Received: 15 April 2024 | Accepted: 19 November 2024

DOI: 10.1111/1365-2435.14729

Functional Ecology

RESEARCH ARTICLE

Mycorrhizal Networks

Plant mycorrhizal status indicates partner selectivity in arbuscular mycorrhizal interaction networks

Kadri Koorem[1] | Siim-Kaarel Sepp[1] | C. Guillermo Bueno[1,2] | John Davison[1] | Siqiao Liu[1] | Yiming Meng[1] | Marina Semchenko[1] | Martti Vasar[1] | Martin Zobel[1] | Mari Moora[1]

[1]Institute of Ecology and Earth Sciences, University of Tartu, Tartu, Estonia

[2]Pyrenean Institute of Ecology (IPE) CSIC, Jaca, Huesca, Spain

Correspondence
Kadri Koorem
Email: kadri.koorem@ut.ee

Funding information
H2020 European Research Council, Grant/Award Number: 101044424; Eesti Teadusagentuur, Grant/Award Number: PRG1065 and PRG1836; Estonian Ministry of Science and Education, Grant/Award Number: CentreofExcellenceAgroCropFuture

Handling Editor: Katie Field

Abstract

1. Mycorrhizal symbiosis, specifically arbuscular mycorrhiza, is one of Earth's oldest and most widespread symbiosis. Existing evidence suggests that plant species differ in their associations with mycorrhizal partners, with different species reported to be always (obligately mycorrhizal, OM), sometimes (facultatively mycorrhizal, FM) or never (non-mycorrhizal, NM) associating with arbuscular mycorrhizal (AM) fungi and this plant reliance on AM fungi is called plant mycorrhizal status. However, very little is known about how host plant mycorrhizal status shapes the network topology of interacting AM fungi.
2. Here, we use a standardized sampling scheme to test whether plant species with different mycorrhizal statuses differ in mean AM fungal hyphal colonization and various indices of the AM fungal networks such as nestedness rank and resource range.
3. We collected the roots and rhizosphere soil of 19 plant species representing five families. Each plant species was sampled from three distinct habitats. We determined AM fungal colonization in the roots and AM fungal community composition in roots and rhizosphere soil using molecular methods.
4. We found that previously reported NM plant species had lower mean AM fungal colonization than FM plant species, but no differences were found between FM and OM plant species. Network analyses indicated that AM fungal communities in the roots of FM plant species had higher nestedness rank and resource range than networks associated with OM plant species, suggesting that OM plant species are more generalist regarding partner selection and interact with a wider range of fungal partners.
5. Our results suggest that plant mycorrhizal status conveys useful information about the characteristics of AM fungal interaction networks, revealing that plant species consistently associated with AM fungi are less selective towards their fungal partners.

KEYWORDS
contrasting habitats, facultatively mycorrhizal plant species, intraspecific trait variation, mycorrhizal traits, non-mycorrhizal plant species, obligately mycorrhizal plant species, plant population

1 | INTRODUCTION

Some symbiotic relationships formed by extant plant species are as old as land plants, having existed for more than 400 million years (Remy et al., 1994; Strullu-Derrien et al., 2018). Among the most ancient symbionts of plants are fungi that form arbuscular mycorrhiza, which are believed to colonize the roots of more than 70% of extant terrestrial plant species (Brundrett & Tedersoo, 2018; Meng et al., 2023; Smith & Read, 2010). In this symbiosis, the fungal partner receives carbon compounds from the host plant in exchange for enhanced nutrient access and improved tolerance to abiotic and biotic stress (Smith & Read, 2010). Changing environmental conditions during evolutionary time have spurred the development of other types of mycorrhiza alongside the emergence of plant species that do not form mycorrhizal symbioses at all (Brundrett & Tedersoo, 2018; Strullu-Derrien et al., 2018). Approximately 8%–14% of vascular plant species are non-mycorrhizal, while 7%–18% are facultatively mycorrhizal, being sometimes but not always associating with AM fungi (Brundrett & Tedersoo, 2018; Meng et al., 2023).

The characteristic of plant species to always (obligately; OM), never (non-mycorrhizal; NM) or sometimes (facultatively; FM) associate with AM fungi is referred to as plant mycorrhizal status (Moora, 2014; Smith & Read, 2010). Thus, plant mycorrhizal status indicates how frequently a plant species is mycorrhizal. Plant mycorrhizal status is assumed to be mainly driven by the characteristics of the plant partner (Chaudhary et al., 2022) and has been linked to other plant characteristics, such as dispersal structures (Correia et al., 2018). The proportion of OM, FM and NM plant species in a community has been used to gain insights into the drivers shaping plant and microbial communities at large scales (Gerz et al., 2016; Leon et al., 2022, 2024; Vahter et al., 2020). At larger scales, the proportion of FM plant species has been found to increase with latitude, while that of OM plant species decreases (Bueno et al., 2017; Meng et al., 2023). The share of FM plant species has been shown to depend positively on environmental factors such as variation in temperature (Bueno et al., 2017) as well as negatively on pH and positively on precipitation (Hempel et al., 2013). A recent study demonstrated that a higher proportion of OM and a lower proportion of FM plants are found in soils with low nutrient (C, N, P) content (Meng et al., 2023). This suggests that plant species are more extensively associated with mycorrhizal fungi in conditions of low nutrient availability. However, it is unknown whether the same tendency applies at the intraspecific level, especially among populations within FM plant species.

Facultatively mycorrhizal plant species can grow in a wide range of habitats, reflecting their broader niches compared with OM and NM plant species (Gerz et al., 2018; Hempel et al., 2013). FM plant species are also successful in establishing outside their native ranges (Moyano et al., 2020; Pyšek et al., 2019), making them the most widespread plant species globally (Zobel et al., 2024). The success of FM plant species may at least partly stem from their ability to adjust the extent of their association with mycorrhizal fungi to suit their abiotic and biotic environment. Indeed, FM species are often found to be more responsive to environmental cues compared to NM or OM species, which appear to be more constrained by phylogenetic factors (Meng et al., 2023). Moreover, within FM plants, there is a higher variability in the intensity of mycorrhizal colonization compared to OM plants (Soudzilovskaia et al., 2020). This variability suggests that FM plants may exert stronger control over their mycorrhizal associations depending on prevailing environmental conditions. However, these observed patterns may, at least partially, arise from differences in geographical and ecological conditions where AM fungal colonization in the roots of FM and OM plants has been assessed.

Facultatively mycorrhizal plant species have shown to associate with different AM fungal communities compared with OM plants, with OM plant species having higher beta diversity (Davison et al., 2020) and more generalist partner selection (Sepp et al., 2019). This suggests that facultatively mycorrhizal plant species have greater filtering ability, allowing them to preferentially select the most suitable AM fungal partners (Lekberg & Koide, 2014; Sepp et al., 2019). However, there are multiple aspects of partner specificity within the interaction, generalizable as different measures of network topology. Relevant network indices range from simple characteristics, such as the number of partners a plant species interacts with (e.g. normalized degree), to more specific measures describing, for instance, plant species discrimination towards interacting partners (resource range, Poisot et al., 2012) or relevance for the partners in the network (species strength, Bascompte et al., 2006), and species position in the generalist-specialist continuum of the wider bipartite interaction network (nestedness rank, Alarcón et al., 2008). So far, we have very little information about possible differences in interaction network topology in relation to plant mycorrhizal statuses.

This research aimed to test whether plant mycorrhizal status provides information about AM fungal colonization and the topography of the AM fungal interaction network. As plant mycorrhizal status is expected to be related to environmental conditions (Han et al., 2020; Meng et al., 2023; Qin et al., 2020), we also tested if mean AM fungal colonization of a plant species in a population can be used as an alternative measure for evaluating the topology of AM fungal interaction network. We used 19 common plant species in Estonia as test species and used a standardized sampling of

individual plants from a wide range of habitats. We hypothesized that (1) AM fungal colonization is inversely related to soil nutrient content, and the pattern is strongest for FM plant species; (2) FM plant species have lower AM fungal richness and beta-diversity in their roots compared with those associated with OM plant species, and both richness and beta-diversity of AM fungal communities in plant roots are positively related to average AM fungal colonization; (3) AM fungal communities in the roots of FM plant species represent limited subsets of the AM fungal communities present in soil, reflecting the ability of plants with this mycorrhizal status to favour specific AM fungal taxa (measured as resource range) and indicating that FM plants are less important than OM species for sustaining AM fungal networks in the soil (measured as species strength).

2 | MATERIALS AND METHODS

Sampling was conducted in a wide range of habitats within Estonia in the middle of the 2020 growing season. We sampled roots and rhizosphere soil of each target plant species from three sites. Expert opinion was used to select sites representing significantly different growing conditions for each target plant species. We sampled 19 plant species from 5 different families, each represented by all of FM, OM and NM plant species where possible (Table S1). Mycorrhizal statuses were assigned to species based on the most up-to-date literature available (Bueno et al., 2017; Gerz et al., 2018; Harley & Harley, 1987; Hempel et al., 2013; Soudzilovskaia et al., 2020; Wang & Qiu, 2006), following the colonization approach (Bueno et al., 2021). The number of references available for plant species mycorrhizal status showed a non-significant trend for NM plant species to have fewer references than OM and FM plant species (Figure S1). All plant species except *Lupinus polyphyllus* Lindl. are native to Estonia. Three individuals per species were sampled from each selected site and were used for AM fungal colonization and community composition analyses (below). Soil from the rhizosphere of the target plant species was sampled and divided into two parts. One part was used to characterize the composition of the AM fungal community present in the soil. The second part of the rhizosphere soil was pooled within site and used for soil nutrient analyses. This design (19 plant species, 3 habitats, 3 individuals) generated 171 root samples and 171 soil samples during the sampling phase of the study.

2.1 | AM fungal colonization

The fine roots of sampled plant individuals were divided into two subsamples; one subsample was used for molecular analyses (below), and the other was stained with trypan blue (Koske & Gemma, 1989). Stained roots (approximately 20 cm in total) were mounted on slides, and AM fungal colonization of the roots was estimated using the magnified grid-line intersection method (McGonigle et al., 1990), counting AM fungal structures (hyphae, vesicles, arbuscules, coils) in 100 intersections of root and vertical crosshair per plant. Counting was performed using a ZEISS Axioscope 5 Digital Microscope at 400× magnification.

2.2 | Molecular identification of AM fungi

DNA was extracted from plant roots using the PowerSoil Pro Kit and from the soil using PowerMax Soil Kit (MO BIO Laboratories, Inc. California, USA) according to the manufacturer's instructions. AM fungal community composition was estimated by targeting the SSU rRNA gene using the WANDA (Dumbrell et al., 2011) and AML2 (Lee et al., 2008) primer pair. DNA concentration per plate was unified, and plates were subsequently subjected to a 2×300 bp paired-read sequencing approach on an Illumina MiSeq sequencing platform at Asper Biogene (Tartu, Estonia).

2.3 | Bioinformatics

Paired-end Illumina reads were cleaned using the gDAT pipeline (Vasar et al., 2021). All sequence reads were demultiplexed into samples using an 8-bp barcode allowing one mismatch for both forward and reverse reads. Demultiplexed reads were checked for correct forward (WANDA) and reverse primers (AML2), allowing one mismatch for both pairs. Both reads were retained if the average quality was ≥30. Filtered paired-end reads were combined using FLASH (v1.2.11, Magoč & Salzberg, 2011) with the default parameters (overlap ≥10 bp, identity ≥75%). Chimeric sequences were removed using VSEARCH (v2.15.0, Rognes et al., 2016) with the default parameters and comparison against a reference database (MaarjAM database, Öpik et al., 2010, status 2021). The MaarjAM database, supplemented with some unassigned phylogroups, was used to assign obtained reads to virtual taxa (VT; cf. Öpik et al., 2010) using a BLAST+ search (v2.10.1, Camacho et al., 2009). Following a BLAST+ search for each read, the best hit was identified using 97% identity and 95% alignment thresholds. Reads that did not find a match among the MaarjAM database (nohits) were subjected to a further BLAST+ search against the INSDC non-redundant nucleotide database (status 2021, Karsch-Mizrachi et al., 2018) to detect any potential novel VT not present in the MaarjAM database (with ≥90% similarity and alignment length not differing from the shorter of the query and subject by 10% of the length). VT represented by one read (singletons) were removed from further analysis. Only samples where both the soil and root samples yielded sequences (127 pairs of root and soil samples) were included in further statistical analyses.

Illumina MiSeq sequencing resulted in 3,415,788 reads after filtering, of which 1,199,386 were identified as AM fungi. On average, roots yielded 3520 and soils 5923 sequences per sample with 17 and 30 VT per sample, respectively. Arbuscular mycorrhizal hyphal colonization was significantly correlated with the number of AM fungal sequences in plant roots (Spearman $\rho = 0.33$, $p < 0.001$).

Raw reads from this targeted locus study have been deposited in the National Center for Biotechnology Information Sequence Read Archive (BioProject PRJNA1183728).

2.4 | Statistical analysis

The richness and diversity of AM fungal communities were estimated using extrapolated taxon richness and Shannon diversity (Hill numbers $q=0$ and $q=1$, respectively, Hill, 1973). These measures were calculated with the asymptotic diversity estimation functions from the "iNEXT" package (Hsieh et al., 2016) based on the read number of AM fungal VT. Parallel analyses were performed with raw taxon richness and Shannon diversity values, which yielded a similar pattern. Analysis of AM fungal community composition was based on Hellinger-transformed matrices of AM fungal abundance in samples.

For phylogenetically-informed pairwise community distance analyses, we constructed a phylogenetic tree of representative sequences of all AM fungal taxa (VT) using BEAST 2.5 (Bouckaert et al., 2019). A read in our dataset with the highest BLAST+ score was selected as the representative for each AM fungal VT, indicating their closest proximity to the VT type sequence in the MaarjAM database. In the MaarjAM database, a type sequence is assigned to each VT, around which the VT would evolve if the taxon splits or merges with others following the inclusion of additional sequences (Öpik et al., 2010). Phylogenetic analysis was conducted using substitution model averaging facilitated by the BEAST package bModelTest (Bouckaert & Drummond, 2017). Three separate MCMC chains of 30,000,000 iterations were constructed and combined after the removal of 10% burn-in; this resulted in a posterior estimate effective sample size (ESS) >200. The results were summarized on a maximum clade credibility tree.

To test the strength of co-variation between root AM fungal communities and surrounding soil AM fungal communities, we first ordinated the soil and root Hellinger-transformed matrices, as well as soil pH_{KCl}, N, P, K, Ca and Mg variables using NMDS [metaMDS() in R package vegan (Oksanen et al., 2022)], using both the Horn-Morisita distance and the UniFraq phylogenetic distance (Lozupone & Knight, 2005) for AM fungal and Euclidean distance for soil parameters. We then fit multivariate linear regressions of both root and soil AM fungal community NMDS axes against soil chemistry to partial out variation in soil parameters. Following that, we performed a Procrustes rotation [function procrustes() in R package vegan] of the residual NMDS axes and extracted residuals from the rotation. These residuals were used as the dependent variables in linear models with the mycorrhizal status of the plant species included as an explanatory variable.

We used the R package bipartite to calculate species-level indices in the plant—AM fungal taxon interaction network (Dormann, 2011). We focused on the normalized degree, resource range, specialization (d'), species strength and nestedness rank of the species. The normalized degree is the number of VT with which the plant species interacts, divided by the number of all possible partners. The larger the degree, the more VT out of all possible partners the plant species interacts with. The resource range ranges from 0, when a plant species interacts with all available AM fungal VT, to 1 when it interacts with only 1, being a proxy of specialization (Poisot et al., 2012). Species strength quantifies the importance of the plant species as a partner of AM fungal taxa (Bascompte et al., 2006). d' is the specialization of the plant species based on its partner preference from a random selection of partners (Blüthgen et al., 2006). The nestedness rank (Alarcón et al., 2008) is the rank of a species in a matrix sorted for maximum nestedness; a lower-ranked plant individual interacts with more AM fungal taxa, including both generalist and specialist AM fungi, meaning that the plant individual is generalist regarding partner selection.

To account for the spatial configuration of study sites, we calculated the Principal Coordinates of Neighbourhood Matrix (PCNM) [pcnm() in R package vegan] and incorporated the first three PCNM vectors into relevant analyses. To account for variation in soil chemistry, that is N, P, K, Ca, Mg contents and pH_{KCl}, we conducted a principal components analysis on the soil parameters scaled to unit variance [prcomp() in R package stats]. We incorporated the first two principal components, describing 38.3% and 31.3% of the total variance in soil parameters, respectively, into relevant analyses.

We tested the effects of two main explanatory variables of interest: plant species mycorrhizal status and mean AM fungal hyphal colonization. Depending on the scale of the dependent variable, the mean AM fungal hyphal colonization was calculated either at the level of the plant species or at the level of a single population of the plant species (i.e. individuals of a species in one site). The dependent variables were grouped at three scales—plant individual, plant population and plant species.

The plant individual level dependent variables were AM fungal root hyphal colonization, AM fungal VT richness and Shannon diversity in the plant roots, and the discrepancy (Procrustes residuals) between soil and root AM fungal communities. At the plant individual level, we fit linear mixed-effects models [lmer in R package lme4 (Bates et al., 2015)], using the R package lmerTest (Kuznetsova et al., 2017) to test model significance with the main explanatory variable of interest, the soil PCA axes and spatial PCNM vectors of the site (population) as fixed-effects terms, and plant population nested in plant species as the random-effect term. Marginal coefficients of determination (analogue of R^2) for individual explanatory variables were calculated using the function partR2 (..., R2_type = "marginal", nboot = 100) in R package partR2 (Stoffel et al., 2021).

The plant species level dependent variables were the species-level network topological indices (normalized degree, resource range, d', species strength, nestedness rank). At the plant species level, we fit linear mixed models with the main explanatory variable of interest as the fixed-effects term [using Anova() in R package car (Fox & Weisberg, 2019) to test for model significance].

Where significant effects of model terms were identified ($p<0.05$), Tukey's HSD post hoc test was used to evaluate differences

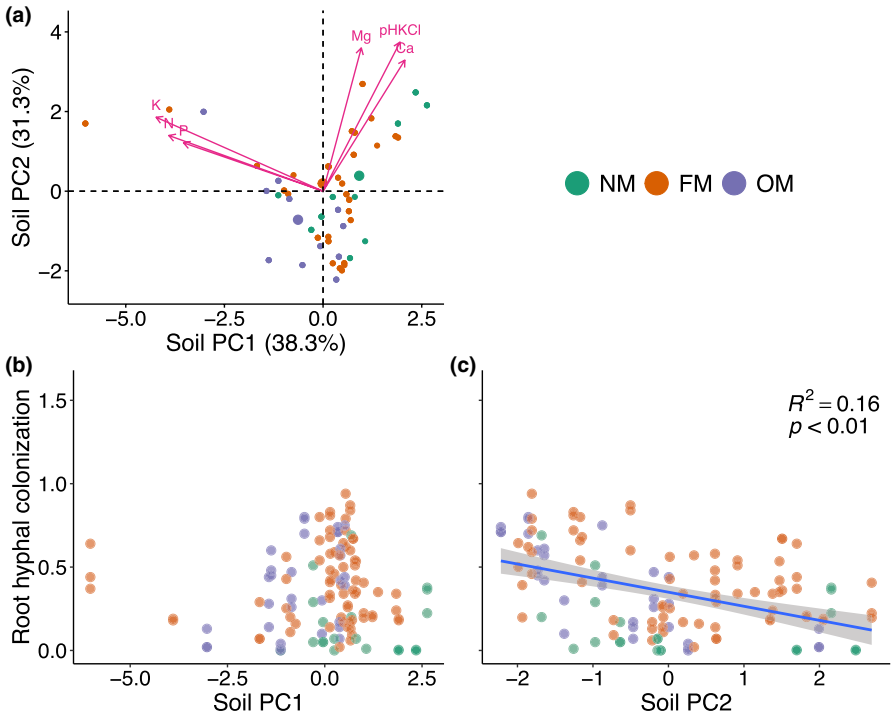

FIGURE 1 Variation in the soil chemistry (N, P, K, Mg, Ca, and pH_{KCl}) of study sites according to Principal Components Analysis (a). The dependence of AM fungal root colonization on variation in soil chemistry (Soil PC1 and PC2) is shown in panels (b) and (c). Colours indicate different plant mycorrhizal statuses: NM (green)—non-mycorrhizal; FM (orange)—facultatively mycorrhizal; OM (blue)—obligately mycorrhizal. Each point on the graph represents a plant individual (a–c).

among all explanatory variable levels using the emmeans R package (Lenth, 2024). All analyses were conducted with R version 4.3.3 (R Core Team, 2024).

3 | RESULTS

Soil pH_{KCl} at the sampled sites ranged from 2.96 to 8.18, soil P content from 11 to 276 mg/kg, and soil N from 0.11 to 24 mg/kg. PCA indicated that most variation in soil parameters (PC1, explaining 38.3% of variation) was explained simultaneously by P, N, and K content, while a second fraction of the variation (PC2, explaining 31.3% of variation) was explained by Mg, pH_{KCl} and Ca (Figure 1a). Arbuscular mycorrhizal fungal colonization in plant roots was significantly negatively influenced by PC2 ($p = 0.003$) but not by PC1 of soil parameters (Figure 1b,c).

Arbuscular mycorrhizal hyphal colonization was significantly lower in NM plants than in FM plants but did not differ between FM and OM plants (Table 1; Figure 2A). Three of the sampled putatively NM plant species had individuals with no AM fungal colonization detected in their roots (*Dianthus deltoides*—2 individuals, *Galium boreale*—1 individual, *Galium uliginosum*—2 individuals), while the roots of all individuals of two other sampled putatively NM plant species (*Astragalus glycophyllos*, *Carex tomentosa*) were colonized. The effects of mycorrhizal status and mean hyphal colonization on variation in AM fungal colonization were also significant at the species level ($p < 0.05$, Figures S2 and S3, respectively).

There were no differences in the richness or Shannon diversity of AM fungal communities associated with plant species with different mycorrhizal statuses. The richness of AM fungi in roots was, however, positively correlated with the population-level mean hyphal colonization % of the plant roots (Table 1; Figure 2C). There were no significant differences between plants of different mycorrhizal status in the intraspecific beta diversity of AM fungal communities, considering both Morisita-Horn distance of species, and UniFraq distance, which accounts for phylogenetic distances between fungal species in samples. According to the Procrustes analysis, host plants of different mycorrhizal status did not significantly differ in the strength of correlation between AM fungal communities in roots and bulk soil.

Regarding plant species level network indices, plants with different mycorrhizal statuses significantly differed in nestedness rank, normalized degree, resource range, and species strength, but not in d' (Table 1). Facultatively mycorrhizal plant species had significantly higher nestedness rank (Figure 3A) and significantly lower species strength (Figure 3D) than OM plant species. Facultatively mycorrhizal and putatively NM plant species had significantly lower normalized degree (Figure 3B) and higher resource range (Figure 3C) than OM plant species.

4 | DISCUSSION

Association with mycorrhizal fungi is one of the most ubiquitous plant symbioses, providing multiple benefits for host plants (Smith & Read, 2008); however, this association can also impose costs on a host plant, when plants allocate carbon to fungi that they might otherwise allocate to their own growth. Thus, the ability of host plants to regulate the occurrence and extent of the symbiosis may be a crucial asset underlying plant species success (Zobel et al., 2024). Here, we used standardized sampling of 19 plant species across a diverse range of habitats to examine whether plant mycorrhizal status

TABLE 1 Effects of plant mycorrhizal status and mean AM fungal colonization in a plant population (columns) on AM fungal community parameters (rows).

	Mycorrhizal status model *p*-value	NM	FM	OM	Population mean colonization % model *p*-value
AM fungal hyphal colonization	**0.003**	0.14a ± 0.04	0.41b ± 0.03	0.38ab ± 0.05	NA
AM fungal richness	NS	13.4 ± 4.10	12.2 ± 2.13	26.5 ± 8.0	**0.024**
AM fungal Shannon diversity	NS	5.91 ± 0.90	4.88 ± 0.50	6.40 ± 0.87	NS
Intraspecific β-diversity of root AM fungal communities	NS	0.43 ± 0.06	0.44 ± 0.04	0.32 ± 0.06	NS
Discrepancy between soil and root AM fungal communities (Procrustes residuals)	NS	0.03 ± 0.01	0.03 ± 0.004	0.02 ± 0.01	NS
Nestedness rank	**0.009**	0.56ab ± 0.12	0.62a ± 0.07	0.11b ± 0.12	NS
Normalized degree	**0.006**	0.27a ± 0.05	0.24a ± 0.03	0.48b ± 0.05	NS
Resource range	**0.006**	0.73a ± 0.05	0.76a ± 0.03	0.53b ± 0.05	NS
Species strength	**0.038**	6.1ab ± 2.4	6.2a ± 1.5	13.9b ± 2.4	NS
d′ (specialization index)	NS	0.10 ± 0.05	0.11 ± 0.03	0.06 ± 0.05	NS

Note: Group means ± standard errors are shown on the response scale for plant mycorrhizal statuses. In the case of a significant effect, differing letters indicate statistically significant pairwise differences ($p < 0.05$) between plant mycorrhizal statuses. Statistically significant models ($p < 0.05$) are marked in bold.

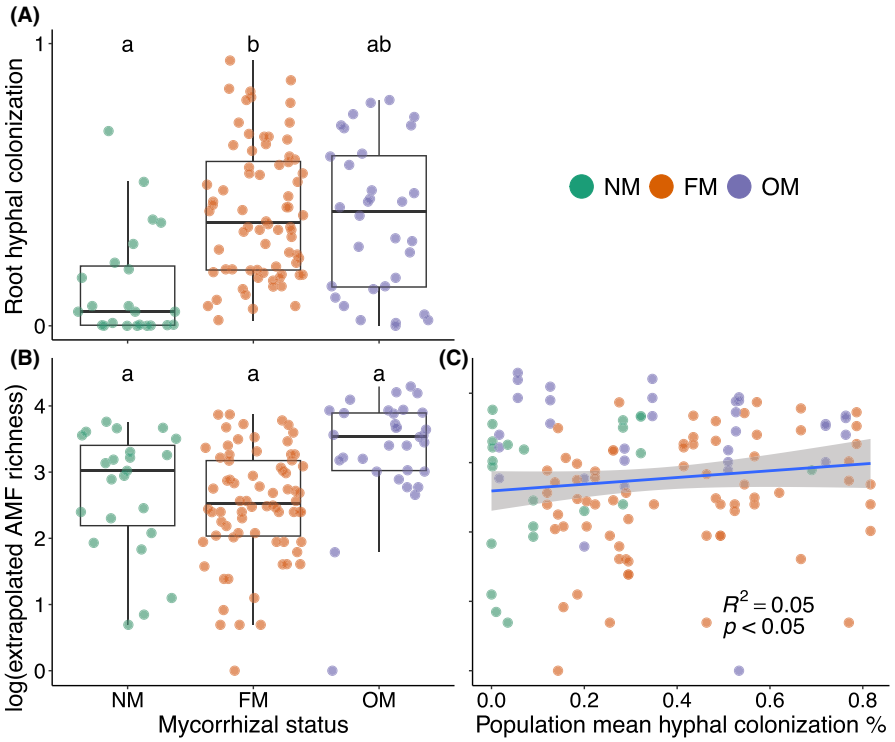

FIGURE 2 Mean hyphal colonization of plant roots (A) and AM fungal richness (B, C) in plant roots, shown in relation to plant mycorrhizal status (A, B) or plant population mean hyphal colonization (C). The boxes show the median, interquartile range (IQR), and potential outliers, with whiskers extending to values within 1.5 times the IQR. Colours indicate different plant mycorrhizal statuses: NM (green)—non-mycorrhizal; FM (orange)—facultatively mycorrhizal; OM (blue)—obligately mycorrhizal; each point on the plots represents a plant individual. Lowercase letters indicate statistically significant differences ($p < 0.05$) between factor levels according to Tukey's HSD post hoc test.

provides useful information about symbiotic mycorrhizal traits such as AM fungal community composition and network indices. Our results suggest that facultatively mycorrhizal (FM) and obligately mycorrhizal (OM) plant species do not differ significantly in terms of hyphal colonization in their roots but have significant differences in terms of fungal partner selection, with OM plant species being more generalist in their partner selection.

4.1 | Variation in AM fungal colonization in host plant roots

In this study, we targeted a wide range of habitats, from Sphagnum bogs to calcareous grasslands, within a fairly small region in order to assess within plant species variation in AM fungal colonization while controlling for larger-scale regional processes. Interestingly, we only

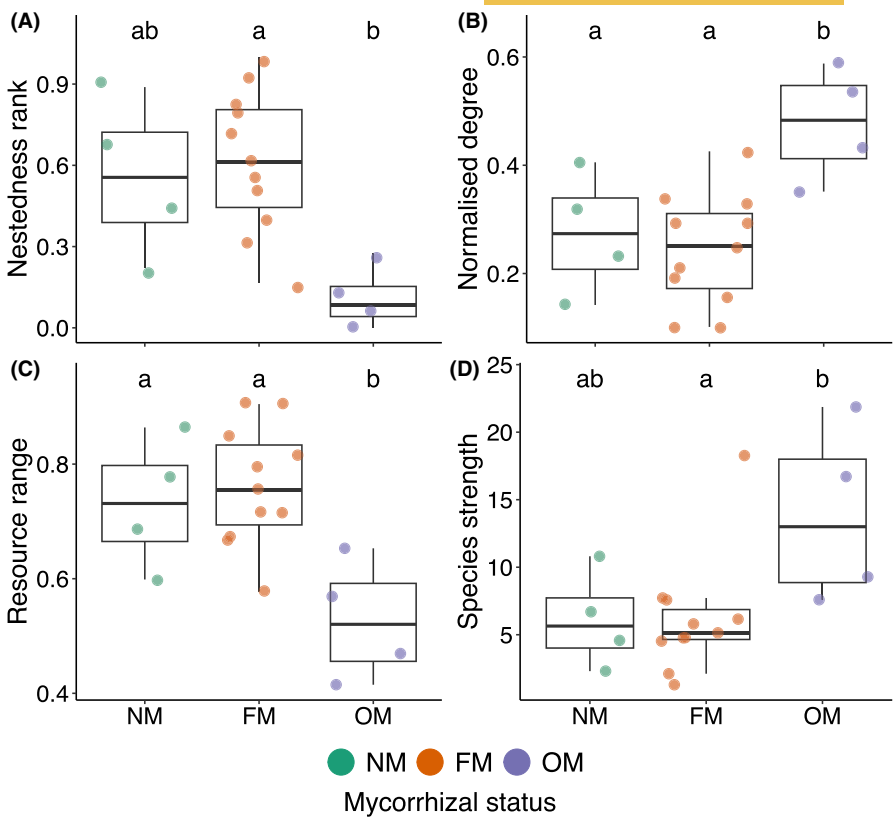

FIGURE 3 The effect of plant species mycorrhizal status on plant species level network topological parameters: nestedness rank (a), normalised degree (b), resource range (c) and species strength (d). The boxes show the median, interquartile range (IQR), and potential outliers, with whiskers extending to values within 1.5 times the IQR. Colours indicate plants of different mycorrhizal status: NM (green)—non-mycorrhizal; FM (orange)—facultatively mycorrhizal; OM (blue)—obligately mycorrhizal; each point on the plots represents a plant species. Lowercase letters indicate statistically significant differences ($p < 0.05$) between factor levels according to Tukey's HSD post hoc test.

identified five plant individuals out of 127 with no AM fungal colonization in their roots despite of the intense sampling effort and inclusion of disturbed sites such as road verges and a construction site. In the sampled area, most of the plant species form AM (Bueno et al., 2017) and previous work has shown that relatively large pools of AM fungal taxa are present even in early successional sites in this area (Garcia de Leon et al., 2016). This suggests that AM fungal species pools in the soil are abundant and active, resulting in high colonization intensity. Indeed, it has been demonstrated that the presence of a neighbour that supports an active and functional AM fungal network increases AM fungal colonization in the roots of plant species that would otherwise not typically associate with AM fungi (Veiga et al., 2012, 2013; Zhang et al., 2019). A recent greenhouse study has demonstrated that AM fungal colonization is positively linked to plant species dependency on AM fungi (Romero et al., 2023) but we did not find support for higher AM fungal colonization in the roots of OM compared to FM plant species, a result that most likely reflects the high degree of variation among sampled habitats.

A recent study highlighted the role of environmental conditions in determining variation in the mycorrhizal status of plant species (Meng et al., 2023). We hypothesized that there is also a significant decrease in AM fungal colonization in plant roots with increasing soil fertility, especially in the case of FM plant species, but this was not supported by our results. The expected trend was, however, evident related to the soil's acidity, with samples collected from sites with higher pH values having lower AM fungal colonization. The opposite trend could have been expected, considering that an earlier study based on German flora demonstrates that OM plant species' distribution is positively related to higher pH (Hempel et al., 2013). Our study highlights that a higher proportion of OM plant species does not necessarily translate into higher AM fungal colonization in plant roots.

4.2 | Variation in AM fungal communities

We found that AM fungal richness in soil was twice as that in plant roots, indicating that a subset of AM fungal species colonizes available plants. Considering that FM plant species are expected to regulate the presence or extent of AM fungal symbiosis (Zobel et al., 2024), we hypothesized that AM fungal communities in the roots of FM plant species are less species-rich than those in the roots of OM plant species. However, despite this trend being apparent, the differences were not statistically significant. At the same time, we did find a positive relationship between the richness of AM fungi and mean AM fungal colonization, demonstrating that plant species that are more colonized by AM fungi harbour also more AM fungal taxa. This positive correlation might stem from differences in plant root morphology. Indeed, species that are more dependent on AM fungi in terms of nutrient transport and allocate more carbon into AM fungi are proposed to have thicker toots, representing the 'outsourcing' strategy of root economics space (Bergmann et al., 2020). Recent studies have linked root traits with AM fungal communities and while positive correlation between root diameter and relative abundance of AM fungi has been reported (Sweeney et al., 2021), no association has been found as well (Hennecke et al., 2023). Thus,

it remains to be tested how plant mycorrhizal status associates with root traits, AM fungal colonization, and AM fungal richness.

We hypothesized that AM fungal communities in the roots of FM plant species are more distinct from communities in soil than communities associating with OM plant species, but this was not supported by the data. The expectation that FM plant species are more selective towards their mycorrhizal partners due to their facultative nature was, however, confirmed with network analyses. The AM fungal network associated with roots of FM plant species had a higher nestedness rank (Alarcón et al., 2008) than that in the roots of OM plant species, indicating that OM plant species are more general in their partner selection. This was also supported by the higher normalized degree and lower resource range of the network in OM compared with FM plants, demonstrating that OM plant species interact with a significantly higher number of possible AM fungal partners than FM plant species. Overall, our network analyses indicate that OM plant species are more relevant to AM fungi in sustaining their network, as demonstrated by the significantly higher species strength of OM than FM plant species networks. These results are consistent with previous findings of the analyses of AM fungal networks in a calcareous grassland (Sepp et al., 2019), suggesting that in arbuscular mycorrhiza, obligate symbiosis means lower selectivity towards fungal partners.

4.3 | Limitations

This is the first study to use a standardized sampling design to quantify variation in AM fungal communities in the roots of OM, FM and NM plant species. We found AM fungal colonization in the roots of some of the individuals of all plant species, which suggests that all the putatively NM plant species used in this study can be categorized as FM according to colonization approach (Bueno et al., 2021). Indeed, the network analyses used in this study also demonstrated that putatively NM and FM plant species had similarities in their interaction networks, highlighting current limitations in our understanding of the symbioses. Indeed, a recent study has quantified that information about plant mycorrhizal traits is currently available for only 4% of the global flora (Meng et al., 2023). Also, the available information is sparse, leading to the possible reclassification of plant species mycorrhizal status as evidence accumulates. In this study, we changed the mycorrhizal status of three of the 19 sampled plant species due to new information emerging between the design of the study and the writing of the manuscript. One previously OM and two previously NM plant species were assigned as FM. While such changes may not influence large-scale patterns of plant species mycorrhizal statuses—for example, in Bueno et al. (2017), random variation in assignation of up to 20% yields the same patterns—they can complicate detection of finer patterns. As we did not sterilize the roots used for estimating AM fungal colonization or community composition, we cannot exclude the possibility that some results might reflect AM fungi attached to the root surface. Despite this uncertainty, our results indicate that irrespective of their mycorrhizal status, all plant species provide some support to sustain AM fungal networks in soil.

5 | CONCLUSIONS

Using an extensive, unified sampling scheme, we found that plant mycorrhizal traits, such as plant mycorrhizal status, can provide information about symbiotic mycorrhizal traits (Chaudhary et al., 2022). Using network analyses, we demonstrate that, compared with FM plant species, OM plant species are less selective towards their AM fungal partners and interact with a higher number of AM fungal taxa. Integrating network analyses with comprehensive descriptions of mycorrhizal fungal communities in both soil and roots represents a promising approach for elucidating the ecological role and mechanism of the frequency of mycorrhizal association in plants.

AUTHOR CONTRIBUTIONS

Kadri Koorem, Martin Zobel and Mari Moora conceived the ideas and designed methodology; Kadri Koorem, C. Guillermo Bueno, John Davison, Siqiao Liu, Yiming Meng, Marina Semchenko, Martin Zobel and Mari Moora collected the data; Siim-Kaarel Sepp and Martti Vasar analysed the data; Kadri Koorem led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication. No licence or permit was needed for the fieldwork.

ACKNOWLEDGEMENTS

We thank Kersti Püssa, Inga Hiiesalu and Merlyn Leigh Dunderdale for technical support during the fieldwork, and Justine Karst for discussions. This research was supported by the European Union (ERC grant PlantSoilAdapt, 101044424), the Centre of Excellence AgroCropFuture and Estonian Research Council (PRG1065, PRG1836).

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Raw reads from this targeted locus study have been deposited in the National Center for Biotechnology Information Sequence Read Archive (BioProject PRJNA1183728).

ORCID

Kadri Koorem https://orcid.org/0000-0002-3376-9372
C. Guillermo Bueno https://orcid.org/0000-0002-7288-2271
John Davison https://orcid.org/0000-0002-0161-6195
Siqiao Liu https://orcid.org/0000-0002-0680-1816
Yiming Meng https://orcid.org/0000-0003-0141-7812
Marina Semchenko https://orcid.org/0000-0001-6196-3562
Martti Vasar https://orcid.org/0000-0002-4674-932X
Martin Zobel https://orcid.org/0000-0001-7957-6704
Mari Moora https://orcid.org/0000-0002-4819-7506

REFERENCES

Alarcón, R., Waser, N. M., & Ollerton, J. (2008). Year-to-year variation in the topology of a plant–pollinator interaction network. *Oikos*, *117*(12), 1796–1807. https://doi.org/10.1111/j.0030-1299.2008.16987.x

Bascompte, J., Jordano, P., & Olesen, J. M. (2006). Asymmetric coevolutionary networks facilitate biodiversity maintenance. *Science*, *312*(5772), 431–433. https://doi.org/10.1126/science.1123412

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Bergmann, J., Weigelt, A., van der Plas, F., Laughlin, D. C., Kuyper, T. W., Guerrero-Ramirez, N., Valverde-Barrantes, O. J., Bruelheide, H., Freschet, G. T., Iversen, C. M., Kattge, J., McCormack, M. L., Meier, I. C., Rillig, M. C., Roumet, C., Semchenko, M., Sweeney, C. J., van Ruijven, J., York, L. M., & Mommer, L. (2020). The fungal collaboration gradient dominates the root economics space in plants. *Science Advances*, *6*(27), eaba3756. https://doi.org/10.1126/sciadv.aba3756

Blüthgen, N., Menzel, F., & Blüthgen, N. (2006). Measuring specialization in species interaction networks. *BMC Ecology*, *6*(1), 9. https://doi.org/10.1186/1472-6785-6-9

Bouckaert, R., Vaughan, T. G., Barido-Sottani, J., Duchêne, S., Fourment, M., Gavryushkina, A., Heled, J., Jones, G., Kühnert, D., Maio, N. D., Matschiner, M., Mendes, F. K., Müller, N. F., Ogilvie, H. A., du Plessis, L., Popinga, A., Rambaut, A., Rasmussen, D., Siveroni, I., … Drummond, A. J. (2019). BEAST 2.5: An advanced software platform for Bayesian evolutionary analysis. *PLoS Computational Biology*, *15*(4), e1006650. https://doi.org/10.1371/journal.pcbi.1006650

Bouckaert, R. R., & Drummond, A. J. (2017). bModelTest: Bayesian phylogenetic site model averaging and model comparison. *BMC Evolutionary Biology*, *17*(1), 42. https://doi.org/10.1186/s12862-017-0890-6

Brundrett, M. C., & Tedersoo, L. (2018). Evolutionary history of mycorrhizal symbioses and global host plant diversity. *New Phytologist*, *220*(4), 1108–1115. https://doi.org/10.1111/nph.14976

Bueno, C. G., Moora, M., Gerz, M., Davison, J., Öpik, M., Pärtel, M., Helm, A., Ronk, A., Kühn, I., & Zobel, M. (2017). Plant mycorrhizal status, but not type, shifts with latitude and elevation in Europe. *Global Ecology and Biogeography*, *26*(6), 690–699. https://doi.org/10.1111/geb.12582

Bueno, C. G., Davison, J., Leon, D., Meng, Y., Öpik, M., Zobel, M., & Moora, M. (2021). Towards a consistent benchmark for plant mycorrhizal association databases. *New Phytologist*, *231*, 913–916. https://doi.org/10.1111/nph.17417

Camacho, C., Coulouris, G., Avagyan, V., Ma, N., Papadopoulos, J., Bealer, K., & Madden, T. L. (2009). BLAST+: Architecture and applications. *BMC Bioinformatics*, *10*(1), 421. https://doi.org/10.1186/1471-2105-10-421

Chaudhary, V. B., Holland, E. P., Charman-Anderson, S., Guzman, A., Bell-Dereske, L., Cheeke, T. E., Corrales, A., Duchicela, J., Egan, C., Gupta, M. M., Hannula, S. E., Hestrin, R., Hoosein, S., Kumar, A., Mhretu, G., Neuenkamp, L., Soti, P., Xie, Y., & Helgason, T. (2022). What are mycorrhizal traits? *Trends in Ecology & Evolution*, *37*, 573–581. https://doi.org/10.1016/j.tree.2022.04.003

Correia, M., Heleno, R., Vargas, P., & Rodríguez-Echeverría, S. (2018). Should I stay or should I go? Mycorrhizal plants are more likely to invest in long-distance seed dispersal than non-mycorrhizal plants. *Ecology Letters*, *21*(5), 683–691. https://doi.org/10.1111/ele.12936

Davison, J., García de León, D., Zobel, M., Moora, M., Bueno, C. G., Barceló, M., Gerz, M., León, D., Meng, Y., Pillar, V. D., Sepp, S.-K., Soudzilovaskaia, N. A., Tedersoo, L., Vaessen, S., Vahter, T., Winck, B., & Öpik, M. (2020). Plant functional groups associate with distinct arbuscular mycorrhizal fungal communities. *New Phytologist*, *226*(4), 1117–1128. https://doi.org/10.1111/nph.16423

Dormann, C. F. (2011). How to be a specialist? Quantifying specialisation in pollination networks. *Network Biology*, *1*(1), 1–20.

Dumbrell, A. J., Ashton, P. D., Aziz, N., Feng, G., Nelson, M., Dytham, C., Fitter, A. H., & Helgason, T. (2011). Distinct seasonal assemblages of arbuscular mycorrhizal fungi revealed by massively parallel pyrosequencing. *New Phytologist*, *190*(3), 794–804. https://doi.org/10.1111/j.1469-8137.2010.03636.x

Fox, J., & Weisberg, S. (2019). *An R companion to applied regression* (3rd ed.). Sage.

Garcia de Leon, D., Moora, M., Öpik, M., Neuenkamp, L., Gerz, M., Jairus, T., Vasar, M., Bueno, C. G., Davison, J., & Zobel, M. (2016). Symbiont dynamics during ecosystem succession: Co-occurring plant and arbuscular mycorrhizal. *FEMS Microbiology Ecology*, *92*(7), fiw097. https://doi.org/10.1093/femsec/fiw097

Gerz, M., Bueno, C. G., Zobel, M., & 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. https://doi.org/10.1111/jvs.12338

Gerz, M., Bueno, G. C., Ozinga, W. A., Zobel, M., & Moora, M. (2018). Niche differentiation and expansion of plant species are associated with mycorrhizal symbiosis. *Journal of Ecology*, *106*(1), 254–264. https://doi.org/10.1111/1365-2745.12873

Han, Y., Feng, J., Han, M., & Zhu, B. (2020). Responses of arbuscular mycorrhizal fungi to nitrogen addition: A meta-analysis. *Global Change Biology*, *26*(12), 7229–7241. https://doi.org/10.1111/gcb.15369

Harley, J., & Harley, E. L. (1987). A check-list of mycorrhiza in the British flora. *New Phytologist*, *105*, 1–102. https://doi.org/10.1111/j.1469-8137.1987.tb00674.x

Hempel, S., Gotzenberger, L., Kuhn, I., Michalski, S. G., Rillig, M. C., Zobel, M., & Moora, M. (2013). Mycorrhizas in the central European flora: Relationships with plant life history traits and ecology. *Ecology*, *94*(6), 1389–1399. https://doi.org/10.1890/12-1700.1

Hennecke, J., Bassi, L., Mommer, L., Albracht, C., Bergmann, J., Eisenhauer, N., Guerra, C. A., Heintz-Buschart, A., Kuyper, T. W., Lange, M., Solbach, M. D., & Weigelt, A. (2023). Responses of rhizosphere fungi to the root economics space in grassland monocultures of different age. *New Phytologist*, *240*(5), 2035–2049. https://doi.org/10.1111/nph.19261

Hill, M. O. (1973). Diversity and evenness: A unifying notation and its consequences. *Ecology*, *54*(2), 427–432. https://doi.org/10.2307/1934352

Hsieh, T. C., Ma, K. H., & Chao, A. (2016). iNEXT: An R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods in Ecology and Evolution*, *7*(12), 1451–1456. https://doi.org/10.1111/2041-210X.12613

Karsch-Mizrachi, I., Takagi, T., Cochrane, G., & International Nucleotide Sequence Database Collaboration. (2018). The international nucleotide sequence database collaboration. *Nucleic Acids Research*, *46*(D1), D48–D51. https://doi.org/10.1093/nar/gkx1097

Koske, R. E., & Gemma, J. N. (1989). A modified procedure for staining roots to detect VA mycorrhizas. *Mycological Research*, *92*(4), 486–488. https://doi.org/10.1016/S0953-7562(89)80195-9

Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). lmerTest package: Tests in linear mixed effects models. *Journal of Statistical Software*, *82*(13), 1–26. https://doi.org/10.18637/jss.v082.i13

Lee, J., Lee, S., & Young, J. P. W. (2008). Improved PCR primers for the detection and identification of arbuscular mycorrhizal fungi. *FEMS Microbiology Ecology*, *65*(2), 339–349. https://doi.org/10.1111/j.1574-6941.2008.00531.x

Lekberg, Y., & Koide, R. T. (2014). Integrating physiological, community, and evolutionary perspectives on the arbuscular mycorrhizal symbiosis 1. *Botany*, *92*(4), 241–251. https://doi.org/10.1139/cjb-2013-0182

Lenth, R. V. (2024). *emmeans: Estimated marginal means, aka least-squares means*. https://CRAN.R-project.org/package=emmeans

Leon, D., Bueno, C. G., Zobel, M., Bennett, J. A., Puglielli, G., Davison, J., Riibak, K., Pärtel, M., & Moora, M. (2022). Plant diversity but not productivity is associated with community mycorrhization in temperate grasslands. *Journal of Vegetation Science*, *33*(1), e13107. https://doi.org/10.1111/jvs.13107

Leon, D., Peyre, G., Zobel, M., Moora, M., Meng, Y., Diaz, M., & Bueno, C. G. (2024). Mycorrhizal symbioses in the Andean paramo. *Mycorrhiza*, *34*(1–2), 107–117. https://doi.org/10.1007/s00572-023-01133-5

Lozupone, C., & Knight, R. (2005). UniFrac: A new phylogenetic method for comparing microbial communities. *Applied and Environmental Microbiology*, *71*(12), 8228–8235. https://doi.org/10.1128/AEM.71.12.8228-8235.2005

Magoč, T., & Salzberg, S. L. (2011). FLASH: Fast length adjustment of short reads to improve genome assemblies. *Bioinformatics*, *27*(21), 2957–2963. https://doi.org/10.1093/bioinformatics/btr507

McGonigle, T. P., Miller, M. H., Evans, D. G., Fairchild, G. L., & Swan, J. A. (1990). A new method which gives an objective measure of colonization of roots by vesicular—arbuscular mycorrhizal fungi. *New Phytologist*, *115*(3), 495–501. https://doi.org/10.1111/j.1469-8137.1990.tb00476.x

Meng, Y., Davison, J., Clarke, J. T., Zobel, M., Gerz, M., Moora, M., Öpik, M., & Bueno, C. G. (2023). Environmental modulation of plant mycorrhizal traits in the global flora. *Ecology Letters*, *26*(11), 1862–1876. https://doi.org/10.1111/ele.14309

Moora, M. (2014). Mycorrhizal traits and plant communities: Perspectives for integration. *Journal of Vegetation Science*, *25*(5), 1126–1132. https://doi.org/10.1111/jvs.12177

Moyano, J., Dickie, I. A., Rodriguez-cabal, M. A., & Nuñez, M. A. (2020). Patterns of plant naturalization show that facultative mycorrhizal plants are more likely to succeed outside their native Eurasian ranges. *Ecography*, *43*(5), 648–659. https://doi.org/10.1111/ecog.04877

Oksanen, J., Simpson, G. L., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Solymos, P., Stevens, M. H. H., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., Caceres, M. D., Durand, S., … Weedon, J. (2022). *vegan: Community ecology package*. https://CRAN.R-project.org/package=vegan

Öpik, M., Vanatoa, A., Vanatoa, E., Moora, M., Davison, J., Kalwij, J. M., Reier, Ü., & Zobel, M. (2010). The online database MaarjAM reveals global and ecosystemic distribution patterns in arbuscular mycorrhizal fungi (Glomeromycota). *New Phytologist*, *188*(1), 223–241. https://doi.org/10.1111/j.1469-8137.2010.03334.x

Poisot, T., Canard, E., Mouquet, N., & Hochberg, M. E. (2012). A comparative study of ecological specialization estimators. *Methods in Ecology and Evolution*, *3*(3), 537–544. https://doi.org/10.1111/j.2041-210X.2011.00174.x

Pyšek, P., Guo, W. Y., Štajerová, K., Moora, M., Bueno, C. G., Dawson, W., Essl, F., Gerz, M., Kreft, H., Pergl, J., van Kleunen, M., Weigelt, P., Winter, M., & Zobel, M. (2019). Facultative mycorrhizal associations promote plant naturalization worldwide. *Ecosphere*, *10*(11), e02937. https://doi.org/10.1002/ecs2.2937

Qin, Z., Zhang, H., Feng, G., Christie, P., Zhang, J., Li, X., & Gai, J. (2020). Soil phosphorus availability modifies the relationship between AM fungal diversity and mycorrhizal benefits to maize in an agricultural soil. *Soil Biology and Biochemistry*, *144*, 107790. https://doi.org/10.1016/j.soilbio.2020.107790

R Core Team. (2024). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Remy, W., Taylor, T. N., Hass, H., & Kerp, H. (1994). Four hundred-million-year-old vesicular arbuscular mycorrhizae. *Proceedings of the National Academy of Sciences*, *91*(25), 11841–11843. https://doi.org/10.1073/pnas.91.25.11841

Rognes, T., Flouri, T., Nichols, B., Quince, C., & Mahé, F. (2016). VSEARCH: A versatile open source tool for metagenomics. *PeerJ*, *4*, e2584. https://doi.org/10.7717/peerj.2584

Romero, F., Argüello, A., de Bruin, S., & van der Heijden, M. G. A. (2023). The plant–mycorrhizal fungi collaboration gradient depends on plant functional group. *Functional Ecology*, *37*(9), 2386–2398. https://doi.org/10.1111/1365-2435.14395

Sepp, S. K., Davison, J., Jairus, T., Vasar, M., Zobel, M., & Öpik, M. (2019). Non-random association patterns in a plant—Mycorrhizal fungal network reveal host—Symbiont specificity. *Molecular Ecology*, *28*(2), 365–378. https://doi.org/10.1111/mec.14924

Smith, S., & Read, D. (2008). *Mycorrhizal symbioses*. Academic Press.

Smith, S. E., & Read, D. J. (2010). *Mycorrhizal symbiosis*. Academic Press.

Soudzilovskaia, N. A., Vaessen, S., Barcelo, M., He, J., Rahimlou, S., Abarenkov, K., Brundrett, M. C., Gomes, S. I. F., Merckx, V., & Tedersoo, L. (2020). FungalRoot: Global online database of plant mycorrhizal associations. *New Phytologist*, *227*(3), 955–966. https://doi.org/10.1111/nph.16569

Stoffel, M. A., Nakagawa, S., & Schielzeth, H. (2021). partR2: Partitioning R2 in generalized linear mixed models. *PeerJ*, *9*, e11414. https://doi.org/10.7717/peerj.11414

Strullu-Derrien, C., Selosse, M.-A., Kenrick, P., & Martin, F. M. (2018). The origin and evolution of mycorrhizal symbioses: From palaeomycology to phylogenomics. *New Phytologist*, *220*(4), 1012–1030. https://doi.org/10.1111/nph.15076

Sweeney, C. J., de Vries, F. T., van Dongen, B. E., & Bardgett, R. D. (2021). Root traits explain rhizosphere fungal community composition among temperate grassland plant species. *New Phytologist*, *229*(3), 1492–1507. https://doi.org/10.1111/nph.16976

Vahter, T., Guillermo, C., John, B., Koit, D., Hiiesalu, I., Jane, L. K., Pål, O., Olsson, A., Zobel, S. S. M., Vasar, M., & Öpik, M. (2020). Co-introduction of native mycorrhizal fungi and plant seeds accelerates restoration of post-mining landscapes. *Journal of Applied Ecology*, *57*(9), 1741–1751. https://doi.org/10.1111/1365-2664.13663

Vasar, M., Davison, J., Neuenkamp, L., Sepp, S., Young, J. P. W., Moora, M., & Öpik, M. (2021). User-friendly bioinformatics pipeline gDAT (graphical downstream analysis tool) for analysing rDNA sequences. *Molecular Ecology Resources*, *21*(4), 1380–1392. https://doi.org/10.1111/1755-0998.13340

Veiga, R. S. L., Faccio, A., Genre, A., Pieterse, C. M. J., Bonfante, P., & van der Heijden, M. G. A. (2013). Arbuscular mycorrhizal fungi reduce growth and infect roots of the non-host plant Arabidopsis thaliana. *Plant, Cell & Environment*, *36*(11), 1926–1937. https://doi.org/10.1111/pce.12102

Veiga, R. S. L., Howard, K., & van der Heijden, M. G. A. (2012). No evidence for allelopathic effects of arbuscular mycorrhizal fungi on the non-host plant Stellaria media. *Plant and Soil*, *360*(1), 319–331. https://doi.org/10.1007/s11104-012-1256-x

Wang, B., & Qiu, Y.-L. (2006). Phylogenetic distribution and evolution of mycorrhizas in land plants. *Mycorrhiza*, *16*, 299–363. https://doi.org/10.1007/s00572-005-0033-6

Zhang, H., Qin, Z., Chu, Y., Li, X., Christie, P., Zhang, J., & Gai, J. (2019). Interactions between arbuscular mycorrhizal fungi and non-host *Carex capillacea*. *Mycorrhiza*, *29*(2), 149–157. https://doi.org/10.1007/s00572-019-00882-6

Zobel, M., Koorem, K., Moora, M., Semchenko, M., & Davison, J. (2024). Symbiont plasticity as a driver of plant success. *New Phytologist*, *241*(6), 2340–2352. https://doi.org/10.1111/nph.19566

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1: The number of references available for determining the mycorrhizal status of the plant species included in the study. Colors

indicate plants with different mycorrhizal status: NM (green)—non-mycorrhizal; FM (orange)—facultatively mycorrhizal; OM (blue)—obligately mycorrhizal; each point on the plots represents a plant species.

Figure S2: The effect of the mycorrhizal status of a plant species on the variability of arbuscular mycorrhizal hyphal colonization (coefficient of variation) of the species. Colors indicate plants with different mycorrhizal status: NM (green)—non-mycorrhizal; FM (orange)—facultatively mycorrhizal; OM (blue)—obligately mycorrhizal; each point on the plots represents a plant species. Differing letters indicate statistically significant pairwise differences.

Figure S3: The effect of the mean arbuscular mycorrhizal hyphal colonization of a plant species on the variability of arbuscular mycorrhizal hyphal colonization (coefficient of variation) of the species. Colors indicate plants with different mycorrhizal status: NM (green)—non-mycorrhizal; FM (orange)—facultatively mycorrhizal; OM (blue)—obligately mycorrhizal; each point on the plots represents a plant species.

Table S1: Summary table of plant species in the study. Population-level mean proportion of arbuscular mycorrhizal hyphal colonization (Col) and mean arbuscular mycorrhizal fungal richness (VT) are shown.

How to cite this article: Koorem, K., Sepp, S.-K., Bueno, C. G., Davison, J., Liu, S., Meng, Y., Semchenko, M., Vasar, M., Zobel, M., & Moora, M. (2024). Plant mycorrhizal status indicates partner selectivity in arbuscular mycorrhizal interaction networks. *Functional Ecology*, *00*, 1–11. https://doi.org/10.1111/1365-2435.14729