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REVIEW ARTICLE

The role of arbuscular mycorrhizal fungi in plant invasion trajectory

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Background Invasive plant species pose a global threat because they alter ecosystem functioning and biodiversity. The majority of plants form mutualistic mycorrhizal associations with mycorrhizal fungi, which contribute to the nutrient and water supply as well as diversity, competitive ability, and ecosystem productivity. In addition, the role of mycorrhizal interactions in plant invasiveness and the susceptibility or resistance of a habitat to invasion is increasingly recognized. However, the mechanisms by which mycorrhizae contribute to invasion remain unresolved.

Scope Here, we provide an overview of the empirical evidence and discuss the prospects for mycorrhizaemediated plant invasion. Overall, mycorrhizal fungi appear to have impacts on plant invasion that depend on the similarities between the mycorrhizal associations of the alien and native plants. We introduce plant mycorrhizal niche space (PMNS) as a plant's ability to exploit and shape the mycorrhizal fungi pool of a habitat based on its dependency on mycorrhizal fungi, traits and priority effects.

Conclusions Collectively, the available evidence supports the idea that PMNS is independent of place of origin (invasive status). Understanding the drivers of the PMNS of both native and alien plant species may help to predict the potential invasiveness of plants and the invasibility of a habitat, to elucidate the role of the mycorrhizal fungal community in plant invasion and the impact of plant invasion on the structure of the mycorrhizal fungal community in new habitats (i.e., neighbour effect) and to improve restoration planning. In this regard, we highlight a number of knowledge gaps and discuss future research directions.

Keywords Mycorrhizal adaptation · Plant-mycobiome interactions · Invasion ecology · Fungal diversity · Symbiosis

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Introduction

The spread of invasive plants - plants that spread vigorously outside of their native ranges - is rapidly increasing as a result of increased climate change-associated disturbances and human activities, posing a global threat by shifting plant species community composition and ecosystem functioning (Castro-Díez et al. 2016; Aerts et al. 2017) and reducing the species richness of native plants and animals (Vilà et al. 2015) with potential economic losses (Pimentel et al. 2005). It is thus important to determine the relative importance of factors facilitating or inhibiting plant invasion in order to improve management practices.

The performance of plants outside their native ranges at least partly depends on their association with symbiotic microbes. Arbuscular mycorrhizal fungi (AMF) are an ecologically and economically important fungal guild that establishes mutualistic associations with approximately 71% of vascular plant species (Cosme et al. 2018). Recent evidence suggests that mycorrhizal symbiosis with AMF mediates the competitiveness, diversity and community structure of plant species (Lin et al. 2015; Bennett et al. 2017; Teste et al. 2017), thus contributing to plant invasion success/failure (Gerz et al. 2018). Recent gene-based identification studies of fungi support the hypothesis that AMF abundance and composition may affect plant survival, establishment and invasion in a new habitat (Yang et al. 2014), depending on plant mycorrhizal dependency (i.e., mycorrhizal traits) (Neuenkamp et al. 2018), phenological and functional traits (Lin et al. 2015), invasive status and legacy effects (Jordan et al. 2012). A meta-analysis of 304 studies demonstrated that functional groups and life histories of plant species differentially altered the effects of AMF on the competition and structure of the plant communities (Lin et al. 2015). Dassen et al. (2017) showed that AMF community composition in bulk soils was significantly influenced by plant species diversity and functional groups (such as grasses, legumes, small herbs and tall herbs). By analysing the occupied range of 266 invasive plants across Germany in relation to combinations of their mycorrhizal status and plant traits using a generalized linear model, Menzel et al. (2017) demonstrated that mycorrhizal traits are significantly correlated with the geographic expansion of alien plants, such that mycorrhizal alien plants can expand across a larger range compared to non-mycorrhizal (NM) plants. In addition, there is evidence that the identity of AMF taxa can affect the coexistence and competitiveness of plants (Zhou et al. (2018). Studies on other organisms also support the idea that plant diversity and invasion success may be influenced by symbiotic relationships (Traveset and Richardson 2014; Pauw 2013). For example, plants with similar floral traits share similar flower visitors, resulting in higher competition between native and invasive plant species. This finding was also supported by Gibson et al. (2012), who reported that floral traits have indirect impacts on pollinator-mediated plant invasion and that the similarity of floral traits explains the invasion impact of *Acacia saligna* on the co-occurring native species.

However, several studies have reported contrasting results regarding the effects of mycorrhizal fungi on plant invasion, from finding significant (Busby et al. 2013) to negligible (Rodríguez-Caballero et al. 2018) effects. Furthermore, there have been different observations regarding the mycorrhizal status of invasive plants and their potential invasiveness. For instance, Menzel et al. (2017) showed that mycorrhizal invasive plants can outcompete NM invasive plants, whereas NM plant species comprise a greater proportion of invasive plants globally (Pringle et al. 2009). The relationship between mycorrhizae and plant invasion has been the subject of two review articles. Pringle et al. (2009) provided a framework based on the mycorrhizal status of invasive plants and the distribution and availability of mycorrhizae in novel habitats (biogeography and dispersal). The framework facilitates the prediction of invasiveness of an alien plant species based on whether the alien plant is NM, facultative, and flexible, i.e., able to associate with local mycorrhizal fungi in new habitats. In their review, Shah et al. (2009) highlighted the impact of the mycorrhizal status of invasive plants on the nutrient competition between native and invasive plants and the feedback between invasive plants and mycorrhizal fungi. These reviews and most of the research studies focused on the place of origin (invasive status) of plants and mycorrhizal status of invasive plants to explain the mycorrhizae-mediated plant invasion. We argue that these factors may not be sufficient to explain the potential invasiveness of a plant species and that other drivers may also be at play. Here, we aim to address this by focusing on research on how plant invasion is mediated by the plant mycorrhizal niche space (PMNS) of both native and invasive species, defined as their potential to exploit and shape the mycorrhizal fungi pool of a habitat depending on their dependence on mycorrhizal fungi, traits, place of origin (invasive status) and priority effects. Based on their PMNS, we can classify plant species into different groups according to their mycorrhizal association similarities. This classification could be useful for a) predicting the potential invasiveness of each plant in a particular habitat, b) predicting plant invasion impacts on the mycorrhizal communities in a new habitat, and c) enhancing our knowledge in order to restore invaded areas. In addition, we explained the role of plant response to mycorrhizal communities in plant invasion using PMNS. We conclude that a better understanding of the factors driving the mycorrhizal niche of plants will inform ecologists about the magnitude and direction of the role of mycorrhizal fungi in plant invasion trajectories as well as the impact of plant invasion on the structure of soil fungal communities in new habitats.

Mycorrhizal association traits

Depending on their ability to grow with or without mycorrhizal association, plants range from flexible to inflexible (Moora 2014). Flexible plants, such as facultative mycorrhizal (FM) can grow in various environmental conditions with a wide range of mycorrhizal fungi, whereas inflexible plants such as obligate mycorrhizal (OM) and non-mycorrhizal (NM) plants fail to do so (Moora 2014). Facultative mycorrhizal plants do not strictly need mycorrhizal fungi to meet their nutrient requirements and can regulate their traits with mycorrhizal fungi according to local environmental conditions (Moora 2014). The flexibility of this type of mycorrhizal relationship enables facultative mycorrhizal plants to reduce their mycorrhizal dependency (plant control over mycorrhizal colonization) when the costs of carbon allocation outweigh the benefits of the symbiosis (Friede et al. 2016) or when AMF diversity is low (for instance, after a major soil disturbance) (Traveset and Richardson 2014). As a result, the strength of the association between plant and AMF community compositions depends on the mycorrhizal traits of the plant community (Neuenkamp et al. 2018), which may have important consequences for the invasion potential of plants.

A number of studies have compared the performance of mycorrhizal and NM alien plants. Despite having no association with AMF, NM invasive plants can spread outside their native ranges by disrupting AMF associations in the roots of native plants and soils (Zubek et al. 2016; Tanner and Gange 2013; Pakpour and Klironomos 2015). Degradation of AMF mutualisms may lead to lower nutrient uptake, lower fitness, and physiological activity (Hale et al. 2016), thus reducing the competitiveness of local plants against alien plants. Using simulation models, McCary et al. (2019) examined the mechanism of mycorrhizal mutualism disruption in a native plant to understand the processes leading to the invasion success of NM plants (*Alliaria petiolata*) over native species (*Impatiens capensis*). They found that mycorrhizal fungal colonization declines with the increasing population size of the invasive plant and corroborated that the disruption of native mycorrhizal associations depends on the strength of the mutualism with the native plant such that intermediate mutualism shows higher resistance against invasion, while weak and strong mutualisms were susceptible. This study supports the idea that the mycorrhizal traits of native species could also play a role in plant invasion success. Moreover, the reduction in AMF density in the soil results in long-term negative legacy effects such as impaired ecosystem functions of AMF, facilitation of further plant invasions and greater resistance to the restoration of native plant species even after removal of invasive plants (Lankau et al. 2014) owing to the association between plant and AMF communities (Neuenkamp et al. 2018). Production of allelopathic compounds by alien plants may also function as a mechanism for mycorrhizal mutualism degradation (Pinzone et al. 2018; Hale et al. 2016). Another competitive advantage to NM alien plants is that they allocate less carbon belowground, in contrast to mycorrhizal plants that allocate a considerable amount of carbon to their associated mycorrhizal fungi belowground (Traveset and Richardson 2014). Taken together, NM plant invasions may have important consequences for the AMF community in a new habitat, particularly by disrupting AMF-native plant associations (Fig. 1).

Several survey studies suggest that the potential invasiveness of OM plants may also depend on the degree of specialization of plant species. Some OM plants are specialists and require specific AMF taxa to associate with (Torrez et al. 2016), whereas generalist plants are able to form associations with non-host-specific AMF taxa distributed in a broad geographical range and in the roots of a wide range of hosts (generalists) (Moora et al. 2011). There are a few studies assessing the performance of plant specialists and generalists outside of their native habitats. Using inoculation with a specific

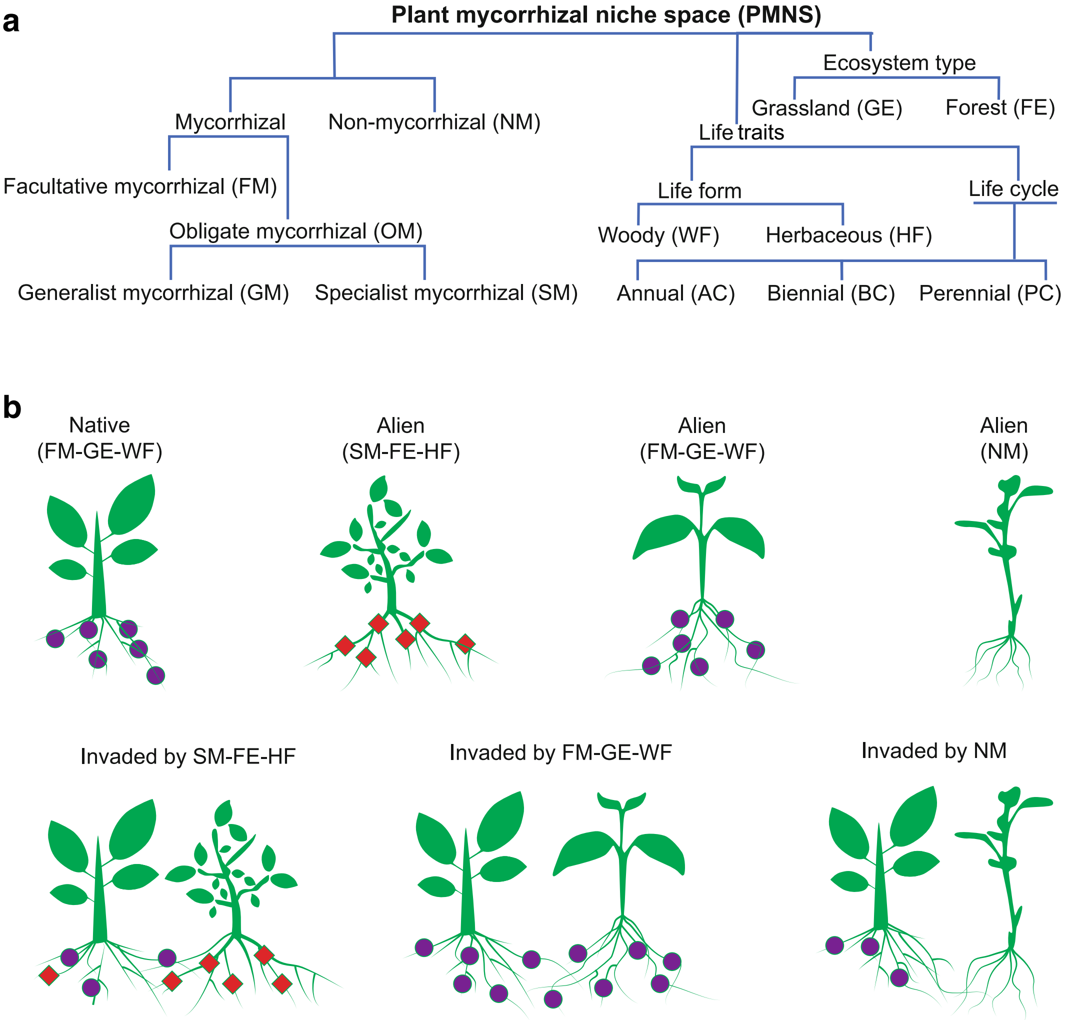

Fig. 1 A schematic view to explain the plant mycorrhizal niche space (PMNS) components. **a**) Plants can be distinguished based on mycorrhizal traits and ecological types. For example, facultative-forest plants are considered a group and can then be compared with grassland-specialist plants. Furthermore, life cycle (annual and perennial) and life form (herbaceous versus woody) could be applied for further clustering. Therefore, we suggest that plants within each group would have more similar PMNS and thus harbour similar mycorrhizal communities. **b**) The relationship between mycorrhizae-mediated plant invasion and PMNS of native and alien plant species. There is a negative relationship between PMNS similarity and the role of mycorrhizal fungi in plant invasion and mycorrhizal fungal community shifts following plant invasion (neighbour effect). Similar PMNS (e.g.a native plant invaded by alien FM-GE-WF) leads to a lower contribution of mycorrhizal fungi to a successful plant invasion and the plant invasion impacts on the mycorrhizal community in a native habitat. In addition, an alien plant can degrade the native mutualism (invaded by NM) and alter the diversity and composition of mycorrhizae (invaded by SM-FE-HF). Therefore, the PMNS of native and alien plants can be considered as a predictor of plant invasiveness, impacts of plant invasion on the structure of mycorrhizae in a new habitat, and resistance or susceptibility of the invaded areas to newly arrived plants

AMF inoculum in a field experiment, Torrez et al. (2016) observed a significant increase in species richness and diversity of plant specialist species compared to that in control plots without inoculum. A large-scale study of *Trachycarpus fortunei* in native, invasive and experimentally introduced ranges revealed that this generalist mycorrhizal species can replace its native AMF with the geographically widespread generalist AMF taxa present in introduced ranges (Moora et al. 2011). Swift et al. (2018) also demonstrated that the potential of multiple populations of *Anoectochilus sandvicensis* to associate with generalist AMF enabled this plant to spread across remote oceanic islands. Rodríguez-Caballero et al. (2018) showed that *Pennisetum setaceum* can establish and spread across five Mediterranean semiarid locations with different AMF communities because of its flexibility to associate with local AMF taxa. Taken together, associating with and benefiting from a diverse range of AMF may enable invasive plants to outcompete native plants, and hosting widely distributed generalist AMF taxa increases plant invasiveness owing to their adaptation to a wider range of environmental conditions (Pringle et al. 2009).

The spread of a specialist mycorrhizal plant species could be constrained by the lack of specific AMF taxa or by a poor performance of AMF taxa in introduced ranges (Egidi and Franks 2018). For example, plants may perform better when associated with AMF from their native range than with those from non-native ranges (Callaway et al. 2011). Co-invasion or introduction of symbionts independently can overcome this constraint. Hayward et al. (2015a) indicated that co-invasion of a single ectomycorrhizal fungus, *Suillus luteus*, is sufficient to enable *Pinus contorta* to become invasive in Coyhaique, Chile. A recent review article also highlights that pine trees always associate with suilloid fungi in both native and non-native habitats, reflecting the importance of the suilloid fungi group in the invasion success of pine (Policelli et al. 2019). While several studies have shown that ectomycorrhizal fungi are potentially co-introduced and may become co-invasive (Nuñez et al. 2009; Dickie et al. 2010; Bahram et al. 2013; Hayward et al. 2015b; Sulzbacher et al. 2018), to the best of our knowledge, the co-invasion potential of AMF has been reported only in one study (Spence et al. 2011). The rarity of AMF invasion reports can be at least partly ascribed to the widespread AMF distribution and commercial fungal inocula used in agricultural and horticultural contexts (Davison et al. 2015).

Mycorrhizal traits could mediate plant niche partitioning and expansion (Gerz et al. 2018). Native and invasive plant species (archaeophytes and neophytes) can occur in different geographic ranges due to their different degrees of mycorrhizal flexibility (Menzel et al. 2018), suggesting that the mycorrhizae-plant relationship may correlate with potential invasion in specific environmental conditions. In particular, the mycorrhizal traits of alien plants strongly determine their influence on the abundance, richness, and composition of mycorrhizal communities in new habitats (Hausmann and Hawkes 2009). For example, Zubek et al. (2016) found that the invasion of *Reynoutria japonica*, *Rudbeckia laciniata*, and *Solidago gigantea* decreased the abundance and diversity of the AMF community in new habitats to various degrees depending on their mycorrhizal traits. In a mesocosm study, Vogelsang and Bever (2009) showed that AMF mediated competition between a native mycorrhizal herbaceous forb (*Gnaphalium californicum*) and an invasive herbaceous forb (*Carduus pycnocephalus*) with low mycorrhizal dependency and that the invasive plant outcompeted the native species by disrupting its mutualisms with AMF.

There are only a few studies comparing the distribution of invasive plants based on their mycorrhizal traits. The mycorrhizal traits of only 33 invasive plants are known from a list of plants ($n = 82$) provided by the U.S. Invasive Species Impact Rank (Pringle et al. 2009). Menzel et al. (2017) showed that mycorrhizal invasive plants (FM and mycorrhizal plants) have an advantage over their NM counterparts, especially in the early stage of invasion, because their nutritional benefits gained from symbiosis seem to exceed the costs of carbon allocation. Moreover, FM species show a wider geographic distribution and ecological niche than mycorrhizal plant species (Menzel et al. 2017; Hempel et al. 2013; Gerz et al. 2018; Menzel et al. 2018). This is also in agreement with the observation of Gerz et al. (2018), who reported that FM plants consistently show wider niches compared to inflexible plants in relation to environmental variation, e.g., along soil fertility, moisture, pH and temperature gradients. There may be a strong relationship between mycorrhizal traits and habitat preference of plant species such that mycorrhizal plant species prefer to occupy soils with a lower nutrient and moisture content and a higher pH and temperature, while FM species show intermediate preferences and thus occupy wider ecological niches (Hempel et al. 2013). In addition, mycorrhizal plant species tend to be distributed at lower latitudes according to Bueno et al. (2017). Gerz et al. (2018) also observed niche differentiation among plants with different mycorrhizal traits. The authors showed that FM species have a wider distribution than plants with other mycorrhizal traits, such as mycorrhizal plants and NM species. In contrast, a review of the mycorrhizal traits of invasive plants showed that NM plant species comprise a greater proportion of invasive plants compared to mycorrhizal plants (Pringle et al. 2009). However, the limited available data on the mycorrhizal traits of invasive plants in their study may have resulted in an underestimation of the fraction of invasive mycorrhizal plants. In another study, investigation of three invasive plant species in the native AMF community revealed that the magnitude of plant invasion impact depends on their mycorrhizal dependency (Zubek et al. 2016). In addition, the impact of mycorrhizal dependency on the plant distribution may be confounded by the effects of environmental parameters, e.g., higher annual temperature enhances the proportion of mycorrhizal plants (Menzel et al. 2016).

Overall, although more controlled experiment studies are needed to support this, available data suggest that plant mycorrhizal traits influence PMNS and thus a) the establishment of alien plants, b) the strength of the neighbour effect and c) the role of AMF in plant invasion. In the case of generalist and FM plant species invasion, there may be shared AMF associations between invasive and native plants (Rodríguez-Caballero et al. 2018) (similar PMNS), implying that the AMF may have a neutral impact on plant invasion and that the AMF composition may not be severely altered (weak neighbour effect) (Fig. 1). This is supported by a study by Bunn et al. (2014), who found weak mycorrhizae-mediated invasion potential of *Centaurea stoebe* and *Potentilla recta* in the USA, reflected in negligible shifts in soil and root AMF communities across regions with different densities of invading exotic plants.

Plant traits

Growing evidence indicates that host plant traits have a significant impact on the structure of AMF communities across various habitats (Becklin et al. 2012), successional stages (Martínez-García et al. 2015) and elevational gradients (Li et al. 2014; Saitta et al. 2018). Despite shifts in soil properties, variation in AMF community composition over different ecosystem successional stages is explained by changes in plant communities (Martínez-García et al. 2015). Numerous studies have shown that plant diversity is a main factor driving mycorrhizal fungal richness and community composition across a range of habitats (e.g., Bahram et al. 2012; Martínez-García et al. 2015; García de León et al. 2016; Tedersoo et al. 2013; Krüger et al. 2017; Saitta et al. 2018). In addition, a global-scale meta-analysis showed that plant community composition is directly associated with AMF community composition, whereas the effect of climate and other ecosystem properties remained indirect and secondarily mediated by host plants (Yang et al. 2012).

However, little is known about the relationship between plant traits and associated mycorrhizal fungi, and various phenological and functional traits of alien plants may affect the structure of AMF communities (from a plant trait-based filter). The life cycle is a plant trait that could affect AMF communities. Annual and perennial plants can harbour different AMF communities in the root, rhizosphere and bulk soil (Alguacil et al. 2012). For instance, the root (not rhizosphere soil) of an annual herbaceous plant species harboured a higher diversity of AMF compared to that of a perennial herbaceous species (Torrecillas et al. 2012). Beauchamp et al. (2006) also observed that the structure of AMF communities in a riparian area depended on the richness of annual and perennial species.

Plant-life form (herbaceous versus woody) can also act as a major determinant of AMF community structure. Varela-Cervero et al. (2015) reported that similar AMF communities were harboured by herbaceous plant species (*Thymus zygis* and *Thymus mastichina*). López-García et al. (2014) found that plants with different life forms (annual herbs, perennial herbs and perennial semi-woody plants) are associated with distinct AMF communities. The AMF richness of forbs may be higher than that of grasses (Lekberg et al. 2013). Comparison between root samples of a native (*Leymus mollis*) and an invasive (*Ammophila arenaria*) dune grass revealed that both plant species share similar AMF communities (Johansen et al. 2016). In line with these findings, Lekberg et al., (2013) and Bunn et al. (2015) showed that AMF communities depended more strongly on the functional groups rather than the place of origin (or different invasive status) of plants.

Mycorrhizal colonization also depends on belowground traits such as root dry matter content, root C:N (Legay et al. 2016), root diameter, and first-order root length (Li et al. 2017). Roots with higher C:N and dry matter content, thickness, and longer first-order roots have higher mycorrhizal colonization. However, a recent study found no link between root length and AMF colonization associated with *Brachypodium distachyon* (Donn et al. 2017).

Another major component of PMNS stems from ecological adaptations (ecosystem type) or ecological requirements of plant species (Öpik et al. 2009) (Fig. 1). In this context, plants associate with AMF according to their habitat preferences (habitat range). Veresoglou and Rillig (2014) suggested that the ecosystem type of plants, rather than their phylogenetic relatedness, determines the structure of AMF communities. For instance, forest specialist and habitat generalist plants tend to associate with specialist and generalist AMF, respectively (Davison et al. 2011; Öpik et al. 2009). In a global-scale study, a comparison of AMF richness between grassland and forest ecosystems demonstrated that the diversity of the AMF community was consistently higher in grasslands (Davison et al. 2015).

Plant traits can contribute to the structure of AMF communities either directly by altering abiotic soil characteristics (Kamutando et al. 2017; Stefanowicz et al. 2017, 2018) and releasing allelochemicals (Cipollini et al. 2012; Ruckli et al. 2016) or indirectly through suppression of native plant growth (exposing the native plant to C limitation) and changing the light intensity (Bunn et al. 2015; Jandová et al. 2014). Kamutando et al. (2017) showed that the invasive tree *Acacia dealbata* can modify the rhizospheric soil chemistry (pH, C, NO3, NH4, P, Mg) and consequently the structure of microbial communities. Gaggini et al. (2018) reported that *Impatiens glandulifera* significantly impacted the richness and composition of soil fungal communities by increasing soil moisture and pH. In addition, Stefanowicz et al. (2018) showed that the growth of four invasive and two native plants resulted in a considerable divergence in the physical and chemical properties of the soil. Even at the landscape scale, Martínez-García et al. (2011) found that shrub species provide different nutrient contents in the rhizosphere soil, explaining most of the landscape-scale variation in the AMF composition and diversity. Benzoxazinoids secreted by maize roots mediate the alteration of microbiota structure and composition in the rhizosphere (Hu et al. 2018). Zhalnina et al. (2018) demonstrated that plant root exudation traits in combination with microbial substrate preferences shape the rhizosphere-associated microbial communities. In contrast, a meta-analysis of 67 studies by Bunn et al. (2015) revealed no difference in the AMF colonization rate when native and invasive plants were grown separately, although the AMF colonization of native plants declined in the presence of the invasive plant. The authors suggested that this could result from shading and carbon limitations of the native plant. In another study, Jandová et al. (2014) showed that *Heracleum mantegazzianum* was responsible for changing the composition of soil microbial communities in the invaded communities by altering the environment and light conditions of the soil as a result of high biomass production.

In addition to plant traits, phylogenetic relatedness of alien and native plants may affect their AMF community relatedness, similar to what is observed in ectomycorrhizal fungal communities (Tedersoo et al. 2013). In contrast to ectomycorrhizal plants, however, phylogenetically similar arbuscular mycorrhizal plants tend to associate with compositionally more dissimilar AMF communities (Reinhart and Anacker 2014; Veresoglou and Rillig 2014). Nevertheless, it is important to consider the influence of ecosystem type to draw conclusions about the effect of plant phylogenetic relatedness on AMF, because closely related plants can originate from different ecosystem types (Veresoglou and Rillig 2014). The different ecosystem origins of plants could promote their coexistence in a community (Reinhart and Anacker 2014). Montesinos-Navarro et al. (2012) considered a broader plant phylogenetic diversity and suggested that there is no relationship between the phylogenetic relatedness of plants and the similarity of their associated AMF communities.

Regardless of whether similar plants associate with similar AMF communities, there is strong evidence that association with dissimilar AMF communities can promote coexistence among plants (Reinhart and Anacker 2014; Montesinos-Navarro et al. 2012). This is because distinct AMF taxa occupy different niches and provide plants with complementary resources, which could reflect the establishment potential of alien plants in a new habitat (Pringle et al. 2009). Enhanced resource partitioning (Montesinos-Navarro et al. 2018) and increased resource availability (Jiang et al. 2017) mediated by plant-AMF interactions could promote plant coexistences.

Taken together, although the available data are not sufficient to draw a definite conclusion, exploring the effects of plant traits and phylogeny on their associated mycorrhizal fungi as an important component of PMNS is an important step towards a more predictive understanding of invasiveness and invasibility.

Neighbour effect and priority effect

A growing body of literature shows that alien plants influence the structure of AMF communities in new habitats (known as neighbour effect) (Hausmann and Hawkes 2009, 2010; Werner and Kiers 2015; Helsen et al. 2016; Weidlich et al. 2017). Depending on the traits and mycorrhizal dependency of alien and native plants and their interactions, neighbour effects can be categorized into three types: controlling, synergistic, and neutral effects. A controlling effect occurs when alien plants skew the AMF composition of the new habitat towards the AMF composition of one of the host plants. A synergistic effect results in a novel AMF community not previously present in either host, whereas a neutral effect is observed when invasive plants have no effect on the AMF community in a new habitat or when native and alien plants have similar PMNS (Hausmann et al. 2009). Neighbour effects can facilitate or prevent the establishment of newly arriving alien plants (priority effect) (Weidlich et al. 2017) depending on the PMNS of the alien plants and the AMF community in the native habitat reshaped by neighbour effects.

Alien plants with synergistic and controlling impacts on the native habitat can act as a biotic filter on the ecological pool of AMF and consequently affect subsequent invasion by other alien plants (Hausmann and Hawkes 2010). The functional group of newcomer plants has a strong effect on the plant community composition. For instance, legumes can facilitate the growth of grasses and non-leguminous forbs when legumes are sown earlier (Weidlich et al. 2017). Sikes et al. (2016) showed that the emergence and biomass of plant species depend on the early introduction of native or alien fungi species. The biomass declined when native fungi were introduced early; however, early introduction of alien fungi species promoted an increase in their biomass. On the other hand, the abundance and colonization of AMF taxa co-invaded with the alien plant species is influenced by the priority effect imposed by earlier arriving AMF taxa. The abundance of *Rhizophagus irregularis* was higher than that of *Glomus aggregatum* when they were inoculated simultaneously, but the priority effect of *G. aggregatum* neutralized this effect and suppressed the subsequent AMF invader (Werner et al. 2015).

Collectively, available data suggest that plant invasion not only has a direct impact on the AMF and plant community of invaded habitats but also creates a long-lasting effect by facilitating further invasions by other plants. The strength of this effect depends on the degree of host specificity and mycorrhizal traits and thus the PMNS of the invasive and native plants. In extreme cases, such as when alien and native plants have similar PMNS or when the alien plant is a generalist or facultative mycorrhizal plant (i.e., able to associate with the native plant AMF community), the invasion may result in the smallest priority effects, i.e., a neutral effect on the establishment of next alien plant. Therefore, the priority effect is an important factor to consider in predicting the invasibility of a habitat and to enhance habitat resistance via early sowing or removing specific species (Lang et al. 2017).

Invasive status (plant provenance)

The impacts of plant invasive status on PMNS could be significant when exotic and native plants with similar plant traits and mycorrhizal dependency associate with dissimilar mycorrhizal fungi communities. This allows us to disentangle the effect of invasive status from other factors driving PMNS. Mummey and Rillig (2006) demonstrated that *Centaurea maculosa* invasion caused a significant reduction in AMF diversity outside *C. maculosa*’s native ranges. In contrast, a study on AMF and ectomycorrhizal communities associated with the bulk soil and roots of an invasive plant (*Schinus terebinthifolius*) and two native plants (*Hamelia patens* and *Bidens alba*) demonstrated a greater diversity of AMF and ectomycorrhizal fungi in the bulk soil and rhizosphere of invasive plants compared to in that of native plants (Dawkins and Esiobu 2017). In these studies, however, the effect of invasive status may have been confounded by other parameters, such as functional traits and mycorrhizal traits.

Only a few studies have addressed the contribution of invasive status in mycorrhizae-mediated plant invasion in relation to other factors. Lekberg et al. (2013) studied the vegetation types of invasive and native plants (forb and grass) on AMF associations and found that the colonization rate and diversity remained similar among similar functional groups of plants regardless of their invasive status.

Bunn et al. (2015) also performed a meta-analysis to determine the factors driving changes in AMF communities following invasion. The authors found that AMF colonization and abundance did not differ between native and invasive plants, whereas there were significant differences among functional groups, e.g., forbs were generally more colonized by AMF compared to grasses. In an experimental study, Gomes et al. (2018) evaluated not only the invasive status impact but also the proportion of plant identity and functional traits in shaping mycorrhizal diversity, finding that in addition to the invasive status, plant functional groups can explain mycorrhizal shifts following plant invasion. An evaluation of four invasive and two expansive native plant species on the abundance, richness, and composition of soil AMF communities as well as the growth of a native plant showed a stronger effect of plant identity than its invasive status due to their differences in mycorrhizal traits (Majewska et al. 2018).

In addition, the relationship between invasive status and the responsiveness of plants to AMF was evaluated by Reinhart et al. (2017), whose findings corroborated that invasive status has no effect on plant responsiveness to AMF. These findings suggest that the influence of plant species on AMF communities is more predictable based on plant functional traits rather than on plant invasive status. Thus, plant invasive status may not determine PMNS or the AMF shifts in mycorrhizal associations.

Plant response to mycorrhizal fungi

The response of plant species to mycorrhizal fungi ranged from positive to negative, depending on the combination of plant and fungal species (Klironomos 2003). Plant response to mycorrhizal communities is also considered a factor influencing mycorrhizae-mediated plant invasion. A recent study showed that invasive trees responded positively to soil AMF communities from different elevations, while native trees benefited only from soil AMF collected from their altitudinal distribution range (Urcelay et al. 2019). Plant responses to mycorrhizal communities of novel habitat can be explained by PMNS. Native and invasive plant species with dissimilar PMNS are expected to respond differently to AMF communities, independent of invasive status (Bunn et al. 2015). Rather than invasive status, the plant functional group was observed as a predictor of plant response to AMF association, e.g., forbs responded positively, while grasses showed neutral or negative responses (Bunn et al. 2015). Waller et al. (2016) showed that an invasive plant (*Centaurea solstitialis*) in both native and non-native ranges is less responsive to mycorrhizal fungal association than the native plant (*Stipa pulchra*) due to differences in mycorrhizal traits. There is a relationship between mycorrhizal association traits and plant responsiveness to AMF in which the response of mycorrhizal specialist plants is stronger than that of FM plants (Veresoglou et al. 2018).

On the other hand, it is not clear how alien plants with similar PMNS to native plants would respond to AMF communities in new habitats. High similarities between the PMNS of native and alien plants could enable alien plants to associate with their specific mycorrhizal fungi in new habitats, suggesting that the success of each competitor depends on their response to mycorrhizal fungi. For instance, a long-term field study comparing perennial native and exotic species with similar phylogenetic and functional groups showed that invasive plant species across functional groups could benefit more from the same mycorrhizal community in the new habitat through a higher colonization rate (Sielaff et al. n.d.). Thus, plant response to mycorrhizal communities in a new habitat could be a determinant factor for invasion success of an alien plant.

Current knowledge gaps and future research

Most of the mycorrhizae-mediated plant invasion studies to date rely on the mycorrhizal status and invasive status of invasive plants to assess (1) how they alter mycorrhizal fungi communities of new habitats to outcompete the native plants and (2) how the mycorrhizal status of invasive plants could translate into their potential invasiveness. The impacts of plant invasive status on the potential invasiveness can be determined by comparing alien and native plants with similar plant functional and mycorrhizal traits while considering the neighbour effect. By doing so, we can disentangle the effect of invasive status from other factors driving mycorrhizae-mediated plant invasion. There have been different observations regarding the impact of alien plants on the AMF communities in new habitats, from reduced (Mummey and Rillig 2006) to enhanced diversity (Dawkins and Esiobu 2017) of AMF in the soil and roots of native plants. In these studies, the effect of invasive status may have been confounded with other parameters, such as functional and mycorrhizal traits. This approach has led to the classification of invasive plants into a few groups, such as flexible and non-flexible or mycorrhizal and NM invasive plants. However, our review indicates that this approach may have limitations for a) uncovereing the mechanisms behind AMF community changes in new habitats following invasion and b) predicting the potential invasiveness of a plant species and the invasibility of a habitat, the role of AMF in plant invasion and the impact of invasion of a particular species on the AMF communities. Our review indicates that the magnitude and direction of native host plant impact on the invasion potential of alien plants remains largely understudied. In addition, most of the studies have focused on a few plant traits without evaluating the neighbour effect and the role of native plant communities, which may confound host plant effects. As a next major step towards mechanistic understanding of mycorrhizae-mediated plant invasion, further studies are needed to elucidate the factors driving mycorrhizal associations of plant species, especially plant quantitative and quantitative traits, to predict the PMNS of plant species. In particular, studies on the response of plants with similar PMNS to mycorrhizal communities may unravel mechanisms underlying the different invasiveness of plants and invasibility of habitats.

Summary

Given the significant impact of mycorrhizal fungi on the diversity, competitive ability, composition and distribution of plants and on ecosystem productivity, their effect on invasion is inevitable, yet under-recognized. Here, we attempted to highlight the importance of AMF in plant invasion by linking PMNS and plant invasiveness by characterizing some biotic factors that influence PMNS, including plant mycorrhizal and functional traits, priority effect and invasive status. We defined PMNS as a plant's ability to exploit and shape the mycorrhizal fungal pool outside its native range depending on its dependency on mycorrhizal fungi, traits, place of origin (invasive status) and priority effects. The relative contribution of mycorrhizal traits, qualitative and quantitative traits of both invasive and native plants, and neighbour effects provide an opportunity to develop models to classify plant species into different PMNS. The model could help to predict the potential invasiveness of each plant in a particular habitat by comparing PMNS distance between native and invasive plants. These classifications enhance our understanding of the role of mycorrhizae in plant invasion trajectories and the impacts of invasion on the mycorrhizal communities of native habitats. Comparing the PMNS of alien and native species enables us to understand mycorrhizae-mediated plant invasion. The invasive and native PMNS reflect the role of mycorrhizal fungi in plant invasion and alien plant impact on the mycorrhizal fungi composition of the native community (strength of neighbour effect) such that there is a negative relation between the similarity of PMNS and the role of mycorrhizal fungi in plant invasion and alteration of mycorrhizal fungi following invasion. Differences between native and alien plants in terms of PMNS also determine the invasion strategy of alien plants. Alien plants with dissimilar PMNS can disrupt native mycorrhizal associations and hence alter the diversity, abundance and composition of mycorrhizae. On the other hand, plant response to mycorrhizal communities can be a determinant factor when both native and invasive plants tend to associate with similar mycorrhizal communities. Plants that can benefit more from associated mycorrhizal communities could win the competition. Multiple lines of evidence suggest that plant invasion may be independent of invasive status. Thus, a better understanding of mycorrhizae associated with alien and native plants could be obtained by unravelling relationships between the features of plants associated with the AMF community, which could provide an enhanced perspective to move towards a more predictive understanding of invasiveness and invasibility for restoration planning.

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