RESEARCH ARTICLE

Arbuscular mycorrhizal fungal communities in plant roots are not random assemblages

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Abstract

We investigated whether arbuscular mycorrhizal fungal (AMF) communities in plant roots are random subsets of the local taxon pool or whether they reflect the action of certain community assembly rules. We studied AMF small subunit rRNA gene sequence groups in the roots of plant individuals belonging to 11 temperate forest understorey species. Empirical data were compared with null models assuming random association. Distinct fungal species pools were present in young and old successional forest. In both forest types, the richness of plant–AMF associations was lower than expected by chance, indicating a degree of partner selectivity. AMF communities were generally not characteristic of individual plant species, but those associated with ecological groups of plant species – habitat generalists and forest specialists – were nonrandom subsets of the available pool of fungal taxa and differed significantly from each other. Moreover, these AMF communities were the least distinctive in spring, but developed later in the season. Comparison with a global database showed that generalist plants tend to associate with generalist AMF. Thus, the habitat range of the host and a possible interaction with season played a role in the assembly of AMF communities in individual plant root systems.

Introduction

Arbuscular mycorrhizal fungi (AMF) (phylum *Glomeromycota*) colonize the roots of most terrestrial plants, facilitating mineral nutrient uptake from soil in exchange for plant-assimilated carbon (Smith & Read, 2008). While AMF have repeatedly been shown to exhibit host-specific growth responses (Bever, 2003) and to induce differential growth responses in host plant species (van der Heijden *et al.*, 1998; Klironomos, 2003), the degree of selectivity in natural associations remains unresolved. Many observations suggest that there is little or no partner specificity (i.e. exclusive association with a single taxon) in plant–AMF combinations (Smith & Read, 2008, p. 35). Indeed, the low number of AMF species [over 200 morphospecies – A. Schüßler's *Glomeromycota* phylogeny, http://www.lrz.de/~schuessler/amphylo/, or nearly 300 small subunit (SSU) rRNA gene sequence groups – Öpik *et al.*, 2010] compared with the very large number of potential host species (perhaps 200 000 or 80–90% of terrestrial plants) implies that each fungal taxon must have many hosts.

However, the results of studies assessing plant–AMF compatibility using spore inoculation (Giovannetti & Hepper, 1985; Bever *et al.*, 1996; Smith & Read, 2008) and more recently molecular studies addressing AMF communities in plant roots have started to reveal a more complex picture. Although most AMF taxa may be capable of colonizing a number of plant species, there is significant evidence to suggest that not all combinations of plant–fungal associations are equally likely to occur (Fitter, 2005; Helgason & Fitter, 2005). Öpik *et al.* (2010) summarized current knowledge about the global distribution of SSU-rRNA-gene-based AMF molecular taxa and found that they are unevenly distributed among vascular plant superorders. Case studies have also described divergent AMF communities in the roots of different coexisting plant species (Helgason *et al.*, 2002; Vandenkoornhuyse *et al.*, 2002, 2003; Scheublin *et al.*, 2004; Pivato *et al.*, 2007; Santos-Gonzalez *et al.*, 2007; Sýkorová *et al.*, 2007b; Öpik *et al.*, 2008; Li *et al.*, 2010). In principle, such findings could be related to the abundance (Dumbrell *et al.*, 2010a), life history (Sýkorová *et al.*, 2007a) or ecology (Chaudhary *et al.*, 2008; Dumbrell *et al.*, 2010b) of either fungal or plant partners. For

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example, Öpik *et al.* (2009) found that plant species and fungal taxa that could be characterized as habitat generalists frequently associated with one another, while forest specialist plants and fungi were similarly associated.

Although information about AMF communities in the roots of different plant species is accumulating, the related question of whether such communities are truly a nonrandom selection of taxa from the relevant local fungal taxon pool remains unclear. Community ecology has for decades considered so-called assembly rules, i.e., the processes governing the nonrandom component in community composition, which can be deduced by comparing certain parameters of an observed data set with the same parameters in multiple randomized data sets (Gotelli & Graves, 1996; Gotelli, 2000; Watkins & Wilson, 2003). However, the approaches used hitherto to study AMF communities have not sampled a sufficiently large number of plants (individuals and species) for the underlying pool of AMF taxa to be described with accuracy. Moreover, the analytical approaches used previously have generally been limited to simple permutation of data matrices to infer the importance of experimental or environmental factors in shaping AMF communities. In order to evaluate whether AMF communities in the roots of plant species are nonrandom assemblages, data are required from a representative number of plant individuals and species, collected from the same area and thus exposed to the same AMF taxon pool.

Here, we report new information on AMF communities at the level of plant individuals belonging to six forest understorey species. Using this information and published data from a further five species from the same location, we investigate whether the AMF communities in plant roots are random subsets of the local taxon pool or whether they reflect the action of community assembly rules. We compare the actual distribution of AMF taxa among plant individuals against null models that represent random colonization of plants by AMF taxa. If there are rules governing community assembly, we aim to investigate how these are related to the seasonal and successional dynamics of plant communities. Further, we test Öpik *et al.*'s (2009) hypothesis in the framework of assembly rules by considering whether AMF and plants exhibit deviations from random assembly at the level of ecological groups.

Materials and methods

Study area and sampling

The study was carried out in Koeru boreo-nemoral forest, Estonia (58°58′N; 26°03′E), which is home to one of the best-studied AMF communities (Öpik *et al.*, 2008, 2009; Moora *et al.*, 2011; Powell *et al.*, 2011; Unterseher *et al.*, 2011), and from where 46 AMF SSU rRNA gene sequence groups have been recorded previously (according to Öpik *et al.*, 2010; 51 according to the nomenclature in Öpik *et al.*, 2009). The study area consists of 130 ha of spruce *Picea abies* forest (*Hepatica nobilis* Mill. site type) on a calcaric cambisol. Detailed descriptions of the area are provided by Moora *et al.* (2007, 2009) and Zobel *et al.* (2007).

In a previous study (Öpik *et al.*, 2008), we described AMF communities in 90 individuals belonging to five plant species: *Fragaria vesca*, *Galeobdolon luteum* (note that *Lamiastrum galeobdolon* is a synonym for this species), *H. nobilis*, *Oxalis acetosella* and *Trifolium pratense* (Table 1).

Table 1. Sampling of plant species and individuals in relation to sampling month and forest habitat type

	Young forest stands			Old forest stands				
Plant	June	July	October	June	July	October	Total	Sources
Generalists								
Fragaria vesca	2 (32)	0(0)	3 (44)	4 (28)	5 (44)	5 (58)	19 (206)	Öpik *et al.* (2008)
Geranium pratense	0 (0)	3 (31)	5 (57)	1 (9)	3 (42)	4 (51)	16 (190)	This study
Geum rivale	0 (0)	5 (65)	5 (63)	0 (0)	2 (27)	3 (53)	15 (208)	This study
Hypericum maculatum	1 (11)	4 (41)	2 (29)	2 (26)	2 (28)	2 (30)	13 (165)	This study
Trifolium pratense	NA	3 (31)	4 (26)	NP	NP	NP	7 (57)	Öpik *et al.* (2008)
Veronica chamaedrys	5 (49)	5 (51)	4 (55)	2 (28)	6 (77)	7 (96)	29 (356)	This study
Forest specialists								
Galeobdolon luteum	NP	NP	NP	NP	3 (36)	3 (39)	6 (75)	Öpik *et al.* (2008)
Hepatica nobilis	5 (41)	6 (74)	6 (64)	5 (31)	4 (50)	5 (48)	31 (308)	Öpik *et al.* (2008)
Oxalis acetosella	2 (27)	6 (67)	3 (26)	4 (33)	5 (19)	6 (48)	26 (220)	Öpik *et al.* (2008)
Paris quadrifolia	3 (44)	5 (73)	2 (29)	4 (48)	6 (91)	NP	20 (285)	This study
Viola mirabilis	4 (71)	6 (93)	6 (80)	2 (18)	6 (74)	6 (80)	30 (416)	This study
Total	22 (275)	43 (526)	40 (473)	24 (221)	42 (488)	41 (503)	212 (2486)	

Numbers of plant individuals from which DNA was successfully amplified are shown, with the number of recovered AMF SSU rRNA gene clones in parentheses. Numbers of plant individuals from which DNA was successfully amplified are shown (six individuals per sampling month per stand were subjected to analyses if not stated otherwise). NP indicates that the species was not present, while NA indicates that it was not analysed. Sequencing data for different plant species were generated in this study or taken from Öpik *et al.* (2008).

This information is used in the current analysis. In addition, we present new data from 123 individuals belonging to six further plant species: *Geranium pratense*, *Geum rivale*, *Hypericum maculatum*, *Paris quadrifolia*, *Veronica chamaedrys* and *Viola mirabilis* (Table 1). All sampled plant species were classified into two groups according to their habitat preference as presented in the BiolFlor database (Klotz *et al.*, 2002): typical forest plant species (five species, hereafter called forest specialists) and plant species growing in a wide range of habitats including grasslands and forests (six species, hereafter called generalists; Table 1). This classification is consistent with the habitat preferences of the study species in Estonia according to Paal (1997), as well as descriptive studies of forest (Moora *et al.*, 2007; Aavik *et al.*, 2009) and grassland vegetation (Pärtel *et al.*, 1999; Aavik *et al.*, 2008).

Sampling of the six additional plant species followed the same procedures as described in Öpik *et al.* (2008). Briefly, this consisted of sampling two forest ecosystems of different age and management intensity: three mature old growth spruce forest stands (old forest stands) and three early successional stands in areas that were clear-cut approximately 25 years ago (young forest stands). Individual plants were sampled from a 10×10 m plot in each stand at the beginning of June, the end of July and the beginning of October in 2003. These sampling times were chosen to represent the beginning of the plant growth season, the mid-season and the end of the growth season in the study ecosystem. Entire plant individuals of each species were excavated from the sampling area if present. Roots were cleaned in the laboratory, dried with silica gel and stored before analysis. Generally, a maximum of two individuals from each plant species per plot per sampling time were included in subsequent analyses (Table 1; a third individual of *V. chamaedrys* was sampled from one old forest stand in October).

Molecular analyses

Molecular analyses followed those described by Öpik *et al.* (2008), with the sole difference being the cloning vector used (pCR2.1-TOPO vector as opposed to pGEM-T Easy). In brief, a 20-cm subsample of the root system of each plant individual was pulverized and DNA extracted using the Nucleospin® 96 Plant kit (Macherey-Nagel, Düren, Germany). Subsequent PCR reactions contained Expand High Fidelity Buffer (Roche Applied Science, Mannheim, Germany) with 15 mM $MgCl_2$, 100 nM of each of the dNTPs, 200 nM of each of primers NS31 and AM1 (Simon *et al.*, 1992; Helgason *et al.*, 1998), 20 mg mL^{-1} bovine serum albumin, 0.7 U of Expand High Fidelity enzyme mix (Roche Applied Science) and 5 μL of DNA. Thermocycling conditions were as follows: 94 °C for 2 min; 10 cycles of 94 °C for 15 s, 58 °C for 30 s and 72 °C for 45 s; 20 cycles of 94 °C for 15 s, 58 °C for 30 s and 72 °C for 45 s+5 s per cycle; and 72 °C for 7 min using a DNAEngine PTC Dyad thermocycler (MJ Research, Reno, NV).

PCR products were purified using the MinElute PCR Purification kit (Qiagen, Crawley, UK), and cloned and sequenced following the method of Griffiths *et al.* (2006). Purified PCR products were inserted into the pCR2.1-TOPO vector (Invitrogen, Paisley, UK) by the College of Life Sciences Cloning Service at the University of Dundee, Dundee, UK. From each sample, 48 white or light blue colonies were selected and stored. Colonies were grown in 1 mL of 2 × Luria–Bertani broth with 0.15 mg mL^{-1} ampicillin in deep-well microtitre plates. Plasmids were purified using a Multiscreen Plasmid Minipreparation Kit (Millipore, Bedford, MA). Sequencing of 16 clones per sample was performed using the BigDye® Terminator v3.1 Cycle Sequencing kit (Applied Biosystems, Warrington, UK) with vector primers directed against the SP6 or T7 promoter regions. Sequencing reactions were purified using 96- or 384-well Geneclean plates (Genetix, Queensway, New Milton, UK) and run on an ABI Prism 3700 DNA Analyzer (Applied Biosystems). For some samples, 16 further randomly chosen clones were sequenced in order to obtain enough sequences of good quality.

Phylogenetic analysis

The new sequences, those from Öpik *et al.* (2008) and *Glomeromycota* reference sequences from the Maarj*AM* database (http://maarjam.botany.ut.ee/; Öpik *et al.*, 2010) were aligned automatically using the MAFFT multiple sequence alignment web service in JALVIEW version 2.6.1 (Waterhouse *et al.*, 2009), and subjected to neighbour-joining (NJ) analysis (F84 model with gamma substitution rates) in TOPALI version 2.5 (Milne *et al.*, 2004). Sequence groups containing the Koeru sequences of interest in this study (i.e. the new sequences and those from Öpik *et al.*, 2008) were delimited based on the NJ tree at ≥97% sequence similarity. Representative sequences from each sequence group were subjected to BLAST searches with default settings against the Maarj*AM* (status 28.01.2011, Öpik *et al.*, 2010) and GenBank databases. Fifty-seven sequences appeared to belong to Ascomycetes and Basidiomycetes and were excluded from further analyses. In total, 2486 good-quality *Glomeromycota* sequences were retained in the analysis (Table 1). For subsequent analyses, the phylogenetically delimited sequence groups were assigned to the respective virtual taxa (VT) from the Maarj*AM* database (Supporting Information, Table S1) on the basis of the NJ tree and the BLAST against Maarj*AM*. Representative sequences of detected sequence groups were submitted to the European Molecular Biology Laboratory Nucleotide Sequence Database (accession numbers FR728433–FR728626 and FR837672-

FR837673). For illustrative purposes, a phylogenetic tree containing sequences from major clades of *Glomeromycota* and the representatives of each sequence group was generated using BEAST (version 1.5.3; Drummond & Rambaut, 2007). The HKY+I+G nucleotide substitution model was selected on the basis of AIC (JMODELTEST; Posada, 2008). A burn-in corresponding to 10% of samples was discarded and trees were drawn every 1000 generations from three independent runs of 10 000 000 generations. The results are summarized on a maximum clade credibility tree.

Statistical data analyses

Null model construction

Selectivity in plant–AMF associations was analysed in the framework of assembly rules (Gotelli, 2000; Watkins & Wilson, 2003). The nonrandom component of plant–AMF associations was detected by comparing the characteristics of an observed data matrix with those from multiple randomized matrices. The observed data consisted of a matrix with 212 individual plants in rows (i) and 40 fungal VT in columns (j). Thus, cell i, j of the matrix was filled with the count of clones corresponding to VT j derived from plant individual i.

The choice of the randomization algorithm is important for ensuring that randomized matrices represent the desired null model (i.e. the null hypothesis that the observed pattern is a product of chance). Ecological mechanisms that are excluded from the null model can generate deviation from a random pattern. We used two algorithms in order to impose slightly different constraints and assumptions:

(1) *Randomization algorithm 1* – '*permatswap*': Clones were assumed to be independent; thus, different clones from a single sample could be separately redistributed throughout the matrix during randomization. We fixed row and column sums and matrix fill, so that in both the original and every randomized matrix (i), plant individuals were associated with the same number of fungal clones; (ii) the overall counts of particular VT did not vary; and (iii) the overall number of plant–AMF associations did not vary. Thus, while the number of plant–AMF associations was strongly constrained by the randomization procedure, the precise identity of the associations was not. The quasiswapcount algorithm, implemented using the permatswap function in the R package vegan (Oksanen *et al.*, 2010), was used for this randomization.

(2) *Randomization algorithm 2* – '*permatfull*': AMF form individual structures that may extend spatially over areas that exceed the size of the sampling units used in this study (Rosendahl & Stukenbrock, 2004). In order to reflect the potential nonindependence between clones, we replicated the analysis using a less constrained, but sample-based procedure (i.e. permutation of matrix cells) within the permatfull function in R package vegan. Using this approach, column sums were constrained during randomization, and matrix fill remained constant as a result of the permutation, but row sums were allowed to vary. Thus, the overall count for each VT and the overall number of plant–AMF associations were held constant, but the numbers of fungal clones associated with plant individuals varied.

Although located in a homogeneous habitat, sampling was conducted in six spatially distinct stands within the forest. Therefore, both algorithms were further constrained to perform randomization separately within each stand. The combinations of constraints used by both randomization algorithms are considered to be conservative because of expected low type I error (Gotelli, 2000; the approaches correspond to Gotelli's Sim2 and Sim9).

Factors influencing AMF community composition in Koeru

For an overview of AMF communities in Koeru, the effects of certain factors were investigated using the permutational multivariate analysis of variance (PERMANOVA) function *adonis* from vegan, with the Bray–Curtis distance (BC) used as a measure of community dissimilarity. Separate models were constructed containing the following factors: forest successional stage (young or old), season (June, July or October) and either plant species (11 species) or plant ecological group (generalist or forest specialist). Rather than using the default permutation test to assess the significance of effects, we repeated the PERMANOVA procedure 999 times on data matrices randomized according to the permatswap algorithm (which meets the requirement of constant row fill), and the number of randomized pseudo-F statistics more extreme than the observed value was used to estimate P.

Selectivity in associations between plants and AMF

Because our focus was primarily on selectivity in associations between AMF and plants, the following questions were investigated:

(1) *Richness*: Are AMF richness per plant species or plant ecological group, and plant richness per AMF VT lower than expected by chance? Low richness may be indicative of host preference. Richness measures from the original data matrix were compared with analogous measures from 999 randomized matrices.

(2) *Community assembly* (BC_{diff}): Do the AMF communities associated with particular plant species and ecological groups differ from random subsets of the local fungal taxon pool? Species- or ecological group-level BC was calculated

between the observed matrix and each of 999 randomized matrices (BC[observed vs. random] = BC_{or}). In parallel, BC was calculated for 999 randomized vs. randomized matrices (BC[random vs. random] = BC_{rr}). The latter calculation provided a population of BC measures that might be expected to arise by chance. The vector of 999 BC_{rr} values was subtracted from the vector of 999 BC_{or} in a random pairwise manner to produce a final vector of 999 values ($BC_{diff} = BC_{or} - BC_{rr}$). BC_{diff} has an expected value of 0 if the community composition is random.

(3) *Pairwise comparison of communities* (BC_{pair}): Are plant species and ecological groups associated with different communities of AMF? BC was calculated between the AMF communities associated with all pairs of plant species and between habitat generalist and forest specialist plants in the observed matrix (BC[group1 vs. group2] = BC_{pair}). Each value was compared with 999 analogous measures from randomized matrices.

We applied these analyses to subsets of the data matrix representing different successional stages or seasons in order to assess whether the assembly rule varied in relation to these factors. For approaches (i) and (iii), 95% quantiles within the 999 randomized values were calculated, and the *P* values were approximated based on the number of randomized values more extreme than the observed value. For approach (ii), 95% quantiles of BC_{diff} were calculated, and *P* values were approximated based on the number of BC_{diff} values below 0.

Indicator species analyses

To identify the organisms involved in nonrandom associations, we tested whether any fungal VT could be characterized as 'indicator species' for certain plant species or ecological groups. We used Dufrêne–Legendre indicator analysis (Dufrêne & Legendre, 1997) as implemented by the indval function from the R package labdsv (Roberts, 2010). This index varies from 0 to 1 and would be maximal if all examples of a VT were distributed among all individuals of only one plant species or ecological group. The indval function uses unconstrained permutation; hence, the randomization procedure is not directly comparable to those used in other analyses. For each indicative fungal VT, the previously recorded habitat range was compiled (in August 2010) using the metadata that accompany accessions in the Maarj*AM* database. The proportion of accessions coming from forest habitat was calculated for each taxon. All analyses were carried out using R 2.10.1.

Results

Glomeromycota diversity in Koeru forest

Forty VT were detected in a combined set of new and previously published (Öpik *et al.*, 2008) sequences from 11 plant species in Koeru forest. The sequences belonged to *Glomeraceae* (27 VT), *Gigasporaceae* (2), *Acaulosporaceae* (7) and *Diversisporaceae* (4) (Fig. S1, Table S1). Seven of the detected VT were new to Koeru forest (not detected by Öpik *et al.*, 2008, 2009) and included two VT not previously detected elsewhere (VT 315, VT 316). This analysis brings the number of known *Glomeromycota* VT recorded at the site to 53. The AMF community composition at Koeru was significantly influenced by plant identity – both in models containing plant species (PERMANOVA: pseudo-$F = 1.96$, $P < 0.01$) and plant ecological group (pseudo-$F = 5.06$, $P < 0.01$) – and forest successional stage (in a model containing plant species: pseudo-$F = 5.10$, $P < 0.01$; in a model containing plant ecological group: pseudo-$F = 4.98$, $P < 0.01$), but not by season or any interaction between factors.

Richness of partners in plant–fungal associations

Plant species were on average associated with 16.8 AMF VT, which was significantly fewer than expected from either randomization approach ($P < 0.01$; Fig. 1; Table S2). The mean AMF richness was higher among forest specialist (18.8) than generalist (15.2) plants. Fungal VT were also associated with significantly fewer of the studied plant species (4.6 on average) than expected by chance ($P < 0.01$; Fig. 1). Significantly fewer associations between plant species and fungal VT than expected by chance were recorded in both successional stages and all seasons using permatswap (all $P < 0.01$) and in the young forest successional stage and the June and July sampling times ($P < 0.05$) using permatfull (Table S2). Overall, four out of 11 plant species (two generalists and two forest specialists) were associated with fewer fungal VT than expected using permatswap, while there was only one species-level deviation (*H. maculatum* – generalist) from random using permatfull (Table S2). Meanwhile, four out of 40 fungal VT were associated with fewer plant species than expected using permatswap, while permatfull did not reveal any VT-level deviations from random (Table S2). When the data were split by season or successional stage, fewer taxa differed significantly in the richness of their associations (Table S2).

Composition of AMF communities associated with plant species and plant ecological groups

In general, the composition of AMF communities associated with plant species did not differ significantly from random subsets of the local AMF pool (as measured by BC_{diff}), except the community associated with *V. mirabilis* (95% quantiles of $BC_{diff} = 0.01 - 0.245$, $P < 0.05$ using permatswap; Table S3). However, the fungal communities associated with the two ecological groups of plants differed significantly from random (Fig. 2). When the data were restricted

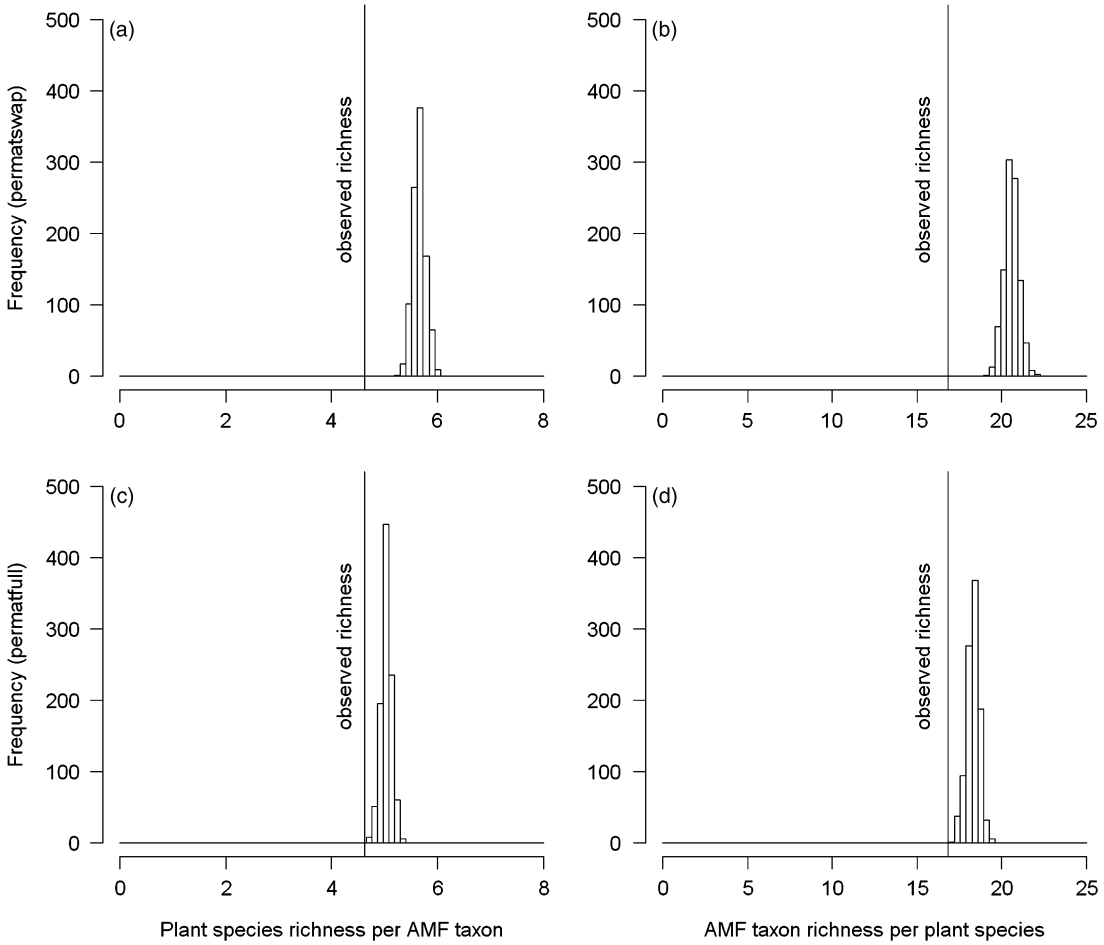

Fig. 1. Richness of the associations between plant species and AMF sequence groups. The mean richness of sequence groups associating with study plant species and the mean number of study plant species associating with sequence groups are shown. Bars show the distribution of mean richness values resulting from 999 randomizations of the data matrix; the solid line indicates the observed richness value. (a, b) Randomized values from the permatswap algorithm; (c, d) values from the permatfull algorithm (see Materials and methods for further details). In all cases, observed richness was lower than expected from randomization.

to particular seasons or successional stages, the only deviations from random occurred among the plant ecological groups during the July sampling time using the permatswap algorithm (forest specialists: 95% quantiles of $BC_{diff} = 0.007 - 0.153$, $P < 0.05$; generalists: 95% quantiles of $BC_{diff} = 0.009 - 0.201$, $P < 0.05$; Table S3).

The AMF communities associated with pairs of plant species differed significantly in certain cases (i.e. BC_{pair}; permatswap: $P < 0.05$ in 14/55 pairs; permatfull: $P < 0.05$ in 7/55 pairs; Table S4). Pairwise differences were most frequently observed between plant species corresponding to the two different ecological groups: using permatswap, 16% of the within-ecological group comparisons (i.e. a forest specialist species vs. forest specialist species or generalist species vs. generalist) exhibited significant differences, compared with 33% of the between-ecological group comparisons (i.e. a forest specialist species vs. generalist species; Table S4).

Correspondingly, the AMF communities associated with the two ecological groups of plants were clearly distinct from each other ($P < 0.01$ using both randomization algorithms; Fig. 3). Significant differences between the two groups were observed in both young and old stands using both randomization algorithms ($P < 0.01$; Table 2). Meanwhile, forest specialist and generalist plant species were not associated with significantly different AMF communities in June, but later in the season, AMF communities emerged that differed significantly between the ecological groups of plants ($P < 0.05$ using both randomization algorithms; Table 2).

Indicator VT

Certain AMF VT were significantly indicative of particular plant species or plant ecological groups in the overall data matrix or in subsets of the data split according to

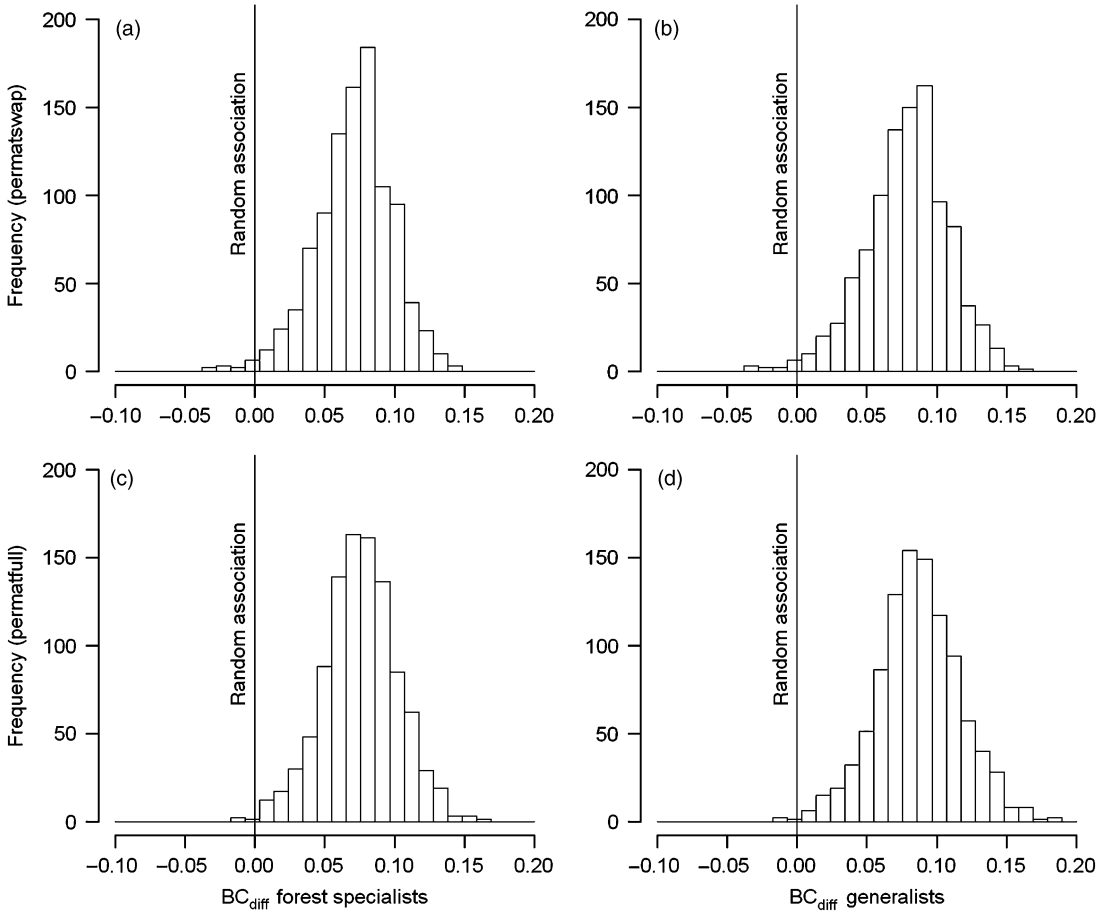

Fig. 2. Difference in BC between real and randomized AMF communities (BC_{diff}) associated with habitat generalist and forest specialist plant species. For a precise calculation of BC_{diff} see Materials and methods. Bars indicate the values of BC_{diff} resulting from 999 randomizations. (a, b) Randomized values from the permatswap algorithm; (c, d) values from the permatfull algorithm. The solid line at 0 indicates the expected value if the AMF communities associated with each group are not different from random. In all instances, the 95% quantiles within the BC_{diff} values were > 0 ($P < 0.05$).

successional stage or season (Table 3). Notably, fewest fungal taxa (2) were at all indicative of any plant or plant ecological group during the first sampling time (June; Table 3). Accessions in the Maarj*AM* database (Öpik *et al.*, 2010) representing the VT that were important indicators of forest plants overall in this study were more frequently recovered from forest habitats (18/29 or 62% of accessions) than those associated with VT that were indicative of generalist plants (28/141 or 20% of accessions; $\chi^2 = 19.6$, d.f. = 1, $P < 0.01$).

Discussion

Arbuscular mycorrhizal fungi have traditionally been regarded as low-specificity mutualists that associate with a wide range of plant partners (Smith & Read, 2008). Nonetheless, it is becoming increasingly clear that distinct AMF communities are present in the rhizosphere (Bever *et al.*, 1996, 2001; Eom *et al.*, 2000) and associate with the roots of different plant species (Helgason *et al.*, 2002; Vandenkoornhuyse *et al.*, 2002, 2003; Scheublin *et al.*, 2004; Pivato *et al.*, 2007; Santos-Gonzalez *et al.*, 2007; Sýkorová *et al.*, 2007b; Mummey & Rillig, 2008; Öpik *et al.*, 2008; Li *et al.*, 2010). However, to the best of our knowledge, no previous studies have made a statistical comparison of the AMF associating with a large number of plant species from the same plant community. Thus, it is largely unclear to what extent plant-species- or plant-ecological-group-level AMF communities simply reflect a random sample of the local AMF taxon pools.

The assembly rules approach attempts to identify the processes influencing biological communities by comparing the parameters of real community matrices with the same parameters in matrices that have been randomized according to a chosen algorithm. The randomization algorithm is not merely a mathematical construct, but also the

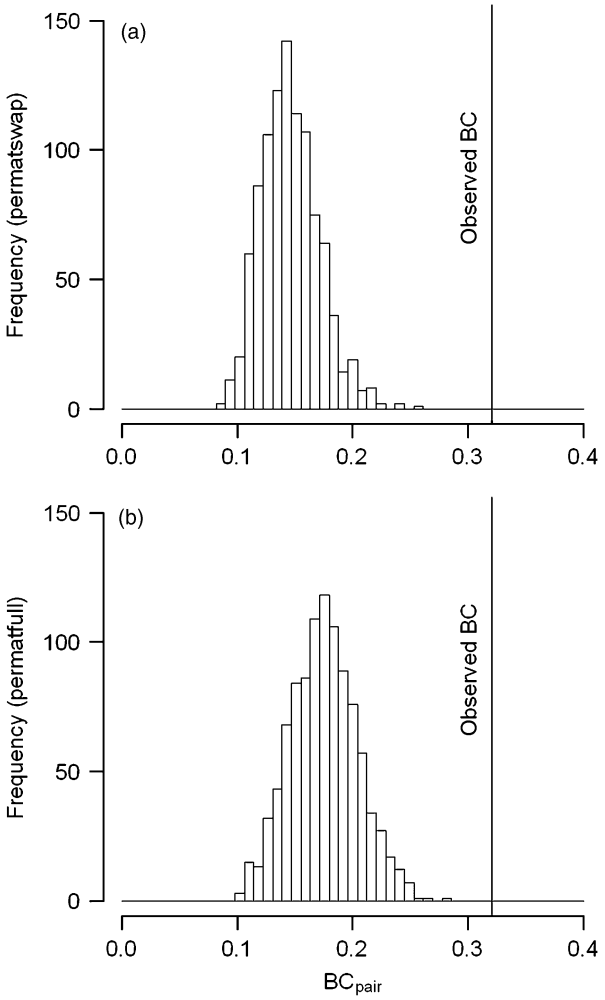

Fig. 3. BC between the AMF communities associated with forest specialist and habitat generalist plant species (BC_{pair}). Bars denote the BC values from 999 randomized data sets; the solid line indicates the BC distance observed in the real data set. (a) Randomized values from the permatswap algorithm; (b) values from the permatfull algorithm (see Materials and methods for further details). In both cases, the distance between AMF communities in the roots of habitat generalist and forest specialist plants was greater than expected at random.

expression of a specific ecological hypothesis to be tested. While this approach has a long history in plant and animal ecology (Gotelli & Graves, 1996; Gotelli, 2000; Manly, 2007), it has only recently been adopted by microbial ecologists (Horner-Devine *et al.*, 2007). Although the majority of studies considering assembly rules have analysed species presence–absence matrices, quantitative approaches that incorporate taxon abundance are expected to be ecologically more sound (Watkins & Wilson, 2003). Here, we present the first attempt to address assembly rules in AMF communities. We applied a quantitative statistical approach that used the counts of clones as a proxy for the relative abundance of AMF taxa in a sample. Potential biases in PCR resulting from possible preferential amplification of VT and plant-species-specific PCR inhibitors may mean that the sequence counts for each fungal VT do not necessarily reflect their natural relative abundance. Nonetheless, the constraints we imposed on randomization (in the permatswap algorithm) meant that counts of clones associated with each fungal VT and plant individual were fixed. Thus, any bias should not have resulted in artefactual identification of preferential associations between particular plant and fungal taxa. Moreover, it is worth noting that in our previous work (Öpik *et al.*, 2009), we found significant and important concordance between measures of AMF taxon relative abundance in samples generated by independent analysis of the same plant root samples with independent PCRs, followed by cloning and Sanger sequencing or with pyrosequencing.

Table 2. BC between observed AMF communities associated with habitat generalist and forest specialist plants (BC_{pair}) in the entire data matrix and subsets of the matrix split according to successional stage or sampling month

Data subset	BC_{pair}	permatswap	permatfull
All data	0.33	0.104–0.202**	0.121–0.236**
Young forest stands	0.31	0.122–0.25**	0.124–0.257**
Old forest stands	0.40	0.13–0.297**	0.173–0.342**
June	0.37	0.29–0.452	0.254–0.48
July	0.46	0.179–0.333**	0.181–0.355**
October	0.37	0.201–0.342*	0.188–0.355*

The columns permatswap and permatfull show the 95% quantiles of BC_{pair} measures taken from 999 matrices randomized according to the two different algorithms (permatswap and permatfull; see Materials and methods for further explanation); significant differences between observed and randomized measures of BC_{pair} are taken to reflect community assembly rules acting on the AMF communities associating with the different plant ecological groups.
**$P < 0.01$; *$P < 0.05$.

A further methodological issue that could potentially influence interpretation of the results is the unbalanced nature of the dataset with respect to the factors potentially influencing community composition (season and successional stage). Nonetheless, we used a PERMANOVA procedure that accounts for unbalanced designs, and partial reanalysis of the selectivity analyses using only those species that were present in every successional stage and season (i.e. excluding *G. luteum*, *G. rivale* and *T. pratense*) produced very similar results to those based on the full data (Supporting Information).

The PERMANOVA analysis showed that the AMF community present at the Koeru site did not differ between seasons, indicating that the same suite of taxa was consistently present. However, different AMF communities were associated with forest stands of different ages, effectively presenting plants in the two forest stand types with different fungal species pools. A classic study of AMF spores derived from soil samples along a successional gradient from

Table 3. AMF sequence groups (VT) that are significantly indicative of plant species and ecological groups, specifically habitat generalists and forest specialists

Plant species/ecological group	All data	Young forest stands	Old forest stands	June	July	October
Habitat generalists						
Fragaria vesca	–	**VT115 0.25**** VT194 0.24* VT46 0.20*	–	–	**VT219 0.25***	–
Geranium pratense	–	**VT315 0.25*** **VT316 0.25***	**VT191 0.34****	**VT191 0.78*** **VT219 0.55***	–	–
Geum rivale	–	–	–	–	–	–
Hypericum maculatum	–	–	–	–	–	–
Trifolium pratense	–	–	–	–	**VT114 0.29***	–
Veronica chamaedrys	–	–	–	–	–	–
Generalists pooled	**VT113 0.49**** **VT115 0.35*** VT219 0.09* VT37 0.06*	**VT113 0.53**** **VT115 0.39***	**VT113 0.44*** VT219 0.20* VT37 0.15**	–	**VT113 0.50**** VT37 0.11* VT219 0.11*	**VT113 0.54**** **VT115 0.44***
Forest specialists						
Galeobdolon luteum	**VT67 0.26**** VT65 0.17 *	–	VT67 0.20*	–	**VT67 0.67****	–
Hepatica nobilis	–	–	–	–	**VT199 0.28***	–
Oxalis acetosella	–	–	–	–	–	–
Paris quadrifolia	–	–	VT60 0.19*	–	–	**VT135 0.58**** **VT160 0.41*** **VT166 0.29***
Viola mirabilis	–	VT160 0.22*	–	–	–	–
Forest specialists pooled	VT199 0.21* VT143 0.16* VT140 0.06*	VT140 0.12*	**VT199 0.35****	–	**VT199 0.31***	–

Sequence groups that can be considered importantly indicative are taken as those with an indicator value ≥ 0.25 as suggested by Dufrêne & Legendre (1997) and are shown in bold type.

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

VT are sequence groups delimited over currently published datasets in the Maarj*AM* database on the basis of bootstrap support and sequence similarity $\geq 97\%$ (http://maarjam.botany.ut.ee/; Öpik *et al.*, 2010).

grassland to forest similarly revealed changes in the AMF community, which the authors attributed to the characteristics of the host plant communities or the soil (Johnson *et al.*, 1991). However, AMF communities can be robust to successional change; for example, Liu *et al.* (2009) found no differences in the AMF communities associating with a chronosequence of *Caragana korshinskii* plantations spanning 35 years. In our study, the use of a constant set of host plant species and the lack of an interaction between plant identity and successional stage suggests that the effect of successional stage was not a direct result of host plant identity.

The PERMANOVA also provided evidence for selectivity in associations between AMF and plants, both at the level of plant species and plant ecological groups. In our more detailed analysis of selectivity, both the number of AMF VT associated with particular plant species and the number of plant species associated with particular AMF VT were significantly lower than expected, indicating some level of partner selectivity. While we found only limited evidence of plant-species-level differences in associated AMF communities, significantly different AMF communities were associated with generalist and forest specialist plant groups. This result lends support to the contention that ecological groups of plants harbour different AMF communities (Öpik *et al.*, 2009). While the contrast in the absolute richness of fungal species associating with forest specialist and generalist plant species is present, but fairly small, Öpik *et al.* (2009) detected a twofold difference in richness by utilizing a 454 sequencing approach that yielded counts of sequences that were orders of magnitude higher than those presented here. This comparison suggests that the (forest) specialist fungi might be infrequent, and that there can be substantial quantitative limitations in the ability of different approaches to detect nonrandom patterns in AMF communities. Our results also encourage further consideration of the mechanisms underlying selectivity in AM associations. Under experimental conditions, plant species 'pick up' different fungal communities from the same soil environment (Gollotte *et al.*, 2004; Aldrich-Wolfe, 2007; Uibopuu *et al.*, 2009),

with the identity of neighbouring plant species potentially able to influence this process as well (Hausmann & Hawkes, 2009, 2010). AMF taxa differ in terms of their symbiotic function (Helgason *et al.*, 2007), and there is evidence of preferential allocation of photosynthates by host plants to the more beneficial fungal partners (Bever *et al.*, 2009). Moreover, studies of mutant plant individuals have shown that mutations in a single gene can induce barriers to colonization by AMF that affect AMF species to different degrees (Smith & Read, 2008). However, there also exists the potential for AMF host preference. AMF exhibit variation both in their mutualistic effects and in their competitive abilities, and there is some evidence of a trade-off between these characteristics (Bennett & Bever, 2009). Thus, successfully colonizing AMF may not always be the most beneficial for the host plant.

The taxon composition of AMF communities in soil (Dumbrell *et al.*, 2011) and plant roots (Bever *et al.*, 2001; Daniell *et al.*, 2001; Husband *et al.*, 2002; Öpik *et al.*, 2003; Liu *et al.*, 2009) is known to undergo seasonal changes. Our results suggest a novel detail in these seasonal dynamics: that it reflects a gradual organization of community assembly. In both the full and the reduced (balanced) data sets, the distinctiveness of AMF communities associated with plant ecological groups was the least in spring, but developed later in the season. Similarly, no AMF taxa were significantly indicative of the plant ecological groups in spring, but were by the later sampling times. In the study ecosystem, root growth of herbaceous plants halts in the winter and root functioning in spring is mostly in the form of new roots. On this basis, the fungal communities associating with individual plants presumably reform each year to some degree. Our results may therefore indicate that the colonization of new plant roots by AMF in spring is largely random, with selectivity only becoming apparent later in the season. This interpretation would be consistent with the feedback model of Bever *et al.* (1997), and would have the practical consequence that snapshot surveys of AMF communities may be unrepresentative of broader patterns. It should be noted, however, that the PERMANOVA did not produce a significant interaction between season and ecological group, and neither did a similar, but less powerful analysis by Öpik *et al.* (2008) when analysing the previously published subset of the data. Therefore, only very tentative conclusions can be drawn.

Accessions in the Maarj*AM* database (Öpik *et al.*, 2010) corresponding to VT that were important indicators of forest specialist plants overall were more frequently recovered from forest habitats than those associated with habitat generalist plants. This difference is largely attributable to the widespread VT113, which was a good indicator of generalist plants and is infrequently recovered from forest habitats (16/106 or 15% of its accessions in Maarj*AM*). Nonetheless, it supports Öpik *et al.*'s (2009) finding from the same site that generalist plants tend to associate with generalist AMF taxa, while forest specialist plants associate with a mix of forest specialist and generalist AMF taxa.

The characteristics of those fungal taxa that were significantly and importantly indicative of plant ecological groups can also shed further light on the associations revealed in this analysis. AMF *Glomus* VT113 was the best indicator of generalist plant species. It is also the dominant fungus at the Koeru boreo-nemoral forest site (Öpik *et al.*, 2008, 2009, this study), was the most abundant taxon in a large-scale study of AMF associating with an experimentally introduced plant species across European wooded habitats (Moora *et al.*, 2011) and is the most commonly recorded VT in the Maarj*AM* database (Öpik *et al.*, 2010). The molecular taxon contains sequences from cultures of *Glomus fasciculatum* (BEG53) and *Glomus intraradices* (unidentified cultures), which are both known to be generalist fungi (e.g. Börstler *et al.*, 2010; Oehl *et al.*, 2010) as is VT113 (Öpik *et al.*, 2006, 2010). *Glomus* VT115, which includes sequences from cultures of *G. intraradices*, *Glomus irregulare* and *Glomus vesiculiferum*, is closely related to VT113, and it has not been distinguished from VT113 in several studies (cf. Maarj*AM* database). Studies of *G. intraradices* have also illustrated that single AMF species can exhibit complex responses to different host plants (e.g. Klironomos, 2003). *Glomus intraradices* genotype richness can also vary between locations and is positively related to disturbance, and there may be little overlap of genotypes between sites (Börstler *et al.*, 2010), suggesting the presence of considerable functional diversity within the taxon. The currently unresolved taxonomic complexity of the *G. intraradices* species aggregate (Stockinger *et al.*, 2009) calls for further investigation to clarify whether it represents a true generalist species with multiple ecotypes or whether the apparent widespread nature of the species is attributable to several cryptic species of more limited distribution. *Glomus* VT199, which includes sequences from cultures of *Glomus hoi*, is a dominant taxon in Koeru (Öpik *et al.*, 2008, 2009, this study) and was a significant indicator of forest specialist plants. Elsewhere, it is commonly recorded in temperate forests and grasslands. This taxon has shown selectivity towards *Acer* among forest plants in field samples, but not under pot experiment conditions (as Glo9, Helgason *et al.*, 2002). Although somewhat fragmentary, this information also supports the notion that the fungal taxa preferentially associating with generalist plants tend to be widespread or phenotypically variable, i.e., generalists themselves.

Selectivity in associations between plant and AMF taxa may shed light on other aspects of plant and fungal ecology. It potentially has important consequences for the study of plant community interactions, both for the formulation of new hypotheses and for designing studies that are not confounded by the effects of specific mutualists. The

association of generalist plants with generalist AMF taxa may also have an important role to play in determining the success of biotic invasions (Moora *et al*., 2011).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Maximum clade credibility tree of SSU rRNA gene sequences of *Glomeromycota* obtained from Koeru in this study (indicated in bold) or earlier (in italics; Öpik *et al*., 2008; Powell *et al*., 2011), and reference sequences.
Table S1. Counts of clones of AMF sequence groups recovered from different plant species.
Table S2. Richness of associations between plant species and AMF VT (according to Öpik *et al*., 2010).
Table S3. Deviation of observed AMF communities associated with plant species and ecological groups from random assemblages created either with permatswap or permatfull algorithms.
Table S4. Comparison of AMF communities associating with pairs of plant species.

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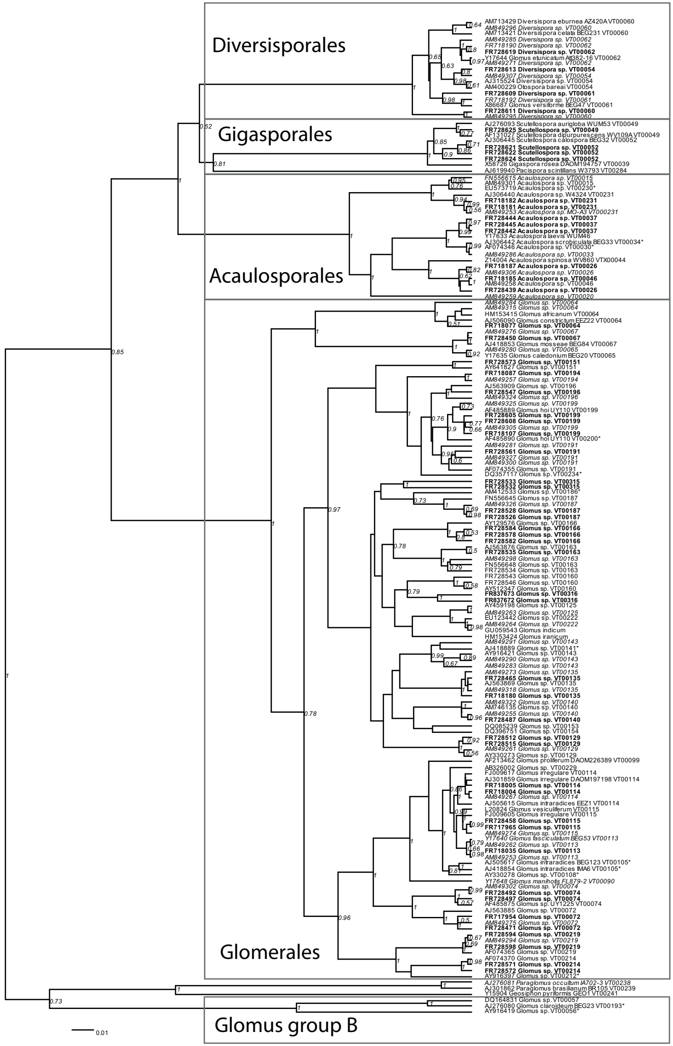
Figure S1. Maximum clade credibility tree of SSU rRNA gene sequences of Glomeromycota obtained from Koeru in this study (indicated in bold) or earlier (in italics; Öpik et al., 2008; Powell et al., 2011), and reference sequences. Fungi detected from Koeru only as BLAST hits of 454 sequences against MaarjAM database are denoted with * (Öpik et al., 2009; Moora et al., 2011). The virtual taxon (VT) nomenclature of the MaarjAM database (Öpik et al., 2010) is shown. Representative sequences are deposited in the EMBL data library (accession numbers FR728433-FR728626 & FR837672-FR837673).



Diversisporales
Gigasporales
Acaulosporales
Glomerales
Glomus group B
AM713429 Diversispora eburnea AZ420A VT00060
AM849296 Diversispora sp. VT00060
AM713421 Diversispora celata BEG231 VT00060
AM849285 Diversispora sp. VT00062
FR718190 Diversispora sp. VT00062
FR728619 Diversispora sp. VT00062
Y17644 Glomus etunicatum Att382-16 VT00062
AM849271 Diversispora sp. VT00062
FR728613 Diversispora sp. VT00054
AM849307 Diversispora sp. VT00054
AJ315524 Diversispora sp. VT00054
AM400229 Otospora bareai VT00054
FR728609 Diversispora sp. VT00061
FR718192 Diversispora sp. VT00061
X86687 Glomus versiforme BEG47 VT00061
FR728611 Diversispora sp. VT00060
AM849295 Diversispora sp. VT00060
AJ276093 Scutellospora aurigloba WUM53 VT00049
FR728625 Scutellospora sp. VT00049
AF131027 Scutellospora dipurpurescens WV109A VT00049
AJ306445 Scutellospora calospora BEG32 VT00052
FR728621 Scutellospora sp. VT00052
FR728622 Scutellospora sp. VT00052
FR728624 Scutellospora sp. VT00052
X58726 Gigaspora rosea DAOM194757 VT00039
AJ619940 Pacispora scintillans W3793 VT00284
FN556615 Acaulospora sp. VT00015
AM849301 Acaulospora sp. VT00015
EU573719 Acaulospora sp. VT00230*
AJ306440 Acaulospora sp. W4324 VT00231
FR718182 Acaulospora sp. VT00231
FR718181 Acaulospora sp. VT00231
AM849253 Acaulospora sp. MO-A3 VT000231
FR728444 Acaulospora sp. VT00037
FR728445 Acaulospora sp. VT00037
FR728442 Acaulospora sp. VT00037
Y17633 Acaulospora laevis WUM46
AJ306442 Acaulospora scrobiculata BEG33 VT00034*
AF074346 Acaulospora sp. VT00030*
AM849286 Acaulospora sp. VT00033
Z14004 Acaulospora spinosa WV860 VTX00044
FR718187 Acaulospora sp. VT00026
AM849306 Acaulospora sp. VT00026
FR718185 Acaulospora sp. VT00046
AM849258 Acaulospora sp. VT00046
FR728439 Acaulospora sp. VT00026
AM849259 Acaulospora sp. VT00020
AM849284 Glomus sp. VT00064
AM849315 Glomus sp. VT00064
HM153415 Glomus africanum VT00064
AJ506090 Glomus constrictum EEZ22 VT00064
FR718077 Glomus sp. VT00064
AM849276 Glomus sp. VT00067
FR728450 Glomus sp. VT00067
AJ418853 Glomus mosseae BEG84 VT00067
AM849280 Glomus sp. VT00065
Y17635 Glomus caledonium BEG20 VT00065
FR728573 Glomus sp. VT00151
AY641827 Glomus sp. VT00151
FR718087 Glomus sp. VT00194
AM849257 Glomus sp. VT00194
AJ563909 Glomus sp. VT00196
FR728547 Glomus sp. VT00196
AM849324 Glomus sp. VT00196
AM849325 Glomus sp. VT00199
AF485889 Glomus hoi UY110 VT00199
FR728605 Glomus sp. VT00199
FR728608 Glomus sp. VT00199
AM849305 Glomus sp. VT00199
FR718107 Glomus sp. VT00199
AF485890 Glomus hoi UY110 VT00200*
AM849281 Glomus sp. VT00191
FR728561 Glomus sp. VT00191
AM849327 Glomus sp. VT00191
AM849300 Glomus sp. VT00191
AF074355 Glomus sp. VT00191
DQ357117 Glomus sp. VT00234*
FR728533 Glomus sp. VT00315
FR728532 Glomus sp. VT00315
AM412533 Glomus sp. VT00186*
FN556645 Glomus sp. VT00187
AM849326 Glomus sp. VT00187
FR728528 Glomus sp. VT00187
FR728526 Glomus sp. VT00187
AY129576 Glomus sp. VT00166
FR728584 Glomus sp. VT00166
FR728578 Glomus sp. VT00166
FR728582 Glomus sp. VT00166
AJ563876 Glomus sp. VT00163
FR728535 Glomus sp. VT00163
AM849298 Glomus sp. VT00163
FN556648 Glomus sp. VT00163
FR728534 Glomus sp. VT00163
FR728543 Glomus sp. VT00160
FR728546 Glomus sp. VT00160
AY512347 Glomus sp. VT00160
FR837673 Glomus sp. VT00316
FR837672 Glomus sp. VT00316
AY459198 Glomus sp. VT00125
AM849263 Glomus sp. VT00125
EU123442 Glomus sp. VT00222
AM849264 Glomus sp. VT00222
GU059543 Glomus indicum
HM153424 Glomus iranicum
AM849291 Glomus sp. VT00143
AJ418889 Glomus sp. VT00141*
AY916421 Glomus sp. VT00143
AM849290 Glomus sp. VT00143
AM849283 Glomus sp. VT00143
AM849273 Glomus sp. VT00135
FR728465 Glomus sp. VT00135
AJ563869 Glomus sp. VT00135
AM849318 Glomus sp. VT00135
FR718180 Glomus sp. VT00135
AM849322 Glomus sp. VT00140
AM746135 Glomus sp. VT00140
AM849255 Glomus sp. VT00140
FR728487 Glomus sp. VT00140
DQ085239 Glomus sp. VT00153
DQ396751 Glomus sp. VT00154
FR728512 Glomus sp. VT00129
FR728515 Glomus sp. VT00129
AM849261 Glomus sp. VT00129
AY330273 Glomus sp. VT00129
AF213462 Glomus proliferum DAOM226389 VT00099
AB326002 Glomus sp. VT00229
FJ009617 Glomus irregulare VT00114
AJ301859 Glomus irregulare DAOM197198 VT00114
FR718005 Glomus sp. VT00114
FR718004 Glomus sp. VT00114
AM849267 Glomus sp. VT00114
AJ505615 Glomus intraradices EEZ1 VT00114
L20824 Glomus vesiculiferum VT00115
FJ009605 Glomus irregulare VT00115
FR728458 Glomus sp. VT00115
FR717965 Glomus sp. VT00115
AM849274 Glomus sp. VT00115
Y17640 Glomus fasciculatum BEG53 VT00113
AM849262 Glomus sp. VT00113
FR718035 Glomus sp. VT00113
AM849253 Glomus sp. VT00113
AJ505617 Glomus intraradices BEG123 VT00105*
AJ418854 Glomus intraradices IMA6 VT00105*
AY330278 Glomus sp. VT00108*
Y17648 Glomus manihotis FL879-2 VT00090
AM849302 Glomus sp. VT00074
FR728492 Glomus sp. VT00074
FR728497 Glomus sp. VT00074
AF485875 Glomus sp. UY1225 VT00074
AJ563885 Glomus sp. VT00072
FR717954 Glomus sp. VT00072
AM849275 Glomus sp. VT00072
FR728471 Glomus sp. VT00072
FR728594 Glomus sp. VT00219
AM849294 Glomus sp. VT00219
FR728598 Glomus sp. VT00219
AF074365 Glomus sp. VT00219
AF074370 Glomus sp. VT00214
FR728571 Glomus sp. VT00214
FR728572 Glomus sp. VT00214
AY916397 Glomus sp. VT00212*
AJ276081 Paraglomus occultum IA702-3 VT00238
AJ301862 Paraglomus brasilianum BR105 VT00239
Y15904 Geosiphon pyriformis GEO1 VT00241
DQ164831 Glomus sp. VT00057
AJ276080 Glomus claroideum BEG23 VT00193*
AY916419 Glomus sp. VT00056*
0.01

Table S1. Counts of clones of AM fungal sequence groups recovered from different plant species. Virtual taxon (VT) nomenclature according to the Maarj*AM* database (http://maarjam.botany.ut.ee/; Öpik *et al.*, 2010) is also shown. Virtual taxa are sequence groups delimited over all datasets in the database on the basis of bootstrap support and sequence similarity ≥97%. VT new to Koeru (but recorded from elsewhere) are denoted with *; new VT with no former records are denoted with **.

			Generalists						Forest specialists				
Family	Genus	Virtual Taxon (VT)	*Fragaria vesca*	*Geranium pratense*	*Geum rivale*	*Hypericum maculatum*	*Trifolium pratense*	*Veronica chamaedrys*	*Galeobdolon luteum*	*Hepatica nobilis*	*Oxalis acetosella*	*Paris quadrifolia*	*Viola mirabilis*
Acaulosporaceae	Acaulospora	VT15	0	0	0	0	0	0	0	1	0	0	0
Acaulosporaceae	Acaulospora	VT20	1	0	0	0	0	0	0	0	0	0	0
Acaulosporaceae	Acaulospora	VT26	0	0	3	0	0	3	0	10	0	2	3
Acaulosporaceae	Acaulospora	VT33	0	3	0	0	0	5	0	0	4	0	1
Acaulosporaceae	Acaulospora	VT37	1	0	5	3	0	26	0	4	0	0	0
Acaulosporaceae	Acaulospora	VT46*	2	0	0	0	0	0	0	1	0	0	0
Acaulosporaceae	Acaulospora	VT231*	0	0	0	0	0	0	0	2	0	0	0
Diversisporaceae	Diversispora	VT60	1	0	0	0	0	5	0	0	2	4	6
Diversisporaceae	Diversispora	VT61	1	0	0	0	0	0	0	0	0	5	0
Diversisporaceae	Diversispora	VT62	2	0	0	0	0	7	0	2	1	27	6
Diversisporaceae	Otospora	VT54	0	0	0	0	0	0	0	1	0	0	2
Gigasporaceae	Scutellospora	VT49*	0	0	0	0	0	4	0	0	0	0	2
Gigasporaceae	Scutellospora	VT52*	0	0	0	0	0	6	0	0	0	0	0
Glomeraceae	Glomus	VT64	9	4	0	1	0	10	0	7	2	4	1
Glomeraceae	Glomus	VT65	0	0	0	0	0	0	1	0	0	0	0
Glomeraceae	Glomus	VT67	0	0	0	0	0	0	2	0	0	0	3
Glomeraceae	Glomus	VT72	0	7	0	9	0	2	1	4	0	0	10
Glomeraceae	Glomus	VT74	0	4	0	7	0	0	0	3	16	18	7
Glomeraceae	Glomus	VT113	85	42	88	79	27	103	19	60	80	46	48
Glomeraceae	Glomus	VT114	4	0	0	0	2	0	0	0	1	0	0
Glomeraceae	Glomus	VT115	49	18	43	21	14	42	14	28	34	26	47
Glomeraceae	Glomus	VT125	0	0	0	0	0	0	0	0	3	0	0

Glomeraceae	Glomus	VT129	9	19	12	0	0	11	0	1	5	7	12
Glomeraceae	Glomus	VT135	1	0	0	0	0	6	0	7	1	5	9
Glomeraceae	Glomus	VT140	0	0	1	0	0	0	0	2	0	8	5
Glomeraceae	Glomus	VT143	2	15	4	1	2	4	8	24	8	16	25
Glomeraceae	Glomus	VT151*	0	0	0	0	0	1	0	0	0	0	0
Glomeraceae	Glomus	VT160	0	14	7	1	1	12	0	11	3	10	64
Glomeraceae	Glomus	VT163	0	1	0	0	0	8	0	3	8	0	0
Glomeraceae	Glomus	VT166	6	10	17	32	2	26	5	33	13	68	77
Glomeraceae	Glomus	VT187	1	2	4	1	0	2	0	3	0	9	10
Glomeraceae	Glomus	VT191	0	27	2	0	5	9	2	26	1	6	23
Glomeraceae	Glomus	VT194	4	0	0	0	0	1	0	8	0	0	0
Glomeraceae	Glomus	VT196	0	0	0	0	0	1	0	1	0	0	0
Glomeraceae	Glomus	VT199	9	13	10	0	4	25	8	62	23	24	36
Glomeraceae	Glomus	VT214	0	0	0	0	0	0	0	0	0	0	14
Glomeraceae	Glomus	VT219	19	6	12	10	0	37	15	4	14	0	5
Glomeraceae	Glomus	VT222	0	0	0	0	0	0	0	0	1	0	0
Glomeraceae	Glomus	VT315**	0	2	0	0	0	0	0	0	0	0	0
Glomeraceae	Glomus	VT316**	0	3	0	0	0	0	0	0	0	0	0

Table S2. Richness of associations between plant species and AM fungal virtual taxa (according to Öpik *et al.,* 2010). The table shows whether the number of fungal VT in the roots of particular plant species, or the number of plant species associated with particular VT, differs from randomised datasets, created either with the permatswap or permatfull algorithm. Observed richness is presented with the 95% quantiles of richness from 999 randomised data sets in parentheses. Significant differences between observed and random patterns are indicated by: * $P < 0.05$ ** $P < 0.01$. Italics is used to show one cell where observed richness is greater than expected (i.e. contrary to the pattern expected to result from selectivity)

Taxon	All data	Young forest stands	Old forest stands	June	July	October
Permatswap						
Richness of AMF sequence groups in plant roots						
Plant species						
Generalist						
Fragaria vesca	18 (17 – 26)	8 (7 – 14)	14 (14 – 22)	8 (7 – 14)	5 (6 – 12)*	15 (11 – 19)
Geranium pratense	17 (16 – 26)	13 (10 – 17)	14 (11 – 19)	4 (1 – 5)	11 (8 – 16)	17 (12 – 20)
Geum rivale	13 (15 – 24)**	11 (10 – 18)	8 (8 – 16)	-	9 (9 – 17)	13 (10 – 18)
Hypericum maculatum	11 (15 – 23)**	5 (9 – 16)**	9 (9 – 18)	5 (4 – 11)	7 (8 – 15)*	5 (7 – 14)
Trifolium pratense	8 (7 – 13)	8 (7 – 13)	-	-	5 (4 – 9)	6 (5 – 10)
Veronica chamaedrys	24 (21 – 29)	17 (13 – 21)	16 (15 – 23)	13 (9 – 16)	13 (12 – 20)	18 (13 – 22)
Forest						
Galeobdolon luteum	10 (8 – 16)	-	10 (8 – 16)	-	6 (4 – 10)	8 (4 – 10)
Hepatica nobilis	25 (22 – 30)	20 (14 – 22)	17 (15 – 22)	18 (14 – 21)	14 (12 – 20)	13 (12 – 20)
Oxalis acetosella	19 (20 – 28)*	11 (11 – 18)	14 (14 – 23)	9 (9 – 16)	12 (11 – 18)	9 (10 – 18)
Paris quadrifolia	17 (18 – 28)**	12 (12 – 19)	14 (13 – 21)	11 (10 – 18)	17 (13 – 21)	7 (4 – 10)
Viola mirabilis	23 (21 – 30)	12 (13 – 21)*	20 (15 – 22)	8 (8 – 14)	16 (13 – 21)	15 (13 – 21)
Mean	16.8 (19.7 – 21.5)**	11.7 (13.4 – 14.9)**	13.6 (15.2 – 16.9)**	9.5 (10.4 – 11.8)**	10.5 (11.7 – 13.2)**	11.5 (12.2 – 13.5)**
The number of plant species associated with particular AMF VT						

VT						
VT00015	1 (1 – 1)	0 (0 – 0)	1 (1 – 1)	1 (1 – 1)	0 (0 – 0)	0 (0 – 0)
VT00020	1 (1 – 1)	1 (1 – 1)	0 (0 – 0)	0 (0 – 0)	0 (0 – 0)	1 (1 – 1)
VT00026	5 (4 – 9)	3 (2 – 5)	4 (3 – 7)	2 (2 – 4)	4 (2 – 6)	1 (1 – 3)
VT00033	4 (3 – 7)	0 (0 – 0)	4 (3 – 8)	2 (2 – 4)	1 (1 – 2)	3 (1 – 4)
VT00037	5 (6 – 10)*	1 (1 – 4)	4 (5 – 9)	1 (1 – 1)	2 (3 – 7)**	3 (3 – 7)
VT00046	2 (1 – 3)	1 (1 – 2)	1 (1 – 1)	1 (1 – 1)	0 (0 – 0)	1 (1 – 2)
VT00049	2 (2 – 5)	0 (0 – 0)	2 (2 – 5)	0 (0 – 0)	1 (1 – 2)	1 (1 – 3)
VT00052	1 (2 – 5)*	0 (0 – 0)	1 (2 – 5)	0 (0 – 0)	0 (0 – 0)	1 (2 – 4)*
VT00054	2 (1 – 3)	0 (0 – 0)	2 (1 – 3)	1 (1 – 1)	1 (1 – 2)	0 (0 – 0)
VT00060	5 (5 – 9)	2 (2 – 5)	5 (3 – 7)	2 (2 – 5)	3 (2 – 5)	3 (1 – 3)
VT00061	2 (2 – 5)	0 (0 – 0)	2 (2 – 5)	1 (1 – 1)	1 (1 – 4)	0 (0 – 0)
VT00062	6 (6 – 11)	4 (4 – 8)	5 (4 – 8)	4 (3 – 6)	3 (4 – 7)*	2 (1 – 3)
VT00064	8 (6 – 10)	2 (1 – 3)	7 (5 – 9)	6 (3 – 6)	5 (2 – 6)	4 (3 – 8)
VT00065	1 (1 – 1)	0 (0 – 0)	1 (1 – 1)	0 (0 – 0)	0 (0 – 0)	1 (1 – 1)
VT00067	2 (2 – 5)	0 (0 – 0)	2 (2 – 5)	0 (0 – 0)	1 (1 – 2)	1 (1 – 3)
VT00072	6 (5 – 9)	4 (3 – 7)	4 (3 – 7)	1 (1 – 1)	3 (2 – 6)	4 (4 – 8)
VT00074	6 (6 – 10)	1 (1 – 2)	6 (6 – 10)	3 (3 – 6)	5 (4 – 8)	1 (1 – 3)
VT00113	11 (10 – 11)	10 (10 – 10)	10 (9 – 10)	7 (6 – 8)	11 (9 – 11)	11 (9 – 11)
VT00114	3 (3 – 6)	2 (1 – 3)	1 (2 – 4)	0 (0 – 0)	2 (1 – 3)	1 (1 – 4)
VT00115	11 (10 – 11)	10 (9 – 10)	10 (8 – 10)	7 (6 – 8)	11 (8 – 11)	11 (8 – 11)
VT00125	1 (1 – 3)	1 (1 – 3)	0 (0 – 0)	0 (0 – 0)	1 (1 – 3)	0 (0 – 0)
VT00129	8 (8 – 11)	6 (4 – 8)	6 (6 – 10)	2 (2 – 5)	5 (6 – 10)*	4 (3 – 7)
VT00135	6 (6 – 10)	4 (5 – 9)*	3 (2 – 5)	1 (1 – 1)	4 (2 – 5)	4 (4 – 9)
VT00140	4 (4 – 8)	4 (4 – 8)	0 (0 – 0)	2 (1 – 2)	2 (2 – 6)	2 (2 – 5)
VT00143	11 (9 – 11)	9 (7 – 10)	10 (6 – 10)	5 (3 – 6)	6 (6 – 10)	10 (6 – 10)
VT00151	1 (1 – 1)	1 (1 – 1)	0 (0 – 0)	0 (0 – 0)	0 (0 – 0)	1 (1 – 1)
VT00160	9 (8 – 11)	8 (8 – 10)	2 (1 – 2)	1 (2 – 6)**	8 (5 – 9)	7 (6 – 10)
VT00163	4 (4 – 8)	2 (1 – 3)	3 (3 – 7)	1 (1 – 2)	0 (0 – 0)	4 (3 – 7)
VT00166	11 (10 – 11)	9 (8 – 10)	10 (8 – 10)	6 (4 – 7)	10 (9 – 11)	10 (8 – 11)
VT00187	8 (6 – 10)	6 (5 – 9)	6 (3 – 7)	4 (3 – 6)	5 (3 – 7)	6 (2 – 6)
VT00191	9 (8 – 11)	8 (7 – 10)	5 (6 – 10)	4 (3 – 7)	6 (6 – 10)	8 (6 – 10)
VT00194	3 (4 – 8)*	3 (4 – 8)*	0 (0 – 0)	3 (2 – 6)	0 (0 – 0)	1 (1 – 1)
VT00196	2 (1 – 2)	2 (1 – 2)	0 (0 – 0)	1 (1 – 1)	1 (1 – 1)	0 (0 – 0)

VT00199	10 (9 – 11)	9 (8 – 10)	8 (7 – 10)	4 (5 – 8)	8 (7 – 11)	9 (7 – 11)
VT00214	1 (2 – 5)*	0 (0 – 0)	1 (1 – 5)	0 (0 – 0)	0 (0 – 0)	1 (1 – 4)
VT00219	9 (7 – 10)	0 (0 – 0)	9 (7 – 10)	2 (1 – 4)	3 (4 – 8)	7 (5 – 8)
VT00222	1 (1 – 1)	1 (1 – 1)	0 (0 – 0)	0 (0 – 0)	1 (1 – 1)	0 (0 – 0)
VT00231	1 (1 – 2)	1 (1 – 1)	1 (1 – 1)	1 (1 – 2)	0 (0 – 0)	0 (0 – 0)
VT00315	1 (1 – 2)	1 (1 – 2)	0 (0 – 0)	0 (0 – 0)	0 (0 – 0)	1 (1 – 2)
VT00316	1 (1 – 3)	1 (1 – 3)	0 (0 – 0)	0 (0 – 0)	1 (1 – 1)	1 (1 – 2)
Mean	4.6 (5.4 – 5.9)**	2.9 (3.4 – 3.7)**	3.4 (3.8 – 4.2)**	1.9 (2.1 – 2.4)**	2.9 (3.2 – 3.6)**	3.2 (3.4 – 3.7)**
Permatfull						
Richness of AMF VT in plant roots						
Plant species						
Generalist						
Fragaria vesca	18 (15 – 24)	8 (5 – 13)	14 (12 – 21)	8 (6 – 14)	5 (6 – 13)*	15 (9 – 17)
Geranium pratense	17 (14 – 23)	13 (8 – 16)	14 (9 – 17)	4 (1 – 6)	11 (6 – 14)	17 (10 – 19)
Geum rivale	13 (12 – 21)	11 (9 – 17)	8 (6 – 14)		9 (7 – 15)	13 (9 – 17)
Hypericum maculatum	11 (12 – 21)*	5 (7 – 15)**	9 (7 – 15)	5 (3 – 10)	7 (6 – 13)	5 (6 – 14)*
Trifolium pratense	8 (7 – 13)	8 (7 – 13)			5 (4 – 9)	6 (5 – 10)
Veronica chamaedrys	24 (19 – 28)	17 (11 – 19)	16 (13 – 21)	13 (8 – 15)	13 (11 – 19)	18 (11 – 20)
Forest						
Galeobdolon luteum	10 (7 – 15)		10 (6 – 15)		6 (4 – 10)	8 (3 – 10)
Hepatica nobilis	25 (19 – 28)	20 (12 – 20)	17 (12 – 21)	18 (13 – 21)	14 (10 – 18)	13 (11 – 19)
Oxalis acetosella	19 (17 – 26)	11 (9 – 16)	14 (13 – 22)	9 (8 – 15)	12 (10 – 18)	9 (9 – 17)
Paris quadrifolia	17 (16 – 25)	12 (10 – 18)	14 (10 – 19)	11 (9 – 18)	17 (10 – 18)	7 (3 – 10)
Viola mirabilis	23 (18 – 27)	12 (11 – 19)	20 (12 – 21)	8 (7 – 14)	16 (11 – 19)	15 (12 – 20)
Mean	16.8 (17.5 – 19.1)**	11.7 (12.1 – 13.2)**	13.6 (13.5 – 14.8)	9.5 (9.6 – 11.0)*	10.5 (10.7 – 11.9)**	11.5 (11.2 – 12.4)
The number of plant species associated with AMF sequence groups						

VT						
VT00015	1 (1 – 1)	0 (0 – 0)	1 (1 – 1)	1 (1 – 1)	0 (0 – 0)	0 (0 – 0)
VT00020	1 (1 – 1)	1 (1 – 1)	0 (0 – 0)	0 (0 – 0)	0 (0 – 0)	1 (1 – 1)
VT00026	5 (4 – 8)	3 (2 – 4)	4 (3 – 5)	2 (2 – 3)	4 (3 – 5)	1 (1 – 1)
VT00033	4 (3 – 6)	0 (0 – 0)	4 (3 – 6)	2 (1 – 2)	1 (1 – 1)	3 (2 – 3)
VT00037	5 (4 – 7)	1 (1 – 1)	4 (4 – 7)	1 (1 – 1)	2 (2 – 4)	3 (2 – 3)
VT00046	2 (1 – 2)	1 (1 – 1)	1 (1 – 1)	1 (1 – 1)	0 (0 – 0)	1 (1 – 1)
VT00049	2 (1 – 2)	0 (0 – 0)	2 (1 – 2)	0 (0 – 0)	1 (1 – 1)	1 (1 – 1)
VT00052	1 (1 – 2)	0 (0 – 0)	1 (1 – 2)	0 (0 – 0)	0 (0 – 0)	1 (1 – 2)
VT00054	2 (1 – 2)	0 (0 – 0)	2 (1 – 2)	1 (1 – 1)	1 (1 – 1)	0 (0 – 0)
VT00060	5 (5 – 9)	2 (1 – 2)	5 (4 – 8)	2 (2 – 4)	3 (2 – 3)	3 (2 – 4)
VT00061	2 (1 – 2)	0 (0 – 0)	2 (1 – 2)	1 (1 – 1)	1 (1 – 1)	0 (0 – 0)
VT00062	6 (6 – 10)	4 (2 – 4)	5 (5 – 8)	4 (3 – 6)	3 (3 – 6)	2 (1 – 2)
VT00064	8 (7 – 10)	2 (2 – 3)	7 (7 – 10)	6 (3 – 6)	5 (3 – 7)	4 (4 – 8)
VT00065	1 (1 – 1)	0 (0 – 0)	1 (1 – 1)	0 (0 – 0)	0 (0 – 0)	1 (1 – 1)
VT00067	2 (2 – 3)	0 (0 – 0)	2 (2 – 3)	0 (0 – 0)	1 (1 – 2)	1 (1 – 1)
VT00072	6 (4 – 7)	4 (2 – 4)	4 (2 – 4)	1 (1 – 1)	3 (2 – 3)	4 (2 – 4)
VT00074	6 (5 – 9)	1 (1 – 1)	6 (4 – 8)	3 (2 – 3)	5 (3 – 6)	1 (1 – 2)
VT00113	11 (11 – 11)	10 (10 – 10)	10 (10 – 10)	7 (7 – 8)	11 (10 – 11)	11 (10 – 11)
VT00114	3 (2 – 4)	2 (1 – 2)	1 (1 – 2)	0 (0 – 0)	2 (1 – 2)	1 (1 – 2)
VT00115	11 (11 – 11)	10 (10 – 10)	10 (9 – 10)	7 (6 – 8)	11 (10 – 11)	11 (9 – 11)
VT00125	1 (1 – 1)	1 (1 – 1)	0 (0 – 0)	0 (0 – 0)	1 (1 – 1)	0 (0 – 0)
VT00129	8 (6 – 10)	6 (4 – 7)	6 (3 – 7)	2 (2 – 3)	5 (4 – 7)	4 (2 – 4)
VT00135	6 (5 – 9)	4 (4 – 7)	3 (2 – 3)	1 (1 – 1)	4 (2 – 4)	4 (3 – 6)
VT00140	4 (4 – 7)	4 (4 – 7)	0 (0 – 0)	2 (1 – 2)	2 (2 – 3)	2 (2 – 3)
VT00143	11 (9 – 11)	9 (7 – 10)	*10 (6 – 9)**	5 (4 – 7)	6 (6 – 10)	10 (6 – 10)
VT00151	1 (1 – 1)	1 (1 – 1)	0 (0 – 0)	0 (0 – 0)	0 (0 – 0)	1 (1 – 1)
VT00160	9 (8 – 11)	8 (8 – 10)	2 (1 – 2)	1 (1 – 2)	8 (6 – 10)	7 (6 – 9)
VT00163	4 (3 – 6)	2 (1 – 2)	3 (2 – 4)	1 (1 – 1)	0 (0 – 0)	4 (3 – 5)
VT00166	11 (10 – 11)	9 (9 – 10)	10 (8 – 10)	6 (4 – 7)	10 (9 – 11)	10 (9 – 11)
VT00187	8 (7 – 11)	6 (6 – 9)	6 (4 – 7)	4 (3 – 6)	5 (4 – 8)	6 (4 – 7)
VT00191	9 (8 – 11)	8 (7 – 10)	5 (5 – 8)	4 (3 – 5)	6 (5 – 9)	8 (6 – 10)
VT00194	3 (3 – 5)	3 (3 – 5)	0 (0 – 0)	3 (2 – 4)	0 (0 – 0)	1 (1 – 1)
VT00196	2 (1 – 2)	2 (1 – 2)	0 (0 – 0)	1 (1 – 1)	1 (1 – 1)	0 (0 – 0)

VT00199	10 (9 – 11)	9 (8 – 10)	8 (8 – 10)	4 (5 – 8)**	8 (8 – 11)	9 (7 – 11)
VT00214	1 (1 – 1)	0 (0 – 0)	1 (1 – 1)	0 (0 – 0)	0 (0 – 0)	1 (1 – 1)
VT00219	9 (6 – 10)	0 (0 – 0)	9 (6 – 10)	2 (1 – 2)	3 (2 – 4)	7 (5 – 8)
VT00222	1 (1 – 1)	1 (1 – 1)	0 (0 – 0)	0 (0 – 0)	1 (1 – 1)	0 (0 – 0)
VT00231	1 (1 – 2)	1 (1 – 1)	1 (1 – 1)	1 (1 – 2)	0 (0 – 0)	0 (0 – 0)
VT00315	1 (1 – 2)	1 (1 – 2)	0 (0 – 0)	0 (0 – 0)	0 (0 – 0)	1 (1 – 2)
VT00316	1 (1 – 2)	1 (1 – 2)	0 (0 – 0)	0 (0 – 0)	1 (1 – 1)	1 (1 – 1)
Mean	4.6 (4.8 – 5.3)**	2.9 (3.0 – 3.3)**	3.4 (3.4 – 3.7)	1.9 (1.9 – 2.2)*	2.9 (3.0 – 3.3)**	3.2 (3.1 – 3.4)

Table S3. Deviation of observed AM fungal communities associated with plant species and ecological groups from random assemblages created either with permatswap or permatfull algorithms. The data in the table are the 95% quantiles of Bray-Curtis distances between observed and random datasets (BC[diff], see Materials and Methods for calculation). BCdiff has an expected value of zero if community composition is random; therefore overlap of the 95% quantiles with 0 indicates no difference to random assemblage. * indicates a difference at $P < 0.05$.

Plant species/ Ecogroup	All data	Young forest stands	Old forest stands	June	July	October
Permatswap						
Fragaria vesca	-0.131 – 0.218	-0.224 – 0.263	-0.192 – 0.231	-0.267 – 0.234	-0.364 – 0.341	-0.216 – 0.235
Geranium pratense	-0.121 – 0.163	-0.205 – 0.17	-0.118 – 0.275	-0.444 – 0.778	-0.219 – 0.301	-0.185 – 0.148
Geum rivale	-0.144 – 0.164	-0.204 – 0.148	-0.325 – 0.213	-	-0.272 – 0.25	-0.224 – 0.129
Hypericum maculatum	-0.121 – 0.236	-0.21 – 0.333	-0.238 – 0.202	-0.432 – 0.324	-0.217 – 0.29	-0.305 – 0.187
Trifolium pratense	-0.299 – 0.229	-0.298 – 0.246	-	-	-0.419 – 0.389	-0.385 – 0.231
Veronica chamaedrys	-0.082 – 0.121	-0.155 – 0.123	-0.09 – 0.214	-0.169 – 0.299	-0.133 – 0.25	-0.146 – 0.212
Galeobdolon luteum	-0.32 – 0.16	-	-0.307 – 0.187	-	-0.417 – 0.306	-0.386 – 0.282
Hepatica nobilis	-0.068 – 0.156	-0.134 – 0.162	-0.132 – 0.194	-0.181 – 0.181	-0.113 – 0.282	-0.196 – 0.116
Oxalis acetosella	-0.105 – 0.182	-0.142 – 0.225	-0.17 – 0.17	-0.233 – 0.267	-0.233 – 0.151	-0.23 – 0.216
Paris quadrifolia	-0.053 – 0.232	-0.123 – 0.24	-0.144 – 0.259	-0.163 – 0.141	-0.122 – 0.244	-0.345 – 0.379
Viola mirabilis	0.01 – 0.245*	-0.004 – 0.299	-0.099 – 0.291	-0.124 – 0.292	-0.102 – 0.263	-0.013 – 0.344
Forest specialist	0.014 – 0.12*	-0.016 – 0.121	-0.002 – 0.143	-0.061 – 0.067	0.007 – 0.153*	-0.053 – 0.138
Generalist	0.015 – 0.133*	-0.019 – 0.142	-0.002 – 0.147	-0.104 – 0.115	0.009 – 0.201*	-0.039 – 0.101
Permatfull						
Fragaria vesca	-0.128 – 0.195	-0.265 – 0.289	-0.158 – 0.193	-0.255 – 0.245	-0.303 – 0.303	-0.198 – 0.253
Geranium pratense	-0.138 – 0.17	-0.215 – 0.174	-0.185 – 0.239	-0.513 – 0.778	-0.245 – 0.293	-0.189 – 0.14
Geum rivale	-0.143 – 0.176	-0.222 – 0.139	-0.327 – 0.261	-	-0.278 – 0.209	-0.245 – 0.17
Hypericum maculatum	-0.116 – 0.236	-0.177 – 0.279	-0.284 – 0.228	-0.404 – 0.287	-0.226 – 0.273	-0.301 – 0.227

Trifolium pratense	-0.245 – 0.175	-0.236 – 0.173	-	-	-0.348 – 0.286	-0.26 – 0.288
Veronica chamaedrys	-0.097 – 0.106	-0.155 – 0.113	-0.15 – 0.195	-0.156 – 0.322	-0.197 – 0.205	-0.179 – 0.21
Galeobdolon luteum	-0.346 – 0.18	-	-0.312 – 0.173	-	-0.46 – 0.255	-0.47 – 0.277
Hepatica nobilis	-0.054 – 0.191	-0.089 – 0.203	-0.142 – 0.221	-0.139 – 0.21	-0.145 – 0.269	-0.21 – 0.136
Oxalis acetosella	-0.094 – 0.134	-0.163 – 0.204	-0.087 – 0.257	-0.261 – 0.297	-0.191 – 0.161	-0.236 – 0.176
Paris quadrifolia	-0.086 – 0.183	-0.143 – 0.205	-0.177 – 0.202	-0.253 – 0.147	-0.175 – 0.209	-0.381 – 0.327
Viola mirabilis	-0.021 – 0.213	-0.066 – 0.247	-0.111 – 0.284	-0.224 – 0.249	-0.147 – 0.235	-0.075 – 0.34
Forest specialist	0.009 – 0.117*	-0.037 – 0.098	-0.003 – 0.146	-0.084 – 0.065	-0.025 – 0.138	-0.031 – 0.13
Generalist	0.005 – 0.13*	-0.033 – 0.113	-0.024 – 0.157	-0.13 – 0.107	-0.029 – 0.182	-0.04 – 0.098

Table S4 Comparison of AM fungal communities associating with pairs of plant species. The table contains Bray-Curtis distances calculated between the pairs of fungal communities (see question (iii) in the Materials and Methods) and P values approximated by comparing the observed value with analogous measured calculated from multiple randomised data matrices. Cells are highlighted in bold type when the observed value was significantly larger than the randomised measures; and in italics when the observed value was significantly lower than the randomised measures. The P values above the diagonal in the table were derived using the permatfull algorithm; those below the diagonal were derived using the permatswap algorithm. Cells that reflect pairwise comparisons within plant ecological group (i.e., forest specialist vs forest specialist or generalist vs generalist) are shaded; comparisons between plants belonging to the different ecological groups are unshaded.

		Generalist						Forest specialist				
		Fragaria vesca	Geranium pratense	Geum rivale	Hypericum maculatum	Trifolium pratense	Veronica chamaedrys	Galeobdolon luteum	Hepatica nobilis	Oxalis acetosella	Paris quadrifolia	Viola mirabilis
Generalist	Fragaria vesca	NA	0.51 P = 0.07	*0.19* *P < 0.002*	0.35 P = 0.42	0.61 P = 0.5	0.33 P = 0.37	0.55 P = 0.28	0.51 P = 0.18	0.27 P = 0.11	**0.57** **P = 0.01**	**0.58** **P = 0.02**
	Geranium pratense	**0.51** **P = 0.04**	NA	0.43 P = 0.26	0.49 P = 0.17	0.55 P = 0.56	0.5 P = 0.24	0.52 P = 0.42	0.38 P = 0.44	0.43 P = 0.59	0.45 P = 0.21	0.45 P = 0.72
	Geum rivale	*0.19* *P < 0.002*	0.43 P = 0.18	NA	0.29 P = 0.2	0.61 P = 0.2	*0.28* *P = 0.04*	0.55 P = 0.27	0.44 P = 0.95	*0.24* *P = 0.01*	0.49 P = 0.09	0.5 P = 0.39
	Hypericum maculatum	0.35 P = 0.89	0.49 P = 0.06	0.29 P = 0.35	NA	0.59 P = 0.13	0.44 P = 0.63	0.58 P = 0.89	0.45 P = 0.43	0.31 P = 0.05	0.51 P = 0.14	0.57 P = 0.3
	Trifolium pratense	0.61 P = 0.57	0.55 P = 0.17	0.61 P = 0.71	0.59 P = 0.6	NA	0.73 P = 0.23	*0.35* *P = 0.03*	0.7 P = 0.69	0.62 P = 0.98	0.68 P = 0.32	0.77 P = 0.08
	Veronica chamaedrys	0.33 P = 0.25	**0.5** **P = 0.04**	*0.28* *P = 0.01*	0.44 P = 0.87	0.73 P = 0.61	NA	0.68 P = 0.8	**0.4** **P = 0.02**	0.32 P = 0.39	**0.46** **P < 0.002**	**0.46** **P = 0.01**
Forest specialist	Galeobdolon luteum	0.55 P = 0.49	0.52 P = 0.26	0.55 P = 0.34	0.58 P = 0.79	**0.35** **P = 0.04**	0.68 P = 0.5	NA	0.68 P = 0.29	**0.53** **P = 0.01**	0.69 P = 0.92	0.74 P = 0.99
	Hepatica nobilis	**0.51** **P = 0.01**	0.38 P = 0.6	**0.44** **P = 0.03**	0.45 P = 0.23	0.7 P = 0.55	**0.4** **P = 0.04**	0.68 P = 0.9	NA	0.43 P = 0.05	0.38 P = 0.82	0.35 P = 0.17
	Oxalis acetosella	0.27 P = 0.3	0.43 P = 0.1	0.24 P = 0.19	0.31 P = 0.58	0.62 P = 0.96	0.32 P = 0.68	0.53 P = 0.18	**0.43** **P = 0.05**	NA	0.42 P = 0.22	**0.52** **P < 0.002**
	Paris quadrifolia	**0.57** **P < 0.002**	0.45 P = 0.12	**0.49** **P < 0.002**	**0.51** **P = 0.04**	0.68 P = 0.18	0.46 P = 0.12	0.69 P = 0.56	0.38 P = 0.08	0.42 P = 0.13	NA	0.31 P = 0.39
	Viola mirabilis	**0.58** **P < 0.002**	0.45 P = 0.93	**0.5** **P = 0.02**	**0.57** **P = 0.02**	0.77 P = 0.75	**0.46** **P < 0.002**	0.74 P = 0.83	0.35 P = 0.24	**0.52** **P = 0.01**	0.31 P = 0.99	NA

Reanalysis of balanced data set; excluding *Trifolium pratense*, *Galeobdolon luteum* and *Geum rivale* (* P < 0.05 ** P < 0.01)

PERMANOVA (main effects; no significant interactions)

Model with plant: season pseudo-F = 1.18 P = 0.68, successional stage pseudo-F = 4.45 P < 0.01, plant pseudo-F = 2.22 P = 0.01

Model with ecogroup: season pseudo-F = 1.15 P = 0.71, successional stage pseudo-F = 4.27 P < 0.01, ecological group pseudo-F = 3.96 P < 0.01

Overall data set

BCdiff

Forest: permatswap 0.001 – 0.104* permatfull 0.002 – 0.096*
Generalist: permatswap 0.001 – 0.14* -permatfull 0.005 – 0.128

BCpair

Forest vs generalist: 0.33 permatswap 0.171 – 0.257** permatfull 0.175 – 0.325*

Richness

VT per plant species: 19.25 permatswap 22.37 – 24.25** permatfull 20.00 – 21.75**
Plant species per VT: 3.85 permatswap 4.47 – 4.85** permatfull 4.00 – 4.35**

Young forest

BCdiff

Forest: permatswap -0.015 – 0.141 permatfull -0.008 – 0.146
Generalist: permatswap -0.015 – 0.147 -permatfull -0.028 – 0.157

BCpair

Forest vs generalist: 0.42 permatswap 0.145 – 0.308** permatfull 0.192 – 0.362**

Richness

VT per plant species: 14.75 permatswap 16.38 – 18.25 ** permatfull 14.50 – 16.13
Plant species per VT: 2.95 permatswap 3.28 – 3.65 ** permatfull 2.90 – 3.23

Old forest

BCdiff

Forest: permatswap -0.028 – 0.086 permatfull -0.044 – 0.068
Generalist: permatswap -0.048 – 0.148 permatfull -0.064 – 0.122

BCpair

Forest vs generalist: 0.34 permatswap 0.278 – 0.363 permatfull 0.199 – 0.400

Richness

VT per plant species: 12.25 permatswap 14.00 – 15.62 ** permatfull 12.75 – 14.00**
Plant species per VT: 2.45 permatswap 2.80 – 3.12 ** permatfull 2.55 – 2.80**

June

BCdiff

Forest: permatswap -0.051 – 0.067 permatfull -0.080 – 0.061
Generalist: permatswap -0.087 – 0.115 permatfull -0.132 – 0.105

BCpair

Forest vs generalist: 0.37 permatswap 0.290 – 0.456 permatfull 0.250 – 0.492

Richness

VT per plant species: 9.5 permatswap 10.37 – 11.75 ** permatfull 9.63 – 11.00 **
Plant species per VT: 1.90 permatswap 2.07 – 2.35 ** permatfull 1.92 – 2.20 **

July

BCdiff

Forest: permatswap -0.024 – 0.118 permatfull -0.05 – 0.115
Generalist: permatswap -0.041 – 0.204 permatfull -0.064 – 0.192

BCpair

Forest vs generalist: 0.50 permatswap 0.289 – 0.425** permatfull 0.247 – 0.467*

Richness

VT per plant species: 11.88 permatswap 13.13 – 14.75** permatfull 12.00 – 13.50*
Plant species per VT: 2.38 permatswap 2.63 – 2.95** permatfull 2.40 – 2.70*

October

BCdiff

Forest: permatswap -0.051 – 0.133 permatfull -0.049 – 0.129
Generalist: permatswap -0.045 – 0.119 permatfull -0.068 – 0.114

BCpair

Forest vs generalist: 0.39 permatswap 0.17 – 0.33* permatfull 0.20 – 0.37*

Richness

VT per plant species: 13.88 permatswap 13.50 – 15.13** permatfull 12.25 – 13.75
Plant species per VT: 2.48 permatswap 2.70 – 3.03** permatfull 2.45 – 2.75