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Plant functional groups associate with distinct arbuscular mycorrhizal fungal communities

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Summary

- The benefits of the arbuscular mycorrhizal (AM) symbiosis between plants and fungi are modulated by the functional characteristics of both partners. However, it is unknown to what extent functionally distinct groups of plants naturally associate with different AM fungi.
- We reanalysed 14 high-throughput sequencing data sets describing AM fungal communities associating with plant individuals (2427) belonging to 297 species. We examined how root-associating AM fungal communities varied between plants with different growth forms, photosynthetic pathways, CSR (competitor, stress-tolerator, ruderal) strategies, mycorrhizal statuses and N-fixing statuses.
- AM fungal community composition differed in relation to all studied plant functional groups. Grasses, C₄ and nonruderal plants were characterised by high AM fungal alpha diversity, while C₄, ruderal and obligately mycorrhizal plants were characterised by high beta diversity. The phylogenetic diversity of AM fungi, a potential surrogate for functional diversity, was higher among forbs than other plant growth forms. Putatively ruderal (previously cultured) AM fungi were disproportionately associated with forbs and ruderal plants. There was phylogenetic correlation among AM fungi in the degree of association with different plant growth forms and photosynthetic pathways.
- Associated AM fungal communities constitute an important component of plant ecological strategies. Functionally different plants associate with distinct AM fungal communities, linking mycorrhizal associations with functional diversity in ecosystems.

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Introduction

Arbuscular mycorrhizal (AM) fungi (subphylum Glomeromycotina, Spatafora *et al.*, 2016) are root symbionts that associate with > 80% of plant species in terrestrial ecosystems (Brundrett & Tedersoo, 2018). AM fungi typically receive plant-synthesised carbon, while conferring plant hosts with increased nutrient uptake and stress tolerance (Smith & Read, 2008). Although strict species-level partner specificity does not seem to occur in plant–AM fungal interactions, there is a degree of selectivity; that is, AM fungal taxa associate nonrandomly with different plant species (Bainard *et al.*, 2014; Davison *et al.*, 2016; Sepp *et al.*, 2019). Indeed, AM fungi are able to allocate more mineral nutrients to the most C-rewarding plants, while plants may allocate

more C to the fungus providing the greatest mineral nutrition (Bever *et al.*, 2009; Kiers *et al.*, 2011; Fellbaum *et al.*, 2012). On this basis, functionally similar plant species might be expected to associate with the same or functionally similar AM fungi, and, conversely, different functional types of plant might harbour distinctive AM fungal communities. The dominance of different plant functional groups is known to have fluctuated in response to past environmental changes (Willerslev *et al.*, 2014; Zobel *et al.*, 2018). Identifying linkages between plant functional groups and AM fungal community characteristics would importantly inform predictions about future ecosystem-level dynamics.

There have been limited attempts to assess whether AM fungal communities in host roots differ between plants displaying different ecological strategies (hereafter plant functional groups). There is some evidence that AM fungal community richness and composition differ between plant growth forms (e.g. forb, grass and

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woody plant species; Vandenkoornhuyse *et al.*, 2002; López-García *et al.*, 2017; Sepp *et al.*, 2019), forest specialist and generalist plant species (Öpik *et al.*, 2009; Davison *et al.*, 2011), and shade-avoidant and shade-tolerant plant species (Koorem *et al.*, 2017). AM fungal colonisation is also known to differ among certain plants with contrasting photosynthetic pathways (e.g. C₃ vs C₄; Grman, 2012) and CSR (competitor, stress-tolerator, ruderal) strategy types (Betekhtina & Veselkin, 2011). However, these observations were based on comparisons of small numbers of plant species. There have been no large-scale, systematic attempts to empirically investigate how the diversity and composition of associated AM fungal communities vary between plants exhibiting these and other ecological strategies.

In addition to the plant functional groups previously considered, it would be highly informative to consider associations with different microbial mutualists, such as whether plants associate with N-fixing bacteria, or comparisons between plant mycorrhizal statuses, which indicate the degree of reliance of AM plants on AM fungi (Moora, 2014). Gerz *et al.* (2018) showed that, compared with obligately mycorrhizal (OM; i.e. consistently forming mycorrhiza) plant species, facultatively mycorrhizal (FM; i.e. sometimes forming mycorrhiza) species have wider realised ecological niches along soil fertility, moisture, pH, salinity, light and temperature gradients. Neuenkamp *et al.* (2018) found that covariation in plant and AM fungal communities increases with the fraction of OM plants in the community. However, there is no information about whether FM (those individuals forming mycorrhiza) and OM plant species differ systematically in the composition of their associated AM fungal communities.

Theoretical studies have sought to predict how the characteristics of associating plant and AM fungal symbionts might interact. For instance, using the CSR framework, Chagnon *et al.* (2013, 2015) suggested that stress-tolerant plants, whose strategy is predicated on carbon-use efficiency, may preferentially associate with AM fungi that are able to complete their life cycle with low biomass or turnover. However, while plant strategies can be inferred and scrutinised using direct observation, measuring the traits and strategies of AM fungi, including many known only from environmental DNA, is far more challenging. Nonetheless, phylogenetic relationships between fungi are known to correlate with some functional characteristics (Powell *et al.*, 2009), and phylogeny is sometimes used as a coarse proxy for function (Davison *et al.*, 2016). Several studies have also indicated that molecular taxa containing representative sequences from described AM fungal species grown in culture are, in comparison with uncultured taxa, more strongly associated with disturbed habitats (Ohsowski *et al.*, 2014; García de León *et al.*, 2016; Davison *et al.*, 2018) and cultivated plants (Ohsowski *et al.*, 2014). However, whether such AM fungal taxa (hereafter referred to as 'putatively ruderal') preferentially associate with ruderal plant species in nature has not been investigated.

In this study, we perform a meta-reanalysis of existing plant–AM fungal data sets with global sampling to examine relationships between plant functional groups and measures of AM fungal diversity. Specifically, we: investigate taxonomic and

phylogenetic alpha and beta diversity of associated AM fungal communities among groups of plants corresponding to different growth forms (forbs, grasses or woody plants), CSR strategies (ruderal or other strategies), photosynthetic pathways (C₃ or C₄), mycorrhizal statuses (FM or OM) and N-fixing statuses (associating with N-fixing bacteria or not); assess whether plants with a ruderal strategy disproportionately associate with putatively ruderal AM fungi; assess whether fungal taxa differ in the extent to which they associate with different plant groups; and determine whether clades of fungal taxa with conserved patterns of association may be identified.

Materials and Methods

Data collation

We collated 14 data sets that used similar sampling and molecular approaches to generate information on AM fungi present in the roots of plant individuals, based on 454-sequencing of the small subunit (SSU) rRNA gene: Moora *et al.* (2011), Öpik *et al.* (2013), Saks *et al.* (2013), Davison *et al.* (2015), Gazol *et al.* (2016), Moora *et al.* (2016), Koorem *et al.* (2017), Pärtel *et al.* (2017), Vasar *et al.* (2017), Davison *et al.* (2018), García de León *et al.* (2018a), Sepp *et al.* (2018), Sepp *et al.* (2019) and L. Neuenkamp *et al.* (unpublished). Data collation was limited to 454-sequencing data sets because these successfully capture AM fungal diversity using SSU markers, and a larger number of suitable data sets have been produced using 454-sequencing than other platforms. Furthermore, mixing data from different platforms would require platform-specific bioinformatics approaches and might still systematically influence diversity estimates (Vasar *et al.*, 2017). All raw sequencing data were reanalysed as follows to generate a single consistent data set. Sequencing reads were retained only if they had an average quality score > 25, carried the correct barcode and forward primer sequence (one mismatch allowed), and were ≥ 199 bp long (including the barcode and primer sequence). Chimeras were identified and removed using UCHIME (v7.0.1090; Edgar *et al.*, 2011) in reference database mode (MaarjAM database) with the default settings. MaarjAM contains published Glomeromycotina sequences and classifies the middle part of Glomeromycotina SSU rRNA gene sequences into phylogenetically delimited sequence clusters – virtual taxa (VT; Öpik *et al.*, 2010). Retained reads were then matched against VT using a BLAST search (BLAST+ v2.5.0; Camacho *et al.*, 2009; soft masking of DUST filter) against the MaarjAM database (status June 2019) with the following criteria required for a match: sequence similarity ≥ 97%; an alignment length not differing from the length of the shorter of the query (454-read) and subject (reference database sequence) sequences by more than 5%; and a BLAST *e*-value < 1e-50. Samples yielding fewer than matched 10 reads and VT represented by a single read were removed from the data set, leaving in total 2 812 429 reads and 290 VT. The final, combined data set comprised 2427 plant individuals, 297 plant species and 148 locations (Fig. 1; Supporting Information Table S1). In further analyses we considered both presence/absence of VT, and read abundance as a proxy of VT abundance.

Fig. 1 Sampling locations represented in the 14 studies used in the analysis. Points are slightly jittered to allow close locations to be better distinguished (total number of study locations = 148).

Information about plant functional groups (Table S1) was compiled for the plant species used in the analyses from a variety of sources. For plant mycorrhizal status (OM or FM), we used and updated (i.e. incorporating newly identified records of mycorrhizal symbiosis) information from Bueno *et al.* (2017) and Gerz *et al.* (2018) (Table S2). Information about Grime's CSR strategy (Grime, 1977) and plant photosynthetic pathway (C_3 or C_4) was taken from the Biolflor (Klotz *et al.*, 2002) and TRY (Kattge *et al.*, 2011) databases. Due to the relatively low number of species with CSR information, and in order to assess the association of ruderal fungi with ruderal plants, the CSR strategy type was simplified along the ruderality axis: all strategies containing *R* (i.e. including secondary strategies) were assigned to *R* (ruderal), while other strategies (*C*, *S* and *CS*, but not *CSR* which was omitted as it contains all strategies) were assigned to *CS* (nonruderal). N-fixing status (yes/no) was taken from Tedersoo *et al.* (2018). The following numbers of species could be assigned to different functional groups: growth form (forb = 180, grass = 57, woody = 57); photosynthetic pathway (C_3 = 125, C_4 = 25); CSR

(*R* = 6, *CS* = 33); mycorrhizal status (FM = 58, OM = 170); and N-fixing (no = 277, yes = 20).

Following several earlier authors (e.g. Ohsowski *et al.*, 2014; García de León *et al.*, 2016), putatively ruderal AM fungal VT were identified as those VT containing sequences from taxonomically described species maintained in culture, according to records in the MaarjAM database (status June 2019). There were 51 such VT in the data set (Table S3). The most recent dated phylogeny of VT in Davison *et al.* (2018) was used as a source of AM fungal phylogenetic information. The phylogeny did not include 28 VT recorded in this analysis (i.e. 10% of taxa; comprising 2% of reads), so these taxa were not included in phylogenetic calculations.

Statistical analyses

There were varying degrees of association between different plant functional groupings in the data set (Fig. S1). Only growth form and photosynthetic pathway exhibited a strong and significant

Table 1 Differences in the composition of arbuscular mycorrhizal (AM) fungal communities associating with plants with different growth forms, photosynthetic pathways, CSR strategies, mycorrhizal statuses and N-fixing statuses.

Explanatory variable	Presence-absence		Abundance-weighted	
	Sørensen	Phylogenetic beta diversity	Bray-Curtis	Phylogenetic beta diversity
Growth form	$F = 3.9^{**}$ ($F = 2.5^{**}$)	$F = 3.6^{**}$ ($F = 2.2^{**}$)	$F = 3.2^{**}$ ($F = 1.7^{**}$)	$F = 4.7^{**}$ ($F = 2.2^*$)
Photosynthetic pathway	$F = 6.4^{**}$ ($F = 3.5^{**}$)	$F = 5.0^{**}$ ($F = 3.5^{**}$)	$F = 6.9^{**}$ ($F = 4.3^{**}$)	$F = 8.4^{**}$ ($F = 4.5^{**}$)
CSR	$F = 3.7^{**}$	$F = 2.0^*$	$F = 2.3^{**}$	$F = 3.1^*$
Mycorrhizal status	$F = 7.9^{**}$ ($F = 7.9^{**}$)	$F = 4.9^{**}$ ($F = 3.0^{**}$)	$F = 5.5^{**}$ ($F = 2.3^{**}$)	$F = 5.2^{**}$ ($F = 2.0^*$)
N-fixing	$F = 2.0^{**}$ ($F = 1.9^*$)	$F = 2.4^{**}$ ($F = 1.9^*$)	$F = 2.1^{**}$ ($F = 1.9^{**}$)	$F = 5.3^{**}$ ($F = 5.3^{**}$)

The results of distance-based redundancy analyses (db-RDA) are shown. Taxonomic (Sørensen and Bray-Curtis) and phylogenetic measures of composition were considered, and distance measures based on the presence-absence of AM fungal taxa (Sørensen and phylogenetic beta diversity) or estimated taxon abundance (Bray-Curtis and phylogenetic beta diversity) were used. Results in parentheses show marginal effects, after accounting for the effects of other correlated variables (see Supporting Information Fig. S1). Significant effects ($P < 0.05$) are shown in bold type.

*, $P < 0.05$; **, $P < 0.01$.

correlation; however, there were also weak but significant correlations between growth form and N-fixing status, and between photosynthetic pathway and mycorrhizal status. Because complete plant functional group information was only available for 27 plant species, explanatory variables (plant functional groups) were generally included one at a time in models. However, to investigate how functional correlations could influence effects attributed to particular groups, models were also constructed containing all predictor groups that displayed significant correlation (see Fig. S1), and marginal effects were estimated for each group.

Distance-based redundancy analysis (db-RDA; *dbRDA* from R package *VEGAN*; Oksanen *et al.*, 2019) was used to identify differences in fungal community composition in relation to plant growth form, photosynthetic pathway, CSR strategy type, mycorrhizal status and plant N-fixing status, with Sørensen and Bray–Curtis distances used for presence–absence and abundance analyses, respectively. Phylogenetic beta diversity was calculated using the mean pairwise phylogenetic distance (MPD) between taxa in pairs of samples (function *comdist* from the R package *PICANTE*; Kembel *et al.*, 2010). MPD was weighted by VT abundance for abundance-based analyses. To account for the fact that plant functional grouping was available at the level of plant species, while observations were collected at the level of plant individuals, response matrices used in the db-RDAs took the form of matrices of Euclidean distances between species centroids derived from principal coordinates analysis of the Sørensen or Bray–Curtis distance matrices.

Linear mixed models (using R package *LME4*; Bates *et al.*, 2015) were used to assess differences between plant functional groups in associated AM fungal alpha diversity, beta diversity, phylogenetic (alpha) diversity, phylogenetic beta diversity, and the log ratio between counts of putatively ruderal and putatively nonruderal AM fungi. In presence–absence analyses, richness and Sørensen distance were used as measures of alpha and beta diversity; in abundance-based analyses, the asymptotic Shannon index (from the R package *INEXT*; Hsieh *et al.*, 2019) and Bray–Curtis distance were used. Phylogenetic alpha diversity was estimated using MPD (function *mpd* from the R package *PICANTE*). For abundance-based analysis of phylogenetic alpha and beta diversity, MPD was weighted by VT abundance. Beta diversity within categories of plant ecological groups was measured as the multivariate distance of individual data points to the centroid of all points from the corresponding category (function *betadisper* from R package *VEGAN*). Models included sampling location (total $n = 148$) and plant species (total $n = 297$) as random effects. Spatial variograms confirmed that model residuals did not exhibit spatial autocorrelation.

Indicator species analysis was performed using VT abundance data at the level of plant individuals (Dufrêne & Legendre, 1997). Phylogenetic correlograms (Gittleman & Kot, 1990) were constructed to assess correlation in indicator values in relation to the phylogenetic relatedness between VT, and to identify clades associating with particular plant ecological groups. Multivariate correlation, incorporating the indicator values for each functional group category (e.g. in the growth form analysis, the values for

Fig. 2 Compositional differences in arbuscular mycorrhizal (AM) fungal communities associating with different functional groups of plants. R, ruderal plants; CS, nonruderal plants; OM, obligately mycorrhizal; FM, facultatively mycorrhizal. Sørensen and phylogenetic beta diversity (presence–absence) were used as response distance matrices in the distance-based redundancy analysis (db-RDA). For display purposes, data points represent species-level centroids derived from individual plant-level observations. Ellipses represent one SD around group centroids.

Fig. 3 Richness and beta diversity of arbuscular mycorrhizal (AM) fungal communities associating with different functional groups of plants. R, ruderal plants; CS, nonruderal plants; OM, obligately mycorrhizal; FM, facultatively mycorrhizal. Beta diversity was estimated as the distance in multivariate space (based on Sorensen distance) of a plant from the centroid of all plants belonging to the same functional group. For display purposes, data points (grey points) represent species-level means of individual plant-level observations. Large white points indicate means; bars indicate medians; boxes indicate interquartile ranges (IR); whiskers indicate minima and maxima ($< 1.5 \times \text{IR}$). Letters above boxes indicate significant differences between groups.

forbs, grasses and woody taxa were analysed simultaneously), was measured using Mantel's r . A confidence envelope was constructed using bootstrapping ($n = 500$). In the Results, means are given $\pm \text{SE}$.

Results

The composition of AM fungal communities differed between plants with different growth forms, photosynthetic pathways, CSR strategies, mycorrhizal statuses and N-fixing strategies in both presence-absence and abundance-weighted data sets (Table 1; Figs 2, S2).

The richness of associated AM fungal communities differed between plants with different growth forms and CSR strategies, with richness highest among grasses (forbs = 17.7 ± 0.3 , grasses = 21.5 ± 0.6 , woody = 16.6 ± 0.6) and nonruderal (CS = 18.6 ± 0.6 , R = 13.2 ± 1.1) plants (Fig. 3; Table 2). Phylogenetic alpha diversity based on presence-absence data also differed between plants with different growth forms, although it was

highest among forbs (forbs = 377.1 ± 2.7 , grasses = 354.8 ± 4.2 , woody = 339.2 ± 4.5 ; Fig. 4). There were no significant differences in Shannon diversity or in abundance-weighted phylogenetic diversity between any plant groups (Table 2; Figs S3, S4).

Presence-absence and abundance-weighted measures of beta diversity (Sørensen and Bray-Curtis; distance from multivariate centroid) differed between plants with different mycorrhizal statuses and CSR strategies, with higher beta diversity among OM (presence-absence FM = 0.51 ± 0.1 , OM = 0.58 ± 0.01 ; abundance-weighted FM = 0.59 ± 0.01 , OM = 0.65 ± 0.01) and ruderal (presence-absence CS = 0.49 ± 0.01 , R = 0.54 ± 0.02 ; abundance-weighted CS = 0.59 ± 0.01 , R = 0.63 ± 0.01) species (Figs 3, S3; Table 2). Based on presence-absence data there were also differences between plants with different photosynthetic pathways, with C_4 plants exhibiting highest beta diversity (C_3 = 0.55 ± 0.01 , C_4 = 0.57 ± 0.01). Phylogenetic beta diversity differed between plants with different growth forms (only in presence-absence data), photosynthetic pathway, CSR strategy (only in abundance data) and N-fixing status (only in abundance

Table 2 Differences in the diversity of arbuscular mycorrhizal (AM) fungal communities associating with plants with different growth forms, photosynthetic pathways, CSR strategies, mycorrhizal statuses and N-fixing statuses.

Explanatory variable	Presence-absence				Abundance-weighted			
	Richness	Beta diversity	Phylogenetic diversity	Phylogenetic beta diversity	Ruderal AM fungal taxa	Shannon	Beta diversity	Phylogenetic diversity
Growth form	$F_{2,252} = 7.4^{***}$ ($F_{2,138} = 4.9^{***}$)	$F_{2,245} = 2.0$	$F_{2,242} = 6.1^{***}$ ($F_{2,117} = 5.1^{***}$)	$F_{2,239} = 5.7^{***}$	$F_{2,217} = 3.1^{**}$ ($F_{2,98} = 1.9$)	$F_{2,271} = 2.7^*$ ($F_{2,142} = 2.7^*$)	$F_{2,275} = 1.3$	$F_{2,252} = 2.5^*$ ($F_{2,128} = 2.9^*$)
Photosynthetic pathway	$F_{1,186} = 3.5^*$ ($F_{1,155} = 0.4$)	$F_{1,180} = 16.7^{***}$	$F_{1,186} = 1.3$ ($F_{1,148} = 1.9$)	$F_{1,188} = 5.5^{**}$	$F_{1,187} = 3.5^*$ ($F_{1,133} = 0.29$)	$F_{1,175} = 0.4$ ($F_{1,141} = 3.7^*$)	$F_{1,186} < 0.1$	$F_{1,177} = 2.1$ ($F_{1,152} = 1.9$)
CSR strategy	$F_{1,48} = 6.5^{**}$	$F_{1,58} = 32.9^{***}$	$F_{1,58} = 0.2$	$F_{1,63} = 0.5$	$F_{1,104} = 7.1^{***}$	$F_{1,50} = 1.9$	$F_{1,50} = 4.1^{**}$	$F_{1,50} = 0.1$
Mycorrhizal status	$F_{1,175} = 2.0$ ($F_{1,107} = 0.8$)	$F_{1,173} = 16.5^{***}$	$F_{1,159} = 1.4$ ($F_{1,94} = 1.6$)	$F_{1,155} = 0.3$	$F_{1,137} = 1.6$ ($F_{1,84} < 0.1$)	$F_{1,191} < 0.1$ ($F_{1,111} < 0.1$)	$F_{1,180} = 10.1^{***}$	$F_{1,158} = 2.0$ ($F_{1,95} = 2.8^*$)
N-fixing	$F_{1,312} = 1.5$ ($F_{1,313} = 0.1$)	$F_{1,319} = 3.6^*$	$F_{1,333} = 1.0$ ($F_{1,335} = 0.1$)	$F_{1,340} = 2.2$	$F_{1,359} = 0.4$ ($F_{1,335} = 0.5$)	$F_{1,336} = 0.8$ ($F_{1,335} = 0.3$)	$F_{1,309} = 0.6$	$F_{1,350} = 2.2$ ($F_{1,351} = 1.7$)
								$F_{1,332} = 0.4$ ($F_{1,333} = 0.6$)

F values, with Kenward–Rogers estimated degrees of freedom, resulting from linear mixed models are shown. The response variable ‘Ruderal AM fungal taxa’ was calculated as $\log_e(N_e/N_{\text{total}})$, where N_e and N_{total} are the counts of putatively ruderal (containing sequences from taxonomically described species) and putatively nonruderal VT, respectively. Results in parentheses show marginal effects, after accounting for the effects of other correlated variables (see Supporting Information Fig. S1); note that multivariate beta diversity estimates are defined in relation to a single grouping factor, so no multipredictor models were constructed to explain these variables. Significant effects ($P < 0.05$) are shown in bold type. *, $P < 0.1$; **, $P < 0.05$; ***, $P < 0.01$.

data), with diversity highest in forbs (forbs = 268 ± 2 , grasses = 255 ± 3 , woody = 244 ± 3), C_3 (presence-absence $C_3 = 265 \pm 2$, $C_4 = 242 \pm 5$; abundance-weighted $C_3 = 230 \pm 3$, $C_4 = 187 \pm 7$), ruderal plants (CS = 220 ± 4 , R = 263 ± 24) and non-N-fixing plants (N-fixing = 191 ± 12 non-N-fixing = 228 ± 2 ; Figs 4, S4; Table 2).

The proportion of putatively ruderal taxa in associating AM fungal communities differed between plants with different growth forms, photosynthetic pathways (only when using abundance-weighted data) and CSR strategy (only when using presence-absence data), with a higher fraction or abundance of putatively ruderal taxa associated with forbs (log ratio(ruderal/nonruderal): presence-absence forbs = -1.32 ± 0.02 , grasses = -1.55 ± 0.04 , woody = -1.62 ± 0.05 ; abundance-weighted forbs = -1.56 ± 0.06 , grasses = -2.35 ± 0.09 , woody = -2.58 ± 0.11), C_3 (log ratio(ruderal/nonruderal): $C_3 = -1.60 \pm 0.06$, $C_4 = -2.70 \pm 0.14$) and ruderal (log ratio(ruderal/nonruderal): CS = -1.34 ± 0.04 , R = -0.59 ± 0.19) plants (Figs 5, S5; Table 2). However, the differences between growth forms were no longer significant in models also containing correlated functional groupings (Table 2).

Significant indicator taxa were found for all ecological groups of plants, although most were apparent for woody, C_4 and FM plants (Table S4). In total, 173 AM fungal VT (60%) were a significant indicator for one or more plant functional category, and 88 (30%) could be considered a relatively strong indicator taxon (indicator value > 0.25) for one or more category. There was positive phylogenetic correlation in indicator values for growth form and mycorrhizal status (Figs 6, S6, S7). These indicated that the family Glomeraceae harbours distinct clades that predominately associate with different plant growth forms, and notable clades in Glomeraceae and Claroideoglomeraceae that associate with FM plants. However, negative phylogenetic correlation close to the root appeared to represent a generally stronger association with OM among Glomeraceae, compared with other families.

Discussion

We found that different ecological groups of plants were associated with distinct communities of AM fungi, often exhibiting differences in taxonomic and phylogenetic alpha and beta diversity. A relatively large proportion (*c.* 30%) of AM fungal taxa were significant, and relatively strong, indicators for particular plant groups. There was also phylogenetic signal in certain patterns of association, with closely related AM fungal taxa likely to exhibit similar associations with particular plant growth forms and mycorrhizal statuses. The only AM fungal functional characteristic we could include in the analysis, putatively ruderal status, varied in relation to the ruderality of plant species: ruderal plant species were associated with a higher fraction of putatively ruderal AM fungal taxa. Incorporating functional information into the study of shared plant-AM fungal dynamics opens new perspectives on the functioning of the symbiosis and on links with ecosystem-level processes.

Fig. 4 Phylogenetic alpha and beta diversity (unweighted by abundance) in arbuscular mycorrhizal (AM) fungal communities associating with different functional groups of plants. R, ruderal plants; CS, nonruderal plants; OM, obligately mycorrhizal; FM, facultatively mycorrhizal. For display purposes, data points (grey points) represent species-level means of individual plant-level observations. Large white points indicate means; bars indicate medians; boxes indicate interquartile ranges (IR); whiskers indicate minima and maxima ($< 1.5 \times \text{IR}$). Letters above boxes indicate significant differences between groups.

The differences we observed in relation to plant growth form build on previous meta-analyses reporting plant functional group as a major driver of plant responses to AM fungal inoculation (Hoeksema *et al.*, 2010) and differences in the extent of root AM fungal colonisation (Bunn *et al.*, 2015). Differences in AM fungal community composition in relation to plant growth form have only previously been reported from a very limited set of plant species (Vandenkoornhuyse *et al.*, 2002; López-García *et al.*, 2017; Sepp *et al.*, 2019). Among a taxonomically and geographically wide set of plants, we observed highest richness in AM fungal communities associating with grasses, with forbs and especially woody plants harbouring lower richness. This matches the earlier observation that woody plants harbour fewer AM fungi than nonwoody plants, which was ascribed to greater specialism among the former (Pölme *et al.*, 2016), and the finding that grasses associate with a larger number of nonspecialised partners, compared with forbs (Sepp *et al.*, 2019). The differences in diversity between growth forms – especially woody vs other growth forms – are also consistent with earlier analyses noting lower alpha diversity, and higher beta diversity, of AM fungal

communities in forests compared with grasslands at sample, plot and site scales (Davison *et al.*, 2015, 2016; Pärtel *et al.*, 2017). Notably, the patterns of richness and taxonomic beta diversity were not mirrored by those of phylogenetic diversity, with both phylogenetic alpha and beta diversity highest among forbs. Taken together, the results may be indicative of alternative strategies among grasses and forbs, whereby grasses tend to form a large number of nonspecific associations, while forbs tend to form fewer partnerships but favour different characteristics among partner fungi. It is notable that forbs generally show stronger responses to inoculation with AM fungi, compared with other plant growth forms (Hoeksema *et al.*, 2010). By associating with a phylogenetically diverse range of AM fungi, forbs might receive additive nutritional and nonnutritional (e.g. pathogen protection) mycorrhizal benefits, which are to some degree phylogenetically conserved among AM fungi (Powell *et al.*, 2009). Forbs also associated with a relatively large number of putatively ruderal AM fungi. While there may be explanations connected with growth form *per se* or with the plant growth forms associated with the culturing of AM fungi, it should be noted that forbs are more

Fig. 5 Fraction of putatively ruderal taxa in arbuscular mycorrhizal (AM) fungal communities associating with different functional groups of plants. R, ruderal plants; CS, nonruderal plants; OM, obligately mycorrhizal; FM – facultatively mycorrhizal. The ruderal fraction was calculated as $\log_e(N_c/N_u)$, where N_c and N_u are the counts of putatively ruderal (containing sequences from taxonomically described species) and putatively nonruderal VT, respectively. For display purposes, data points (grey points) represent species-level means of individual plant-level observations. Large white points indicate means; bars indicate medians; boxes indicate interquartile ranges (IR); whiskers indicate minima and maxima ($< 1.5 \times \text{IR}$). Letters above boxes indicate significant differences between groups.

likely than other growth forms to be ruderal. This was not clear in the current data set – probably due to missing CSR strategy data for many species – whereas in Biolflor (Klotz *et al.*, 2002), which contains information about > 3000 plant species, 25% of forbs are ruderal, compared with 4% among the other plant growth forms. It should also be noted that differences between growth forms in the abundance of associating ruderal fungi were no longer significant when correlated functional groups were included in the models.

We found that AM fungal community composition differed between C_4 and C_3 plants. Hoeksema *et al.* (2010) and Grman (2012) reported that C_3 grasses have lower mycorrhizal responsiveness and root colonisation than C_4 grasses, but, to our knowledge, there have been no earlier studies investigating the composition of AM fungal communities associating with these two plant groups. We found that there was a trend for C_4 plants to associate with a higher number of partners, and, interestingly, while taxonomic beta diversity was higher among communities associating with C_4 plants, phylogenetic beta diversity was higher among communities associating with C_3 plants. This suggests that C_4 plants associate in particular with certain fairly closely related clades of AM fungal taxa; however, this pattern was not clearly apparent in the phylogenetic correlation analysis. Further studies should target differences between C_4 and C_3 plants under controlled conditions to assess the physiological basis for differences in associations with AM fungal partners.

Root AM fungal communities differed among plant groups according to a simplification of CSR strategies: the distinction between ruderal and other strategies. The communities of AM fungi associating with ruderal plants exhibited lower richness, had higher beta diversity and comprised a greater fraction of putatively ruderal taxa, compared with those associating with other plants. It is notable that significant differences were apparent even though CSR information was available for small numbers of plant species and the models consequently had low power. The precision of estimates could be improved by obtaining AM fungal community data from further plant species and by assigning CSR status to new species. The finding of low-diversity AM fungal communities among ruderal plants mirrors the low levels of mycorrhizal fungal colonisation recorded among such plants (Betekhtina & Veselkin, 2011) and may reflect the same selective pressures (e.g. symbiont limitation, high nutrient availability) that are believed to favour nonmycorrhizal plants in disturbed habitats (Harley & Harley, 1987; Peat & Fitter, 1993; Brundrett, 2009). Recent studies have suggested that unstable environmental conditions favour putatively ruderal AM fungal taxa (García de León *et al.*, 2018a,b,c). Our study confirms that this is reflected in the symbiotic partnerships that emerge in such environments, such that ruderal plants form associations with ruderal AM fungal taxa. The extent to which this reflects co-adaptation to common environmental conditions or is driven by the characteristics of either or both partner groups is unclear.

Fig. 6 Phylogenetic correlation in arbuscular mycorrhizal (AM) fungal VT indicator values (IV) for (a) plant growth forms and (b) mycorrhizal statuses. In each panel the barplot at the tips of the phylogenetic tree shows the maximal indicator value for each VT and the plant functional group category represented by the maximal value. Points next to bars indicate significant ($P < 0.05$) indicator values. At the bottom of each panel a phylogenetic correlogram shows how correlation between VT indicator values changes as a function of VT relatedness (i.e. evolutionary age). The dashed line shows the point correlation coefficient estimate, while the grey envelope shows the 95% confidence interval derived from bootstrapping. AC, Acaulosporaceae; AMB, Ambisporaceae; AR, Archaeosporaceae; CL, Claroideoglomeraceae; DIV, Diversisporaceae; GIG, Gigasporaceae; GL, Glomeraceae; PAC, Pacisporaceae; PAR, Paraglomeraceae.

Plant mycorrhizal status clearly correlated with the beta diversity of associated AM fungal communities, with higher diversity among OM plants. While earlier studies have reported positive

correlations in the beta diversity of plant and AM fungal communities (Yang *et al.*, 2017; Chen *et al.*, 2018), and argued that plant community composition drives AM fungal beta diversity, this is the first study to record a difference in the beta diversity of AM fungal communities associating with different plant functional groups. The result is consistent with Sepp *et al.* (2019) who found that, compared with FM plants, OM plants exhibited less specialised associations with AM fungi. There was phylogenetic signal in AM fungal indicator values for plants with different mycorrhizal statuses, such that certain within-family clades of AM fungal taxa exhibited consistently stronger associations with one or other of the plant groups. Negative phylogenetic correlation close to the root of the phylogeny appeared to indicate that Glomeraceae overall formed stronger associations with OM plants, while other families associated relatively more with FM plants.

Only minor differences in AM fungal alpha, beta or phylogenetic diversity were detected in relation to plant N-fixing status. This is likely to be in part a question of statistical power, stemming from the relatively low number of data points representing plants that associate with N-fixing symbionts. Nonetheless, there was a systematic compositional difference between AM fungal communities associating with N-fixing and non-N-fixing plants, as well as slightly higher phylogenetic beta diversity among the latter group. Further investigation of these phenomena could yield important insights into the factors controlling the establishment of the AM symbiosis, and of the functioning of multipartite symbiotic networks in nature.

The findings described here indicate that plant adaptations to environmental conditions are inherently related to plant interactions with symbiotic AM fungi, and suggest that symbiont selection is an important adaptation strategy of plants. We also show association between ruderal plants and putatively ruderal AM fungal taxa. However, our understanding of the characteristics and strategies of AM fungal taxa remains largely indirect and incomplete. Future investigations of symbiotic interactions among the full diversity of plant and AM fungal taxa would benefit from parallel use of functional classifications for both partner groups.

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Author contributions

MZ, MM, MÖ and JD conceived the ideas and designed methodology; CGB, MB, MG, DL, YM, VDP, NAS, LT, SV and BW collected the data; DG, JD, SKS and TV analysed the data; DG, MZ and JD led the writing of the manuscript. All

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Mosaic plots showing pairwise relationships between plant functional groupings.

Fig. S2 Compositional differences in arbuscular mycorrhizal (AM) fungal communities associating with different functional groups of plants.

Fig. S3 Shannon index (asymptotic extrapolation; INEXT) and beta diversity of arbuscular mycorrhizal (AM) fungal communities associating with different functional groups of plants.

Fig. S4 Phylogenetic alpha and beta diversity (weighted by abundance) in arbuscular mycorrhizal (AM) fungal communities associating with different functional groups of plants.

Fig. S5 Abundance of putatively ruderal taxa in arbuscular mycorrhizal (AM) fungal communities associating with different functional groups of plants.

Fig. S6 Phylogenetic tree of arbuscular mycorrhizal (AM) fungal VT showing indicator species values for different plant growth forms.

Fig. S7 Phylogenetic tree of arbuscular mycorrhizal (AM) fungal VT showing indicator species values for different plant mycorrhizal statuses.

Table S1 Summary of sampled plant species, functional groupings, locations and studies providing the raw data.

Table S2 Sources used to assign mycorrhizal status to plant species.

Table S3 Virtual taxa (VT) containing sequences from taxonomically described species, maintained in culture, according to records in the MaarjAM database (status June 2019).

Table S4 Significant indicator arbuscular mycorrhizal (AM) fungal virtual taxa (VT) for different plant functional groups.

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