	16	19	0	106
area of agricultural land use	agricultural area	CLC	km^2	58	31	0	123
area of urban land use	urban area	CLC	km^2	8	10	0	104
area of lime as geological parent material	lime area	GEO	km^2	6	19	0	135
area of loess as geological parent material	loess area	GEO	km^2	6	15	0	114
area of sand as geological parent material	sand area	GEO	km^2	45	41	0	135
area of clay as geological parent material	clay area	GEO	km^2	7	19	0	123
mean annual temperature (1901-2000)	mean temperature	ALA	°C	8.4	0.8	4.2	10.6
mean annual temperature range (1901-2000)	temperature range	ALA	°C	25.1	1.7	21.1	29.1
mean annual precipitation (1901-2000)	mean precipitation	ALA	mm	724	130	480	1384
mean annual precipitation range (1901-2000)	precipitation range	ALA	mm	40	13	23	104
number of CORINE land-use classes	number of land-use types	CLC	-	10	2.7	1	23
number of classes of geological parent material	number of geological parent materials	GEO	-	7	2.5	1	24
number of soil types	number of soil types	GEO	-	4	1.7	1	12

Table 2: Summary of predictions relating plant arbuscular mycorrhizal status and the environmental predictors selected for this study.

predictor	background and predictions
stream area	Occurrence of AMF in riparian systems is patchy in space (Harner et al., 2009) and time (Piotrowski et al., 2008; Harner et al., 2011) since local conditions can change dramatically. Consequently, we predict that in riparian ecosystems generalist FM plant species occur in greater proportion than specific OM and NM species.
deciduous, mixed, and coniferous forest area	The abundance of potential AM host plant species is greater in deciduous forest than in coniferous forest (Read, 1991; Lang et al., 2011). Plants grown with coniferous forest soil inoculum exhibit low root AMF colonisation (Moora et al., 2004) and diversity (Öpik et al., 2003). We expect that being FM is more viable than being OM in such conditions. Given that the presence of coniferous trees is associated with soil acidification (Augusto et al., 2003) we also expect fewer OM plant species in coniferous forests (Hempel et al., 2013). At the same time, there is no specific information about the occurrence of NM plant species in different forest types. We therefore predict that the proportion of OM plant species decreases along the transition from deciduous to coniferous forests, which might be associated with an accompanying increase of FM plant species.
agricultural area	Intensive agriculture as practiced in Central Europe shows negative effects on AMF diversity (Oehl et al., 2003, 2010). Main reasons are the supply of fertiliser (Johnson, 1993; Santos et al., 2006) and tillage activities, which rupture the AMF hyphal network (Jansa et al., 2002). In addition, agricultural practices fragment the landscape, leaving patchy fragments of the more natural plant communities. We therefore expect a higher proportion of NM plant species and a general decrease of OM species with increased agricultural land use.

continued on next page

predictor	background and predictions
urban area	(1) Urban areas are highly disturbed and fragmented environments (McDonnell and Pickett, 1990). The same plant species exhibit lower root colonisation by AMF in urban than in rural environment (Bainard et al., 2011). This could be due to increased nitrogen deposition in the soil (Egerton-Warburton and Allen, 2000), for instance caused by air pollution (Cairney and Meharg, 1999); various other factors (other types of pollution, mechanical disturbances) may be important. This may be associated with an increase in NM plant species with urbanity. (2) Urban areas are typically species rich (Kühn et al., 2004). Still, they show a larger share of alien plant species, compared with less urbanised or rural areas (Kühn and Klotz, 2006). As alien plant species are more frequently OM species (Hempel et al., 2013), an increase in OM species with increasing urbanisation is possible.
lime area, loess area, sand area, clay area	Different geological parent materials and the resulting soil types differ in soil pH, nutrient, and water availability. Soil conditions influence the distribution of both plant and AMF species. In particular, soil pH (Dumbrell et al., 2010) or soil type in general (Oehl et al., 2010) may be strong drivers of AMF community composition. Hempel et al. (2013) showed that OM plant species are more frequently those adapted to high pH, dry, and less fertile habitats. We predict that more fertile parent material like loess will lead to a lower proportion of OM species, whereas typically nutrient poor soils like sand will promote OM species instead. We predict that soils derived from lime rich parent material inhabit more OM species, as they show a high microbial and fungal activity due their high pH and saturation with calcium ions.
mean temperature	AMF grow better and show higher plant root colonisation rates in areas of higher temperatures (Tungate et al., 2007) and OM status is positively associated with species' preference of higher temperatures (Hempel et al., 2013). Plant roots show changes in morphology (Haugen and Smith, 1992), growth rate as well as longevity (Forbes et al., 1997) in relation to increased soil temperatures, which may be compensated by increasing growth of extraradical fungal hyphae. Consequently, we expect an increase in OM plant species under higher temperatures.

continued on next page

predictor	background and predictions
temperature range	High temperature variability influences the ecology of plant species and their fungal partners (Heinemeyer and Fitter, 2004). We predict a larger proportion of FM plant species in regions of larger temperature range, as this generalist strategy may allow a greater plant ecological amplitude.
mean precipitation	Plant productivity is often limited by water availability. AMF potentially improve individual plant water uptake by different mechanisms, e.g., by accessing small soil pores and increased absorption rates due to high density of fine hyphae (Augé, 2001) and may reduce plant stress in this way. Worchel et al. (2013) showed that the positive growth response of grasses to AMF increased under drought conditions and Hempel et al. (2013) found a positive association of OM species with their preference of drier habitats. We therefore predict a higher proportion of OM plant species in regions of less precipitation.
precipitation range	As OM plant species are positively associated with dry and NM species with wet conditions (Hempel et al., 2013) we expect a decrease of both statuses and an increase of FM species with an increased precipitation range.
no. of land-use and soil types, no. of geological parent materials	A more heterogeneous, patchy landscape, either due to diversity of land-use types, geological parent material or soil type classes, should promote a larger number of plant species due to a larger amount of distinctive habitats (Deutschewitz et al., 2003; Stein et al., 2014). Since we see no reason for a disproportioned advantage of any of the three statuses under such a scenario, we predict no correlation between any of the three status and grid cell heterogeneity.

Modelling compositional data and residual spatial autocorrelation

Dealing with compositional data poses the problem that by adding up to one, the proportions are not independent of each other. If one proportion decreases, another one has to increase. This so-called 'unit-sum-constraint' can be broken by replacing the observed proportions by logarithms of ratios (log-ratios; Aitchison, 1986; Billheimer et al., 2001; see Kühn et al., 2006 for details). We chose the total number of plant species with FM status as denominator and the other two statuses as numerators for both log-ratios. This resulted in one log-ratio log(OM/FM) representing the relative proportion of obligate arbuscular mycorrhizal plant species and another log-ratio log(NM/FM) representing the relative proportion of non-mycorrhizal plant species. Mathematically, the choice of numerator and denominator is arbitrary and does not affect the results (Aitchison, 1986). Ecologically, however, the choice of numerator and denominator affects the interpretation of the model. We chose OM and NM species as numerators, because we were especially interested in the obligate plant strategies regarding the symbiosis (both, obligate mycorrhizal and obligate non-mycorrhizal). As FM plant species represent the ecologically flexible, intermediate position, we identified this status as the most suiting denominator.

We used a vector generalised additive model (VGAM) – a non-parametric extension of generalised linear models (Yee and Mackenzie, 2002) – for distribution modelling, including a multinomial distribution family (cf. Lososová et al., 2012) that accounts for the described log-ratio procedure. Unlike ordinary GAMs (or GLMs), this technique allows modelling the two selected log-ratios in one model. For each of the 17 initially selected environmental predictors, (vector) smooth terms with a maximum of two degrees of freedom were allowed, i.e., a smoothing function up to a quadratic function per predictor fit. Following the initial predictions, the predictors were backward-selected based on error probabilities. Predictors with one significant p-value ($p \leq 0.05$) for at least one log-ratio were kept in the model. The VGAM was implemented using the respective R package (Yee, 2010).

We used a residuals autocovariate (RAC) approach (Crase et al., 2012) to account for spatial autocorrelation (SAC) within the residuals of the distribution model. This approach derives an autocovariate from the residuals of the environment-only model, instead of deriving it from the response variable itself. Therefore, this approach does not suffer from biased parameter estimates reported in Dormann et al. (2007). As we model two log-ratios, this results in two VGAM residuals per grid cell. Hence, two autocovariates accounting for spatial dependencies were calculated using a mean focal operation including the maximum eight neighbouring cells of each grid cell. Afterwards, both RACs (one for each log-ratio) were added as predictors accounting for residual spatial autocorrelation to the backward-selected environment-only model. A second backward selection process was run to control for changing significance levels of the pre-selected predictors after adding the RACs.

The model's ability to account for SAC is indicated by the reduction of SAC in model residuals. SAC was measured by calculating Moran's Index and plotting these values as correlograms. P-values indicating whether the Moran's I for each distance class where significantly different from zero were sequentially adjusted using Holm's procedure (Holm, 1979). For both, Moran's I calculation and correlogram plotting, we used the package 'spdep' (Bivand et al., 2013). The RAC approach successfully reduced the residual SAC of our distribution model. Subsequently, the residuals could not be distinguished from the pattern expected under a white noise process, as the variance appeared homogenous and the autocorrelation was reduced to a sufficient level. We partitioned the explained variance of our final model into the variance that is explained by the environment-only and by the residual autocovariate-only model. We subtracted the overlap in explained variance of both of these models from the final model's explained variance, including the environmental predictors and residual autocovariates to obtain an adjusted explained variance D^2 (Borcard et al., 1992). We assessed the robustness of the final model with five-fold cross-validation. For this purpose, the data set of 2859 grid cells was split into five equally large, mutually exclusive, and non-random subsets. Thereby we assured to use the spatial heterogeneity in the data set for out-of-area predictions during the cross-validation (Wenger and Olden, 2012). We split the data from west to east, as stronger environmental gradients in Germany are acting from north to south.

As the graphical VGAM output illustrates the relationship of both log-ratios only (Fig. S2), it is not distinguishable whether changes in both log-ratios with environmental predictors are due to changes in OM and NM proportions, respectively, or due to a change in FM species proportion. Therefore, we present the model outcome using loess smoother functions, to illustrate the relationship of all three plant mycorrhizal statuses at the same time. Nevertheless, the VGAM approach does not allow presenting any kind of significance test for the FM proportions.

All statistical analyses were performed using the statistical software R (version 3.0.2; R Development Core Team, 2013).

Results

Nine of the initially 17 environmental predictors remained in our final distribution model of plant species AM status across Germany (Fig. 1), additionally including the two residual autocovariates. These nine predictors were at least significant for one of the two log-ratios (Table 3). The final model explained 54% of the variation within the distribution data, corrected for the overlap in explained variance by environmental (D^2=0.47) and residual spatial covariates (D^2=0.39). Predictions showed a root-mean-square error (RMSE) of 0.013 (cross-validated: 0.021) for proportions of OM, 0.013 (cross-validated: 0.021) for proportions of FM, and 0.007 (cross-validated: 0.009) for proportions of NM plant species

(Table S1). The assemblages of proportions of plant species with different mycorrhizal status (Fig. 2) followed a non-random spatial distribution, even at the chosen intermediate geographical extent with a relatively coarse grid cell grain of c. 130km^2 per cell. OM plant species proportion was highest along the Central and South-Western basins of Germany and lowest in the North German Plain, drawing a clear line along the upland range (Fig. 2). The relative FM plant species distribution showed an opposing pattern with highest values in the North German Plain and along the low mountain ranges at the Czech-German border (Fig. 2). NM plant species proportion was highest in northern Germany, but showing a relatively scattered distribution within the rest of Germany (Fig. 2).

Table 3: The relationship between the two chosen log-ratios representing the ratio of obligate to facultative arbuscular mycorrhizal plant species log(OM/FM) and the ratio of non-mycorrhizal to facultative arbuscular mycorrhizal plant species log(NM/FM) as well as the nine final environmental predictors using a vector generalised additive model (VGAM). Degrees of freedom; approximate chi-square values as measure of non-parametric effect size and significance levels: $0.01<p\leq0.05$ *, $0.001<p\leq0.01$ **, $p\leq0.001$ ***

predictor	df	chi-square	p(chi)
mixed forest area: log(OM/FM)	1	5	*
mixed forest area: log(NM/FM)	1	1	-
coniferous forest area: log(OM/FM)	1	23	***
coniferous forest area: log(NM/FM)	1	1	-
urban area: log(OM/FM)	1	7	**
urban area: log(NM/FM)	1	4	-
lime area: log(OM/FM)	1	10	**
lime area: log(NM/FM)	1	1	-
mean temperature: log(OM/FM)	1	4	*
mean temperature: log(NM/FM)	1	1	-
temperature range: log(OM/FM)	1	53	***
temperature range: log(NM/FM)	1	9	**
mean precipitation: log(OM/FM)	1	1	-
mean precipitation: log(NM/FM)	1	8	**
precipitation range: log(OM/FM)	1	6	*
precipitation range: log(NM/FM)	1	2	-
number of soil types: log(OM/FM)	1	1	-
number of soil types: log(NM/FM)	1	5	*

Annual temperature range was the only predictor significantly explaining the distribution of both statistically modelled log-ratios and it was by far the most powerful environmental predictor in terms of effect size (Table 3). With an increase in temperature range per grid cell we detected a strong relative increase in OM species (Fig. 1). NM plant species proportion was highest at low and high values of temperature range, having

Table 4: Concordance of the relationship of initial environmental predictors to one of the three plant arbuscular mycorrhizal statuses (OM: obligate arbuscular mycorrhizal, FM: facultative arbuscular mycorrhizal, NM: non-mycorrhizal) derived from our initial predictions (cf. Table 1) and compared to the outcome of the vector generalised additive model.

	predictions			model outcome		
predictor	OM	FM	NM	OM	FM	NM
stream area	-	↑	-	-	-	-
deciduous forest area	-	-	-	-	-	-
mixed forest area	↓	-	-	↓	-	-
coniferous forest area	↓	-	-	↓	-	-
agricultural area	↓	-	↑	-	-	-
urban area	↑	-	↑	↑	-	-
lime area	↑	-	-	↑	-	-
loess area	↓	-	-	-	-	-
sand area	↑	-	-	-	-	-
clay area	-	-	-	-	-	-
mean temperature	↑	-	-	↑	-	-
temperature range	-	↑	-	↑	-	↓
mean precipitation	↓	-	-	-	-	↓
precipitation range	↓	↑	↓	↑	-	-
number of land-use types	-	-	-	-	-	-
number of geological parent materials	-	-	-	-	-	-
number of soil types	-	-	-	-	-	↑

a minimum in intermediate annual temperature range (Fig. 1). Area of mixed forest and area of coniferous forest per grid cell were significantly negatively related to the relative occurrence of OM plant species (Fig. 1). An increase in urban area per grid cell resulted in an increase in OM proportions (Fig. 1). Likewise, an increase in area of geological parental material originating from lime and mean annual temperature per grid cell were significantly positively related to the proportion of OM plant species (Fig. 1). Mean precipitation and the number of soil types were the two predictors exclusively explaining the distribution of NM plant species (Table 3). There was a strong decline of NM species proportion with an increase in mean precipitation, showing a peak in grid cell regions of low annual precipitation (Fig. 1). NM species proportion increased with an increasing number of soil types (Fig. 1). In regions of low annual precipitation range, there was a decrease in OM proportions. As the annual precipitation range per grid cell increased, this relationship slightly flipped (Fig. 1).

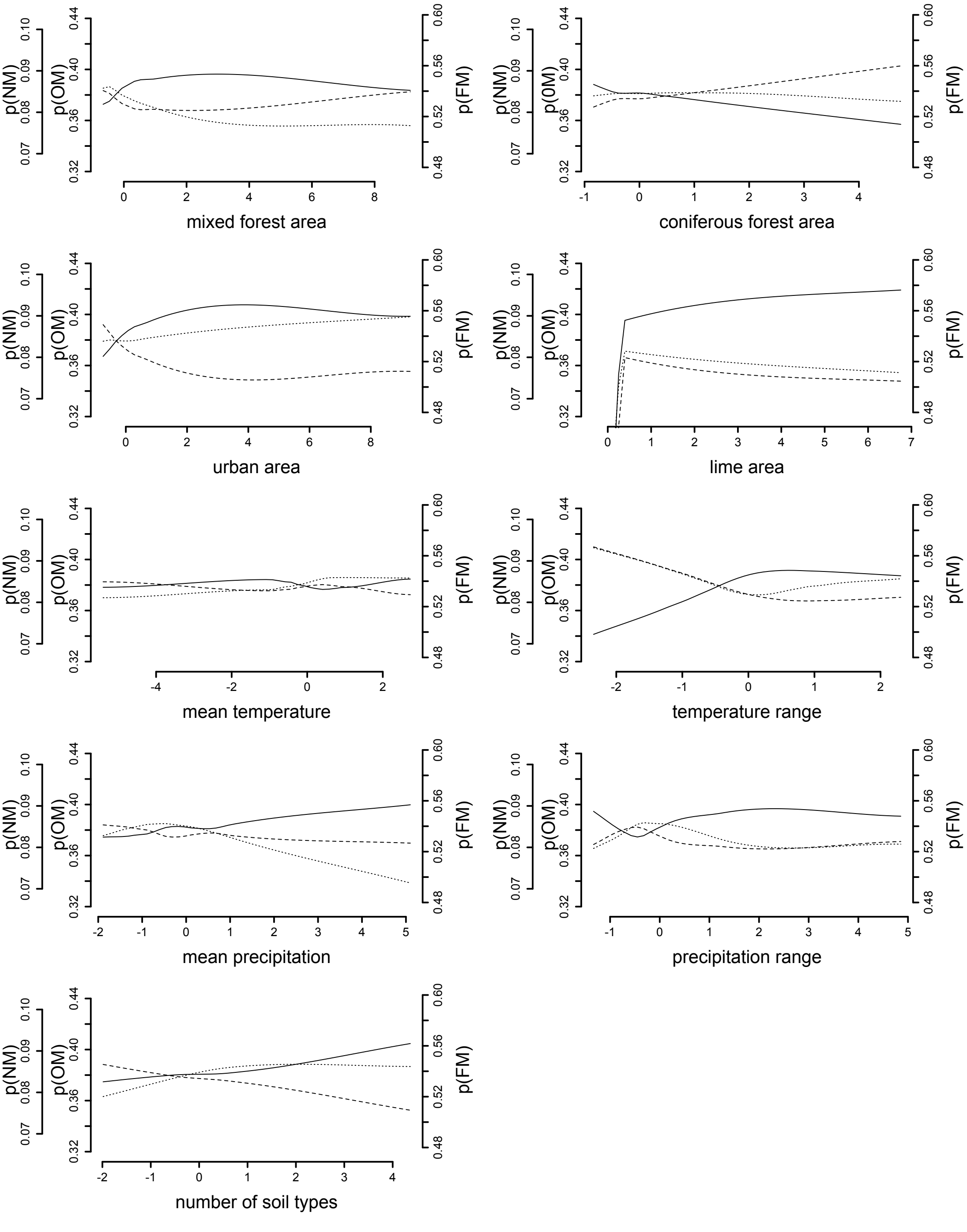


Figure 1: Loess-smoother functions for all finally selected environmental predictors and the predicted VGAM values for the three mycorrhizal status proportions: p(OM) – solid line (left axis), p(FM) – dashed line (right axis), p(NM) – dotted line (far left axis). Each environmental predictor was centred by subtracting its mean and scaled by dividing the centred value by their respective standard deviation.

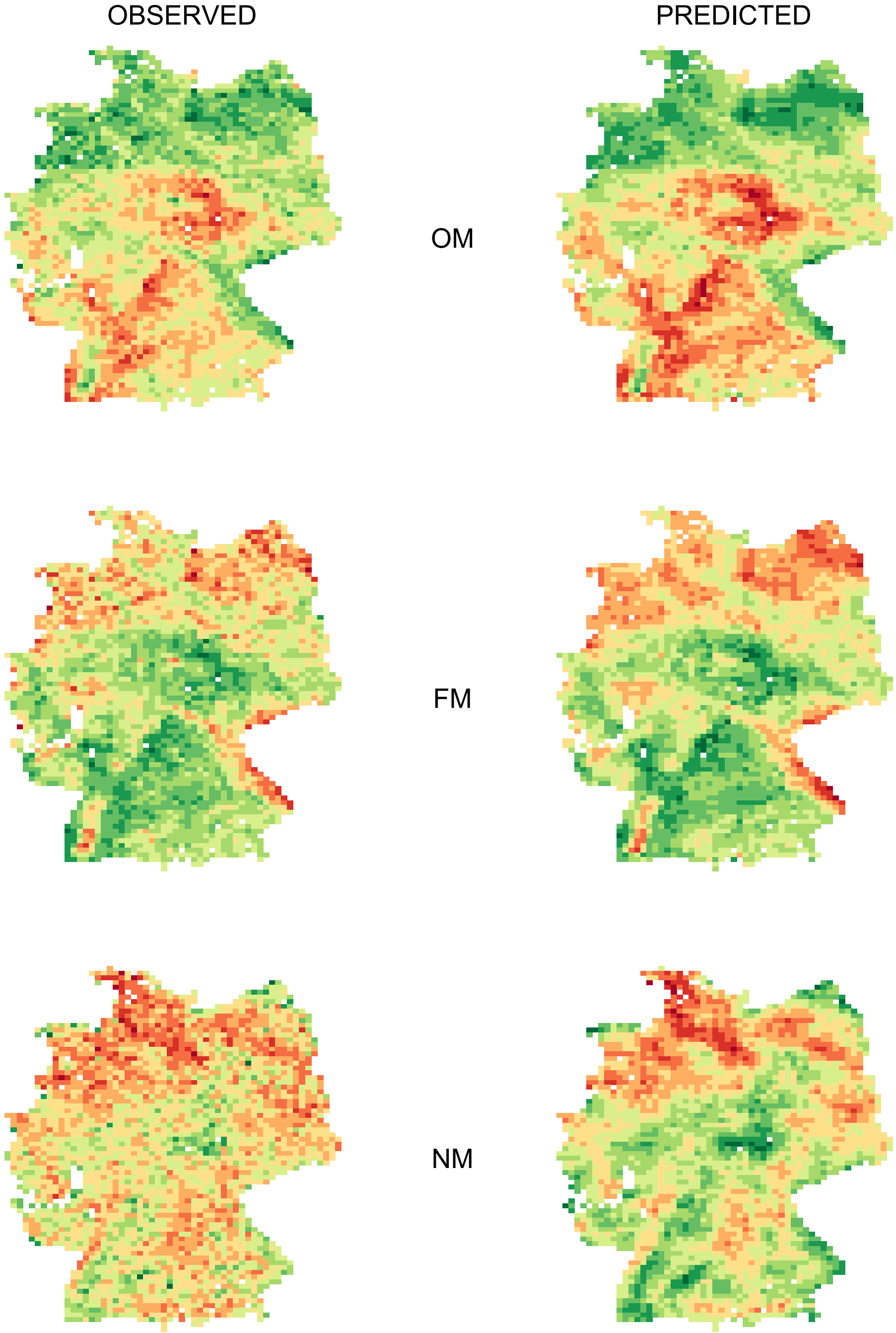


Figure 2: Observed and predicted distribution of arbuscular mycorrhizal plant status of the 2995 grid cells representing Germany. Compared are the observed values (left column) for the three plant arbuscular mycorrhizal status proportions 1) OM – obligate arbuscular mycorrhizal, 2) FM – facultative arbuscular mycorrhizal 3) NM – non mycorrhizal, and their predicted values of the final VGAM distribution model (right column). To better compare the maps, classes for proportions of plant arbuscular mycorrhizal status are decantiles (i.e., ten classes of equal size with different class limits for each map). High values are indicated by red, low values by green colour. Grid cells classified as insufficiently mapped and excluded from the analysis are illustrated in white.

Discussion

We analysed whether plant species assemblages across an intermediate spatial scale are composed of different proportions of species regarding their AM status, and if the variation of these proportions are linked to the geographical variation of ecological and environmental conditions. We detected distinct spatial distribution patterns of the proportion of plant species with different AM status across Germany (i.e., 2859 grid cells, each *c.* 130km^2) and found correlations of these distributions with a set of environmental predictors. Thus, we extended and substantiated many of our initial predictions on associations of plant AM status and the addressed geographical variation of ecological and environmental conditions (Table 4).

The model's outcome matches our initial expectations concerning area of forest stands per grid cell (Table 4). We assume that the inversely proportional relationship (Fig. 1) results from an increase in soil acidity with a higher proportion of coniferous tree species (Augusto et al., 2003), which inhibits AMF activity (van Aarle et al., 2003) and the association of OM with plant species in general (Hempel et al., 2013). Secondly, Europe's coniferous forests in recent silvicultural practice are mostly even-aged stands (Kuuluvainen, 2009) with structurally altered (Moora et al., 2009) and species poor herbal understories (Koorem and Moora, 2010). Therefore, they are predominantly lacking a plant layer that is mostly dominated by potential AMF host plants. As a third point, at least some deciduous tree species are arbuscular mycorrhizal – in addition to being ectomycorrhizal – whereas coniferous tree species are not commonly arbuscular mycorrhizal in Europe.

We presented two initial predictions regarding urban area as a predictor (Table 2). We found an increase of OM plant species proportions with increasing urban area per grid cell (Table 4). We explain this relative gain of OM plant species with an increase of alien plant species in urban areas compared to rural areas (Kühn et al., 2004), which are known to be more frequently OM (Hempel et al., 2013). We do not think that the higher proportion of OM plant species in urban areas is caused by higher average temperatures of cities compared to their surrounding areas (urban heat island; Oke, 1982), as the corresponding environmental predictors urban area and average temperature are – at least at our extent and grain size – not strongly correlated (Fig. S1).

Other land use related environmental predictors, especially the amount of agricultural area per grid cell, did not affect AM plant status distribution (Table 4), although most of the crop species are arbuscular mycorrhizal (Smith and Smith, 2011b). Nevertheless, we do not conclude that agricultural transformations and utilisation are of no importance in shaping the trait distribution. As a predictor in our analysis, agricultural area lumps together agricultural practices differing in land-use intensity, nutrient load, and management practices such as tillage (Jansa et al., 2002) or grazing (Eom et al., 2001). These parameters may influence the trait distribution on a more local scale (Ngosong et al., 2010), which is not captured in our analysis. Other predictors such as precipitation or temperature, which lead to different agricultural practices, may overrule the effects of those practices at the German country scale. The same is true for spatial distributions of nitrogen and phosphorus availability, which influence the composition of plants and their arbuscular mycorrhizal status and are influenced by fertilisation regimes (Landis et al., 2004; Ceulemans et al., 2011). Within our grid system of cells with c. 130km^2, it is not possible to accurately map differences in nutrient availability, which acts on a far finer scale. Considering other environmental predictors as proxy for nutrient availability, e.g., lime area (as discussed in the following paragraph) may mitigate this lack of data availability. Nevertheless, incorporating nutrient level or nutrient availability in our model may substantially improve the model. Unfortunately, such data are not yet available at this scale.

Only lime area significantly explained the distribution of OM plant species proportion, as one of the initial four predictors characterising geological parent material (Table 4). As predicted, we found a relative increase in OM plant species with increasing area of lime per grid cell (Fig. 1). Soils developing on lime-rich parent materials are more alkaline compared to soils on other geological parent materials (Schachtschabel et al., 1998). This promotes AMF activity, favours OM plant species in general (Hempel et al., 2013), and increases the share of AM plants at community level (Gerz et al., 2016). High calcium content of lime-rich parent materials leads to reduced availability of phosphorus, which can be alleviated through external hyphae provided by AMF (Sanders and Tinker, 1971; Smith et al., 2004). Therefore, AM associated plant species may have a (local) competitive advantage in such phosphorus-limited environments (Olsson and Tyler, 2004).

We did not formulate particular expectations towards proportions of mycorrhizal status and the number of soil types. The detected increase in NM plant species proportion with an increase in number of soil types might be explained by an accompanied higher habitat heterogeneity (Deutschewitz et al., 2003; Stein et al., 2014). This increases the probability of occurrences of soil types which favour NM species. As NM plant species are by far the minority among plant species and occupy extreme habitats in terms of soil fertility (Lambers and Teste, 2013), this might explain the exclusive association of this predictor with NM plant species proportion.

With an increase in mean temperature per grid cell we found an increase in OM plant species proportion (Fig. 1). So we corroborated in space what Hempel et al. (2013) found in a cross-species analysis, i.e., that OM plant species are positively associated with higher temperatures. OM plant species may be favoured in warmer habitats driving increased soil temperatures, since AMF are able to compensate temperature induced changes in root morphology (Haugen and Smith, 1992), growth rate, and longevity (Forbes et al., 1997) of host plants, by increasing growth of extraradical fungal hyphae. Additionally, high mean annual temperatures may lead to a higher probability of drought events and OM plant species may cope with drought stress via a variety of mechanisms (Augé, 2001;

Zhu et al., 2011).

Differing from our initial expectation, we found a relative increase in OM plant species with increasing temperature range (Table 4), i.e., highest proportions of OM plant species in Eastern and South-Eastern regions of Germany (Fig. 2), which are climatically the most continental ones (Fig. S3). Contrary to our expectations, the share of FM plant species continuously decreased with increasing temperature range (Fig. 1). Mycorrhizas help to tolerate low (Zhou et al., 2012) and high temperature stress (Maya and Matsubara, 2013), which may explain the relationship of OM plant species and temperature range. On the other hand, NM plant species are associated with high values of temperature range as well (Fig. 1). At present, we can therefore offer no clear explanation of this correlation at our chosen scale. The mechanism relating AM plant status with continentality remains to be elucidated.

Regarding mean annual precipitation as a predictor, our distribution model revealed a relationship distinctly different from our expectations (Table 4); with NM plant species proportions strongly decreasing with increasing annual precipitation and no significant relationship concerning OM plant species (Fig. 1). As we found a relative increase in OM species share in regions having higher mean temperature, and OM plant species have low moisture indicator values (Hempel et al., 2013), this finding may imply that our precipitation related predictors do not fully translate into actual soil moisture conditions. Factors influencing soil moisture such as evapotranspiration and infiltration due to substrate type and texture act on smaller scales, which we cannot address at our chosen extent and grain. We find a decrease in OM plant species proportion in regions of low annual precipitation range (Fig. 1), which turns into a slight increase with increasing precipitation range per grid cell, slightly contradicting our predictions (Table 4). The same trend appears for NM plant species proportions (Fig. 1), but showing an increase in grid cells of low precipitation range and a slight decrease with increasing precipitation range, a pattern more closely aligned with our prediction. Analogously to temperature stress, mycorrhizas were shown to mitigate plant stress under drought conditions (Li et al., 2014), which may explain this correlation. Again, this result may be related to weak transferability of our precipitation related predictors to actual soil moisture conditions. However, precipitation range shows similar relationships with plant mycorrhizal status as temperature range, emphasising the role of continental climate for the trait's distribution. This correlation as a proxy for continental climate is less strong, which can be explained by the less pronounced gradient within Germany, showing peak values of precipitation range in the German Alps and pre-alpine foothills only (Fig. S3).

Our results extend the findings of Hempel et al. (2013) from a cross-species analysis to a spatially explicit context, substantiating their findings regarding the association of plant AM status with information of plant species ecological requirements. We thus bridge the gap between former coarse grained global analyses (Treseder and Cross, 2006; Öpik et al., 2010; Kivlin et al., 2011; Davison et al., 2015) and local greenhouse or field experiments (e.g., van der Heijden et al., 1998; Hartnett and Wilson, 2002; Klironomos et al., 2011). We thereby uncovered new patterns regarding the assemblages of plant species differing in their plant mycorrhizal status at this intermediate scale. Our analysis is not able to disentangle, whether the found AM status distributions are due to the AM status of plants or other plant traits that correlate with AM status; this needs further testing. Still, the distinct spatial distributions of proportions of different plant AM status (Fig. 2) emphasise the importance of plant mycorrhizal status as a useful functional trait, especially considering that root traits are not as commonly and widely used in analyses of plant species distribution and assemblages (Rillig et al., 2015).

Our intermediate study scale may be suitable to questions related to plant mycorrhizal status and its potential capacity to mediate future changes in plant responses due to changes in climatic conditions (Compant et al., 2010; Mohan et al., 2014) or land use. Our results demonstrate that the proportion of plants with different arbuscular mycorrhizal status is dependent on climatic predictors, in particular temperature and precipitation, which present the largest effect size (Table 3). If temperatures in Germany will increase (IPCC, 2013), OM plant species may be favoured according to our results (cf. Bunn et al., 2009).

We encourage including plant mycorrhizal status as a plant trait in future macroecological analyses of plant assemblages and distributions (Moora, 2014). This additional information may help to improve plant species distribution models, for instance in interaction with other traits. Pellissier et al. (2013) could already show such advancement by adding the number of soil fungal operational taxonomic units to a plant species distribution model of the Western Swiss Alps. Nevertheless, there is still a need to improve the existing knowledge regarding plant mycorrhizal traits. Hempel et al. (2013) stated that more abundant plant species are better studied in terms of their mycorrhizal associations. Furthermore, they were able to compile mycorrhizal status information only for half of the plant species of the German flora via the existing literature. This may be a simple explanation for the performance of our distribution model, which is e.g., biased upwards for NM plant species, i.e., the model predicts higher proportions of NM plant species especially in the South and Central part of Germany (Fig. 2). Collecting more data even on rare plant species – both in literature review and experimentally – would substantially improve future analyses involving plants' mycorrhizal status as a plant functional trait. Certainly, investigating the biogeography of AMF themselves (Hazard et al., 2013; Davison et al., 2015) will stimulate usage of plant mycorrhizal status in future analyses of co-variation of plant and AMF communities (Zobel and Öpik, 2014).

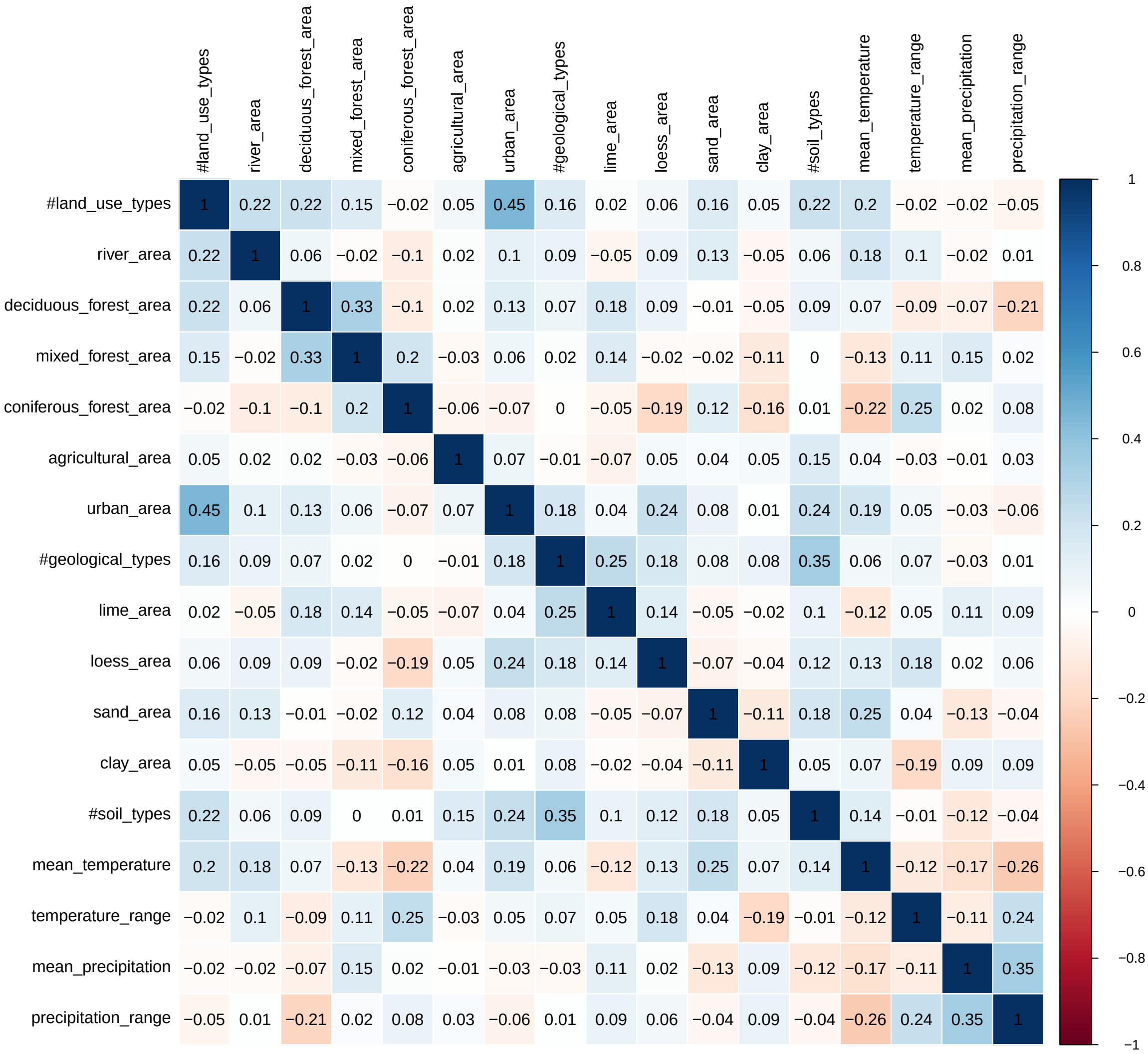
Acknowledgements

MM and MZ were supported by grants from the Estonian Science Foundation (9050) and Estonian Research council (IUT 20-28).

Supplementary data

Table S1: Summary of the cross-validation results. Shown are the sets of finally backward-selected environmental predictors of the final model as well as the five cross-validations. An 'X' illustrates that the predictor was selected in the particular model. Bold rows indicate predictors that were chosen in each of the models. Root-mean-squared errors (RMSE) are given for each of the three proportions of arbuscular mycorrhizal status.

predictor	final model	CV1	CV2	CV3	CV4	CV5
Mixed forest area	**X**	**X**	**X**	**X**	**X**	**X**
Coniferous forest area	**X**	**X**	**X**	**X**	**X**	**X**
Agricultural area			X		X	X
Urban area	**X**	**X**	**X**	**X**	**X**	**X**
Number of classes of geological parent material			X		X	
Number of soil types	**X**	**X**	**X**	**X**	**X**	**X**
Lime area	**X**	**X**	**X**	**X**	**X**	**X**
Loess area						X
Mean temperature	**X**	**X**	**X**	**X**	**X**	**X**
Mean precipitation	**X**	**X**	**X**	**X**	**X**	**X**
Temperature range	**X**	**X**	**X**	**X**	**X**	**X**
Precipitation range	**X**	**X**	**X**	**X**	**X**	**X**
RMSE(pOM)	0.013	0.021	0.019	0.02	0.022	0.025
RMSE(pFM)	0.013	0.02	0.018	0.021	0.019	0.025
RMSE(pNM)	0.007	0.009	0.009	0.009	0.01	0.01



	#land_use_types	river_area	deciduous_forest_area	mixed_forest_area	coniferous_forest_area	agricultural_area	urban_area	#geological_types	lime_area	loess_area	sand_area	clay_area	#soil_types	mean_temperature	temperature_range	mean_precipitation	precipitation_range
#land_use_types	1	0.22	0.22	0.15	−0.02	0.05	0.45	0.16	0.02	0.06	0.16	0.05	0.22	0.2	−0.02	−0.02	−0.05
river_area	0.22	1	0.06	−0.02	−0.1	0.02	0.1	0.09	−0.05	0.09	0.13	−0.05	0.06	0.18	0.1	−0.02	0.01
deciduous_forest_area	0.22	0.06	1	0.33	−0.1	0.02	0.13	0.07	0.18	0.09	−0.01	−0.05	0.09	0.07	−0.09	−0.07	−0.21
mixed_forest_area	0.15	−0.02	0.33	1	0.2	−0.03	0.06	0.02	0.14	−0.02	−0.02	−0.11	0	−0.13	0.11	0.15	0.02
coniferous_forest_area	−0.02	−0.1	−0.1	0.2	1	−0.06	−0.07	0	−0.05	−0.19	0.12	−0.16	0.01	−0.22	0.25	0.02	0.08
agricultural_area	0.05	0.02	0.02	−0.03	−0.06	1	0.07	−0.01	−0.07	0.05	0.04	0.05	0.15	0.04	−0.03	−0.01	0.03
urban_area	0.45	0.1	0.13	0.06	−0.07	0.07	1	0.18	0.04	0.24	0.08	0.01	0.24	0.19	0.05	−0.03	−0.06
#geological_types	0.16	0.09	0.07	0.02	0	−0.01	0.18	1	0.25	0.18	0.08	0.08	0.35	0.06	0.07	−0.03	0.01
lime_area	0.02	−0.05	0.18	0.14	−0.05	−0.07	0.04	0.25	1	0.14	−0.05	−0.02	0.1	−0.12	0.05	0.11	0.09
loess_area	0.06	0.09	0.09	−0.02	−0.19	0.05	0.24	0.18	0.14	1	−0.07	−0.04	0.12	0.13	0.18	0.02	0.06
sand_area	0.16	0.13	−0.01	−0.02	0.12	0.04	0.08	0.08	−0.05	−0.07	1	−0.11	0.18	0.25	0.04	−0.13	−0.04
clay_area	0.05	−0.05	−0.05	−0.11	−0.16	0.05	0.01	0.08	−0.02	−0.04	−0.11	1	0.05	0.07	−0.19	0.09	0.09
#soil_types	0.22	0.06	0.09	0	0.01	0.15	0.24	0.35	0.1	0.12	0.18	0.05	1	0.14	−0.01	−0.12	−0.04
mean_temperature	0.2	0.18	0.07	−0.13	−0.22	0.04	0.19	0.06	−0.12	0.13	0.25	0.07	0.14	1	−0.12	−0.17	−0.26
temperature_range	−0.02	0.1	−0.09	0.11	0.25	−0.03	0.05	0.07	0.05	0.18	0.04	−0.19	−0.01	−0.12	1	−0.11	0.24
mean_precipitation	−0.02	−0.02	−0.07	0.15	0.02	−0.01	−0.03	−0.03	0.11	0.02	−0.13	0.09	−0.12	−0.17	−0.11	1	0.35
precipitation_range	−0.05	0.01	−0.21	0.02	0.08	0.03	−0.06	0.01	0.09	0.06	−0.04	0.09	−0.04	−0.26	0.24	0.35	1

Figure S1: Kendall rank correlation plot of all 17 initially selected environmental predictors. Blue colour indicates a positive correlation coefficient between two predictors; red colour indicates a negative correlation coefficient. Numbers represent the specific correlation coefficient value. The correlation plot was created using the R package 'corrplot' (Wei, 2013).

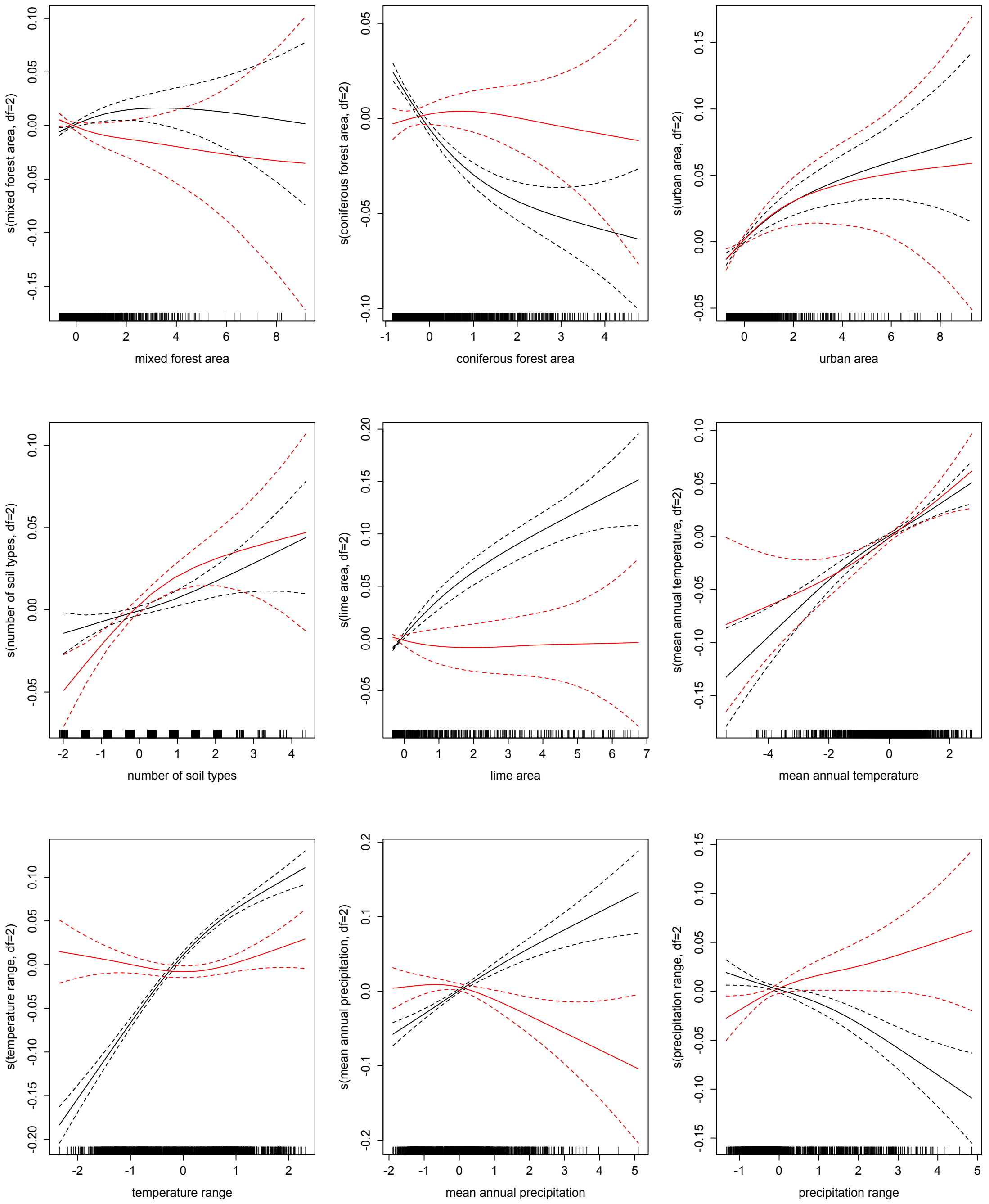
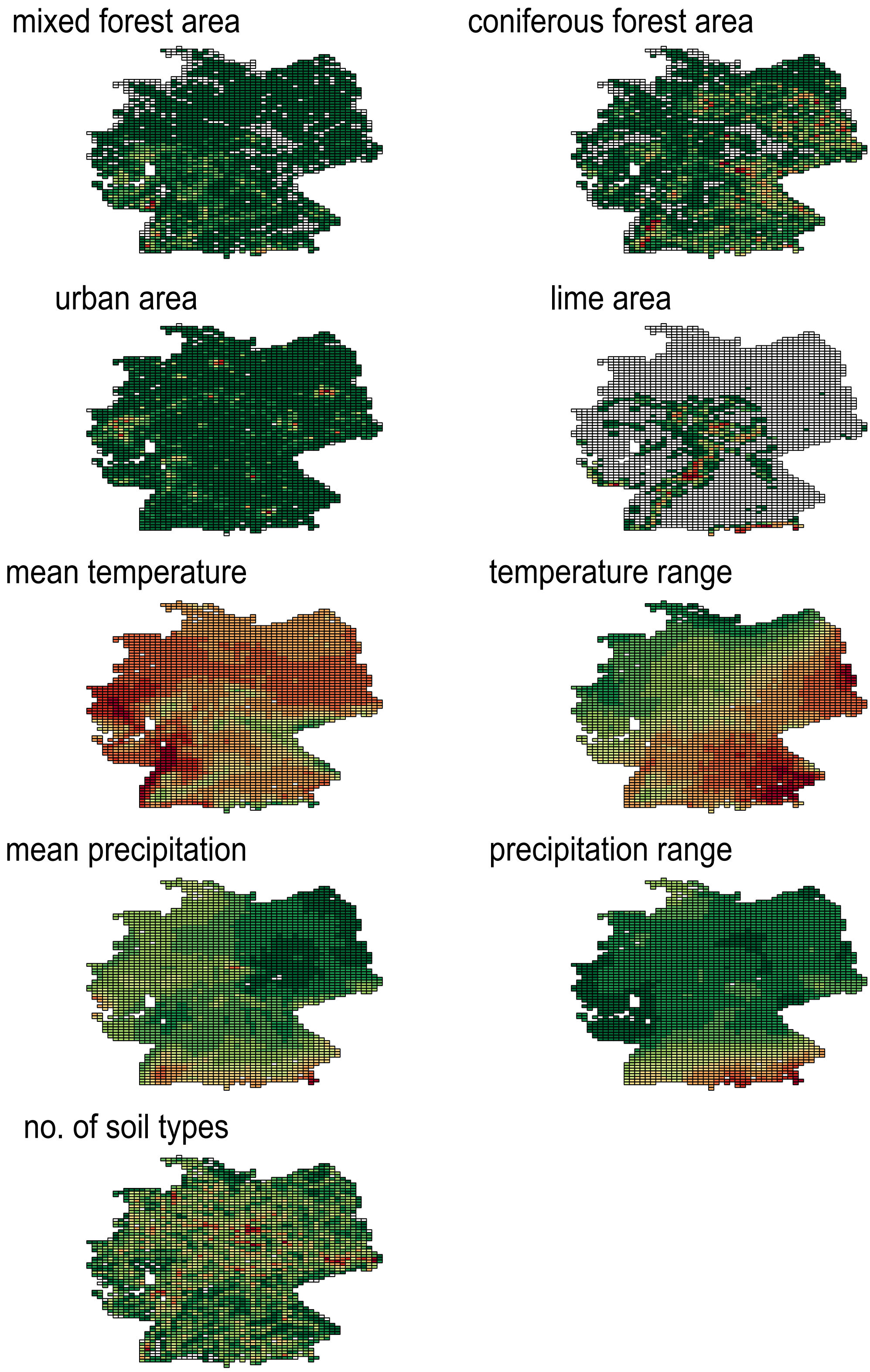


Figure S2: Smoother functions for both log-ratios over all nine finally selected environmental predictors extracted from the vector generalised additive model . Black lines indicate log(OM/FM), red lines indicate log(NM/FM), and the dashed curves indicate ±2 standard error bands. Each environmental predictor was centred by subtracting its mean and scaled by dividing the centred form by their particular standard deviation.



mixed forest area

coniferous forest area

urban area

lime area

mean temperature

temperature range

mean precipitation

precipitation range

no. of soil types

Figure S3: Spatial overview of the nine final environmental predictors throughout Germany. To better compare the maps, classes for the different predictors are decantiles (i.e., ten classes of equal size with different class limits for each map). High values are indicated by red, low values by green colour. Grid cells classified as insufficiently mapped and excluded from the analysis are illustrated in white without border; white cells with border indicate a cell value of zero.

CHAPTER 3

Mycorrhizal Status Helps Explain Invasion Success of Alien Plant Species

Andreas Menzel, Stefan Hempel, Stefan Klotz, Mari Moora, Petr Pyšek, Matthias C. Rillig, Martin Zobel, and Ingolf Kühn

Ecology (accepted)

CHAPTER 3: Mycorrhizal Status Helps Explain Invasion Success of Alien Plant Species

Abstract

It is still debated whether alien plants benefit from being mycorrhizal or if engaging in the mycorrhizal symbiosis constrains their establishment and spread in new regions. Here, we analysed 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. Furthermore, we used generalised linear models to explain the range in Germany, incorporating interactions of mycorrhizal status with additional plant traits related to morphology, reproduction, and life-history. Non-naturalised aliens did not differ in their relative frequency of mycorrhizal status from naturalised aliens. Mycorrhizal status significantly explained the occupied geographical range, with facultative mycorrhizal species inhabiting a larger range than non-mycorrhizal aliens and obligate mycorrhizal plant species taking an intermediate position. Additionally, aliens with storage organs, shoot metamorphoses or specialised structures promoting vegetative dispersal, occupied a larger range if being facultative mycorrhizal. We conclude that being mycorrhizal is important for the establishment and persistence of aliens in Central Europe and constitutes an advantage compared to non-mycorrhizal plants. Being facultative mycorrhizal seems to be especially advantageous for successful spread, as the flexibility of this mycorrhizal status may enable a broader set of ecological strategies.

Keywords: alien plants, biological invasion, Central Europe, functional traits, invasion stage, MycoFlor, mycorrhizal status, neophytes, trait interactions

Introduction

With increasing concern about invasive alien plant species' effects on native plant species, communities, ecosystems as well as their economic consequences (Vilà et al., 2010, 2011; Simberloff et al., 2013), there has been growing interest in studying processes and mechanisms underlying successful invasion, including the role of species traits. Besides a set of functional plant traits known to promote invasion (van Kleunen et al., 2010; Küster 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., 2000b; Traveset and Richardson, 2014). Next to pollination (Pyšek et al., 2011; Bezemer et al., 2014), the mycorrhizal symbiosis is a mutualistic interaction that attracted the attention of invasion ecologists (Reinhart and Callaway, 2006; Pringle et al., 2009; Shah et al., 2009; Bunn et al., 2015). Nevertheless, analyses using mycorrhizal traits to characterise plant species (Moora, 2014) are still rare. Whereas experimental, mostly local studies 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 alien plant species to be more likely from 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 whether alien plant species benefit from being mycorrhizal, or whether engaging in the symbiosis is constraining their establishment and geographical spread in the new environment and region. A few case studies report positive impacts of the mycorrhizal symbiosis on growth and development of alien plant species, resulting in a competitive advantage over native species (Fumanal et al., 2006; Chmura and Gucwa-Przepióra, 2012; Sun and He, 2010). In a meta-analysis conducted by Bunn et al. (2015), the authors did not find a positive correlation between arbuscular mycorrhizal colonisation and growth response in invasive plants, but invasives were more colonised 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 plant 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 functional plant traits may thus help to gain 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 plant species (OM) that are always colonised by mycorrhizal fungi, (2) facultative mycorrhizal plant species (FM) that are colonised under some conditions but not others, and (3) non-mycorrhizal plant species (NM) that are never found to be colonised 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 response under given conditions, mycorrhizal status does not give direct information about the functional significance of mycorrhizal colonisation of the given species' individuals. It rather refers to the mere presence/absence of fungal colonisation 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 carbon 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, 2011a) as well as a significant amount of plant N uptake (Hobbie and Hobbie, 2008), and 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, implying that considering plant ecological strategies improved the explanatory power of their models. 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 the understanding of such 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 infer about the role mycorrhizal status possibly plays in invasion success, as the importance of colonisation by mycorrhizal fungi may change with stages of invasion (Shah et al., 2009; Blackburn et al., 2011). In the present study we aim at answering the following questions: (1) Do neophyte plant species of the German flora at different stages of invasion, i.e., (a) casual (non-naturalised) species, (b) species naturalised only in human-made habitats, and (c) species naturalised also in habitats with (semi)natural vegetation, differ in their relative frequency of mycorrhizal status? (2) Do these groups of neophytes differ from archaeophyte and native plant species in their relative frequency of mycorrhizal status? (3) Are certain combinations of mycorrhizal status and other functional plant traits underlying invasion success?

Material and Methods

Plant species distribution data were obtained from FLORKART, a database of the German Network for Phytodiversity, provided by the German Federal Agency for Nature Conservation (http://www.floraweb.de). 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., c. 130 km^2) size, resulting in 2995 grid cells. We used the number of occupied grid cells as proxy for invasion success of each particular neophyte. Therefore, this measure potentially ranges from 1 to 2995 occupied grid cells.

Information on species status with respect to immigration time (i.e., native, archaeophyte, neophyte species) and stage of invasion, i.e., (a) casual species, that are not a permanent component of the flora and depend on repeated supply of propagules by humans for their occurrence in the wild (Richardson et al., 2000a), (b) species naturalised only in human-made habitats, and (c) species naturalised also in habitats with (semi)natural vegetation, were obtained from BiolFlor (Klotz et al., 2002); and so was the information on plant functional traits (Table 1). In addition to the traits in BiolFlor, we used nitrogen fixation ability as a supplemental trait, since this trait refers to an important mutualistic symbiosis besides the formation of mycorrhizas. We assigned a 'yes – nitrogen fixing' to all plant species of the *Fabaceae* family and the genus *Alnus* and a 'no – not nitrogen fixing' to all other plant species (Table 1). Plant functional traits were selected with respect to potential high energy cost of plant species in terms of carbon and nutrients, which could be supported (in the case of N or P) or inhibited (in the case of carbon) by the symbiosis.

Information on mycorrhizal status for each plant species - OM, FM or NM - was taken from the MycoFlor data base (Hempel et al., 2013). In total, we analysed the invasion success of 266 neophytes of the German flora: 64 plant species were casual, 112 naturalised only in human-made habitats, and 90 also naturalised 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, 7 ectomycorrhizal, 4 ericoid mycorrhizal, and 6 were arbuscular and ectomycorrhizal. Besides mycorrhizal status, the availability of plants' trait information differed among species for the other selected traits (Table 1). We did not analyse very rare attributes (trait values) that are those with less than ten species in the group. This resulted in different numbers of species per plant trait (Table 1).

Four questions were tested using G test 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 in their relative frequency of mycorrhizal status from all neophytes; (2) casual neophytes differ from neophytes naturalised in human-made and/or (semi)natural habitats; (3) casual neophytes differ from archaeophyte and native plant species, and (4) neophytes naturalised in human-made habitats and/or (semi)natural habitats differ from archaeophyte and native plant species.

As a second step, we used the number of occupied grid cells as response to model neophyte invasion success, by using plant mycorrhizal status and the additionally selected plant traits as predictors. We used generalised linear models with negative binomial error distribution to account for overdispersion and established a model for each of the functional plant traits, i.e., including both main effects and the interaction of trait and mycorrhizal status. 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, originally proposed for accounting spatial dependencies by Bini et al. (2009), was used to incorporate phylogenetic relatedness within the generalised linear models. The triangular 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 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 Jarošik, 2006; Williamson et al., 2009; Pyšek et al., 2015). To assure that our analysis is not confounded by residence times of the neophytes considered, we regressed species' introduction time on their occupied geographical range. Information on time of introduction was available for 130 of the 266 from BiolFlor (Klotz et al., 2002). Residence time did not significantly explain the number of grid cells occupied (Appendix B: Table B1).

Differences in the mean number of occupied grid cells in Germany among the three mycorrhizal statuses within each attribute of the plant functional traits were tested by post-hoc Tukey's honestly significant differences (Tukey HSD). Furthermore, we conducted an outlier analysis using Cook's distance (Cook and Weisberg, 1982) to unravel 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 and Hervë, 2015), 'MASS' (Venables and Ripley, 2002), and 'multcomp' (Hothorn et al., 2008). Interaction plots were made with the help of 'ggplot2' (Wickham, 2009).

Table 1: Summary of selected functional plant traits for modelling invasion success in interaction with plant mycorrhizal status.

functional trait	value	no. of 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
nitrogen fixation ability	yes; no	266

For details on traits (except nitrogen 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 A: Figure A1 for trait correlations).

Results

Neophyte plant species at different stages of invasion did not differ in their relative frequency of mycorrhizal status from all neophytes ($G=2.5$, $df=6$, $p=0.87$; Appendix C: Figure C1); neither did casual neophytes differ from naturalised in this respect ($G=1.44$, $df=2$, $p=0.49$; Appendix C: Figure C1). Casual neophytes significantly differed in their relative frequency of mycorrhizal status from archaeophytes ($G=7.24$, $df=2$, $p=0.03$; Appendix C: Figure C2) and native species ($G=6.45$, $df=2$, $p=0.04$; Appendix C: Figure C2), in both cases by being more frequently OM and less frequently FM. Naturalised neophytes significantly differed from archaeophytes ($G=13.9$, $df=2$, $p<0.01$; Appendix C: Figure C3) and native species ($G=28.02$, $df=2$, $p<0.001$; Appendix C: Figure C3) by being more frequently OM and less frequently FM.

Mycorrhizal status had a significant effect on the number of occupied grid cells including all 266 species (df=2, deviance=7.4, p=0.02; Appendix D: Table D1) in a phylogenetically informed generalised linear model. 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 compared to NM neophytes (p=0.08), whereas FM species did not differ from OM 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 compared to shrubs and trees, none of the functional plant traits significantly explained the number of occupied grid cells in a single-trait model (Appendix D: Table D1). However, we found significant interactions between mycorrhizal status and nine out of 13 additional traits, excluding the existence of root metamorphoses, reproduction strategy, leaf persistence, and nitrogen fixation ability (Table 2).

Results of Tukey HSD post-hoc analysis revealed that neophytes with storage organs, shoot metamorphoses or specialised structures promoting vegetative dispersal and propagation, occupied more grid cells if being FM (Figure 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 ones were more successful. For woody (shrub and tree) species and plant species with variable types of life span, OM neophytes occupied the highest number of grid cells and the same was true for those with primary storage root as type of root metamorphoses (Figure 1 and Table 3).

Table 2: Results of phylogenetically informed generalised linear models explaining the number of occupied grid cells as a proxy for invasion success. Displayed are the error probabilities 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.

variable	df	deviance	p
GROWTH FORM			
growth form	**1**	**5.9**	**0.01**
mycorrhizal status	**2**	**7.5**	**0.02**
growth form × mycorrhizal status	**2**	**6.8**	**0.03**
STORAGE ORGAN (EXISTENCE)			
storage organ (existence)	1	0.4	ns
mycorrhizal status	**2**	**7.8**	**0.02**
storage organ (existence) × mycorrhizal status	**2**	**9.8**	**0.007**

continued on next page

variable	df	deviance	p
STORAGE ORGAN			
storage organ	4	5.8	ns
mycorrhizal status	**2**	**10.1**	**0.006**
storage organ × mycorrhizal status	**8**	**17.5**	***0.03***
ROOT METAMORPHOSES (EXISTENCE)			
root metamorphoses (existence)	1	0.2	ns
mycorrhizal status	**2**	**7.4**	**0.02**
root metamorphoses (existence) × mycorrhizal status	2	0.9	ns
ROOT METAMORPHOSES			
root metamorphoses	2	0.5	ns
mycorrhizal status	2	5.5	ns
root metamorphoses × mycorrhizal status	**4**	**9.8**	**0.04**
SHOOT METAMORPHOSES (EXISTENCE)			
shoot metamorphoses (existence)	1	0.2	ns
mycorrhizal status	**2**	**7.8**	**0.02**
shoot metamorphoses (existence) × mycorrhizal status	**2**	**12.5**	**0.002**
SHOOT METAMORPHOSES			
shoot metamorphoses	3	0.8	ns
mycorrhizal status	**2**	**8.6**	**0.01**
shoot metamorphoses × mycorrhizal status	**6**	**13.5**	***0.04***
VEGETATIVE DISPERSAL (EXISTENCE)			
vegetative dispersal (existence)	1	0.3	ns
mycorrhizal status	**2**	**7.6**	**0.02**
vegetative dispersal (existence) × mycorrhizal status	**2**	**9.5**	**0.009**
VEGETATIVE DISPERSAL			
vegetative dispersal	3	2.9	ns
mycorrhizal status	**2**	**7**	**0.03**
vegetative dispersal × mycorrhizal status	**6**	**19.2**	**0.004**
REPRODUCTION STRATEGY			
reproduction strategy	2	1.2	ns
mycorrhizal status	**2**	**7.6**	**0.02**
reproduction strategy × mycorrhizal status	4	9.3	ns

continued on next page

variable	df	deviance	p
LIFE SPAN			
life span	2	1.2	ns
mycorrhizal status	**2**	**7**	**0.03**
life span × mycorrhizal status	**4**	**15.4**	**0.004**
LEAF PERSISTENCE			
leaf persistence	2	4.7	ns
mycorrhizal status	**2**	**6.9**	**0.03**
leaf persistence × mycorrhizal status	4	2.5	ns
NITROGEN FIXATION ABILITY			
nitrogen fixation ability	1	0	ns
mycorrhizal status	**2**	**7.4**	**0.02**
nitrogen fixation ability × mycorrhizal status	2	1.6	ns

Rows in bold indicate a significant error probability pf $p \leq 0.05$. P-values in italic indicate that this term was no longer significant after excluding plant species that were selected by Cook's distance (Cook and Weisberg, 1982) as most influential.

Table 3: Results of the Tukey-post-hoc test following the generalised linear models explaining the number of occupied grid cells. Displayed are the plant functional traits that showed significant interaction effects with mycorrhizal status only (Table 2). A plus sign indicates a significantly higher, a minus sign a significantly lower number of occupied grid cells within each row of the table (Freeman Tukey test: p≤0.05).

		mycorrhizal status	
traits	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
storage organ			
none	ns	ns	ns
pleiocorm	ns	ns	ns
rhizome	-	+	-
runner	ns	ns	ns
vegetative dispersal (existence)			
yes	-	+	ns
no	ns	ns	ns
vegetative dispersal			
none	ns	ns	ns
rhizome	-	+	-
runner	ns	ns	ns
variable	-	ns	+
life span			
annual	ns	ns	ns
perennial	-	+	-
various	+	-	ns
number of positive associations	3	9	1

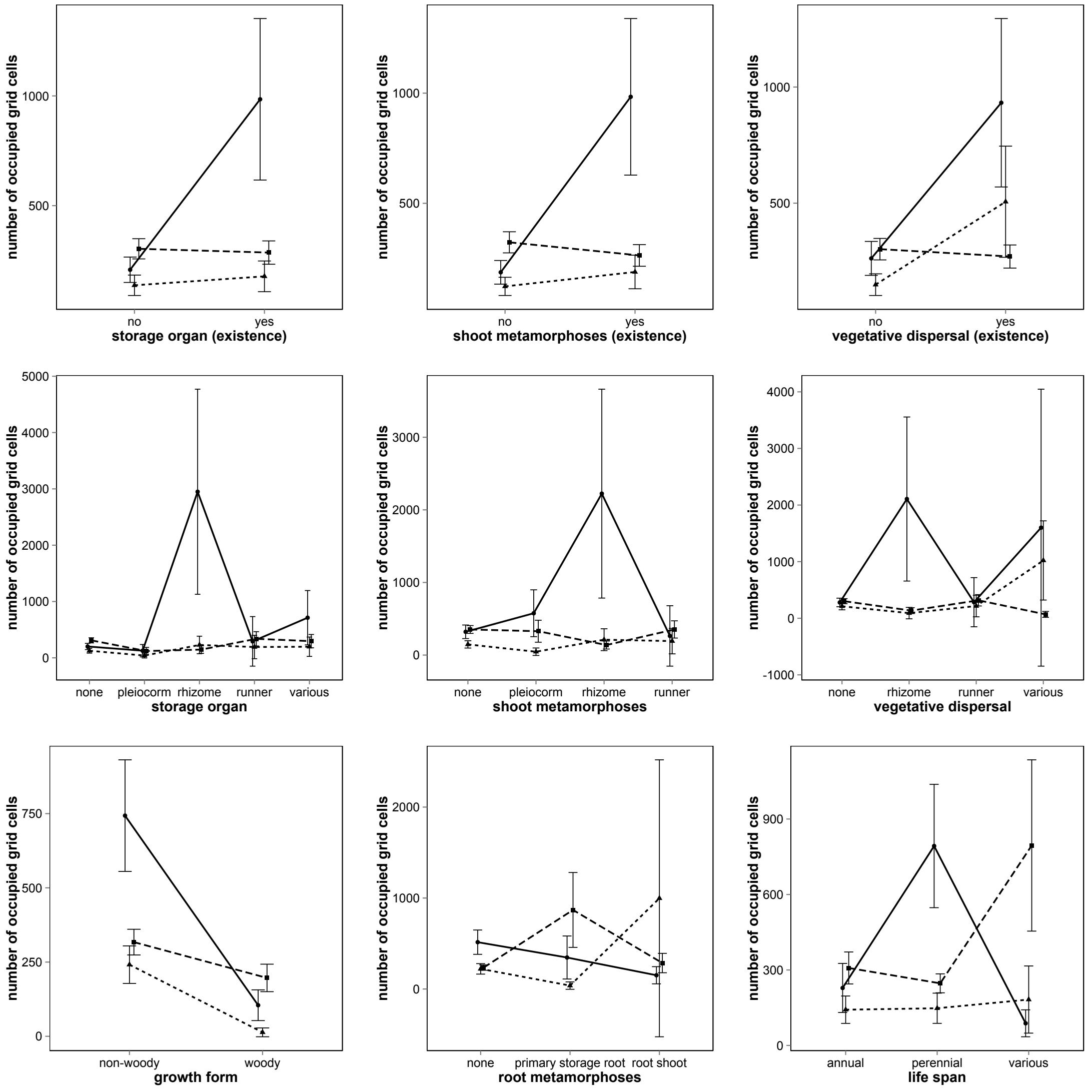


Figure S3: Interaction plots for significant two-way interactions between mycorrhizal status and the shown plant functional traits (Table 2); dashed line - OM, solid line - FM, dotted line - NM. Displayed are the least-squares means (± standard error) per each trait value interaction. Traits referring 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 A: Figure A1 for trait correlations).

Discussion

Our results indicate that being mycorrhizal promotes the invasion success of alien plant species in Germany. This is supported by FM neophytes showing a significantly higher invasion success than NM plant species, and OM neophytes tending towards higher invasion success compared to NM species. Moreover, we found significant interactions between neophyte mycorrhizal status and nine out of 13 functional plant traits. This emphasises the importance of mycorrhizal status in understanding alien plant invasion.

Although neophytes were previously shown to be more likely OM than native and archaeophyte species in Germany (Hempel et al., 2013), this mycorrhizal status does not particularly promote invasion success in terms of occupied geographical range. OM and FM neophytes did not differ in terms of occupied geographical range in Germany. 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 the 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 a successful spread across a large geographical range and a potential sustainment over a longer time period, as the flexibility of FM plants regarding the mycorrhizal symbiosis may enable a broader set of ecological strategies. This is supported by our finding that the relative frequency of neophytes mycorrhizal status did not differ among neophytes at different stages of invasion (casuals against naturalised neophytes; Figure S2), but compared to archaeophyte and native plant species; with the latter showing higher proportions of FM plant species (Figure S3).

Seedling establishment is promoted by the presence of mycorrhizal symbionts (van der Heijden, 2004; Wurst et al., 2011; Koorem et al., 2012). Following that, mycorrhizal aliens potentially have quick access to common mycorrhizal networks (Barto et al., 2012). Alien plants may profit from additional nutrient (Koide, 1991) and water availability (Augé, 2001) at relatively low energy cost, since they do not need to invest into the construction of the existing network at the early stage of establishment. Consequently, resident mycorrhizal networks may serve as an alternative supplier of nutrients and water from a relatively larger soil volume than an independent non-mycorrhizal seedling could afford. Hence, mycorrhizal plant species may obtain a competitive advantage compared to non-mycorrhizal alien plant species. By mediating seedling survival of introduced species, mycorrhizal fungi do have the potential to determine whether an alien plant species persists until a second factor occurs (e.g., an disturbance event) that weakens the competitive strength of natives (Hobbs and Huenneke, 1992) and may allow successful spread. The great majority of mycorrhizal neophytes in our analysis are involved in an arbuscular mycorrhizal relationship (93%), pointing at differences in the establishment of neophyte plant species based on their mycorrhizal type. 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 suggested to act as a barrier (Richardson et al., 2000b; Nuñez et al., 2009), the availability of a fungal partner should not constrain the establishment of alien plants in new environments when they are engaged in an arbuscular mycorrhiza. Nevertheless, the numbers of ectomycorrhizal and ericoid plant species considered in this approach were too small to conduct an additional analysis to gain insights into differences between neophytes associated with different mycorrhizal types. This indicates that our findings are transferable to other regions, as Fitter (2005) found alien plant species to be more likely from plant families that typically associate with mycorrhizal fungi, compared to the native flora of Great Britain – similar to the starting point of our analysis. The contrasting conclusions of Pringle et al. (2009) for alien plants in California might be due to different evolutionary histories of the particular alien floras, especially regarding the strong and long-time exposure of aliens of European origin to intensive agriculture (i.e., North-American aliens; La Sorte and Pyšek, 2009; Seifert et al., 2009). Yet, we do not know an assessment of alien plants' invasion success in North America that is similar to our approach and it therefore remains to be investigated whether our results are similarly relevant for this and other geographical regions. Moreover, additional investigation and discussion 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. Possible qualitative differences in responsiveness towards mycorrhizal fungi between OM and FM species, especially in the stage of seedling establishment, will be worth further investigations.

The mycorrhizal symbiosis potentially affects the nutrient uptake and carbon 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, 2011a) as well as a significant amount of plant N uptake (Hobbie and Hobbie, 2008), and consume up to 50% of a plant's net primary production (Hobbie and Hobbie, 2008). Therefore, despite the benefits plants gain from the symbiosis, there is cost in terms of the carbon provided to the fungal partner. This exchange, although highly variable in its specificity, suggests trade-offs between mycorrhizal status and the expression of other functional plant traits which require further plant investment. Nevertheless, such trade-offs have rarely been tested according to our knowledge (but see Onipchenko and Zobel, 2000; Philip et al., 2001; Varga, 2010). Our study is one of the first to actually demonstrate the significance of interactions between mycorrhizal status and functional plant traits related to morphology, reproduction, and life-history in association with invasion success. Küster et al. (2008) showed that trait interactions help understanding the invasion success of alien plant species, as different combinations of traits and therefore different ecological strategies can facilitate the invasion process. Our analysis reveals the importance of the symbiosis for such strategies and therefore extends their work. Our findings suggest that FM neophytes show a significantly higher invasion success compared to NM and OM neophytes when 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 (Figure 1 and Table 3). This suggests that the flexibility of carbon investments for FM neophytes, with respect to their mycorrhizal strategy, may be a crucial advantage for plants in combination with this 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), this may allow different plant strategies independent of the symbiosis, including the development of such additional structures.

This potentially explains the results of Hempel et al. (2013) – showing that FM species show wider ecological amplitudes and occupy larger geographical ranges – by adding plant traits to the analysis and therefore depicting a more versatile range of ecological strategies available for FM plants. OM and NM neophytes lack this flexibility in their mycorrhizal association. However, the (nutritional or other) benefits gained from the symbiosis seem to exceed the (carbon) costs, as our results indicate that OM neophytes occupy a larger geographical range than NM neophytes. Nevertheless, as plant mycorrhizal status does not give direct information about mycorrhizal dependency or responsiveness (Moora, 2014), 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 status with local abiotic and biotic conditions.

Although the mycorrhizal symbiosis has been in the focus of invasion biologists for a while (Richardson et al., 2000b; Reinhart and Callaway, 2006; Pringle et al., 2009; Shah et al., 2009; Bunn et al., 2015), we do not know any study combining plant mycorrhizal status with other functional plant traits related to morphology, reproduction, and life-history which is similar to our approach. We encourage using mycorrhizal status and related mycorrhizal plant traits in further analyses of invasion success of alien plant species. Including root traits (Maherali, 2014; Yang et al., 2015), introducing three-way-interactions, e.g., with above- and belowground herbivory (Barto and Rillig, 2010; Kempel et al., 2013), and/or understanding traits of mycorrhizal fungi themselves (Öpik and Moora, 2012; Koide et al., 2014; Aguilar-Trigueros et al., 2014, 2015) will enhance the functional understanding of alien plant invasion and will be a fruitful extension to understand the role of the symbiosis in this context.

Acknowledgements

MCR acknowledges funding from Federal Ministry for Education and Research (BMBF) for the project 'Bridging in Biodiversity Science (BIBS)'. MM and MZ were supported by grants from the European Regional Developmental Fund (Centre of Excellence Ecolchange) and Estonian Research council (IUT 20-28). PP was supported by long-term research development project RVO 67985939 (The Czech Academy of Sciences), project no. 14-36079G, Centre of Excellence PLADIAS (Czech Science Foundation), and Praemium Academiae award from The Czech Academy of Sciences.

Supplementary data

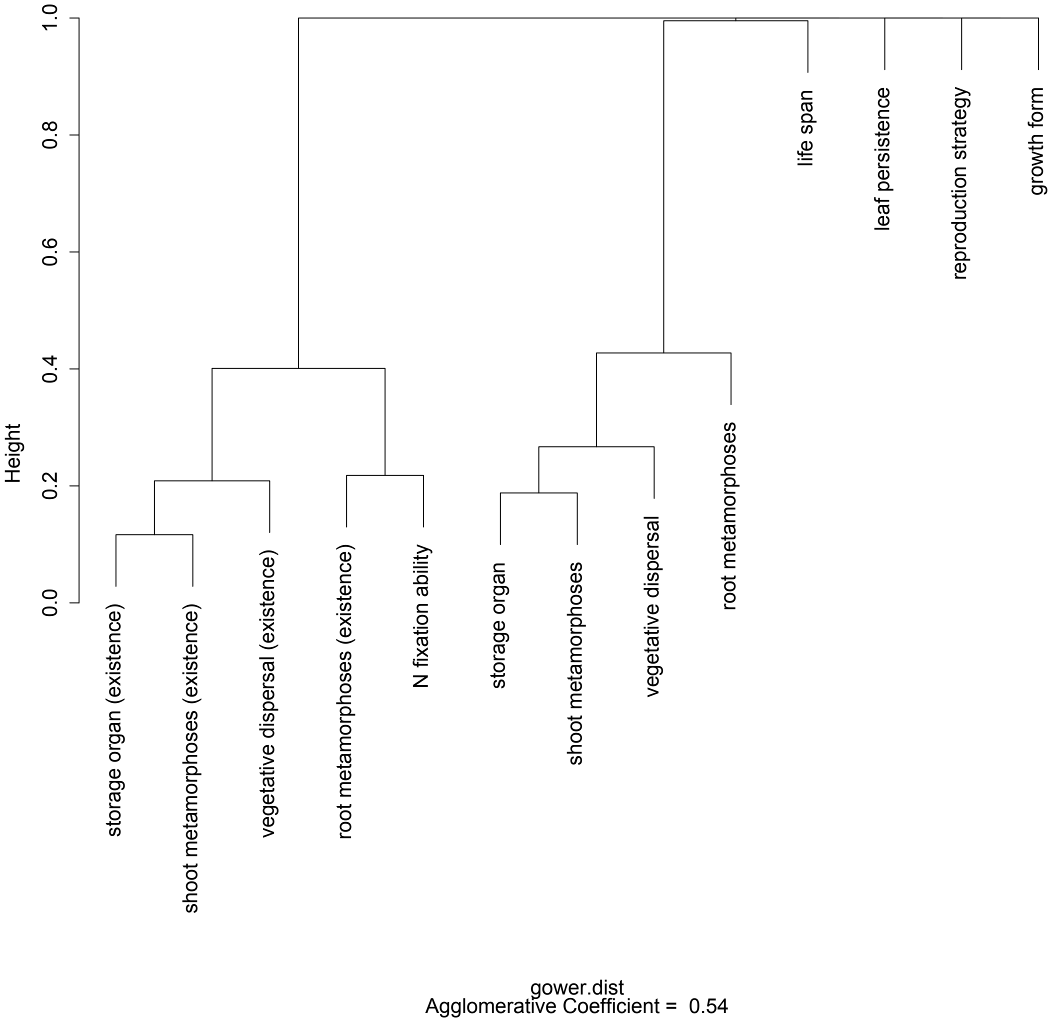


Figure A1: Dendrogram illustrating correlations of the functional traits next to mycorrhizal status, resulting of a cluster analysis based on a Gower's pairwise dissimilarity distance and agglomerative hierarchical clustering. The dendrogram was built using the package 'cluster' (Mächler et al., 2013) in R (version 3.0.2, R Development Core Team, 2013).

Table B1: Summary of the negative binomial generalised linear models with introduction time as predictor and number of occupied grid cells as response variable. As information on neophytes' introduction time was heterogeneous, i.e. a definite year for some species (e.g., 1912) or the century of introduction for other species (e.g., 17th century), we created two variables to account for introduction time: (*model m1*) a categorical variable containing the century of introduction (5 trait values: 16th to 20th century), (*model m2*) a continuous variable containing the definite year; if introduction time was given as century of introduction, the year was coded as the 50th year of the particular century (e.g., 17th century → 1650). Both variables were tested in separate models.

variable	df	deviance	p
model m1			
introduction time (categorical)	4	3.0	0.55
model m2			
introduction time (continuous)	1	0.02	0.87

Asterisks indicate results with *$0.01 < p \leq 0.05$, **$0.001 < p \leq 0.05$, ***$p \leq 0.001$.

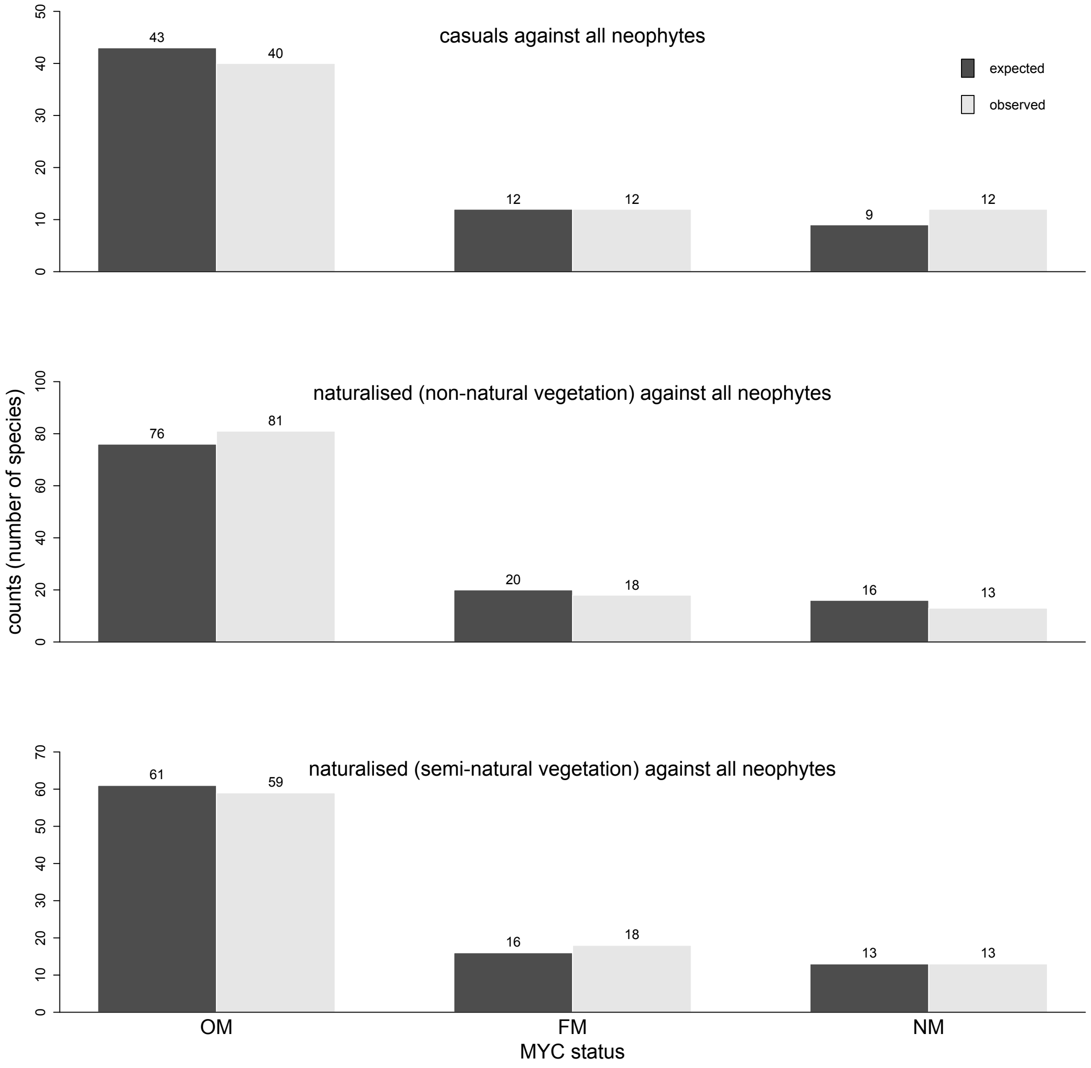


Figure C1: Observed and expected frequencies of mycorrhizal status for casual neophytes, neophytes naturalised only in human-made habitats, and neophytes naturalised also in habitats with (semi)natural vegetation. Values above bars are counts (number of plant species). Expected frequencies are based on the observed values for all neophytes and do not significantly differ from the observed values pooled across all mycorrhizal statuses (G=2.5, df=6, p=0.87)

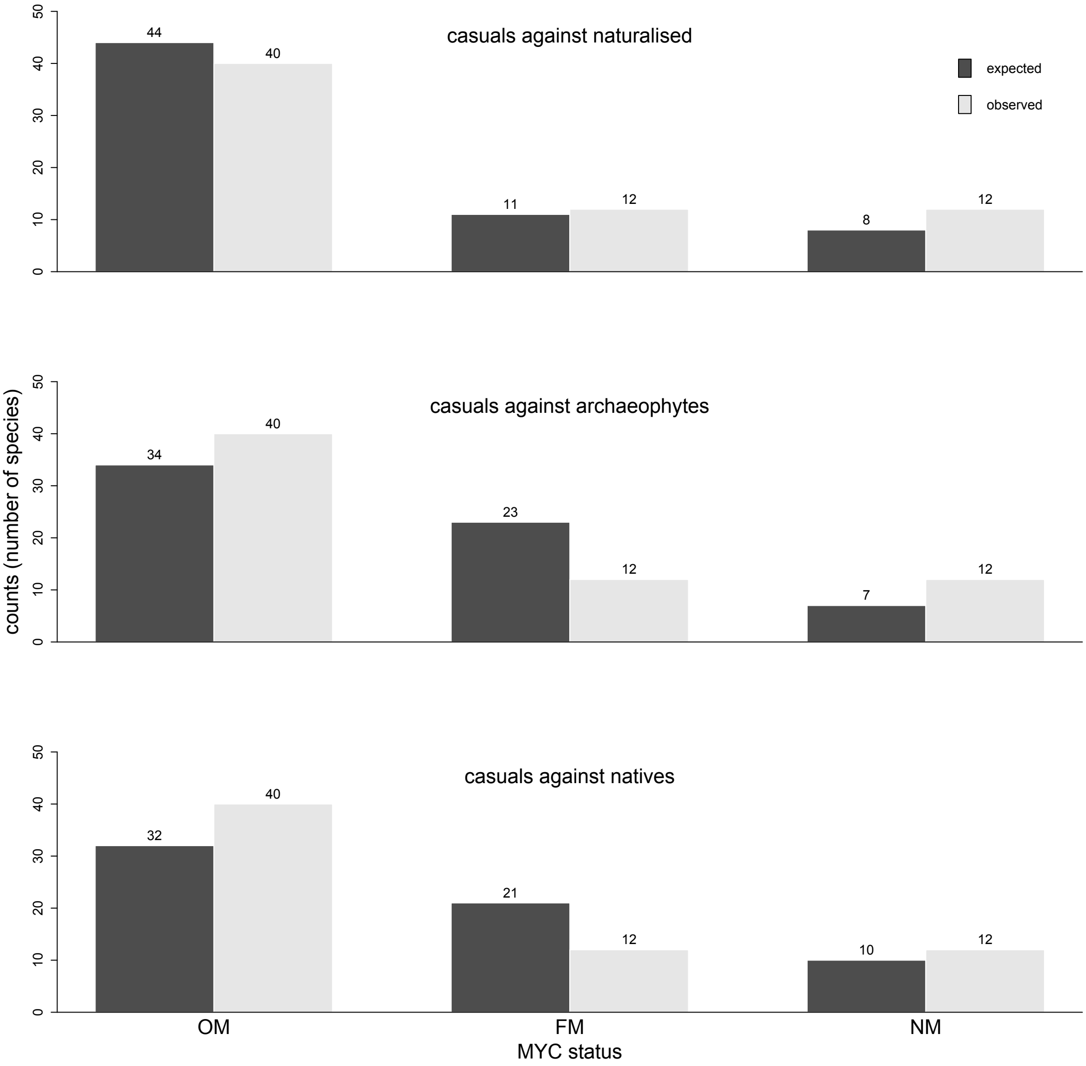


Figure C2: Observed and expected frequencies of mycorrhizal status for casual neophytes compared to (1) naturalised neophytes (naturalised in human-made habitats and/or (semi)natural vegetation), (2) archaeophyte plant species, and (3) native plant species. Values above bars are counts (number of plant species). Expected frequencies are based on the observed values (1) for naturalised neophytes (naturalised in human-made habitats and/or (semi)natural vegetation) and do not significantly differ from these values pooled across all mycorrhizal statuses (G=1.44, df=2, p=0.49), (2) for archaeophytes and do significantly differ from these values (G=7.24, df=2, p=0.03) and (3) for natives and do significantly differ from these values (G=6.45, df=2, p=0.04).

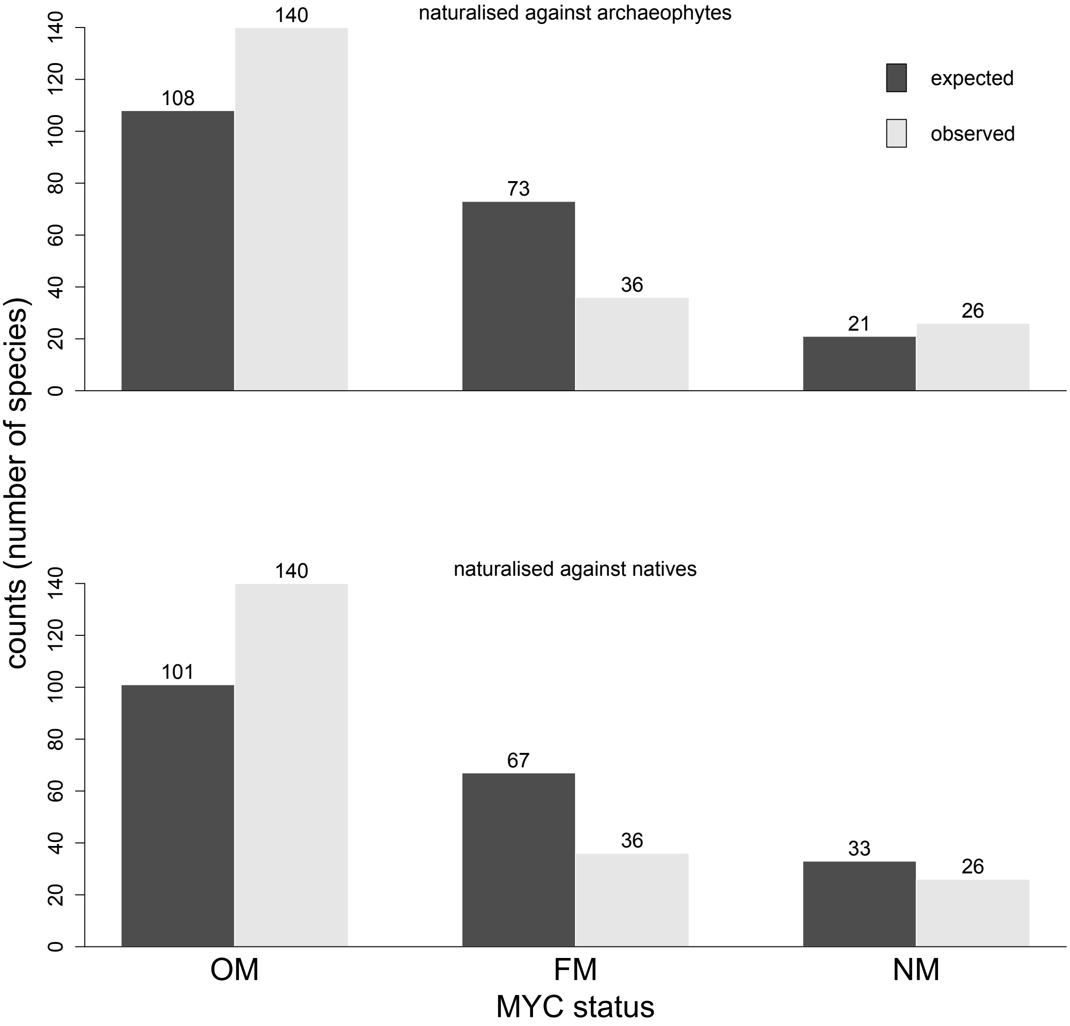


Figure C3: Observed and expected frequencies of mycorrhizal status for (1) naturalised neophytes (naturalised in human-made habitats and/or (semi)natural vegetation) compared to archaeophyte plant species; (2) naturalised neophytes (naturalised in human-made habitats and/or (semi)natural vegetation) compared to natives. Values above bars are counts (number of plant species). Expected frequencies are based on the observed values (1) for archaeophytes and do significantly differ from these values (G=13.9, df=2, $p<0.01$), and (2) for natives and do significantly differ from these values (G=28.02, df=2, $p<0.001$).

Table D1: Results of the phylogenetically informed single trait generalised linear models with number of occupied grid cells as response variable; in each model the particular functional trait served as independent variable together with the pre-selected phylogenetic principal coordinates. Results for phylogenetic covariates are not presented.

variable	df	deviance	p
mycorrhizal status	2	7.4	0.02**
growth form	1	7.7	0.005**
storage organ (existence)	1	0.9	0.35
root metamorphoses (existence)	1	0.3	0.59
shoot metamorphoses (existence)	1	0.8	0.37
reproduction strategy	2	2.3	0.31
vegetative dispersal and propagation (existence)	1	0.6	0.42
nitrogen fixation ability	1	0	0.88
life span	2	0.6	0.76
leaf persistence	2	2.7	0.25
storage organ	4	7.2	0.13
root metamorphoses	2	0.6	0.75
shoot metamorphoses	3	1.6	0.65
vegetative dispersal and propagation	3	2.4	0.5

Asterisks indicate results with *$0.01 < p \leq 0.05$, **$0.001 < p \leq 0.05$, ***$p \leq 0.001$.

CHAPTER 4

Trait Interactions Reveal Differences in Arbuscular Mycorrhizal Associations Between Native and Alien Plant Species

Andreas Menzel, Stefan Hempel, Stefan Klotz, Mari Moora,
Petr Pyšek, Matthias C. Rillig, Martin Zobel, and Ingolf Kühn

CHAPTER 4: Trait Interactions Reveal Differences in Arbuscular Mycorrhizal Associations Between Native and Alien Plant Species

Abstract

It is still debated whether alien plants benefit from being mycorrhizal and whether widespread alien plants differ in their association with mycorrhizal fungi from widespread native plants. Here, we compare whether species differing in their floristic status (natives, archaeophytes, neophytes) and arbuscular mycorrhizal status (obligate, facultative, non-mycorrhizal) differ in their area of occupancy in Germany. We used generalised linear models to explain the area of occupancy in Germany. To this end, we incorporated main effects as well as three-way interactions combining arbuscular mycorrhizal status, floristic status, and plant functional traits. The latter were chosen with respect to potential high energy costs, which could be supported (in the case of N and P) or inhibited (in the case of carbon) by the symbiosis. Arbuscular mycorrhizal status significantly explained the area of occupancy of natives and neophytes, with facultative mycorrhizal species occupying the largest area in both groups. This relationship was absent in archaeophytes. Significant trait interactions between mycorrhizal status and other plant traits were almost exclusively detected for neophytes. Whereas facultative mycorrhizal neophytic species benefit from trade-offs with other traits related to high carbon cost, such trade-offs are almost absent from natives. This indicates that natives and neophytes benefit differently from the symbiosis and that the benefits received by natives are independent of carbon allocation.

Keywords: alien plants, biological invasion, Central Europe, floristic status, functional traits, MycoFlor, mycorrhizal status, trait interactions

Introduction

With increasing concern about invasive alien plant species' effects on native plant species, communities, ecosystems as well as their economic consequences (Vilà et al., 2010, 2011; Simberloff et al., 2013), there has been increasing interest in studying processes and mechanisms underlying successful invasions. Next to the susceptibility of an ecosystem (invasibility), the invasion success of alien plant species depends on species' traits (invasiveness; Lonsdale, 1999). The integration of biotic interactions (Mitchell et al., 2006) and particularly mutualistic associations (Richardson et al., 2000b; Traveset and Richardson, 2014; Aslan et al., 2015) to frameworks assessing alien plant invasions has gained increased interest, as they help bridging invasibility (facilitated by mutualists of the receiving habitat) and invasiveness (exerted by introduced mutualists). The large majority of terrestrial plant species is associated with arbuscular mycorrhizal fungi (AMF; Smith and Read, 2008; Brundrett, 2009) and it has been demonstrated that AMF are of great importance in shaping the ecology of plant species and plant communities (van der Heijden et al., 2003; Callaway et al., 2004; Klironomos et al., 2011). Therefore, interest in the arbuscular mycorrhizal symbiosis has emerged in the context of alien plant invasions (Pringle et al., 2009; Shah et al., 2009; Bunn et al., 2015). This was facilitated by the publications of comprehensive data sets compiling information on plants and whether they form mycorrhizal associations (Wang and Qiu, 2006; Akhmetzhanova et al., 2012; Hempel et al., 2013) as well as conceptualising plant mycorrhizal traits, including plant mycorrhizal status (Moora, 2014). In this study, we classify plant species according to their arbuscular mycorrhizal status: (1) obligate mycorrhizal plant species (OM) that are always colonised by arbuscular mycorrhizal fungi, (2) facultative mycorrhizal plant species (FM) that are colonised under some conditions but not others, and (3) non-mycorrhizal plant species (NM) that are never found to be colonised by mycorrhizal fungi (Smith and Read, 2008; Moora, 2014).

It is an ongoing debate whether alien plants benefit from being mycorrhizal or if engaging in the symbiosis constrains their establishment and spread in new regions (Pringle et al., 2009; Shah et al., 2009; Bunn et al., 2015). Whereas small-scaled field studies report the majority of alien plant species to be mycorrhizal (Štajerová et al., 2009; Moora et al., 2011; Nuñez and Dickie, 2014), the functional significance of the mycorrhizal association on invasion success remains either unknown or is seen as highly context-dependent (Johnson et al., 1997; Klironomos, 2003; Hoeksema et al., 2010). In a meta-analysis, Bunn et al. (2015) did not find a positive correlation between arbuscular mycorrhizal colonisation and growth response in invasive plants, but invasives were more strongly colonised by mycorrhizal fungi when grown in direct competition with natives. Studies including a larger number of species remain scarce or yield ambiguous results. Fitter (2005) found alien plant species to be more likely from 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. Concerning the German flora, Hempel et al. (2013) showed that neophyte plant species (i.e., those aliens species introduced after the year 1500; Pyšek et al., 2004) are more frequently OM compared to archaeophytes (introduced before the year 1500) and native species. Using the same data set, Menzel et al. (chapter 3) found that the mycorrhizal status significantly explained the invasion success of neophyte plant species in Germany. Their results indicated that being mycorrhizal (OM and FM) is important for the establishment of neophyte plants in the new environment, most likely as being involved in the symbiosis promotes seedling establishment (van der Heijden, 2004; Wurst et al., 2011; Koorem et al., 2012), and constitutes a competitive advantage over non-mycorrhizal plants (Fumanal et al., 2006; Sun and He, 2010; Chmura and Gucwa-Przepióra, 2012). The arbuscular mycorrhizal symbiosis potentially affects nutrient uptake and carbon economy of plant species. AMF can supply up to 90% of plant P uptake, up to 20% of plant N uptake, and consume a significant amount of plant's net primary production (van der Heijden et al., 2015, and references therein). Hence, despite the benefits plants gain from the symbiosis, there is cost in terms of carbon provided to the fungal partner. Thus, trade-offs between mycorrhizal status and the expression of other plant traits can be expected (Peat and Fitter, 1993; Reinhart et al., 2012). In fact, Menzel et al. (chapter 3) demonstrated that being FM is beneficial for successful spread and persistence of neophytes, as the advantage to flexibly choose the strategy or property to invest in enables a broader set of available ecological strategies, i.e., it allows additional high energy cost plant strategies such as the development of storage organs, rhizomes or a perennial life span.

Based on the analysis by Menzel et al. (chapter 3), we aim at increasing the generality of trade-offs between arbuscular mycorrhizal status and other plant functional traits. To this end, we extended the set of plant traits in the respective study by the following traits. We included plants' functional group, as it was suggested that differences in functional group influence plant-soil feedbacks and invasion trajectories rather than plants' floristic status (Meisner et al., 2014; Bunn et al., 2015). We especially aimed to include root traits, as the plant-root interface is the direct link between the mycorrhizal symbionts. It has been shown that plant species with thick and slow-growing roots, abundantly covered with root hairs are known to rely much more on mycorrhizal fungi, than plants with fine, fast-growing, and less root-hair covered roots (Hetrick et al., 1992; Peat and Fitter, 1993; McCormack et al., 2014). Moreover, plant species with tap root architecture were reported to be more dependent on the symbiosis than plants with fibrous root systems (Marler et al., 1999; Yang et al., 2015), indicating that highly branched roots and mycorrhizal fungi are alternative strategies for absorbing nutrients (Wilson and Hartnett, 1998). We included plants species' seed dry mass, as NM species were reported to produce smaller seeds (Peat and Fitter, 1993) and we therefore expect competing carbon costs between retention of the symbiosis and the production of larger and heavier seeds. Lighter seeds may positively affect dispersal rates of wind dispersed plants (Greene and Johnson, 1993;

Skarpaas et al., 2011) whereas germination and establishment success were shown to jointly increase with seed mass (Turnbull et al., 1999, 2004; Moles and Westoby, 2004). Following the same argumentation, we included trait information concerning the existence of seed appendages as well as seedling vigour, as both traits represent a more or less plant investment in nutrient reserves. We included specific leaf area (SLA), as it is tightly correlated with plants' photosynthetic capacity (Wright et al., 2004; Shipley et al., 2006) and provides information about a plant's ability to acquire resources (cf. Lavorel and Grigulis, 2012). This most likely affects the allocation of photosynthates to mycorrhizal fungi. The same is true for including plant growth rate, as taller plants invest more carbon to increase their height and have a generally slower metabolism, potentially affecting the symbiosis. In turn, one of the known physiological plant responses to inoculation with AMF is an increased size (Hoeksema et al., 2010). In general, high values of SLA and plant growth rate are associated with a high plant performance in terms of physiology and fitness and are shown to be characteristics of invasive alien plants (van Kleunen et al., 2010; Pyšek et al., 2015). Lastly, we aimed to include the ability of a plant species to defend itself chemically. Gange and West (1994) suggested that AMF colonisation can alter plants' carbon and nutrient balance in such a way that it leads to an increased allocation to carbon-based defence mechanisms. Contrastingly, De Deyn et al. (2009) reported that genotypes of *Plantago lanceolata*, which were better chemically defended against root herbivory, were less colonised by AMF than less chemically defended genotypes. Therefore, the production of allelochemicals for plant defence may either benefit or suffer from engagement in the symbiosis and thereby may affect a plant's area of occupancy by reducing or increasing above- or belowground herbivory.

Invasion ecologists are still debating, whether widespread alien plant species differ in their characteristics from widespread native plant species or if they are functionally similar (van Kleunen et al., 2010; Davis et al., 2011; Knapp and Kühn, 2012). There are two possible scenarios concerning the arbuscular mycorrhizal status of plants: (1) the trait interactions indicating trade-offs in carbon allocation strategies (Menzel et al., chapter 3) are specific for neophytes, which would emphasise a peculiar association with mycorrhizal symbionts in recently introduced alien plant species and may explain the differences in composition of mycorrhizal status between natives, archaeophytes and neophytes in Germany (Hempel et al., 2013), (2) the reported trait interactions are consistent across all plant species independent of their floristic status and therefore depict general trade-offs. This is supported by the perception that FM plant species show the largest area of occupancy in neophytes (Menzel et al., chapter 3) as well as across all plant species in Germany for which their mycorrhizal status is known (Hempel et al., 2013). Yet, this was not tested for native and archaeophyte species separately. To this end, we analyse whether or not the area of occupancy of native, archaeophyte, and neophyte plant species in Germany is similarly affected by their arbuscular mycorrhizal status as well as associated trait interactions related to carbon allocation strategies.

Material and Methods

Plant species distribution data were obtained from FLORKART, a database of the German Network for Phytodiversity, provided by the German Federal Agency for Nature Conservation (http://www.floraweb.de). 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., c. 130 km^2) size, resulting in 2995 grid cells. We used the number of occupied grid cells as proxy for area of occupancy for each plant species. Therefore, this measure potentially ranges from 1 to 2995 occupied grid cells.

Information on mycorrhizal status for each plant species - OM, FM or NM - was taken from the MycoFlor data base (Hempel et al., 2013). 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 response under given conditions, mycorrhizal status does not give direct information about the functional significance of mycorrhizal colonisation of the given species' individuals. It rather refers to the mere presence/absence of fungal colonisation and can be used as a proxy for estimating the potential importance of the mycorrhizal symbiosis for plants at species level. Although MycoFlor contains information on a range of mycorrhizal associations, we restricted the analysis to symbioses involving AMF, as they are the most cosmopolitan and largest group represented in MycoFlor. Furthermore, neophyte plant species in Germany are predominantly arbuscular mycorrhizal (Menzel et al., chapter 3). Therefore, restricting the analysis to plant species forming an arbuscular mycorrhizal symbiosis helps to avoid confounding effects, while comparing species with different floristic status. We assigned the NM status to strictly non-mycorrhizal plant species, i.e., non-arbuscular mycorrhizal species that may form dual symbiotic relationships with other mycorrhiza types (e.g., ecto- or ericoid mycorrhiza) were excluded. Information on species' floristic status, i.e., native, archaeophyte or neophyte was obtained from BiolFlor (Klotz et al., 2002). Finally, we analysed the number of occupied grid cells of 1462 plant species of which 1084 were natives, 129 archaeophytes, and 249 neophytes.

Information on plant traits was obtained from TRY, a compilation of worldwide trait data bases (Kattge et al., 2011). We aimed for selecting data bases originating from Europe, as they should represent the German flora in a sound way (Table 1; including source data based included in TRY). Furthermore, we aimed for not merging trait information from different data sources, as the import in TRY does not guarantee similar protocols of trait measurements across data bases (Kattge et al., 2011). We preferentially selected these data bases, which contained information of the largest number of plant species in MycoFlor, i.e., the most information per particular plant trait. Prior to the analysis we assessed the availability of information of each plant functional trait and each floristic status group and decided which traits were included in the analysis based on their particular availability of trait information. Due to the lack in availability of trait information, we did not include the plant functional traits root type, rooting depth, seedling vigour, and availability of chemical plant defence (Table 1). We did not analyse very rare attributes (i.e., trait values) that are those with less than ten species in each group of plants with different floristic status. This resulted in different numbers of species per plant trait (Table 1).

We used the number of occupied grid cells in Germany as response to model the area of occupancy and chose generalised linear models with negative binomial error distribution to account for overdispersion. We established a model for each of the plant functional traits, including the three-way interaction of arbuscular mycorrhizal status, floristic status, and the particular trait. Therefore, the three main effects and all possible two-way interactions were included. Each model was reduced to the simplest possible model, i.e., interaction effects were removed in a backward selection process based on error probabilities or being included in a significant higher-order trait interaction. Furthermore, we split the data set by plants' floristic status and analysed the resulting three data sets separately, as the unbalanced number of native, archaeophyte, and neophyte species may superpose significant interaction terms in each group. Thereby, we included the two-way interaction of arbuscular mycorrhizal status and the particular plant trait. For each of the three separated data sets, differences in the mean number of occupied grid cells in Germany among the three mycorrhizal statuses within each attribute of categorical plant functional traits were tested by post-hoc Tukey's honestly significant differences (Tukey HSD).

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 by using the phylogenetic tree DaPhnE provided by Durka and Michalski (2012). A modification of the approach, originally proposed for accounting spatial dependencies by Bini et al. (2009) was used to incorporate phylogenetic relatedness within each generalised linear models. The triangular 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 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 (version 3.0.2, R Development Core Team 2013), in particular the packages 'ape' (Paradis et al., 2004), 'lsmeans' (Lenth and Hervë, 2015), 'MASS' (Venables and Ripley, 2002), and 'multcomp' (Hothorn et al., 2008).

Table 1: Summary of selected 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% - percentage of missing native species information; arc% - percentage of missing archaeophyte species information; neo% - percentage of missing neophyte species information. The last column indicates whether the functional trait was selected for modelling the area of occupancy in three-way and two-way interactions with plant mycorrhizal status and floristic status or whether it was excluded due to the lack of information. 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 Figure S1 for trait correlations).

functional trait	values	unit	n	nat%	arc%	neo%	references	selected
growth form	non-woody; woody	-	1462	0	0	0	BiolFlor (Klotz et al., 2002)	X
functional group	fern; forb; grass; rush; sedge; shrub/tree	-	1462	0	0	0	-	X
storage organ (existence)	yes; no;	-	1462	0	0	0	BiolFlor (Klotz et al., 2002)	X
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)	X
root metamorphoses (existence)	yes; no;	-	1462	0	0	0	BiolFlor (Klotz et al., 2002)	X
root metamorphoses	none; primary storage root; root shoot; root tuber	-	1462	0	0	0	BiolFlor (Klotz et al., 2002)	X
shoot metamorphoses (existence)	yes; no;	-	1462	0	0	0	BiolFlor (Klotz et al., 2002)	X
shoot metamorphoses	bulb; none; pleiocorm[1]; rhizome[2]; runner[3]; variable	-	1462	0	0	0	BiolFlor (Klotz et al., 2002)	X

continued on next page

functional trait	values	unit	n	nat%	arc%	neo%	references	selected
vegetative propagation and dispersal (existence)	yes; no;	-	1462	0	0	0	BiolFlor (Klotz et al., 2002)	X
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)	X
reproduction strategy	predominantly via seeds; seeds and vegetative; predominantly vegetative	-	1462	0	0	0	BiolFlor (Klotz et al., 2002)	X
life span	annual; perennial; variable	-	1434	0	0	0	BiolFlor (Klotz et al., 2002)	X
leaf persistence	summer green; overwintering green; persistent green	-	1359	5	2	6	BiolFlor (Klotz et al., 2002)	X
nitrogen fixation ability	yes; no	-	1462	0	0	0	-	X
plant defense: chemical	yes; no	-	359	78	63	70	USDA Plants (Green, 2009)	
root type	adventitious; fibrous; tap root; variable	-	265	81	81	85	EcoFlora (Fitter and Peat, 1994)	
tap root persistence[4]	yes; no	-	1095	23	11	41	CLO-PLA (Klimešova and de Bello, 2009)	X
seedling vigour	low; medium; high	-	281	88	88	74	USDA Plants (Green, 2009)	
rooting depth	0-50; >50;	cm	161	87	84	98	EcoFlora (Fitter and Peat, 1994)	
plant growth rate	*continuous*	mm	587	63	40	59	The Xylem Database (Schweingruber and Landolt, 2005)	X

continued on next page

functional trait	values	unit	n	nat%	arc%	neo%	references	selected
seed dry mass	*continuous*	mg	1206	30	6	20	KEW Seed Information Database (http://data.kew.org/sid/)	X
specific leaf area (SLA)	*continuous*	mm^2/mg	1061	25	17	43	LEDA (Kleyer et al., 2008)	X
seed morphology: appendages	yes; no; both	-	1005	31	12	40	LEDA (Kleyer et al., 2008)	X

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

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

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

[4] tap root persistence describes whether the primary root survives over the entire life span or not or whether both cases are reported.

Results

Mycorrhizal status had a significant effect on the number of occupied grid cells in a phylogenetically informed generalised linear model including all 1462 plant species (df=2, deviance=55.7, $p<0.001$), 1084 natives (df=2, deviance=36, $p<0.001$), and 249 neophyte plant species (df=2, deviance=8.4, p=0.02) but did not significantly explain archaeophytes' area of occupancy in Germany (df=2, deviance=3.1, p=0.21). For each of the significant cases, subsequent post-hoc tests revealed that FM species occupied a significantly greater number of grid cells than NM (all species: $p<0.001$, natives: p=0.01, neophytes: $p<0.001$) and OM ($p<0.001$, $p<0.001$, p=0.02) species. NM species occupied a marginally significant larger number of grid cells than OM species using all plant species (p=0.06) and native species (p=0.05). Contrastingly, OM neophyte plant species showed a tendency to occupy a larger number of grid cells than NM neophytes, but this difference was not significant (p=0.18).

We found significant three-way interactions of arbuscular mycorrhizal status, floristic status, and functional group, mode of shoot metamorphoses, the existence and mode of vegetative propagation and dispersal as well as the existence of seed appendages (Table 2). Furthermore, the three-way interaction of arbuscular mycorrhizal status, floristic status, and growth form, reproduction strategy, nitrogen fixation ability, seed dry mass, and SLA were marginally significant (Table 2). We found significant two-way interactions between mycorrhizal status and 13 out of 19 additional traits for neophytes and one trait interaction for archaeophytes and natives respectively (Table 3). Results of Tukey HSD post-hoc analysis revealed that neophytes with storage organs, shoot metamorphoses or specialised structures promoting vegetative dispersal and propagation, occupied more grid cells if being FM (Table 3). In particular, rhizomatous FM neophytes exhibited a positive association with the number of grid cells occupied. Among perennial and non-woody as well as forb species in particular, neophytes being FM were most successful. OM neophytes were most successful when likewise not developing storage organs nor structures promoting vegetative dispersal and propagation as well as if they were variable in their life span (Table 3).

Table 2: Summary of phylogenetically informed generalised linear models explaining the number of occupied grid cells. Displayed are the error probabilities for the main effect of mycorrhizal status, floristic status, and each particular trait as well as all possible two-way interactions and the three-way interactions of all three predictors. M=mycorrhizal status; F=floristic status; t=functional trait. Each cell includes degrees of freedom (df), deviance (dev) and significance levels: ns – non-significant, 0.05<p≤0.1 +, 0.01<p≤0.05 *, 0.001<p≤0.01 **, p≤0.001 ***

functional trait	M×F×t	M×t	M×F	F×t	M	t	F
growth form	*df=2 dev=5 +*	*df=2 dev=6.1 **	*df=4 dev=2.7 ns*	*df=1 dev=1.5 ns*	*df=2 dev=58 ****	*df=1 dev=6.6 **	*df=2 dev=104 ****
functional group	**df=5 dev=12 ***	**df=9 dev=15 ***	**df=4 dev=1.5 +**	**df=7 dev=18 ns**	**df=2 dev=58 *****	**df=5 dev=12 ***	**df=2 dev=105 *****
storage organ (existence)	-	-	-	-	df=2 dev=58 ***	df=1 dev=.3 ns	df=2 dev=106 ***
storage organ	-	-	-	df=4 dev=9.2 +	df=2 dev=58 ***	df=8 dev=43 ***	df=2 dev=106 ***
root metamorphoses (existence)	-	-	-	-	df=2 dev=59 ***	df=1 dev=7.5 **	df=2 dev=105 ***
root metamorphoses	-	-	-	df=3 dev=8.9 *	df=2 dev=59 ***	df=4 dev=8.5 +	df=2 dev=104 ***
shoot metamorphoses (existence)	-	-	-	-	df=2 dev=58 ***	df=1 dev=.1 ns	df=2 dev=107 ***
shoot metamorphoses	**df=7 dev=15 ***	**df=9 dev=7.5 ns**	**df=4 dev=4.6 ns**	**df=4 dev=3.6 ns**	**df=2 dev=57 *****	**df=5 dev=19 ****	**df=2 dev=94 *****

continued on next page

functional trait	M×F×t	M×t	M×F	F×t	M	t	F
vegetative propagation and dispersal (existence)	**df=3** **dev=8** *****	**df=2** **dev=.7** **ns**	**df=4** **dev=2.8** **ns**	**df=2** **dev=.1** **ns**	**df=2** **dev=58** *******	**df=1** **dev=.8** **ns**	**df=2** **dev=106** *******
vegetative propagation and dispersal	**df=7** **dev=21** ******	**df=11** **dev=9.4** **ns**	**df=4** **dev=3.6** **ns**	**df=4** **dev=8.1** **ns**	**df=2** **dev=56** *******	**df=6** **dev=18** ******	**df=2** **dev=99** *******
reproduction strategy	*df=4* *dev=9* *+*	*df=4* *dev=2.6* *ns*	*df=4* *dev=2.2* *ns*	*df=2* *dev=2.4* *ns*	*df=2* *dev=57* *****	*df=2* *dev=.5* *ns*	*df=2* *dev=109* *****
life span	-	-	-	-	df=2 dev=60 ***	df=2 dev=2.5 ns	df=2 dev=104 ***
leaf persistence	-	-	-	-	df=2 dev=53 ***	df=2 dev=8.1 *	df=2 dev=93 ***
nitrogen fixation ability	*df=2* *dev=4.8* *+*	*df=2* *dev=1.7* *ns*	*df=4* *dev=3.4* *ns*	*df=1* *dev=5.1* ***	*df=2* *dev=59* *****	*df=1* *dev=2.8* *+*	*df=2* *dev=106* *****
tap root persistence	-	df=2 dev=5.2 +	-	-	df=2 dev=56 ***	df=1 dev=.6 ns	df=2 dev=46 ***
plant growth rate	-	-	-	-	df=2 dev=14 ***	df=1 dev=.8 ns	df=2 dev=44 ***
seed dry mass	*df=4* *dev=9.2* *+*	*df=2* *dev=1.2* *ns*	*df=4* *dev=2.7* *ns*	*df=2* *dev=17* *****	*df=2* *dev=47* *****	*df=1* *dev=4.2* ***	*df=2* *dev=124* *****

continued on next page

functional trait	M×F×t	M×t	M×F	F×t	M	t	F
specific leaf area	*df=4* *dev=8.1* *+*	*df=2* *dev=6.3* ***	*df=4* *dev=2.7* *ns*	*df=2* *dev=2.5* *ns*	*df=2* *dev=32* *****	*df=1* *dev=8.8* ****	*df=2* *dev=67* *****
seed morphology: appendages	**df=6** **dev=16** *****	**df=4** **dev=4.6** **ns**	**df=4** **dev=.3** **ns**	**df=3** **dev=1.3** **ns**	**df=2** **dev=46** *******	**df=2** **dev=27** *******	**df=2** **dev=85** *******

Bold rows indicate a significant three-way-interaction between mycorrhizal status, floristic status, and the particular functional trait. Italic rows indicate a marginally significant three-way interaction between mycorrhizal status, floristic status, and the particular functional trait.

Table 3: Results of the Tukey post-hoc test following the generalised linear models explaining the number of occupied grid cells. Displayed are the plant functional traits that showed significant interaction effects with mycorrhizal status in each of the three data sets. A plus sign indicates a significantly higher, a minus sign a significantly lower number of occupied grid cells within each row of the table (Freeman Tukey test: $p<0.05$). The table's three parts separate the results for each floristic status.

		mycorrhizal status		
traits		OM	FM	NM
NEOPHYTES				
growth form				
	non-woody	-	+	-
	woody	ns	ns	ns
functional group				
	forb	-	+	-
	grass	ns	ns	ns
	shrub/tree	ns	ns	ns
storage organ (existence)				
	yes	-	+	-
	no	ns	ns	ns
storage organ				
	none	+	ns	-
	pleiocorm	ns	ns	ns
	rhizome	-	+	-
	runner	ns	ns	ns
	variable	ns	ns	ns
root metamorphoses				
	none	-	+	-
	primary storage root	+	-	ns
	root shoot	ns	ns	ns
shoot metamorphoses (existence)				
	yes	-	+	-
	no	+	ns	-
shoot metamorphoses				
	none	+	ns	-
	pleiocorm	ns	ns	ns
	rhizome	-	+	-
	runner	ns	ns	ns
vegetative dispersal (existence)				
	yes	-	+	-
	no	+	ns	-
vegetative dispersal				
	none	ns	ns	ns
	rhizome	-	+	-
	runner	ns	ns	ns
	variable	-	ns	+

continued on next page

	mycorrhizal status		
traits	OM	FM	NM
reproduction strategy			
predominantly via seeds	ns	+	-
seeds and vegetative	ns	ns	ns
predominantly vegetative	-	+	ns
life span			
annual	ns	ns	ns
perennial	-	+	ns
various	+	-	ns
specific leaf area	+	-	ns
seed morphology: appendages			
yes	ns	ns	ns
no	-	+	ns
both	ns	ns	ns
number of positive associations	7	13	1
NATIVES			
vegetative dispersal			
none	-	+	+
pleiocorm	ns	ns	ns
rhizome	ns	ns	ns
runner	ns	ns	ns
root shoot	-	+	-
variable	-	+	-
number of positive associations	0	3	1
ARCHAEOPHYTES			
specific leaf area	+	-	+
number of positive associations	1	0	1

NS marks non-significant 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 shown trait level combinations and each floristic status. 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 Figure S1 for trait correlations).

Discussion

Plant arbuscular mycorrhizal status significantly explained the area of occupancy of native and neophyte species, but not for archaeophyte plant species. In both significant groups, FM plant species showed the largest area of occupancy, indicating a similar association of plant species with the arbuscular mycorrhizal symbiosis. However, trait interactions between mycorrhizal status and other plant functional traits related to carbon allocation are predominantly present in neophytes and absent from natives. This result suggests differences in the mycorrhizal association and carbon allocation strategies involving the symbiosis of neophytes relative to native plant species. The detected trade-offs may be critical for the invasion success of neophyte plant species. As it is still discussed whether alien plant species benefit from being mycorrhizal or not and whether wide-spread native species differ in their mycorrhizal association from wide-spread alien species (Pringle et al., 2009; Shah et al., 2009; Bunn et al., 2015), our findings add a new perspective to this debate. Overall, our results emphasise the importance of incorporating trait interactions while analysing characteristics of alien plant species that are related to their mycorrhizal association and invasion success (cf. Küster et al., 2008). In general, discriminating alien plants by their floristic status (archaeophytes or neophytes) and mycorrhizal status (i.e., differentiating between OM, FM, and NM species instead of merely between mycorrhizal and non-mycorrhizal species) will refine future studies assessing the effects of the mycorrhizal symbiosis in alien plant invasions.

AMF are suggested not to act as barriers for alien plant invasion, as AMF taxa are globally distributed (Davison et al., 2015) and the arbuscular mycorrhizal symbiosis is generally proposed to be non-specific in terms of plant and fungal partners (Smith and Read, 2008; Moora et al., 2011). Nevertheless, even if the global diversity of AMF is low, the local diversity of AMF communities can be large. Oehl et al. (2010) e.g., found up to 30 AMF species interacting with 50 plant species at field sites of minor land-use intensity. Alien plant species have been shown to be less responsive to native fungal species (Klironomos, 2003; Pringle et al., 2009) and Hetrick and Wilson (1990) demonstrated that this difference was independent of the origin of the fungal partner, implying a general difference in responsiveness. Furthermore, Reinhart and Callaway (2006) suggested that not the mere interaction itself, but the strength and specificity of biotic interactions in new environments are important (see also Endresz et al. 2013). In general, the degree of plant responsiveness towards fungal partners is influenced by several factors such as soil nutrient status, additional resource availability (water and light) as well as plant and fungal identity (Klironomos, 2003; Pringle and Bever, 2008; Werner and Kiers, 2015). Our approach is not able to differentiate between effects of plant-fungi interactions, neither alterations in native fungal communities due to alien plant species (Callaway et al., 2008; Vogelsang and Bever, 2009) nor differences in the abiotic environment. Nevertheless, our results suggest that neophyte plant species in Germany are less responsive to AMF, as the FM status of neophytes simultaneously allows carbon allocation to high-carbon cost plant properties such as storage organs, rhizomes as shoot and root metamorphoses, and a perennial life span; trade-offs that are absent from OM and NM neophytes as well as natives in general. Neophytes typically occupy disturbed and/or urban habitats (Hobbs and Huenneke, 1992; Richardson and Pyšek, 2012), which may favour a larger variety of plant strategies and a lower responsiveness towards the arbuscular mycorrhizal symbiosis. This variety might help to avoid competition over native fungal communities. Therefore, the trade-offs found in FM neophytes may reflect the biotic and abiotic conditions of these environments. It is furthermore possible that facing native fungal communities and therefore new mycorrhizal associations may lead to evolutionary changes in alien plant traits (Bossdorf et al., 2005; Seifert et al., 2009). This might result in the detected differences of trait trade-offs between neophyte and native plant species. Moreover, neophyte OM species show the largest area of occupancy when they are not able to develop additional plant properties like storage organs, shoot metamorphoses or properties of vegetative dispersal. This underlines the perception that the benefits of neophyte plants gained from colonisation by native fungal symbionts are relatively low compared to natives in which these trade-offs are absent. It further indicates that the reported trade-offs indeed result from a reduced carbon allocation to mycorrhizal fungi and not from improved P or N uptake (Zabinski et al., 2002). Otherwise, OM neophyte plant species would have likely shown similar trade-offs as FM neophytes. Yet, it remains to be explained why neophytes in Germany are more frequently OM than natives and archaeophytes (Hempel et al., 2013). Overall, although neophyte FM species show a reduced responsiveness towards native AMF, they are at least partly mycorrhizal. Therefore, it is important to note that the mycorrhizal symbiosis has other meaningful aspects for plant species that are not related to plants' carbon, nutrient or water availability. Taking a plant's perspective, it has been shown that AMF offer pathogen protection (Newsham et al., 1995; Veresoglou and Rillig, 2012) as well as protection against heavy metals (Hildebrandt et al., 2007), and provide stabilisation of soil structure (Rillig et al., 2015). Native plant species may benefit to a larger degree from these facets due to the longer joint (evolutionary) history with native fungal communities, which might as well explain the detected differences in trait interactions found in the analysis.

Alien plant species differ in their ecological adaption to the environment of the recipient range from native plant species for two reasons: (1) most of them were selected by humans for special purposes such as cultivation (di Castri, 1989; Pyšek et al., 2005) and then deliberately introduced (Lambdon et al., 2008). (2) They evolved under different environmental and ecological settings (including different biotic interactors; Pyšek et al., 2005; Seifert et al., 2009). Next to their residence time, neophyte and archaeophyte species differ in their introduction pathways. Whereas entry points of neophytes are typically urban or industrial areas, i.e., habitats with high human impact, archaeophytes are mostly associated with agricultural habitats. Archaeophytes represent an ecologically distinct group compared to both natives and neophytes. They are mostly weed species of arable land and differ in life form and habitat requirements (Pyšek et al., 2004; Pyšek and Jarošik, 2006). Furthermore, archaeophytes have been recruited from less diverse places of origin (Pyšek et al., 2012). Overall, they are a homogenous group of plant species, which is demonstrated by the similarity in trait values in our analysis. They are predominantly forb species, reproduce mainly via seeds, do usually not have storage organs nor propagate or disperse vegetatively, and are not able to fix nitrogen. Our analysis adds that archaeophytes show weak or no association with AMF, which contrasts native and neophyte plant species. This can be explained by their close association with agriculturally used habitats, as management practices such as tillage (Jansa et al., 2002), grazing (Eom et al., 2001) or fertilisation (Johnson, 1993; Oehl et al., 2003) are known to negatively affect existing mycorrhizal networks and associations. Therefore, a plant's retention of the symbiosis becomes obsolete in agricultural habitats with steady availability of nitrogen and phosphorus. Moreover, archaeophyte species may have evolved a reduced mycorrhizal dependence overall (cf. Schultz et al., 2001; Seifert et al., 2009) or did not colonise habitats in their native range in which developing mycorrhizal associations was a useful strategy.

Bunn et al. (2015) suggested that different growth responses to AMF were rather based on plants' functional group than their floristic status, with forb species exhibiting positive growth responses whereas grasses showed neutral to negative effects on growth response when associated with AMF. Further, Yang et al. (2015) suggested that these differences are related to differences in root architecture and root coarseness. In our analysis only neophytes showed an interaction effect between functional group and arbuscular mycorrhizal status and only FM forbs were positively associated with a larger area of occupancy. Therefore, we reinforce the influence of plant species' floristic status, but encourage the further differentiation between plants distinct in their mycorrhizal status. Due to the lack of trait information concerning root traits we were not able to further disentangle this effect in this regard. At present, even large trait data bases like TRY are relatively poor in covering root traits (Table 1). Root traits are commonly neglected in plant functional ecology, although the plant-root interface is the major link between mycorrhizal fungi and plant individuals. Comprehensive measurements of traits like specific root length, root diameter, root hair length or root hair density would be an improvement not only in understanding the belowground compartments of plants, but also the mycorrhizal symbiosis (Ryser, 2006; McCormack et al., 2014; Yang et al., 2015). Different metrics of root traits and root architecture may be combined to reflect a spectrum of root system functioning (Maherali, 2014) including surface area-to-volume ratios and frequency of infection points (Wehner et al., 2014). This would additionally increase our understanding of fungal colonisation and plant-fungi relationships. Moreover, incorporating traits related to plant palatability and herbivory, both above- and belowground, will be a promising approach. High levels of herbivory deplete plant carbon resources and therefore likely reduce carbon allocation to mycorrhizal fungi. In turn, reduced aboveground herbivory is common in alien plant species (Bossdorf et al., 2005) and it has been shown that mycorrhizal associations affect plants' resistance to herbivory, but not in a consistent way (De Deyn et al., 2009; Koricheva et al., 2009; Kempel et al., 2013). Trait interactions may reveal whether alien plant species benefit from associations with mycorrhizal fungi by increased production of allelochemicals or whether a general reduction of herbivory in new environments will generally decrease the necessity to engage in the symbiosis. For this purpose better trait information on plant defence mechanisms in general (chemically and mechanically) are needed. This is not about conceptualising new traits, but rather about increasing the availability of existing ones, e.g., by further description and quantification of the amount and nature of allelochemicals used by a larger number of plant species across different environmental conditions.

On a world-wide basis phosphorus and nitrogen are often the limiting resources for vegetation and it has been suggested that soil nutrient levels play an important role in determining a community's invasibility (Davis et al., 2000; Blumenthal, 2005). The arbuscular mycorrhizal symbiosis profoundly affects the availability of these plant resources in nearly all habitats and across all biomes worldwide (Treseder and Cross, 2006; Brundrett, 2009). Moreover, mycorrhizal fungi are known to be major players in global carbon cycles and carbon sequestration (Wilson et al., 2009; Averill et al., 2014). Yet, the symbiosis and belonging nutritional trade-offs are rarely included in analyses of establishment of alien plant species in new environments. Our study demonstrates that alien and native plant species differ in their association with the arbuscular mycorrhizal symbiosis, which is shown by certain trade-offs linked to carbon allocation that are specific for neophyte plant species in Germany. In future studies, discriminating alien plants by their floristic status (archaeophytes or neophytes) and mycorrhizal status (i.e., differentiating between OM, FM, and NM species instead of merely between mycorrhizal and non-mycorrhizal species) will refine assessing the role of the mycorrhizal symbiosis in alien plant invasions.

Acknowledgements

MCR acknowledges funding from Federal Ministry for Education and Research (BMBF) for the project 'Bridging in Biodiversity Science (BIBS)'. MM and MZ were supported by grants from the European Regional Developmental Fund (Centre of Excellence Ecolchange) and Estonian Research council (IUT 20-28). PP was supported by long-term research development project RVO 67985939 (The Czech Academy of Sciences), project no. 14-36079G, Centre of Excellence PLADIAS (Czech Science Foundation), and Praemium Academiae award from The Czech Academy of Sciences.

We are grateful to the many researchers who contributed to this study by making their data available, helping to check information, and/or providing comments at various stages. The study was supported by the TRY initiative on plant traits (http://www.try-db.org). TRY is hosted at the Max Planck Institute for Biogeochemistry (Jena, Germany) and supported by DIVERSITAS/Future Earth, the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, and BACI (grant ID 640176).

Supplementary data

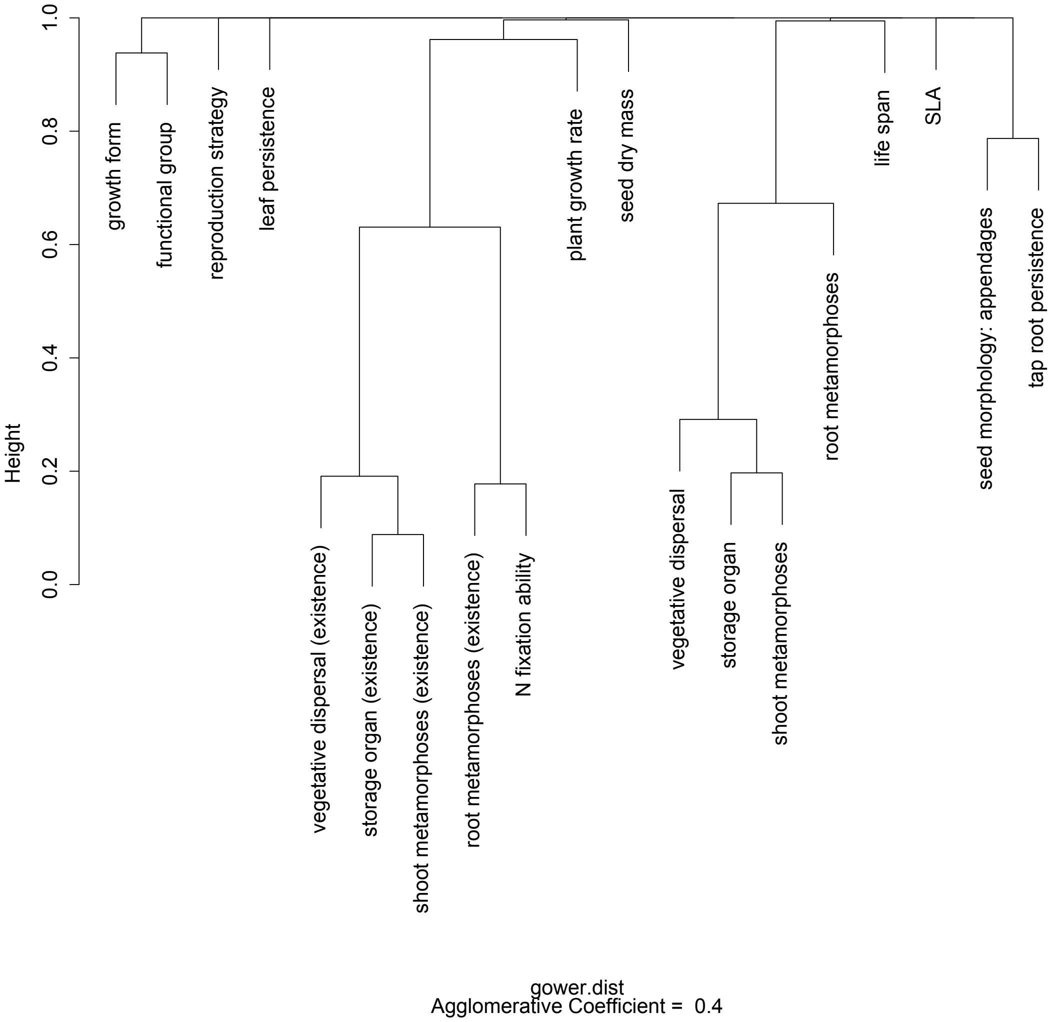


Figure S1: Dendrogram illustrating correlations of the functional traits next to mycorrhizal status, resulting of a cluster analysis based on a Gower's pairwise dissimilarity distance and agglomerative hierarchical clustering. The dendrogram was built using the package 'cluster' (Mächler et al., 2013) in R (version 3.0.2, R Development Core Team, 2013).

CHAPTER 5

SYNTHESIS

CHAPTER 5: Synthesis

This thesis aimed to investigate the effects of the mycorrhizal symbiosis on plant distributions and alien plant invasions at a large spatial scale. By utilising the differentiation between obligate mycorrhizal (OM), facultative mycorrhizal (FM), and non-mycorrhizal (NM) plant species, the presented analyses demonstrate a surplus of accounting for the mycorrhizal symbiosis in such frameworks. The key results are as follows:

- To the best of my knowledge chapter 2 provides the first evidence of spatial patterns of plant assemblages that are composed of species with different arbuscular mycorrhizal status at the German country scale. The patterns are non-random, clearly distinct, and resemble the German topography as well as the associated environmental conditions. Large shares of OM plant species are associated with regions of high temperature and precipitation ranges, high mean temperatures, large limestone and urban areas as well as small areas of mixed and coniferous forest. Contrastingly, large NM shares are associated with regions of low temperature range and low values of mean precipitation as well as a large number of different soil types.

- Chapter 3 and 4 demonstrate that being mycorrhizal benefits the invasion success of alien plant species, but concurrently show the need for differentiation while investigating the effects of the mycorrhizal symbiosis in the context of alien plant invasions: (1) *by floristic status* - the invasion success of neophyte plant species (those introduced to Germany after 1500) is affected by their mycorrhizal status, but this relationship is absent from archaeophyte species (those introduced before 1500), (2) *by mycorrhizal status* - FM plant species inhabit the largest area of occupancy in Germany compared to OM and NM species in both, native and neophyte species. NM natives tend to occupy a larger area than OM natives, whereas this relation is opposite in neophytes, and (3) *including trait interactions* - trait interactions including plant mycorrhizal status revealed differences in arbuscular mycorrhizal associations between neophyte and native plant species. While FM neophytes benefit from their flexibility to choose the carbon sink to invest in (retention of the mycorrhizal symbiosis vs. plant properties such as storage organs), these trade-offs are absent in FM natives. This suggests that native plant species benefit from the symbiosis independent of carbon allocation strategies. OM neophytes show the largest invasion success when not being able to develop additional plant properties.

The mycorrhizal symbiosis affects large-scale plant distributions

Chapter 2 demonstrates the existence of distinct spatial patterns of plant species assemblages differing in their composition of OM, FM, and NM species at the German country scale. Thereby, the analysis emphasises the role of plants' arbuscular mycorrhizal status at such large spatial scale and hierarchical level of plant organisation. Furthermore, the associated model shows that these compositions are affected by environmental conditions acting at this scale and thereby reflecting known responses of plant-fungi relationships to abiotic parameters, which were in turn gained from small-scale studies. Chapter 2 therefore bridges the gap between pot experiments and coarse grained global analyses in studying the mycorrhizal symbiosis. Moreover, it overcomes the comparative character of former studies in mycorrhizal ecology that focus on the level of plant species to a context of plant assemblages and plant distributions. The species compositions follow gradients of acidity, precipitation, and temperature and are in line with the majority of a priori expectations (chapter 2) as well as a study by Soudzilovskaia et al. (2015), which associates plant mycorrhizal colonisation with the abiotic environment at a coarse-grained global scale. However, the large effect of temperature range influencing the spatial distributions of the plant assemblages is surprising (chapter 2). Regions of high temperature range as well as precipitation range, i.e., regions with typically continental climate, were associated with an increase in OM and a decrease of NM species proportions (chapter 2). *A priori* it was expected that such varying conditions in temperature and precipitation would be best tolerated by FM plant species, as they are supposed to be more adaptable to changing environmental conditions due to their flexibility in mycorrhizal association. In general, physiological growth conditions for plant species become harsher with increasing continentality. Welk et al. (2014) found that plant species in Germany, which typically occur in areas of continental climate, are more vulnerable to competition and herbivory as plants typically occurring in regions with oceanic climate. Further, interspecific plant interactions are suggested to turn from competition to facilitation with increasing abiotic stress ('stress-gradient hypothesis'; Bertness and Callaway, 1994; Maestre et al., 2009). The mycorrhizal symbiosis has the potential to similarly alleviate stressful abiotic and biotic conditions of continental climate, which is likely a mechanism explaining the higher proportions of OM plant species in regions with higher temperature and precipitation ranges. Consequently, this would expand the stress-gradient hypothesis from plant-plant to plant-fungi interactions. An alternative explanation is that OM plant species are specialists comprising the extreme ends of temperature and precipitation ranges. Soudzilovskaia et al. (2015), e.g. suggest that the presence of a prolonged frost period increases colonisation intensity of host plant species by arbuscular mycorrhizal fungi (AMF). The next step is to test these model-gained hypotheses experimentally, for instance by conducting reciprocal transplant experiments between regions of continental and oceanic climate using plant species differing in their arbuscular mycorrhizal status (see, e.g., Hoeksema et al., 2010; Doubková et al., 2012; Lankau, 2012). This will not only benefit our understanding of mycorrhizal effects on plant responses to harsh environmental conditions, but will further reveal potential variation in effects of the mycorrhizal symbiosis with scale and hierarchical level of plant organisation (cf. Allison and Goldberg, 2002). Overall, this demonstrates a central point of utilising plant mycorrhizal status in correlative models of large-scale plant distributions. They allow the detection of potential driving processes that could not have emerged at comparable effort and scale from experimental studies under field conditions. Hence, they help generating new hypotheses that can now be tested experimentally (cf. Dormann et al., 2012).

Understanding the co-variation of plants and their mycorrhizal symbionts at large scales starts with observations, descriptions as well as post-hoc explanations of the demonstrated patterns. Therefore, analyses compiling sufficiently large species numbers are necessary to gain a comprehensive picture of underlying processes that shape the co-variation of both symbionts. It would be of great interest, if the reported relationships of plant arbuscular mycorrhizal status and environmental factors related to climate hold true in other biomes, e.g., in the tropics where AMF are the particular dominant mycorrhizal type. Nevertheless, it is important to note that predictions based on correlative distribution models are usually limited in their transferability to other environments and that their inherent assumption of stationarity (i.e., model parameters are constant in space and time) limits their predictive power in scenarios of future environments (Dormann et al., 2012; Heikkinen et al., 2012). The transferability would certainly benefit from accounting for the abundance of species (plant and fungus) instead of their mere presence/absence as well as high-resolution data on soil nutrient availability and climate, to capture fine-scale processes affecting both symbiotic partners (cf. McInerny and Purves, 2011). Unfortunately, such data are predominantly unavailable at the chosen scale.

The mycorrhizal symbiosis affects alien plant invasions

It is still debated, whether alien plant species that arrive in new environments benefit from being mycorrhizal or not and whether they differ in their mycorrhizal association compared to native plant species (Pringle et al., 2009; Shah et al., 2009; Bunn et al., 2015). The analysis presented in chapter 3 demonstrates that neophyte plant species in Germany indeed benefit from being mycorrhizal (both OM and FM). While neophyte plant species are more frequently OM considering all neophytes (Hempel et al., 2013) as well as neophytes across several stages of the invasion process (chapter 3), FM plant species show the greatest invasion success in terms of occupied geographical range. Furthermore, the detected trade-offs between neophyte mycorrhizal status and other plant functional traits (chapter 3), which are related to their invasion success, are not present in native plant species (chapter 4). This demonstrates the peculiarity of trait combinations involving plant mycorrhizal status and other functional plant traits related to morphology, reproduction, and life-history in neophytes. To the best of my knowledge chapters 3 and 4 are the first studies that demonstrate the importance of such trait interactions involving plant mycorrhizal status in association with invasion success. The analyses confirm that considering trait interactions and whole plant ecological strategies help explain the invasion success of alien plant species (Küster et al., 2008) and that the dependence on a fungal partner, particularly in the case of AMF, does not restrict the establishment of alien plants in new environments. Overall, the results indicate that the mycorrhizal association of alien plant species benefits their physiological performance, particularly regarding carbon allocation strategies (e.g., carbon cost of mycorrhizal symbiosis vs. carbon cost of storage organs) and consequently their invasion success. Alternatively, there might be a shift concerning the importance of mycorrhizal colonisation of alien plant species with increasing residence time. Kardol et al. (2006) and Diez et al. (2010) suggest that negative soil feedback accumulates over time for alien plant species, which might be due to increased probability of encountering soil pathogens or parasitic fungi in time and space, but also because of decreased responsiveness to soil mutualists (Seifert et al., 2009). The plant-fungi interaction itself may change its character along the mutualism-parasitism-continuum (Johnson et al., 1997) with time as well as encountering of habitats differing in soil fertility (Neuhauser and Fargione, 2004). After the successful establishment in the new environment, FM alien plant species may regulate their association with mycorrhizal fungi and thereby potentially counteract negative (parasitic) soil feedbacks. Yet, the reasons for sporadic mycorrhizal colonisation, i.e., mycorrhizal flexibility and the underlying regulatory processes in FM plant species are poorly understood (Grman, 2012). However, studies addressing the continuum typically investigate single plant and fungal individuals in pot experiments (Johnson et al., 1997; Klironomos, 2003). At community level and under natural conditions it is likely that plants interact only with mycorrhizal fungi that optimise their fitness by allocating nutrients (Bever et al., 2009; Kiers et al., 2011) and mycorrhizal associations are therefore most likely mutualistic at plant community level. To unravel why neophyte plant species in Germany are still more frequently OM than native plant species (Hempel et al., 2013), additional studies investigating potential physiological differences in mycorrhizal responsiveness of OM and FM plant species are needed. Furthermore, studying differences in non-nutritional benefits provided by the symbiosis, introduction pathways and reasons of introduction of neophyte plant species (e.g., as seed contaminants or escaped crop or ornamental plants) will shed light on the reported differences in frequencies of mycorrhizal status.

Further research at best with a biogeographical context will be crucial for developing further generalisations about the role of the mycorrhizal symbiosis in promoting or inhibiting alien plant species (Reinhart et al., 2012). Next to modelling, experiments under controlled as well as field conditions that assess the symbiosis' function in alien plant invasion *in situ* will be required, e.g., using hyphal ingrowth bags, rotating cores or the manipulation of fungal abundances (Bunn et al., 2015). It remains to be tested whether the positive association of neophyte plant species and retention of the mycorrhizal symbiosis as well as the corresponding trade-offs are general principles that similarly exist in other regions of the world. Seifert et al. (2009) suggest differences in mycorrhizal associations between alien plants in Europe and North America, which are based on different histories of plants and the agricultural practices in the particular regions. This is supported by the documented differences in alien plants' association with mycorrhizal fungi in California (Pringle et al., 2009) on one hand as well as Great Britain (Fitter, 2005) and Germany (Hempel et al., 2013) on the other hand. Moreover, the share of arbuscular mycorrhizal plant species is reported to be comparatively low among invasive aliens in the Fynbos region in South Africa (Richardson et al., 2000b). This indicates that the absence of mycorrhizal dependence may be an advantage for alien plant species in regions diverging from Central European land-use regimes, e.g., in typically nutrient poor (or less nutrient enriched) environments. Furthermore, it has been shown that the regional frequency and number of occupied habitats in the native range are a good proxy of invasion success of alien plant species (Hejda et al., 2015; Pyšek et al., 2015). FM plant species show the largest area of occupancy in Germany (chapter 4) and the largest number of occupied habitat types compared to OM and NM plants (Hempel et al., 2013). Therefore, this mycorrhizal status is a potential characteristic promoting the invasion success of these species in regions they are alien to. Additionally, the detected trade-offs involve traits related to storage organs and clonality (chapter 3 and 4); traits that were shown to be features of successful alien plant species in new environments (Knapp and Kühn, 2012; Pyšek et al., 2015). After all, the involvement in a mycorrhizal symbiosis may not be the major driver of alien plant invasions, but the simple acquisition of fungal symbionts is an important aspect of many ecosystems' susceptibility to the invasion by alien plants (Richardson et al., 2000b). As plants associated with AMF are supposedly of low specificity (Moora et al., 2011) and show low endemism and species richness on a global scale (Davison et al., 2015), the arbuscular mycorrhizal symbiosis is an interesting study object to unravel general mechanisms of alien plant invasion.

As the invasion success of neophyte plants is related to their mycorrhizal status (chapter 3 and 4) and the composition of plant assemblages is linked to environmental conditions (chapter 2), linking both approaches is a reasonable next step. The benefit derived from mutualistic interactions will probably vary with different environmental conditions (Mitchell et al., 2006). Thus, it will be crucial to not only investigate different effects of plants' mycorrhizal status in different locations, but also in the context of their particular abiotic and biotic conditions. Despite the new insights gained from the approaches used in chapter 3 and 4, those analyses are not designed to incorporate fungal communities in the context of alien plant invasion. The composition of native fungal communities itself influences alien plant invasions (Klironomos, 2002; Inderjit and van der Putten, 2010). Likewise, the invasion of alien plant species is reported to change soil fungal communities

(Batten et al., 2006; Mummey and Rillig, 2006; Sun et al., 2013) and non-mycorrhizal invasive plants were shown to supress native fungal symbionts (Callaway et al., 2008; Vogelsang and Bever, 2009). As long as comprehensive information on fungal communities is not available at larger scales, this aspect of alien plant invasion remains to be tested via field experiments. Network analyses of field gained data and studies of the sole or joint introduction of alien fungi and alien plants will promote our understanding of plant-fungi interactions in alien plant invasion. Furthermore, studying the invasion success of alien plant species with static models (chapter 3 and 4) captures only a snap shot of the invasion process and temporal dynamics are being ignored. Therefore, modelling (i.e., correlative, process-based, and hybrid models; Dormann et al., 2012) as well as experimental studies should ideally run in parallel to complement each other (Meisner et al., 2014).

Focus on the arbuscular mycorrhiza and plant-centrism

The analyses presented in chapter 2 and 4 are restricted to plant species forming an arbuscular mycorrhizal symbiosis, as the great majority of angiosperm plant species is engaged in this mycorrhizal type (Brundrett, 2009) and therefore of particular importance while analysing large species numbers at large scales. Furthermore, the majority of examined neophyte plant species (chapter 3) as well as the entirety of examined archaeophytes (chapter 4) in Germany are arbuscular mycorrhizal. Nevertheless, it will be fruitful to assess environmental responses and constraints of different types of mycorrhizal fungi. Ectomycorrhizal fungi probably have higher dispersal rates compared to AMF, due to their aboveground spore release and smaller propagules (Galante et al., 2011). However, in a meta-analysis by Bahram et al. (2015), the authors did not find distinct spatiotemporal patterns of fungal communities dominated by different mycorrhizal types, indicating similar rates of dispersal. Still, global patterns of plant root colonisation were driven by different sets of climatic and soil factors for arbuscular and ectomycorrhizal symbioses (Soudzilovskaia et al., 2015). Additionally, Lankau et al. (2015) showed that ectomycorrhizal fungi can supply their host plants with a greater buffer against environmental conditions compared to AMF. These authors suggest that ectomycorrhizal fungi show a higher diversity in terms of morphology and functioning, e.g., regarding nutrient acquisition strategies. Hence, extending the analyses to other mycorrhizal types will improve our understanding of differences in mycorrhizal functioning between mycorrhizal types.

The presented analysis takes a plant-centric view and neglects the fact that mycorrhizal fungi exhibit specific habitat requirements as well. Traditionally, biogeography and macroecology focussed on plants and animals, whereas microbes were not considered to be restricted by geographical barriers (Baas-Becking hypothesis: 'Everything is everywhere, but the environment selects'; Baas-Becking, 1934; Finlay, 2002; Queloz et al., 2011). In the meantime, microbiologists have discovered the existence of biogeographic patterns of microorganisms (Martiny et al., 2006; Hanson et al., 2012) including fungi (Tedersoo et al., 2014; Davison et al., 2015). Yet, a fungal macroecology is missing and published studies addressing the role of the symbiosis on plant and ecosystem responses are usually of limited duration and limited geographical distribution (Mohan et al., 2014; Bahram et al., 2015). Furthermore, the current limited availability of sufficient distribution data of fungal species respectively fungal (virtual) taxa as well as their communities restricts investigating the mycorrhizal symbiosis from a fungal perspective. Therefore, taking a plant-centric view by linking plant mycorrhizal traits of plant assemblages with large spatial scales is a valuable tool to approach a multi-scale understanding of the symbiosis.

Approaching the mycorrhizal symbiosis with functional traits

As demonstrated, linking functional plant mycorrhizal traits with macroecological analyses of plant distributions (chapter 2) as well as plant invasion ecology (chapter 3 and 4) are promising approaches. Even on its own, plant mycorrhizal status significantly explained the occupied geographical range of neophytes and native species in Germany in single plant trait models (chapter 3 and 4). Moreover, the discovered trade-offs of mycorrhizal status and other functional plant traits emphasise that considering plant mycorrhizal status in such analyses is an important step to get a complete picture of plant species' trait continuums. In particular, these trade-offs substantiate the role of the mycorrhizal symbiosis in plant physiology and plant mycorrhizal traits are therefore a useful addition to the spectrum of commonly used functional plant traits (e.g., Díaz et al., 2016).

MycoFlor (Hempel et al., 2013), as source of mycorrhizal status information in all analyses of this thesis, is purely literature-based and does not compile data specifically sampled for the purposes of the presented analyses. Furthermore, Hempel et al. (2013) reported a bias in the number of references per plant species; with rare species showing lower average reference numbers than common ones, and FM species showing higher average reference numbers than OM and NM species (Table 1). As demonstrated by Dickie et al. (2007), the handling of mycorrhizal status checklists therefore needs appropriate care to ensure the validity of the underlying data, as conflicting data on mycorrhizal associations of plant species exist. Therefore, using a core subset of the available data that only compiles the mycorrhizal status of plant species covered by at least two literature references is reasonable (chapter 2). Unfortunately, this approach was not feasible for the analyses in chapter 3 and 4, as the average reference coverage of neophytes and archaeophytes is lower compared to native species (Table 1). Thus, the procedure would have resulted in excluding a large number of species. Plant mycorrhizal status most likely does not underlie a high intraspecific variability caused by responses to different environmental conditions compared to other plant functional traits (Albert et al., 2010; Violle et al., 2012). However, classifying plant species into OM, FM, and NM species based on existing literature will never completely reassemble actual conditions (which is the case for any kind of averaged trait information derived from data bases; cf. Cordlandwehr et al., 2013) and it should be considered that one additional reference has the potential to transform an OM or NM to an FM species. Still, MycoFlor (Hempel et al., 2013) is one of the best available and most recently compiled data sets on plant mycorrhizal associations to date. Furthermore, it is important to note that plant mycorrhizal status is rather a proxy to estimate the potential importance of the mycorrhizal symbiosis for plants at species level and therefore suitable to the level of precision inherent of the presented analyses investigating large-scale processes.

Table 1: Mean reference numbers (± standard error) per mycorrhizal status and floristic status of plant species compiled in the MycoFlor data base (Hempel et al., 2013). Numbers in brackets display the subset of arbuscular mycorrhizal plant species. As the group of NM plant species is the same independent of whether considering all MycoFlor species or the subset of arbuscular mycorrhizal plant species, the last column ('NM') depicts only one value.

	mycorrhizal status		
floristic status	OM	FM	NM
natives	3.7±0.3 (2.3±0.1)	6.1±0.5 (5.4±0.2)	1.7±0.1
archaeophytes	2.4±0.4 (2.2±0.3)	4.0±0.4 (4.0±0.4)	1.6±0.3
neophytes	2.0±0.2 (1.6±0.1)	2.5±0.2 (2.6±0.2)	1.4±0.1
all plant species	3.2±0.2 (2.2±0.1)	5.5±0.4 (4.9±0.2)	1.6±0.1

Nevertheless, increasing the availability of three groups of functional traits will benefit our future understanding of mycorrhizal functioning: (1) *Plant mycorrhizal traits*: Despite the ubiquity of the symbiosis, it is surprising how little we overall know about the mycorrhizal association of plant species. The MycoFlor data base (Hempel et al., 2013) only contains information on the mycorrhizal association of 48% of the plant species of the German flora, although this flora is one of the best studied worldwide. Missing data on species traits certainly challenge the discovery of general trends in our understanding of the plants' mycorrhizal associations and the effects of the mycorrhizal symbiosis on plant communities. Plant mycorrhizal traits such as mycorrhizal status, mycorrhizal flexibility, and mycorrhizal type (Moora, 2014) can be easily incorporated into analyses of plant distributions and plant community ecology. Therefore, progress in increasing the availability of these plant traits and examining them under a variety of environmental conditions will enhance the explanatory power of corresponding analyses and decrease the uncertainty of related correlative analyses. Reviewing existing data on plant mycorrhizal associations, e.g., archived in museums, administrative agencies, and citizen science programs (cf. Beck et al., 2012) can improve the availability of plant mycorrhizal traits immediately (e.g., Akhmetzhanova et al., 2012). Concurrently, the establishment of complex plant mycorrhizal traits as mycorrhizal dependency (Moora, 2014) will need well-defined protocols of measuring the trait's characteristics (cf. Pérez-Harguindeguy et al., 2013). (2) *Plant root traits*: The plant-root interface is the major link between mycorrhizal fungi and plant individuals as well as between belowground and aboveground systems in general. At present, even large trait data bases are relatively poor in covering root traits (chapter 4), although they have been suggested as highly relevant traits of species' responses to their abiotic and biotic environments (Valverde-Barrantes et al., 2013; McCormack et al., 2014). Comprehensive measurements of traits such as specific root length, root diameter, root hair length or root hair density will lead to an improvement in understanding the belowground compartments of plants (Ryser, 2006; McCormack et al., 2014; Yang et al., 2015). Furthermore, different metrics of root traits and root architecture may be combined to reflect a spectrum of root system functioning (Maherali, 2014), which will certainly be followed by an increased understanding of plant-fungi relationships. (3) *Fungal traits*: The growth response of plants depends on the (functional) identity of both symbionts (Klironomos, 2003). As plant taxa differ in their mycorrhizal dependency, fungal taxa differ in their mycorrhizal effectiveness. This is even the case for obligate plant symbionts such as AMF that likely developed traits to maximise their own fitness (Chagnon et al., 2013). So far, fungal traits have been mainly used to classify fungi in the context of systematics and taxonomy (Kumar et al., 2011) but there have been numerous attempts to conceptually define a functional fungal ecology (Agerer, 2001; van der Heijden and Scheublin, 2007; Powell et al., 2009; Parrent et al., 2010; Behm and Kiers, 2014). Still, fungal ecology lags behind in using traits compared to plant ecology. As traits are measured at the level of individuals, this shortfall is partly based on the difficulty to define a fungus individual (Pringle and Taylor, 2002) and to find consensus on an established species concept (van der Heijden and Scheublin, 2007; Nilsson et al., 2008). Nevertheless, available high-throughput molecular methods already help initiating a fungal community ecology in natural contexts (Öpik et al., 2009; Poisot et al., 2013) and trait-based approaches might make species concepts obsolete at all (cf. Weiher and Keddy, 1995). Recently, requirements of a progressive fungal ecology are phrased in more detail. An excellent overview of possible life-history, morphological, and physiological fungal traits is given by Aguilar-Trigueros et al. (2015) and it has been already demonstrated that spore traits influence fungal distributions (Kivlin et al., 2014). Initiating such a trait-based fungal ecology will be elusive and will require established metrics and methodologies (Lilleskov and Parrent, 2007). While debating inherent features of fungal traits (Crowther et al., 2014; Aguilar-Trigueros et al., 2015), mycologists should also discuss whether adopting established frameworks of plant ecology or defining new concepts of trait-based fungal ecology against the background of extensive molecular insights is a more promising approach (Green et al., 2008). The effort to mutually describe functional plant and fungal traits will certainly improve our understanding of fungal communities, host plant communities, and their interplay (Maherali and Klironomos, 2007; Aguilar-Trigueros et al., 2014; Koide et al., 2014; Zobel and Öpik, 2014).

Concluding remarks

Studies of the mycorrhizal symbiosis are carried out at different hierarchical levels of plant organisation, but with a focus on lower levels. Moving up the hierarchy of complexity (i.e., plant assemblages instead of plant species or individuals) and hierarchy of spatial scales increases the likelihood that observations have greater relevance for answering questions to unravel general principles of mycorrhizal functioning in the context of plant ecology (Figure 1). Small-scale studies are suitable to disentangle mycorrhizal effects on plant physiology at the level of plant individuals, whereas studies addressing larger scales aim at relating the symbiosis to plant community and ecosystem functioning. The precision of analyses may decrease with such higher spatial scales and an increasing amount of studied objects (Figure 1). However, they certainly complement as well as extend the insights gained from pot experiments and molecular approaches in mycorrhizal plant ecology and both will jointly benefit a multiscale view of the symbiosis (Comas et al., 2010).

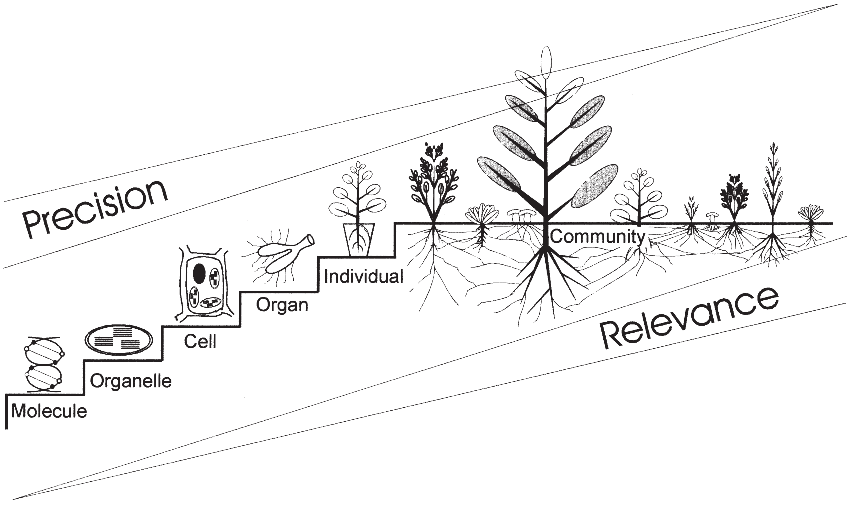


Figure 1: The opposing 'precision-relevance-relationship' in the hierarchy of complexity in answering ecological questions associated with mycorrhizal functioning. Studies of the mycorrhizal symbiosis are carried out at different hierarchical levels of plant organisation, while usually focussing on the lower levels (modified from Read, 2002).

This thesis provides insights into the effects of the mycorrhizal symbioses on plant distributions and their role in alien plant invasions at a large spatial scale. Each chapter demonstrates a surplus of incorporating information regarding the mycorrhizal associations of plant species. Thereby, the thesis concurrently demonstrates a need for differentiation to deepen our understanding of the influence of the mycorrhizal symbiosis in the context of alien plant invasions by plant species' mycorrhizal status (instead of merely differentiating between mycorrhizal and non-mycorrhizal), floristic status, and the incorporation of trait interactions involving the mycorrhizal symbiosis. Moreover, integrating the mycorrhizal symbiosis while studying the underlying processes of plant invasions is a great opportunity to explore general aspects of plant ecology that influence plant community assembly, ecosystem functioning, and/or stability (Sax et al., 2007; Traveset and Richardson, 2014), and will provide additional insights into the joint ecology of both symbiotic partners. Moving beyond a description of plant communities predominantly via eco-physiological traits, including traits related to biotic interactions such as the symbiosis will promote a trait-based ecology addressing all aspects of organisms and lead to a comprehensive understanding of plant distributions and community ecology (McGill, 2015). The present thesis encourages the use of plant mycorrhizal status (and potentially related mycorrhizal traits) as straightforward and simple functional traits to incorporate the mycorrhizal symbiosis to analyses of the abiotic and biotic processes shaping large-scale plant distributions and compositions of plant communities.

REFERENCES

Aerts R. (2002). The role of various types of mycorrhizal fungi in nutrient cycling and plant competition. In: *Mycorrhizal Ecology* (M. van der Heijden and I. Sanders, eds.). Springer Verlag Berlin Heidelberg, pp. 117–133.

Agerer R. (2001). Exploration types of ectomycorrhizae - A proposal to classify ectomycorrhizal mycelial systems according to their patterns of differentiation and putative ecological importance. *Mycorrhiza*, 11: 107–114.

Aguilar-Trigueros C.A., Hempel S., Powell J.R., Anderson I.C., Antonovics J., Bergmann J., et al. (2015). Branching out: Towards a trait-based understanding of fungal ecology. *Fungal Biology Reviews*, 29: 34–41.

Aguilar-Trigueros C.A., Powell J.R., Anderson I.C., Antonovics J. and Rillig M.C. (2014). Ecological understanding of root-infecting fungi using trait-based approaches. *Trends in Plant Science*, 19: 432–438.

Aitchison J. (1986). *The statistical analysis of compositional data.* Chapman & Hall, New York.

Akhmetzhanova A.A., Soudzilovskaia N.A., Onipchenko V.G., Cornwell W.K., Agafonov V.A., Selivanov I.A., et al. (2012). A rediscovered treasure: mycorrhizal intensity database for 3000 vascular plant species across the former Soviet Union. *Ecology*, 93: 689–690.

Albert C.H., Thuiller W., Yoccoz N.G., Soudant A., Boucher F., Saccone P., et al. (2010). Intraspecific functional variability: extent, structure and sources of variation. *Journal of Ecology*, 98: 604–613.

Allison V.J. and Goldberg D.E. (2002). Species-level versus community-level patterns of mycorrhizal dependence on phosphorus: an example of Simpson's paradox. *Functional Ecology*, 16: 346–352.

Aslan C.E., Sikes B.A. and Gedan K.B. (2015). Research on mutualisms between native and non-native partners can contribute critical ecological insights. *Neobiota*, 26: 39–54.

Augé R. (2001). Water relations, drought and vesicular-arbuscular mycorrhizal symbiosis. *Mycorrhiza*, 11: 3–42.

Augusto L., Dupouey J.L. and Ranger J. (2003). Effects of tree species on understory vegetation and environmental conditions in temperate forests. *Annals of Forest Science*, 60: 823–831.

Averill C., Turner B.L. and Finzi A.C. (2014). Mycorrhiza-mediated competition between plants and decomposers drives soil carbon storage. *Nature*, 505: 543–545.

Baas-Becking L.G.M. (1934). *Geobiologie of Inleiding Tot de Milieukunde.* Van Stockkum & Zoon, The Hague.

Bahram M., Peay K.G. and Tedersoo L. (2015). Local-scale biogeography and spatiotemporal variability in communities of mycorrhizal fungi. *New Phytologist*, 205: 1454–1463.

Bainard L.D., Klironomos J.N. and Gordon A.M. (2011). The mycorrhizal status and colonization of 26 tree species growing in urban and rural environments. *Mycorrhiza*, 21: 91–96.

Barto E.K. and Rillig M.C. (2010). Does herbivory really suppress mycorrhiza? A meta-analysis. *Journal of Ecology*, 98: 745–753.

Barto E.K., Weidenhamer J.D., Cipollini D. and Rillig M.C. (2012). Fungal superhighways: do common mycorrhizal networks enhance below ground communication? *Trends in Plant Science*, 17: 633–637.

Batten K.M., Scow K.M., Davies K.F. and Harrison S.P. (2006). Two invasive plants alter soil microbial community composition in serpentine grasslands. *Biological Invasions*, 8: 217–230.

Baylis G.T.S. (1970). Root hairs and phycomycetous mycorrhizas in phosphorus-deficient soil. *Plant and Soil*, 33: 713–716.

Beck J., Ballesteros-Mejia L., Buchmann C.M., Dengler J., Fritz S.A., Gruber B., et al. (2012). What's on the horizon for macroecology? *Ecography*, 35: 673–683.

Behm J.E. and Kiers E.T. (2014). A phenotypic plasticity framework for assessing intraspecific variation in arbuscular mycorrhizal fungal traits. *Journal of Ecology*, 102: 315–327.

Bender S.F., Conen F. and van der Heijden M.G.A. (2015). Mycorrhizal effects on nutrient cycling, nutrient leaching and N_2O production in experimental grassland. *Soil Biology & Biochemistry*, 80: 283–292.

Bernhardt-Römermann M., Römermann C., Nuske R., Parth A., Klotz S., Schmidt W., et al. (2008). On the identification of the most suitable traits for plant functional trait analyses. *Oikos*, 117: 1533–1541.

Bertness M.D. and Callaway R. (1994). Positive interactions in communities. *Trends in Ecology & Evolution*, 9: 191–193.

Bever J.D., Richardson S.C., Lawrence B.M., Holmes J. and Watson M. (2009). Preferential allocation to beneficial symbiont with spatial structure maintains mycorrhizal mutualism. *Ecology Letters*, 12: 13–21.

Bever J.D., Schultz P.A., Pringle A. and Morton J.B. (2001). Arbuscular mycorrhizal fungi: More diverse than meets the eye, and the ecological tale of why. *Bioscience*, 51: 923–931.

Bezemer T.M., Harvey J.A. and Cronin J.T. (2014). Response of native insect communities to invasive plants. *Annual Review of Entomology, Vol 59, 2014*, 59: 119–141.

Billheimer D., Guttorp P. and Fagans W.F. (2001). Statistical interpretation of species composition. *Journal of the American Statistical Association*, 96: 1205–1214.

Bini L., Diniz-Filho A.F., Rangel T.F.L.V.B., Akre T.S.B., Albaladejo R.G., Albuquerque F.S., et al. (2009). Coefficient shifts in geographical ecology: an empirical evaluation of spatial and non-spatial regression. *Ecography*, 32: 193–204.

Bivand R., with contributions by Micah Altman, Anselin L., Assunção R., Berke O., Bernat A., et al. (2013). spdep: Spatial dependence: weighting schemes, statistics and models. Tech. rep. R package version 0.5-56.

Blackburn T. and Gaston K. (2003). Introduction: why macroecology? In: *Macroecology: Concepts and Consequences* (T. Blackburn and K. Gaston, eds.). Blackwell Science Ltd, pp. 1–14.

Blackburn T.M. (2004). Method in macroecology. *Basic and Applied Ecology*, 5: 401–412.

Blackburn T.M., Pyšek P., Bacher S., Carlton J.T., Duncan R.P., Jarošik V., et al. (2011). A proposed unified framework for biological invasions. *Trends in Ecology & Evolution*, 26: 333–339.

Blumenthal D. (2005). Interrelated causes of plant invasion. *Science*, 310: 243–244.

Bogar L.M., Dickie I.A. and Kennedy P.G. (2015). Testing the co-invasion hypothesis: ectomycorrhizal fungal communities on *Alnus glutinosa* and *Salix fragilis* in New Zealand. *Diversity and Distributions*, 21: 268–278.

Borcard D., Legendre P. and Drapeau P. (1992). Partialling out the spatial component of ecological variation. *Ecology*, 73: 1045–1055.

Bossdorf O., Auge H., Lafuma L., Rogers W.E., Siemann E. and Prati D. (2005). Phenotypic and genetic differentiation between native and introduced plant populations. *Oecologia*, 144: 1–11.

Brown J.H. (1995). *Macroecology.* University of Chicago Press.

Brown J.H., Gillooly J.F., Allen A.P., Savage V.M. and West G.B. (2004). Toward a metabolic theory of ecology. *Ecology*, 85: 1771–1789.

Brown J.H. and Maurer B.A. (1989). Macroecology - the division of food and space among species on continents. *Science*, 243: 1145–1150.

Brundrett M. (2002). Coevolution of roots and mycorrhizas of land plants. *New Phytologist*, 154: 275–304.

BRUNDRETT M.C. (2009). Mycorrhizal associations and other means of nutrition of vascular plants: understanding the global diversity of host plants by resolving conflicting information and developing reliable means of diagnosis. *Plant and Soil*, 320: 37–77.

BUNDESANSTALT FÜR GEOWISSENSCHAFTEN UND ROHSTOFFE (1993). Geologische Karte der Bundesrepublik Deutschland 1 : 1 000 000.

BUNN R.A., LEKBERG Y. and ZABINSKI C. (2009). Arbuscular mycorrhizal fungi ameliorate temperature stress in thermophilic plants. *Ecology*, 90: 1378–1388.

BUNN R.A., RAMSEY P.W. and LEKBERG Y. (2015). Do native and invasive plants differ in their interactions with arbuscular mycorrhizal fungi? A meta-analysis. *Journal of Ecology*, 103: 1547–1556.

CAIRNEY J. and MEHARG A. (1999). Influences of anthropogenic pollution on mycorrhizal fungal communities. *Environmental Pollution*, 106: 169–182.

CALLAWAY R.M., CIPOLLINI D., BARTO K., THELEN G.C., HALLETT S.G., PRATI D., ET AL. (2008). Novel weapons: Invasive plant suppresses fungal mutualists in America but not in its native Europe. *Ecology*, 89: 1043–1055.

CALLAWAY R.M., THELEN G.C., BARTH S., RAMSEY P.W. and GANNON J.E. (2004). Soil fungi alter interactions between the invader *Centaurea maculosa* and North American natives. *Ecology*, 85: 1062–1071.

CATFORD J.A., JANSSON R. and NILSSON C. (2009). Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. *Diversity and Distributions*, 15: 22–40.

CEULEMANS T., MERCKX R., HENS M. and HONNAY O. (2011). A trait-based analysis of the role of phosphorus vs. nitrogen enrichment in plant species loss across North-west European grasslands. *Journal of Applied Ecology*, 48: 1155–1163.

CHAGNON P.L., BRADLEY R.L., MAHERALI H. and KLIRONOMOS J.N. (2013). A trait-based framework to understand life history of mycorrhizal fungi. *Trends in Plant Science*, 18: 484–491.

CHAVE J. (2013). The problem of pattern and scale in ecology: what have we learned in 20 years? *Ecology Letters*.

CHMURA D. and GUCWA-PRZEPIÓRA E. (2012). Interactions between arbuscular mycorrhiza and the growth of the invasive alien annual *Impatiens parviflora* DC: A study of forest type and soil properties in nature reserves (S Poland). *Applied Soil Ecology*, 62: 71–80.

COMAS L.H., TUININGA A.R. and CALLAHAN H.S. (2010). Advancing our current understanding of plant-fungal symbioses: bridging scales from local to global. *New Phytologist*, 185: 871–873.

COMPANT S., VAN DER HEIJDEN M.G.A. and SESSITSCH A. (2010). Climate change effects on beneficial plant-microorganism interactions. *FEMS Microbiology Ecology*, 73: 197–214.

COOK R. and WEISBERG S. (1982). *Residuals and influence in regression.* Chapman & Hall, New York.

CORDLANDWEHR V., MEREDITH R.L., OZINGA W.A., BEKKER R.M., VAN GROENENDAEL J.M. and BAKKER J.P. (2013). Do plant traits retrieved from a database accurately predict on-site measurements? *Journal of Ecology*, 101: 662–670.

CORNELISSEN J.H.C., LAVOREL S., GARNIER E., DÍAZ S., BUCHMANN N., GURVICH D.E., ET AL. (2003). A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany*, 51: 335–380.

CRASE B., LIEDLOFF A.C. and WINTLE B.A. (2012). A new method for dealing with residual spatial autocorrelation in species distribution models. *Ecography*, 35: 879–888.

CROWTHER T.W., MAYNARD D.S., CROWTHER T.R., PECCIA J., SMITH J.R. and BRADFORD M.A. (2014). Untangling the fungal niche: the trait-based approach. *Frontiers in Microbiology*, 5: 579.

DARWIN C. (1859). *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life.* Murray, London.

DAVIS M., CHEW M.K., HOBBS R.J., LUGO A.E., EWEL J.J., VERMEIJ G.J., ET AL. (2011). Don't judge species on their origins. *Nature*, 474: 153–154.

DAVIS M., GRIME J. and THOMPSON K. (2000). Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology*, 88: 528–534.

DAVISON J., MOORA M., ÖPIK M., ADHOLEYA A., AINSAAR L., BÂ A., ET AL. (2015). Global assessment of arbuscular mycorrhizal fungus diversity reveals very low endemism. *Science*, 349: 970–973.

DE DEYN G.B., BIERE A., VAN DER PUTTEN W.H., WAGENAAR R. and KLIRONOMOS J.N. (2009). Chemical defense, mycorrhizal colonization and growth responses in *Plantago lanceolata* L. *Oecologia*, 160: 433–442.

DEUTSCHEWITZ K., LAUSCH A., KÜHN I. and KLOTZ S. (2003). Native and alien plant species richness in relation to spatial heterogeneity on a regional scale in Germany. *Global Ecology and Biogeography*, 12: 299–311.

DI CASTRI F. (1989). History of biological invasions with special emphasis on the Old World. In: *Biological Invasions. A Global Perspective* (J. Drake, H. Mooney, F.D. Castri, R. Groves, F. Kruger, M. Rejmánek, and M. Williamson, eds.). Wiley, New York, pp. 1–30.

Díaz S., Hodgson J.G., Thompson K., Cabido M., Cornelissen J.H.C., Jalili A., et al. (2004). The plant traits that drive ecosystems: Evidence from three continents. *Journal of Vegetation Science*, 15: 295–304.

Díaz S., Kattge J., Cornelissen J.H.C., Wright I.J., Lavorel S., Dray S., et al. (2016). The global spectrum of plant form and function. *Nature*, 529: 167–171.

Dickie I.A., Bolstridge N., Cooper J.A. and Peltzer D.A. (2010). Co-invasion by *Pinus* and its mycorrhizal fungi. *New Phytologist*, 187: 475–484.

Dickie I.A., Thomas M.M. and Bellingham P.J. (2007). On the perils of mycorrhizal status lists: the case of *Buddleja davidii*. *Mycorrhiza*, 17: 687–688.

Diez J.M., Dickie I., Edwards G., Hulme P.E., Sullivan J.J. and Duncan R.P. (2010). Negative soil feedbacks accumulate over time for non-native plant species. *Ecology Letters*, 13: 803–809.

Dormann C.F., Elith J., Bacher S., Buchmann C., Carl G., Carre G., et al. (2013). Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, 36: 27–46.

Dormann C.F., McPherson J.M., Araujo M.B., Bivand R., Bolliger J., Carl G., et al. (2007). Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography*, 30: 609–628.

Dormann C.F., Schymanski S.J., Cabral J., Chuine I., Graham C., Hartig F., et al. (2012). Correlation and process in species distribution models: bridging a dichotomy. *Journal of Biogeography*, 39: 2119–2131.

Doubková P., Suda J. and Sudová R. (2012). The symbiosis with arbuscular mycorrhizal fungi contributes to plant tolerance to serpentine edaphic stress. *Soil Biology & Biochemistry*, 44: 56–64.

Drake J., Mooney H., di Castri F., Groves R., Kruger F., Rejmánek M., et al. (1989). *Biological invasions: a global perspective.* Wiley, New York.

Dray S. and Legendre P. (2008). Testing the species traits-environment relationships: the fourth-corner problem revisited. *Ecology*, 89: 3400–3412.

Dumbrell A.J., Nelson M., Helgason T., Dytham C. and Fitter A.H. (2010). Idiosyncrasy and overdominance in the structure of natural communities of arbuscular mycorrhizal fungi: is there a role for stochastic processes? *Journal of Ecology*, 98: 419–428.

Durka W. and Michalski S.G. (2012). Daphne: a dated phylogeny of a large European flora for phylogenetically informed ecological analyses. *Ecology*, 93: 2297–2297.

Egerton-Warburton L.M. and Allen E.B. (2000). Shifts in arbuscular mycorrhizal communities along an anthropogenic nitrogen deposition gradient. *Ecological Applications*, 10: 484–496.

Ellenberg H., Weber H., Düll R., Wirth V., Werner W. and Paulissen D. (1992). Zeigerwerte von Pflanzen in Mitteleuropa. *Scripta Geobotanica*, 18: 1–248.

Ellis E.C. and Ramankutty N. (2008). Putting people in the map: anthropogenic biomes of the world. *Frontiers in Ecology and the Environment*, 6: 439–447.

Elton C. (1958). *The ecology of invasions by animals and plants.* Methuen, London.

Endresz G., Somodi I. and Kalapos T. (2013). Arbuscular mycorrhizal colonisation of roots of grass species differing in invasiveness. *Community Ecology*, 14: 67–76.

Eom A., Wilson G. and Hartnett D. (2001). Effects of ungulate grazers on arbuscular mycorrhizal symbiosis and fungal community structure in tallgrass prairie. *Mycologia*, 93: 233–242.

Felsenstein J. (1985). Phylogenies and the comparative method. *The American Naturalist*, 125: 1–15.

Finlay B.J. (2002). Global dispersal of free-living microbial eukaryote species. *Science*, 296: 1061–1063.

Fitter A.H. (2005). Darkness visible: reflections on underground ecology. *Journal of Ecology*, 93: 231–243.

Fitter A.H. and Moyersoen B. (1996). Evolutionary trends in root-microbe symbioses. *Philosophical Transactions of the Royal Society of London Series B - Biological Sciences*, 351: 1367–1375.

Fitter A.H. and Peat H.J. (1994). The Ecological Flora Database. *Journal of Ecology*, 82: 415–425.

Forbes P., Black K. and Hooker J. (1997). Temperature-induced alteration to root longevity in *Lolium perenne*. *Plant and Soil*, 190: 87–90.

Frank A.B. and Trappe R. (2005). On the nutritional dependence of certain trees on root symbiosis with belowground fungi (an English translation of A.B. Frank's classic paper of 1885). *Mycorrhiza*, 15: 267–275.

Fronzek S., Carter T.R. and Jylhä K. (2012). Representing two centuries of past and future climate for assessing risks to biodiversity in Europe. *Global Ecology and Biogeography*, 21: 19–35.

Fumanal B., Plenchette C., Chauvel B. and Bretagnolle F. (2006). Which role can arbuscular mycorrhizal fungi play in the facilitation of *Ambrosia artemisiifolia* L. invasion in France? *Mycorrhiza*, 17: 25–35.

Galante T.E., Horton T.R. and Swaney D.P. (2011). 95% of basidiospores fall within 1 m of the cap: a field- and modeling-based study. *Mycologia*, 103: 1175–1183.

Gange A.C. and West H.M. (1994). Interactions between arbuscular mycorrhizal fungi and foliar-feeding insects in *Plantago lanceolata* L. *New Phytologist*, 128: 79–87.

GBIF (2016). Global Biodiversity Information Facility - http://www.gbif.org/.

Gerz M., Bueno C.G., Zobel M. and Moora M. (2016). Plant community mycorrhization in temperate forests and grasslands: relations with edaphic properties and plant diversity. *Journal of Vegetation Science*, 27: 89–99.

Green J.L., Bohannan B.J.M. and Whitaker R.J. (2008). Microbial biogeography: From taxonomy to traits. *Science*, 320: 1039–1043.

Green W. (2009). USDA PLANTS Compilation. *version 1, 09-02-02. (http://bricol.net/downloads/data/PLANTSdatabase/) NRCS: The PLANTS Database (http://plants.usda.gov, 1 Feb 2009).*

Greene D.F. and Johnson E.A. (1993). Seed mass and dispersal capacity in wind-dispersed diaspores. *Oikos*, 67: 69–74.

Grime J.P. (1974). Vegetation classification by reference to strategies. *Nature*, 250: 26–31.

Grman E. (2012). Plant species differ in their ability to reduce allocation to non-beneficial arbuscular mycorrhizal fungi. *Ecology*, 93: 711–718.

Grman E., Robinson T.M.P. and Klausmeier C.A. (2012). Ecological specialization and trade affect the outcome of negotiations in mutualism. *The American Naturalist*, 179: 567–581.

Hagemeijer E. and Blair M. (1997). *The EBCC Atlas of European Breeding Birds: their distribution and abundance.* T. & A.D. Poyser, London.

Hanson C.A., Fuhrman J.A., Horner-Devine M.C. and Martiny J.B.H. (2012). Beyond biogeographic patterns: processes shaping the microbial landscape. *Nature Reviews Microbiology*, 10: 497–506.

Harner M.J., Opitz N., Geluso K., Tockner K. and Rillig M.C. (2011). Arbuscular mycorrhizal fungi on developing islands within a dynamic river floodplain: an investigation across successional gradients and soil depth. *Aquatic Sciences*, 73: 35–42.

Harner M.J., Piotrowski J.S., Lekberg Y., Stanford J.A. and Rillig M.C. (2009). Heterogeneity in mycorrhizal inoculum potential of flood-deposited sediments. *Aquatic Sciences*, 71: 331–337.

Hartnett D. and Wilson G. (2002). The role of mycorrhizas in plant community structure and dynamics: lessons from grasslands. *Plant and Soil*, 244: 319–331.

Harvey P. and Pagel M. (1991). *The comparative method in evolutionary biology.* Oxford University Press.

Haugen L. and Smith S. (1992). The effect of high-temperature and fallow period on infection of mung bean and cashew roots by the vesicular-arbuscular mycorrhizal fungus *Glomus intraradices. Plant and Soil*, 145: 71–80.

Hawkes C.V., Belnap J., D'Antonio C. and Firestone M.K. (2006). Arbuscular mycorrhizal assemblages in native plant roots change in the presence of invasive exotic grasses. *Plant and Soil*, 281: 369–380.

Hazard C., Gosling P., van der Gast C.J., Mitchell D.T., Doohan F.M. and Bending G.D. (2013). The role of local environment and geographical distance in determining community composition of arbuscular mycorrhizal fungi at the landscape scale. *The ISME Journal*, 7: 498–508.

Heger T., Pahl A.T., Botta-Dukát Z., Gherardi F., Hoppe C., Hoste I., et al. (2013). Conceptual frameworks and methods for advancing invasion ecology. *Ambio*, 42: 527–540.

Heikkinen R.K., Marmion M. and Luoto M. (2012). Does the interpolation accuracy of species distribution models come at the expense of transferability? *Ecography*, 35: 276–288.

Heinemeyer A. and Fitter A. (2004). Impact of temperature on the arbuscular mycorrhizal (AM) symbiosis: growth responses of the host plant and its AM fungal partner. *Journal of Experimental Botany*, 55: 525–534.

Hejda M., Chytrý M., Pergl J. and Pyšek P. (2015). Native-range habitats of invasive plants: are they similar to invaded-range habitats and do they differ according to the geographical direction of invasion? *Diversity and Distributions*, 21: 312–321.

Hempel S., Götzenberger L., Kühn I., Michalski S.G., Rillig M.C., Zobel M., et al. (2013). Mycorrhizas in the Central European flora - relationships with plant life history traits and ecology. *Ecology*, 94: 1389–1399.

Hetrick B.A.D. and Wilson G.W.T. (1990). Relationship of native and introduced mycorrhizal fungi to mycorrhizal dependence of *Andropogon gerardii* and *Koeleria pyranidata*. *Mycologia*, 82: 779–782.

Hetrick B.A.D., Wilson G.W.T. and Todd T.C. (1992). Relationships of mycorrhizal symbiosis, rooting strategy, and phenology among tallgrass prairie forbs. *Canadian Journal of Botany*, 70: 1521–1528.

Hildebrandt U., Janetta K. and Bothe H. (2002). Towards growth of arbuscular mycorrhizal fungi independent of a plant host. *Applied and Environmental Microbiology*, 68: 1919–1924.

Hildebrandt U., Regvar M. and Bothe H. (2007). Arbuscular mycorrhiza and heavy metal tolerance. *Phytochemistry*, 68: 139–146.

Hobbie E.A. and Hobbie J.E. (2008). Natural abundance of (15)N in nitrogen-limited forests and tundra can estimate nitrogen cycling through mycorrhizal fungi: A review. *Ecosystems*, 11: 815–830.

Hobbs R.J., Arico S., Aronson J., Baron J.S., Bridgewater P., Cramer V.A., et al. (2006). Novel ecosystems: theoretical and management aspects of the new ecological world order. *Global Ecology and Biogeography*, 15: 1–7.

Hobbs R.J. and Huenneke L.F. (1992). Disturbance, diversity, and invasion - implications for conservations. *Conservation Biology*, 6: 324–337.

Hoeksema J.D., Chaudhary V.B., Gehring C.A., Johnson N.C., Karst J., Koide R.T., et al. (2010). A meta-analysis of context-dependency in plant response to inoculation with mycorrhizal fungi. *Ecology Letters*, 13: 394–407.

Holm S. (1979). A simple sequentially rejective multiple test procedue. *Scandinavian Journal of Statistics*, 6: 65–70.

Hothorn T., Bretz F. and Westfall P. (2008). Simultaneous inference in general parametric models. *Biometrical Journal*, 50: 346–363.

Hubbell S.P. (2001). *The unified neutral theory of biodiversity and biogeography.* Monographs in population biology. Princeton University Press.

Hulme P.E. (2009). Trade, transport and trouble: managing invasive species pathways in an era of globalization. *Journal of Applied Ecology*, 46: 10–18.

Inderjit and van der Putten W.H. (2010). Impacts of soil microbial communities on exotic plant invasions. *Trends in Ecology & Evolution*, 25: 512–519.

IPCC (2013). *IPCC, 2013: Summary for Policymakers.* Cambridge University Press, Cambridge, United Kingdom and New York, USA.

Jamil T., Ozinga W.A., Kleyer M. and ter Braak C.J.F. (2013). Selecting traits that explain species-environment relationships: a generalized linear mixed model approach. *Journal of Vegetation Science*, 24: 988–1000.

Jansa J., Mozafar A., Anken T., Ruh R., Sanders I. and Frossard E. (2002). Diversity and structure of AMF communities as affected by tillage in a temperate soil. *Mycorrhiza*, 12: 225–234.

Jayne B. and Quigley M. (2014). Influence of arbuscular mycorrhiza on growth and reproductive response of plants under water deficit: a meta-analysis. *Mycorrhiza*, 24: 109–119.

Jeschke J., Aparicio L.G., Haider S., Heger T., Lortie C., Pyšek P., et al. (2012). Support for major hypotheses in invasion biology is uneven and declining. *NeoBiota*, 14: 1–20.

Johnson D., Martin F., Cairney J.W.G. and Anderson I.C. (2012). The importance of individuals: intraspecific diversity of mycorrhizal plants and fungi in ecosystems. *New Phytologist*, 194: 614–628.

Johnson N.C. (1993). Can fertilization of soil select less mutualistic mycorrhizae? *Ecological Applications*, 3: 749–757.

Johnson N.C., Angelard C., Sanders I.R. and Kiers E.T. (2013). Predicting community and ecosystem outcomes of mycorrhizal responses to global change. *Ecology Letters*, 16: 140–153.

Johnson N.C., Graham J.H. and Smith F.A. (1997). Functioning of mycorrhizal associations along the mutualism-parasitism continuum. *New Phytologist*, 135: 575–586.

Jones M.D. and Smith S.E. (2004). Exploring functional definitions of mycorrhizas: Are mycorrhizas always mutualisms? *Canadian Journal of Botany*, 82: 1089–1109.

Kardol P., Bezemer T.M. and van der Putten W.H. (2006). Temporal variation in plant-soil feedback controls succession. *Ecology Letters*, 9: 1080–1088.

Kattge J., Díaz S., Lavorel S., Prentice C., Leadley P., Bönisch G., et al. (2011). TRY - a global database of plant traits. *Global Change Biology*, 17: 2905–2935.

Kempel A., Nater P., Fischer M. and van Kleunen M. (2013). Plant-microbe-herbivore interactions in invasive and non-invasive alien plant species. *Functional Ecology*, 27: 498–508.

Kiers E.T., Duhamel M., Beesetty Y., Mensah J.A., Franken O., Verbruggen E., et al. (2011). Reciprocal rewards stabilize cooperation in the mycorrhizal symbiosis. *Science*, 333: 880–882.

Kivlin S.N., Hawkes C.V. and Treseder K.K. (2011). Global diversity and distribution of arbuscular mycorrhizal fungi. *Soil Biology & Biochemistry*, 43: 2294–2303.

Kivlin S.N., Winston G.C., Goulden M.L. and Treseder K.K. (2014). Environmental filtering affects soil fungal community composition more than dispersal limitation at regional scales. *Fungal Ecology*, 12: 14–25.

Kleyer M., Bekker R.M., Knevel I.C., Bakker J.P., Thompson K., Sonnenschein M., et al. (2008). The LEDA Traitbase: a database of life-history traits of the Northwest European flora. *Journal of Ecology*, 96: 1266–1274.

Klimešova J. and de Bello F. (2009). CLO-PLA: the database of clonal and bud bank traits of Central European flora. *Journal of Vegetation Science*, 20: 511–516.

Klironomos J. (2002). Feedback with soil biota contributes to plant rarity and invasiveness in communities. *Nature*, 417: 67–70.

Klironomos J., McCune J., Hart M. and Neville J. (2000). The influence of arbuscular mycorrhizae on the relationship between plant diversity and productivity. *Ecology Letters*, 3: 137–141.

Klironomos J., Zobel M., Tibbett M., Stock W.D., Rillig M.C., Parrent J.L., et al. (2011). Forces that structure plant communities: quantifying the importance of the mycorrhizal symbiosis. *New Phytologist*, 189: 366–370.

Klironomos J.N. (2003). Variation in plant response to native and exotic arbuscular mycorrhizal fungi. *Ecology*, 84: 2292–2301.

Klotz S., Kühn I. and Durka W. (2002). BIOLFLOR - Eine Datenbank mit biologisch-ökologischen Merkmalen zur Flora von Deutschland. *Bundesamt für Naturschutz, Bonn.*

Knapp S. and Kühn I. (2012). Origin matters: widely distributed native and non-native species benefit from different functional traits. *Ecology Letters*, 15: 696–703.

Koide R. (1991). Nutrient supply, nutrient demand and plant-response to myorrhizal infection. *New Phytologist*, 117: 365–386.

Koide R. and Dickie I. (2002). Effects of mycorrhizal fungi on plant populations. *Plant and Soil*, 244: 307–317.

Koide R.T., Fernandez C. and Malcolm G. (2014). Determining place and process: functional traits of ectomycorrhizal fungi that affect both community structure and ecosystem function. *New Phytologist*, 201: 433–439.

Koorem K. and Moora M. (2010). Positive association between understory species richness and a dominant shrub species (*Corylus avellana*) in a boreonemoral spruce forest. *Forest Ecology and Management*, 260: 1407–1413.

Koorem K., Saks U., Sober V., Uibopuu A., Öpik M., Zobel M., et al. (2012). Effects of arbuscular mycorrhiza on community composition and seedling recruitment in temperate forest understory. *Basic and Applied Ecology*, 13: 663–672.

Koricheva J., Gange A.C. and Jones T. (2009). Effects of mycorrhizal fungi on insect herbivores: a meta-analysis. *Ecology*, 90: 2088–2097.

Kriticos D.J., Webber B.L., Leriche A., Ota N., Macadam I., Bathols J., et al. (2012). CliMond: global high-resolution historical and future scenario climate surfaces for bioclimatic modelling. *Methods in Ecology and Evolution*, 3: 53–64.

Krüger M., Krüger C., Walker C., Stockinger H. and Schüssler A. (2012). Phylogenetic reference data for systematics and phylotaxonomy of arbuscular mycorrhizal fungi from phylum to species level. *New Phytologist*, 193: 970–984.

Kueffer C., Pyšek P. and Richardson D.M. (2013). Integrative invasion science: model systems, multi-site studies, focused meta-analysis and invasion syndromes. *New Phytologist*, 200: 615–633.

Kühn I., Bierman S.M., Durka W. and Klotz S. (2006). Relating geographical variation in pollination types to environmental and spatial factors using novel statistical methods. *New Phytologist*, 172: 127–139.

Kühn I., Böhning-Gaese K., Cramer W. and Klotz S. (2008). Macroecology meets global change research. *Global Ecology and Biogeography*, 17: 3–4.

Kühn I., Durka W. and Klotz S. (2004). BiolFlor - a new plant-trait database as a tool for plant invasion ecology. *Diversity and Distributions*, 10: 363–365.

Kühn I. and Klotz S. (2006). Urbanization and homogenization - Comparing the floras of urban and rural areas in Germany. *Biological Conservation*, 127: 292–300.

KUMAR T.K.A., CROW J.A., WENNBLOM T.J., ABRIL M., LETCHER P.M., BLACKWELL M., ET AL. (2011). An ontology of fungal subcellular traits. *American Journal of Botany*, 98: 1504–1510.

KÜSTER E.C., DURKA W., KÜHN I. and KLOTZ S. (2010). Differences in the trait compositions of non-indigenous and native plants across Germany. *Biological Invasions*, 12: 2001–2012.

KÜSTER E.C., KÜHN I., BRUELHEIDE H. and KLOTZ S. (2008). Trait interactions help explain plant invasion success in the German flora. *Journal of Ecology*, 96: 860–868.

KUULUVAINEN T. (2009). Forest management and biodiversity conservation based on natural ecosystem dynamics in Northern Europe: the complexity challenge. *Ambio*, 38: 309–315.

LA SORTE F.A. and PYŠEK P. (2009). Extra-regional residence time as a correlate of plant invasiveness: European archaeophytes in North America. *Ecology*, 90: 2589–2597.

LAHTI T. and LAMPINEN R. (1999). From dot maps to bitmaps: *Atlas Florae Europaeae* goes digital. *Acta Botanica Fennica*, 162: 5–9.

LAMBDON P.W., PYŠEK P., BASNOU C., HEJDA M., ARIANOUTSOU M., ESSL F., ET AL. (2008). Alien flora of Europe: species diversity, temporal trends, geographical patterns and research needs. *Preslia*, 80: 101–149.

LAMBERS H. and TESTE F.P. (2013). Interactions between arbuscular mycorrhizal and non-mycorrhizal plants: do non-mycorrhizal species at both extremes of nutrient availability play the same game? *Plant, Cell & Environment*, 36: 1911–1915.

LANDIS F.C., GARGAS A. and GIVNISH T.J. (2004). Relationships among arbuscular mycorrhizal fungi, vascular plants and environmental conditions in oak savannas. *New Phytologist*, 164: 493–504.

LANG C., SEVEN J. and POLLE A. (2011). Host preferences and differential contributions of deciduous tree species shape mycorrhizal species richness in a mixed Central European forest. *Mycorrhiza*, 21: 297–308.

LANKAU R.A. (2012). Coevolution between invasive and native plants driven by chemical competition and soil biota. *Proceedings of the National Academy of Sciences of the United States of America*, 109: 11240–11245.

LANKAU R.A., ZHU K. and ORDONEZ A. (2015). Mycorrhizal strategies of tree species correlate with trailing range edge responses to current and past climate change. *Ecology*, 96: 1451–1458.

LAUGHLIN D.C. (2014). The intrinsic dimensionality of plant traits and its relevance to community assembly. *Journal of Ecology*, 102: 186–193.

LAUGHLIN D.C., JOSHI C., VAN BODEGOM P.M., BASTOW Z.A. and FULE P.Z. (2012). A predictive model of community assembly that incorporates intraspecific trait variation. *Ecology Letters*, 15: 1291–1299.

LAVOREL S. and GARNIER E. (2002). Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology*, 16: 545–556.

LAVOREL S. and GRIGULIS K. (2012). How fundamental plant functional trait relationships scale-up to trade-offs and synergies in ecosystem services. *Journal of Ecology*, 100: 128–140.

LEKBERG Y., GIBBONS S.M., ROSENDAHL S. and RAMSEY P.W. (2013). Severe plant invasions can increase mycorrhizal fungal abundance and diversity. *The ISME Journal*, 7: 1–10.

LEKBERG Y. and KOIDE R.T. (2005). Is plant performance limited by abundance of arbuscular mycorrhizal fungi? A meta-analysis of studies published between 1988 and 2003. *New Phytologist*, 168: 189–204.

LENTH R.V. and HERVË M. (2015). lsmeans: Least-Squares Means. Tech. rep. R package version 2.16.

LEVINE J.M., VILÀ M., D'ANTONIO C.M., DUKES J.S., GRIGULIS K. and LAVOREL S. (2003). Mechanisms underlying the impacts of exotic plant invasions. *Proceedings of the Royal Society B - Biological Sciences*, 270: 775–781.

LI T., LIN G., ZHANG X., CHEN Y., ZHANG S. and CHEN B. (2014). Relative importance of an arbuscular mycorrhizal fungus (*Rhizophagus intraradices*) and root hairs in plant drought tolerance. *Mycorrhiza*, 24: 595–602.

LILLESKOV E.A. and PARRENT J.L. (2007). Can we develop general predictive models of mycorrhizal fungal community-environment relationships? *New Phytologist*, 174: 250–256.

LINDAHL B.D., NILSSON R.H., TEDERSOO L., ABARENKOV K., CARLSEN T., KJOLLER R., ET AL. (2013). Fungal community analysis by high-throughput sequencing of amplified markers - a user's guide. *New Phytologist*, 199: 288–299.

LONSDALE W.M. (1999). Global patterns of plant invasions and the concept of invasibility. *Ecology*, 80: 1522–1536.

LOSOSOVÁ Z., CHYTRÝ M., TICHÝ L., DANIHELKA J., FAJMON K., HÁJEK O., ET AL. (2012). Native and alien floras in urban habitats: a comparison across 32 cities of central Europe. *Global Ecology and Biogeography*, 21: 545–555.

LUTZ F. (1921). Geographic average, a suggested method for the study of distribution. *American Museum Novitates*, 5: 1–7.

MacArthur R. (1972). *Geographical ecology: patterns in the distribution of species*. Harper and Row, New York.

Mächler M., Rousseeuw P., Struyf A., Hubert M. and Hornik K. (2013). *cluster: cluster analysis basics and extensions*. R package version 1.14.4.

Mack R., Simberloff D., Lonsdale W., Evans H., Clout M. and Bazzaz F. (2000). Biotic invasions: Causes, epidemiology, global consequences, and control. *Ecological Applications*, 10: 689–710.

Maestre F.T., Callaway R.M., Valladares F. and Lortie C.J. (2009). Refining the stress-gradient hypothesis for competition and facilitation in plant communities. *Journal of Ecology*, 97: 199–205.

Maherali H. (2014). Is there an association between root architecture and mycorrhizal growth response? *New Phytologist*, 204: 192–200.

Maherali H. and Klironomos J.N. (2007). Influence of phylogeny on fungal community assembly and ecosystem functioning. *Science*, 316: 1746–1748.

Marler M.J., Zabinski C.A. and Callaway R.M. (1999). Mycorrhizae indirectly enhance competitive effects of an invasive forb on a native bunchgrass. *Ecology*, 80: 1180–1186.

Martin F., Aerts A., Ahren D., Brun A., Danchin E.G.J., Duchaussoy F., et al. (2008). The genome of *Laccaria bicolor* provides insights into mycorrhizal symbiosis. *Nature*, 452: 88–92.

Martin F., Cullen D., Hibbett D., Pisabarro A., Spatafora J.W., Baker S.E., et al. (2011). Sequencing the fungal tree of life. *New Phytologist*, 190: 818–821.

Martiny J.B.H., Bohannan B.J.M., Brown J.H., Colwell R.K., Fuhrman J.A., Green J.L., et al. (2006). Microbial biogeography: putting microorganisms on the map. *Nature Reviews Microbiology*, 4: 102–112.

Maya M.A. and Matsubara Y.I. (2013). Influence of arbuscular mycorrhiza on the growth and antioxidative activity in cyclamen under heat stress. *Mycorrhiza*, 23: 381–390.

McCormack M.L., Lavely E. and Ma Z. (2014). Fine-root and mycorrhizal traits help explain ecosystem processes and responses to global change. *New Phytologist*, 204: 455–458.

McDonnell M.J. and Pickett S.T.A. (1990). Ecosystem structure and function along urban rural gradients - an unexploited opportunity for ecology. *Ecology*, 71: 1232–1237.

McGill B. (2015). Steering the trait bandwagon. https://dynamicecology.wordpress.com/2015/07/01/steering-the-trait-bandwagon/. Accessed: 18.03.2016.

McGill B., Enquist B., Weiher E. and Westoby M. (2006). Rebuilding community ecology from functional traits. *Trend in Ecology & Evolution*, 21: 178–185.

McInerny G.J. and Purves D.W. (2011). Fine-scale environmental variation in species distribution modelling: regression dilution, latent variables and neighbourly advice. *Methods in Cell Biology*, 2: 248–257.

Meisner A., Hol W.H.G., de Boer W., Krumins J.A., Wardle D.A. and van der Putten W.H. (2014). Plant-soil feedbacks of exotic plant species across life forms: a meta-analysis. *Biological Invasions*, 16: 2551–2561.

Milbau A. and Stout J.C. (2008). Factors associated with alien plants transitioning from casual, to naturalized, to invasive. *Conservation Biology*, 22: 308–317.

Mitchell C., Agrawal A., Bever J., Gilbert G., Hufbauer R., Klironomos J., et al. (2006). Biotic interactions and plant invasions. *Ecology Letters*, 9: 726–740.

Mohan J.E., Cowden C.C., Baas P., Dawadi A., Frankson P.T., Helmick K., et al. (2014). Mycorrhizal fungi mediation of terrestrial ecosystem responses to global change: mini-review. *Fungal Ecology*, 10: 3–19.

Moles A.T. and Westoby M. (2004). Seedling survival and seed size: a synthesis of the literature. *Journal of Ecology*, 92: 372–383.

Moora M. (2014). Mycorrhizal traits and plant communities: perspectives for integration. *Journal of Vegetation Science*, 25: 1126–1132.

Moora M., Berger S., Davison J., Öpik M., Bommarco R., Bruelheide H., et al. (2011). Alien plants associate with widespread generalist arbuscular mycorrhizal fungal taxa: evidence from a continental-scale study using massively parallel 454 sequencing. *Journal of Biogeography*, 38: 1305–1317.

Moora M., Öpik M., Sen R. and Zobel M. (2004). Native arbuscular mycorrhizal fungal communities differentially influence the seedling performance of rare and common *Pulsatilla* species. *Functional Ecology*, 18: 554–562.

Moora M., Öpik M., Zobel K. and Zobel M. (2009). Understory plant diversity is related to higher variability of vegetative mobility of coexisting species. *Oecologia*, 159: 355–361.

Mummey D.L. and Rillig M.C. (2006). The invasive plant species *Centaurea maculosa* alters arbuscular mycorrhizal fungal communities in the field. *Plant and Soil*, 288: 81–90.

Neuhauser C. and Fargione J.E. (2004). A mutualisim-parasitism continuum model and its application to plant-mycorrhizae interactions. *Ecological Modelling*, 177: 337–352.

Newsham K., Fitter A. and Watkinson A. (1995). Arbuscular mycorrhiza protect an annual grass from root pathogenic fungi in the field. *Journal of Ecology*, 83: 991–1000.

NGOSONG C., JAROSCH M., RAUPP J., NEUMANN E. and RUESS L. (2010). The impact of farming practice on soil microorganisms and arbuscular mycorrhizal fungi: Crop type versus long-term mineral and organic fertilization. *Applied Soil Ecology*, 46: 134–142.

NILSSON R.H., KRISTIANSSON E., RYBERG M., HALLENBERG N. and LARSSON K.H. (2008). Intraspecific ITS variability in the kingdom fungi as expressed in the International Sequence Databases and its implications for molecular species identification. *Evolutionary Bioinformatics*, 4: 193–201.

NUÑEZ M.A. and DICKIE I.A. (2014). Invasive belowground mutualists of woody plants. *Biological Invasions*, 16: 645–661.

NUÑEZ M.A., HORTON T.R. and SIMBERLOFF D. (2009). Lack of belowground mutualisms hinders *Pinaceae* invasions. *Ecology*, 90: 2352–2359.

OEHL F., LACZKO E., BOGENRIEDER A., STAHR K., BOESCH R., VAN DER HEIJDEN M., ET AL. (2010). Soil type and land use intensity determine the composition of arbuscular mycorrhizal fungal communities. *Soil Biology & Biochemistry*, 42: 724–738.

OEHL F., SIEVERDING E., INEICHEN K., MADER P., BOLLER T. and WIEMKEN A. (2003). Impact of land use intensity on the species diversity of arbuscular mycorrhizal fungi in agroecosystems of Central Europe. *Applied and Environmental Microbiology*, 69: 2816–2824.

OHSOWSKI B.M., ZAITSOFF P.D., ÖPIK M. and HART M.M. (2014). Where the wild things are: looking for uncultured *Glomeromycota. New Phytologist*, 204: 171–179.

OKE T.R. (1982). The energetic basis of the urban heat-island. *Quarterly Journal of the Royal Meteorological Society*, 108: 1–24.

OLDROYD G.E.D. (2013). Speak, friend, and enter: signalling systems that promote beneficial symbiotic associations in plants. *Nature Reviews Microbiology*, 11: 252–263.

OLSSON P. and TYLER G. (2004). Occurrence of non-mycorrhizal plant species in south Swedish rocky habitats is related to exchangeable soil phosphate. *Journal of Ecology*, 92: 808–815.

O'NEILL E.G., O'NEILL R.V. and NORBY R.J. (1991). Hierarchy theory as a guide to mycorrhizal research on large-scale problems. *Environmental Pollution*, 73: 271–284.

ONIPCHENKO V. and ZOBEL M. (2000). Mycorrhiza, vegetative mobility and responses to disturbance of alpine plants in the Northwestern Caucasus. *Folia Geobotanica*, 35: 1–11.

ÖPIK M., DAVISON J., MOORA M. and ZOBEL M. (2014). DNA-based detection and identification of *Glomeromycota*: the virtual taxonomy of environmental sequences. *Botany*, 92: 135–147.

Öpik M., Metsis M., Daniell T.J., Zobel M. and Moora M. (2009). Large-scale parallel 454 sequencing reveals host ecological group specificity of arbuscular mycorrhizal fungi in a boreonemoral forest. *New Phytologist*, 184: 424–437.

Öpik M. and Moora M. (2012). Missing nodes and links in mycorrhizal networks. *New Phytologist*, 194: 304–306.

Öpik M., Moora M., Liira J., Koljalg U., Zobel M. and Sen R. (2003). Divergent arbuscular mycorrhizal fungal communities colonize roots of *Pulsatilla* spp. in boreal Scots pine forest and grassland soils. *New Phytologist*, 160: 581–593.

Öpik M., Moora M., Liira J. and Zobel M. (2006). Composition of root-colonizing arbuscular mycorrhizal fungal communities in different ecosystems around the globe. *Journal of Ecology*, 94: 778–790.

Öpik M., Vanatoa A., Vanatoa E., Moora M., Davison J., Kalwij J.M., et al. (2010). The online database MaarjAM reveals global and ecosystemic distribution patterns in arbuscular mycorrhizal fungi (*Glomeromycota*). *New Phytologist*, 188: 223–241.

Öpik M., Zobel M., Cantero J.J., Davison J., Facelli J.M., Hiiesalu I., et al. (2013). Global sampling of plant roots expands the described molecular diversity of arbuscular mycorrhizal fungi. *Mycorrhiza*, 23: 411–430.

Paradis E., Claude J. and Strimmer K. (2004). APE: analyses of phylogenetics and evolution in R language. *Bioinformatics*, 20: 289–290.

Parrent J.L., Peay K., Arnold A.E., Comas L.H., Avis P. and Tuininga A. (2010). Moving from pattern to process in fungal symbioses: linking functional traits, community ecology and phylogenetics. *New Phytologist*, 185: 882–886.

Peat H. and Fitter A. (1993). The distribution of arbuscular mycorrhizas in the British flora. *New Phytologist*, 125: 845–854.

Pellissier L., Pinto-Figueroa E., Niculita-Hirzel H., Moora M., Villard L., Goudet J., et al. (2013). Plant species distributions along environmental gradients: do belowground interactions with fungi matter? *Frontiers in Plant Science*, 4.

Pérez-Harguindeguy N., Díaz S., Garnier E., Lavorel S., Poorter H., Jaureguiberry P., et al. (2013). New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany*, 61: 167–234.

Philip L.J., Posluszny U. and Klironomos J.N. (2001). The influence of mycorrhizal colonization on the vegetative growth and sexual reproductive potential of *Lythrum salicaria* L. *Canadian Journal of Botany*, 79: 381–388.

Piotrowski J.S., Lekberg Y., Harner M.J., Ramsey P.W. and Rillig M.C. (2008). Dynamics of mycorrhizae during development of riparian forests along an unregulated river. *Ecography*, 31: 245–253.

Pirozynski K. and Malloch D. (1975). Origin of land plants - matter of mycotropism. *Biosystems*, 6: 153–164.

Plett J.M., Daguerre Y., Wittulsky S., Vayssieres A., Deveau A., Melton S.J., et al. (2014). Effector MiSSP7 of the mutualistic fungus *Laccaria bicolor* stabilizes the *Populus* JAZ6 protein and represses jasmonic acid (JA) responsive genes. *Proceedings of the National Academy of Sciences of the United States of America*, 111: 8299–8304.

Poisot T., Pequin B. and Gravel D. (2013). High-throughput sequencing: A roadmap toward community ecology. *Ecology and Evolution*, 3: 1125–1139.

Powell J.R., Parrent J.L., Hart M.M., Klironomos J.N., Rillig M.C. and Maherali H. (2009). Phylogenetic trait conservatism and the evolution of functional trade-offs in arbuscular mycorrhizal fungi. *Proceedings of the Royal Society B-biological Sciences*, 276: 4237–4245.

Preston F. (1948). The commonness, and rarity, of species. *Ecology*, 29: 254–283.

Pringle A. and Bever J.D. (2008). Analogous effects of arbuscular mycorrhizal fungi in the laboratory and a North Carolina field. *New Phytologist*, 180: 162–175.

Pringle A., Bever J.D., Gardes M., Parrent J.L., Rillig M.C. and Klironomos J.N. (2009). Mycorrhizal symbioses and plant invasions. *Annual Review of Ecology, Evolution, and Systematics*, 40: 699–715.

Pringle A. and Taylor J.W. (2002). The fitness of filamentous fungi. *Trends in Microbiology*, 10: 474–481.

Pyšek P. and Jarošik V. (2006). Residence time determines the distribution of alien plants. In: *Invasive Plants: Ecological and Agricultural Aspects* (S. Inderjit, ed.). Birkhäuser Verlag, Switzerland, pp. 77–96.

Pyšek P., Jarošik V., Chytrý M., Danihelka J., Kühn I., Pergl J., et al. (2011). Successful invaders co-opt pollinators of native flora and accumulate insect pollinators with increasing residence time. *Ecological Monographs*, 81: 277–293.

Pyšek P., Jarošik V., Chytrý M., Kropac Z., Tichy L. and Wild J. (2005). Alien plants in temperate weed communities: Prehistoric and recent invaders occupy different habitats. *Ecology*, 86: 772–785.

Pyšek P., Jarošik V., Hulme P.E., Kühn I., Wild J., Arianoutsou M., et al. (2010). Disentangling the role of environmental and human pressures on biological invasions across Europe. *Proceedings of the National Academy of Sciences of the United States of America*, 107: 12157–12162.

Pyšek P., Jarošik V., Hulme P.E., Pergl J., Hejda M., Schaffner U., et al. (2012). A global assessment of invasive plant impacts on resident species, communities and ecosystems: the interaction of impact measures, invading species' traits and environment. *Global Change Biology*, 18: 1725–1737.

Pyšek P., Jarošik V., Pergl J., Randall R., Chytrý M., Kühn I., et al. (2009). The global invasion success of Central European plants is related to distribution characteristics in their native range and species traits. *Diversity and Distributions*, 15: 891–903.

Pyšek P., Manceur A.M., Alba C., McGregor K.F., Pergl J., Štajerová K., et al. (2015). Naturalization of Central European plants in North America: species traits, habitats, propagule pressure, residence time. *Ecology*, 96: 762–774.

Pyšek P., Richardson D.M., Pergl J., Jarošik V., Sixtova Z. and Weber E. (2008). Geographical and taxonomic biases in invasion ecology. *Trends in Ecology & Evolution*, 23: 237–244.

Pyšek P., Richardson D.M. and Williamson M. (2004). Predicting and explaining plant invasions through analysis of source area floras: some critical considerations. *Diversity and Distributions*, 10: 179–187.

Queloz V., Sieber T.N., Holdenrieder O., McDonald B.A. and Gruenig C.R. (2011). No biogeographical pattern for a root-associated fungal species complex. *Global Ecology and Biogeography*, 20: 160–169.

R Development Core Team (2013). R: A Language and Environment for Statistical Computing. Tech. rep., Vienna, Austria,.

Read D. (2002). Towards ecological relevance - progress and pitfalls in the path towards an understanding of mycorrhizal functions in nature. In: *Mycorrhizal Ecology* (M. van der Heijden and I. Sanders, eds.). Springer Verlag Berlin Heidelberg, pp. 3–29.

Read D.J. (1991). Mycorrhizas in Ecosystems. *Experientia*, 47: 376–391.

Redecker D., Kodner R. and Graham L.E. (2000). Glomalean fungi from the Ordovician. *Science*, 289: 1920–1921.

Redecker D., Schüssler A., Stockinger H., Stürmer S.L., Morton J.B. and Walker C. (2013). An evidence-based consensus for the classification of arbuscular mycorrhizal fungi (*Glomeromycota*). *Mycorrhiza*, 23: 515–531.

Reich P.B., Wright I.J., Cavender-Bares J., Craine J.M., Oleksyn J., Westoby M., et al. (2003). The evolution of plant functional variation: Traits, spectra, and strategies. *International Journal of Plant Sciences*, 164: 143–164.

Reinhart K.O. and Callaway R.M. (2006). Soil biota and invasive plants. *New Phytologist*, 170: 445–457.

Reinhart K.O., Wilson G.W.T. and Rinella M.J. (2012). Predicting plant responses to mycorrhizae: integrating evolutionary history and plant traits. *Ecology Letters*, 15: 689–695.

Richardson D.M., Allsopp N., D'Antonio C.M., Milton S.J. and Rejmánek M. (2000b). Plant invasions - the role of mutualisms. *Biological Reviews*, 75: 65–93.

Richardson D.M. and Pyšek P. (2012). Naturalization of introduced plants: ecological drivers of biogeographical patterns. *New Phytologist*, 196: 383–396.

Richardson D.M., Pyšek P., Rejmánek M., Barbour M.G., Panetta F.D. and West C.J. (2000a). Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions*, 6: 93–107.

Rillig M.C., Aguilar-Trigueros C.A., Bergmann J., Verbruggen E., Veresoglou S.D. and Lehmann A. (2015). Plant root and mycorrhizal fungal traits for understanding soil aggregation. *New Phytologist*, 205: 1385–1388.

Rillig M.C. and Mummey D.L. (2006). Mycorrhizas and soil structure. *New Phytologist*, 171: 41–53.

Ryser P. (2006). The mysterious root length. *Plant and Soil*, 286: 1–6.

Sala O.E., Chapin F.S., Armesto J.J., Berlow E., Bloomfield J., Dirzo R., et al. (2000). Biodiversity - Global biodiversity scenarios for the year 2100. *Science*, 287: 1770–1774.

Sanders F.E. and Tinker P.B. (1971). Mechanism of absorption of phosphate from soil by endogone mycorrhizas. *Nature*, 233: 278–279.

Santos J.C., Finlay R.D. and Tehler A. (2006). Molecular analysis of arbuscular mycorrhizal fungi colonising a semi-natural grassland along a fertilisation gradient. *New Phytologist*, 172: 159–168.

Sax D.F., Stachowicz J.J., Brown J.H., Bruno J.F., Dawson M.N., Gaines S.D., et al. (2007). Ecological and evolutionary insights from species invasions. *Trends in Ecology & Evolution*, 22: 465–471.

Schachtschabel P., Blume H.P., Brümmer G., Hartge K.H. and Schwertmann U. (1998). *Scheffer/Schachtschabel - Lehrbuch der Bodenkunde*. 14th ed. Ferdinand Verlag.

Schimper A. (1903). *Plant-geography upon a physiological basis*. Oxford University Press.

Schultz P.A., Miller R.M., Jastrow J.D., Rivetta C.V. and Bever J.D. (2001). Evidence of a mycorrhizal mechanism for the adaptation of *Andropogon gerardii* (*Poaceae*) to high- and low-nutrient prairies. *American Journal of Botany*, 88: 1650–1656.

SCHÜSSLER A. (2016). Arthur Schüssler's *Glomeromycota* phylogeny. Accessed: 05.01.2016.

SCHÜSSLER A., SCHWARZOTT D. and WALKER C. (2001). A new fungal phylum, the *Glomeromycota*: phylogeny and evolution. *Mycological Research*, 105: 1413–1421.

SCHWEINGRUBER W. and LANDOLT F. (2005). The Xylem Database.

SEEBENS H., ESSL F., DAWSON W., FUENTES N., MOSER D., PERGL J., ET AL. (2015). Global trade will accelerate plant invasions in emerging economies under climate change. *Global Change Biology*, 21: 4128–4140.

SEIFERT E.K., BEVER J.D. and MARON J.L. (2009). Evidence for the evolution of reduced mycorrhizal dependence during plant invasion. *Ecology*, 90: 1055–1062.

SELOSSE M.A. and ROUSSET F. (2011). The plant-fungal marketplace. *Science*, 333: 828–829.

SHAH M., RESHI Z. and KHASA D. (2009). Arbuscular mycorrhizas: drivers or passengers of alien plant invasion. *The Botanical Review*, 75: 397–417.

SHIPLEY B., VILE D. and GARNIER E. (2006). From plant traits to plant communities: A statistical mechanistic approach to biodiversity. *Science*, 314: 812–814.

SIMBERLOFF D., MARTIN J.L., GENOVESI P., MARIS V., WARDLE D.A., ARONSON J., ET AL. (2013). Impacts of biological invasions: what's what and the way forward. *Trends in Ecology & Evolution*, 28: 58–66.

SIMON L., BOUSQUET J., LEVESQUE R.C. and LALONDE M. (1993). Origin and diversification of endomycorrhizal fungi and coincidence with vascular land plants. *Nature*, 363: 67–69.

SKARPAAS O., SILVERMAN E.J., JONGEJANS E. and SHEA K. (2011). Are the best dispersers the best colonizers? Seed mass, dispersal and establishment in *Carduus* thistles. *Evolutionary Ecology*, 25: 155–169.

SMITH F.A., LYONS S.K., ERNEST S.K.M. and BROWN J.H. (2008). Macroecology: more than the division of food and space among species on continents. *Progress in Physical Geography*, 32: 115–138.

SMITH F.A. and SMITH S.E. (2011b). What is the significance of the arbuscular mycorrhizal colonisation of many economically important crop plants? *Plant and Soil*, 348: 63–79.

SMITH S.E. and READ D. (2008). *Mycorrhizal Symbiosis*. 3rd ed. Elsevier.

SMITH S.E. and SMITH F.A. (2011a). Roles of arbuscular mycorrhizas in plant nutrition and growth: new paradigms from cellular to ecosystem scales. *Annual Review of Plant Biology, Vol 62*, 62: 227–250.

Smith S.E., Smith F.A. and Jakobsen I. (2004). Functional diversity in arbuscular mycorrhizal (AM) symbioses: the contribution of the mycorrhizal P uptake pathway is not correlated with mycorrhizal responses in growth or total P uptake. *New Phytologist*, 162: 511–524.

Sokal R. and Rohlf F. (1995). *Biometry.* Freeman, New York. USA.

Soudzilovskaia N.A., Douma J.C., Akhmetzhanova A.A., van Bodegom P.M., Cornwell W.K., Moens E.J., et al. (2015). Global patterns of plant root colonization intensity by mycorrhizal fungi explained by climate and soil chemistry. *Global Ecology and Biogeography*, 24: 371–382.

Statistisches Bundesamt (1997). Daten zur Bodenbedeckung für die Bundesrepublik Deutschland 1:100.000.

Stein A., Gerstner K. and Kreft H. (2014). Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecology Letters*, 17: 866–880.

Sun X., Gao C. and Guo L.D. (2013). Changes in arbuscular mycorrhizal fungus community along an exotic plant *Eupatorium adenophorum* invasion in a Chinese secondary forest. *Journal of Microbiology*, 51: 295–300.

Sun Z.K. and He W.M. (2010). Evidence for enhanced mutualism hypothesis: *Solidago canadensis* plants from regular soils perform better. *Plos One*, 5: e15418.

Tedersoo L., Bahram M., Polme S., Koljalg U., Yorou N.S., Wijesundera R., et al. (2014). Global diversity and geography of soil fungi. *Science*, 346.

Traveset A. and Richardson D.M. (2014). Mutualistic interactions and biological invasions. *Annual Review of Ecology, Evolution, and Systematics*, 45: 89–113.

Treseder K. and Cross A. (2006). Global distributions of arbuscular mycorrhizal fungi. *Ecosystems*, 9: 305–316.

Tungate K.D., Israel D.W., Watson D.M. and Rufty T.W. (2007). Potential changes in weed competitiveness in an agroecological system with elevated temperatures. *Environmental and Experimental Botany*, 60: 42–49.

Turnbull L.A., Coomes D., Hector A. and Rees M. (2004). Seed mass and the competition/colonization trade-off: competitive interactions and spatial patterns in a guild of annual plants. *Journal of Ecology*, 92: 97–109.

Turnbull L.A., Rees M. and Crawley M.J. (1999). Seed mass and the competition/colonization trade-off: a sowing experiment. *Journal of Ecology*, 87: 899–912.

Valverde-Barrantes O.J., Smemo K.A., Feinstein L.M., Kershner M.W. and Blackwood C.B. (2013). The distribution of below-ground traits is explained by intrinsic species differences and intraspecific plasticity in response to root neighbours. *Journal of Ecology*, 101: 933–942.

van Aarle I.M., Soderstrom B. and Olsson P.A. (2003). Growth and interactions of arbuscular mycorrhizal fungi in soils from limestone and acid rock habitats. *Soil Biology & Biochemistry*, 35: 1557–1564.

van der Heijden M.G.A. (2004). Arbuscular mycorrhizal fungi as support systems for seedling establishment in grassland. *Ecology Letters*, 7: 293–303.

van der Heijden M.G.A. and Horton T.R. (2009). Socialism in soil? The importance of mycorrhizal fungal networks for facilitation in natural ecosystems. *Journal of Ecology*, 97: 1139–1150.

van der Heijden M.G.A., Klironomos J.N., Ursic M., Moutoglis P., Streitwolf-Engel R., Boller T., et al. (1998). Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. *Nature*, 396: 69–72.

van der Heijden M.G.A., Martin F.M., Selosse M.A. and Sanders I.R. (2015). Mycorrhizal ecology and evolution: the past, the present, and the future. *New Phytologist*, 205: 1406–1423.

van der Heijden M.G.A. and Scheublin T.R. (2007). Functional traits in mycorrhizal ecology: their use for predicting the impact of arbuscular mycorrhizal fungal communities on plant growth and ecosystem functioning. *New Phytologist*, 174: 244–250.

van der Heijden M.G.A., Wiemken A. and Sanders I.R. (2003). Different arbuscular mycorrhizal fungi alter coexistence and resource distribution between co-occurring plant. *New Phytologist*, 157: 569–578.

van Kleunen M., Dawson W., Essl F., Pergl J., Winter M., Weber E., et al. (2015). Global exchange and accumulation of non-native plants. *Nature*, 525: 100–103.

van Kleunen M., Weber E. and Fischer M. (2010). A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecology Letters*, 13: 235–245.

Varga S. (2010). Effects of arbuscular mycorrhizas on reproductive traits in sexually dimorphic plants. *Spanish Journal of Agricultural Research*, 8: 11–24.

Venables W.N. and Ripley B.D. (2002). *Modern applied statistics with S*. 4th ed. New York: Springer.

Veresoglou S.D. and Rillig M.C. (2012). Suppression of fungal and nematode plant pathogens through arbuscular mycorrhizal fungi. *Biology Letters*, 8: 214–217.

Vilà M., Basnou C., Pyšek P., Josefsson M., Genovesi P., Gollasch S., et al. (2010). How well do we understand the impacts of alien species on ecosystem services? A pan-European, cross-taxa assessment. *Frontiers in Ecology and the Environment*, 8: 135–144.

VILÀ M., ESPINAR J.L., HEJDA M., HULME P.E., JAROŠIK V., MARON J.L., ET AL. (2011). Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecology Letters*, 14: 702–708.

VIOLLE C., ENQUIST B.J., MCGILL B.J., JIANG L., ALBERT C.H., HULSHOF C., ET AL. (2012). The return of the variance: intraspecific variability in community ecology. *Trends in Ecology & Evolution*, 27: 244–252.

VIOLLE C., NAVAS M.L., VILE D., KAZAKOU E., FORTUNEL C., HUMMEL I., ET AL. (2007). Let the concept of trait be functional! *Oikos*, 116: 882–892.

VIOLLE C., REICH P.B., PACALA S.W., ENQUIST B.J. and KATTGE J. (2014). The emergence and promise of functional biogeography. *Proceedings of the National Academy of Sciences of the United States of America*, 111: 13690–13696.

VOGELSANG K.M. and BEVER J.D. (2009). Mycorrhizal densities decline in association with nonnative plants and contribute to plant invasion. *Ecology*, 90: 399–407.

ŠTAJEROVÁ K., ŠMILAUEROVÁ M. and ŠMILAUER P. (2009). Arbuscular mycorrhizal symbiosis of herbaceous invasive neophytes in the Czech Republic. *Preslia*, 81: 341–355.

WANG B. and QIU Y.L. (2006). Phylogenetic distribution and evolution of mycorrhizas in land plants. *Mycorrhiza*, 16: 299–363.

WEHNER J., POWELL J.R., MULLER L.A.H., CARUSO T., VERESOGLOU S.D., HEMPEL S., ET AL. (2014). Determinants of root-associated fungal communities within *Asteraceae* in a semi-arid grassland. *Journal of Ecology*, 102: 425–436.

WEI T. (2013). corrplot: Visualization of a correlation matrix. Tech. rep. R package version 0.73.

WEIHER E. and KEDDY P. (1995). Assembly rules, null models, and trait dispersion: new questions from old patterns. *Oikos*, 74: 159–164.

WELK A., WELK E. and BRUELHEIDE H. (2014). Biotic interactions overrule plant responses to climate, depending on the species' biogeography. *Plos One*, 9: e111023.

WENGER S.J. and OLDEN J.D. (2012). Assessing transferability of ecological models: an underappreciated aspect of statistical validation. *Methods in Ecology and Evolution*, 3: 260–267.

WERNER G.D.A. and KIERS E.T. (2015). Partner selection in the mycorrhizal mutualism. *New Phytologist*, 205: 1437–1442.

WEST G.B., BROWN J.H. and ENQUIST B.J. (1997). A general model for the origin of allometric scaling laws in biology. *Science*, 276: 122–126.

WESTOBY M. and WRIGHT I.J. (2006). Land-plant ecology on the basis of functional traits. *Trends in Ecology & Evolutions*, 21: 261–268.

WICKHAM H. (2009). *ggplot2: elegant graphics for data analysis.* Springer New York.

Williamson M., Dehnen-Schmutz K., Kühn I., Hill M., Klotz S., Milbau A., et al. (2009). The distribution of range sizes of native and alien plants in four European countries and the effects of residence time. *Diversity and Distributions*, 15: 158–166.

Wilson G.W.T. and Hartnett D.C. (1998). Interspecific variation in plant responses to mycorrhizal colonization in tallgrass prairie. *American Journal of Botany*, 85: 1732–1738.

Wilson J.R.U., Dormontt E.E., Prentis P.J., Lowe A.J. and Richardson D.M. (2009). Something in the way you move: dispersal pathways affect invasion success. *Trends in Ecology & Evolution*, 24: 136–144.

Worchel E.R., Giauque H.E. and Kivlin S.N. (2013). Fungal symbionts alter plant drought response. *Microbial Ecology*, 65: 671–678.

Wright I.J., Reich P.B., Westoby M., Ackerly D.D., Baruch Z., Bongers F., et al. (2004). The worldwide leaf economics spectrum. *Nature*, 428: 821–827.

Wurst S., Gebhardt K. and Rillig M.C. (2011). Independent effects of arbuscular mycorrhiza and earthworms on plant diversity and newcomer plant establishment. *Journal of Vegetation Science*, 22: 1021–1030.

Yang G., Liu N., Lu W., Wang S., Kan H., Zhang Y., et al. (2014). The interaction between arbuscular mycorrhizal fungi and soil phosphorus availability influences plant community productivity and ecosystem stability. *Journal of Ecology*, 102: 1072–1082.

Yang H., Zhang Q., Dai Y., Liu Q., Tang J., Bian X., et al. (2015). Effects of arbuscular mycorrhizal fungi on plant growth depend on root system: a meta-analysis. *Plant and Soil*, 389: 361–374.

Yee T.W. (2010). The VGAM package for categorical data analysis. *Journal of Statistical Software*, 32: 1–34.

Yee T.W. and Mackenzie M. (2002). Vector generalized additive models in plant ecology. *Ecological Modelling*, 157: 141 – 156.

Zabinski C.A., Quinn L. and Callaway R.M. (2002). Phosphorus uptake, not carbon transfer, explains arbuscular mycorrhizal enhancement of *Centaurea maculosa* in the presence of native grassland species. *Functional Ecology*, 16: 758–765.

Zhou Z., Ma H., Liang K., Huang G. and Pinyopusarerk K. (2012). Improved tolerance of teak (*Tectona grandis* L.f.) seedlings to low-temperature stress by the combined effect of arbuscular mycorrhiza and Paclobutrazol. *Journal of Plant Growth Regulation*, 31: 427–435.

Zhu X.C., Song F.B., Liu S.Q. and Liu T.D. (2011). Effects of arbuscular mycorrhizal fungus on photosynthesis and water status of maize under high temperature stress. *Plant and Soil*, 346: 189–199.

ZOBEL M. and ÖPIK M. (2014). Plant and arbuscular mycorrhizal fungal (AMF) communities – which drives which? *Journal of Vegetation Science*, 25: 1133–1140.

DANKSAGUNG

An dieser Stelle bleibt Platz, um mich bei allen Menschen und Institutionen zu bedanken, die mich bei der Anfertigung der vorliegenden Arbeit unterstützt haben.

Mein Dank geht dabei zuerst an Ingolf Kühn für den ursprünglichen Anstoß zu dieser Arbeit und die Betreuung und enge Zusammenarbeit über die letzten Jahre hinweg. Ein Dank für das Diskutieren von Ergebnissen, Methoden und ganzen Manuskripten, für die Begutachtung der Dissertation und für die Möglichkeit, einen Teil meiner Promotionszeit in Chile zu verbringen. Weiterhin danke ich Isabell Hensen und Maarja Öpik für die Bereitschaft zur Begutachtung der vorliegenden Arbeit. Ich danke dem UFZ, dessen Doktorandeninitiative 2012 diese Arbeit erst möglich gemacht hat und der Graduiertenschule HIGRADE für finanzielle Unterstützung in der Schlussphase der Arbeit. Weiterhin danke ich dem DAAD für die Förderung meines Chile-Aufenthaltes.

Mein Dank geht an alle Koautoren, die an den Manuskripten dieser Arbeit beteiligt sind und waren. Danke für die Bereitstellung der MycoFlor-Daten und den schnellen und konstruktiven Austausch per Mail. In den mehr als drei Jahren habe ich es immerhin geschafft, fast jeden einmal persönlich zu treffen.

Ich danke meiner Arbeitsgruppe „Makroökologie“ für die regelmäßigen Gruppentreffen und die damit verbundene Möglichkeit, Zwischenergebnisse vorzustellen und diese und vieles mehr zu diskutieren und zu erfahren.

Ich danke allen Mitgliedern des Departments Biozönoseforschung für die tolle Arbeitsatmosphäre und buchstäblich offene Türen. Ich danke Anja Schmidt für das akribische Korrekturlesen und die konstruktive und kritische Auseinandersetzung mit meiner generellen Einleitung und Synthese. Many thanks to Alexandra Papanikolaou for sharing thoughts about decisions to make, methods to use, and how to survive or not survive in the world of science. Vielen Dank an Ally Siebenkäs für unerschöpfliche Auskünfte gerade in der Schlussphase der Arbeit. Ein Dank allen Mensa-MitstreiterInnen, ganz besonders für das Abgeben von Käseschnitzel-Portionen. Mein Dank gilt natürlich Antje Kautzner und dem glücklichen Zustand, dass wir von Tag eins an ein Büro teilen durften. Danke für unzählige Heißgetränke, zuckrige Mitbringsel, für die Unterstützung in Fragen der Artenkenntnis, Pflanzenmerkmalen und Physiologie sowie die gesamte gemeinsame Zeit inner- und außerhalb des UFZ.

¡Muchas gracias! to the entire Functional Ecology group of Alfredo Saldaña at Universidad de Concepción. I always felt welcome in your lively office. Special thanks to Alfredo, Bartolo, David, Letizzia and Maria for sharing thoughts about Chile and bringing me to a lot of beautiful places. Although our joint time is not included in the thesis scientifically, it was a special part of my time as a PhD for which I am very grateful.

Mein Dank gilt meinen Freunden – an Ann-Christin, Christin und Michael in München, an Caroline, Robert und Uli in Leipzig und alle anderen in Leipzig, Jena, Berlin und Rotterdam. Danke für den steten Zuspruch, Zerstreuung zur rechten Zeit und tollste Zeiten vor Ort und am Telefon.

Liebste Clara, vielen Dank für dein Komplizentum, das gemeinsame Zuhause, die Geduld und das Rückenfreihalten gerade in den letzten Monaten vor Abgabe. Vielen Dank für das gemeinsame Erstellen von Zeitplänen, das Korrekturlesen und das Nachdenken über Begriffe, von denen du zuvor noch nie etwas gehört hattest.

Zuletzt gilt mein Dank meiner Familie für die nun schon so lang andauernde, bedingungslose Unterstützung mit all euren Mitteln und eurem Urvertrauen in die Entscheidungen, die ich getroffen habe.

Dankeschön.

APPENDIX

Curriculum vitae

ANDREAS MENZEL

born	03.02.1987 in Jena
nationality	German
address	Scheffelstraße 48 in 04277 Leipzig
e-mail	andreas.menzel@posteo.de

SCIENTIFIC CAREER

03/2016 - present	postdoc, Department of Community Ecology, Helmholtz Centre for Environmental Research - UFZ, Halle member of EU BON, work package 4: *Link environment to biodiversity: analyses of patterns, processes and trends*
09/2014 - 11/2014	research visit at Universidad de Concepción, Chile Functional Ecology group, Department of Botany, funded by DAAD (ALECHILE): *Land use change and plant functional composition in BíoBío, Chile*
12/2012 - present	PhD candidate, Department of Community Ecology, Helmholtz Centre for Environmental Research - UFZ, Halle
02/2012	diploma degree in biology: grade 'sehr gut' **(1,4)** Friedrich Schiller University Jena *Optimization of diversity experiments by spatial analysis of arthropod distribution patterns* **(1,0)**
2009-2012	The Jena Experiment • evaluation + maintenance of the Jena Experiment data base • installation + assistance of the *Osmia bicornis* cage experiment • mapping, sampling and dissection of pollinator insects
10/2005 - 02/2012	studies in biology Friedrich Schiller University Jena major: ecology; minor: genetics, geography

Conference contributions

09/2016	**talk**, 9th Neobiota Conference, Vianden Menzel A, Hempel S, Klotz S, Moora M, Pyšek P, Rillig MC Zobel M, Kühn I: *’Mycorrhizal status interacting with morphological traits help explaining invasion success of alien plant species’*
09/2015	**talk**, 13th EEF Conference, Rome Menzel A, Hempel S, Götzenberger L, Klotz S, Moora M, Pyšek P, Rillig MC, Zobel M, Kühn I: *’Mycorrhizal status helps explaining invasion success of neophyte plant species in Germany’*
01/2015	**poster**, 7th IBS Conference, Bayreuth Menzel A, Hempel S, Götzenberger L, Manceur MA, Moora M, Rillig MC, Zobel M, Kühn I: *’Large-scale distribution patterns of arbuscular mycorrhizal and non-mycorrhizal plant species’*
09/2013	**talk**, 43rd GfÖ Conference, Potsdam Menzel A, Hempel S, Götzenberger L, Manceur MA, Moora M, Rillig MC, Zobel M, Kühn I: *’What are the environmental drivers of arbuscular mycorrhizal and non-mycorrhizal plant species?’*
09/2012	**talk**, 42nd GfÖ Conference, Lüneburg Menzel A, Rzanny M, Voigt W: *’Optimization of biodiversity experiments by spatial analysis of arthropod distribution patterns’*

List of publications

Menzel A., Hempel S., Manceur A.M., Götzenberger L., Moora M., Rillig M.C., Zobel M., and I. Kühn. Distribution patterns of arbuscular mycorrhizal and non-mycorrhizal plant species in Germany. *Perspectives in Plant Ecology, Evolution, and Systematics* 21: 78-88.

Menzel A., Hempel S., Klotz S., Moora M., Pyšek P., Rillig M.C., Zobel M., and I. Kühn. Mycorrhizal status helps explain invasion success of alien plant species. (*Ecology*, accepted).

Menzel A., Hempel S., Klotz S., Moora M., Pyšek P., Rillig M.C., Zobel M., and I. Kühn. Trait interactions reveal differences in arbuscular mycorrhizal associations between native and alien plant species.

Eigenständigkeitserklärung

Hiermit erkläre ich, dass die vorliegende Arbeit mit dem Titel „Effects of the mycorrhizal symbiosis on plant distributions and alien plant invasions at a large spatial scale“ bisher weder bei der Naturwissenschaftlichen Fakultät I - Biowissenschaften - der Martin-Luther-Universität Halle-Wittenberg noch einer anderen wissenschaftlichen Einrichtung zum Zweck der Promotion vorgelegt wurde.
Darüber hinaus erkläre ich, dass ich die vorliegende Arbeit eigenständig und ohne fremde Hilfe verfasst sowie keine anderen als die im Text angegebenen Quellen und Hilfsmittel verwendet habe. Textstellen, welche aus verwendeten Werken wörtlich oder inhaltlich übernommen wurden, wurden von mir als solche kenntlich gemacht.
Ich erkläre weiterhin, dass ich mich bisher noch nie um einen Doktorgrad beworben habe.

Andreas Menzel
Halle (Saale), 23.03.2016