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Transferred communities of arbuscular mycorrhizal fungal persist in novel climates and soils

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ABSTRACT

Symbiotic mycorrhizal fungi strongly influence plant establishment and growth particularly in harsh environments, whereby sympatric, presumably co-adapted symbionts are considered particularly beneficial. However, the response of transferred sympatric mycorrhizal fungal communities to new environments remains largely ignored. We therefore studied the relative importance of initial inoculum, soil and climatic conditions on the composition, diversity and root colonization ability of arbuscular mycorrhizal fungal (AMF) communities. To do so, we analyzed the AMF communities in an extensive experiment with two ecotypes of *Bouteloua gracilis* planted in their sites of origin and in four new sites differing in climate and soil properties.

After three seasons of growth, the sympatric AMF communities were little changed by the new abiotic conditions. The composition of the AMF communities in plant roots was most strongly determined by the initial inoculum, while the contribution of divergent soil and climatic conditions was an order of magnitude smaller. The levels of root colonization by AMF, in contrast, were significantly influenced by climatic and soil conditions and did not differ among communities of different origins. Their pattern indicates that mycorrhiza formation is facilitated in the plant's sympatric soil and climatic conditions, but also that transferred AMF communities adjust mycorrhiza formation to new abiotic conditions.

1. Introduction

Soil microorganisms are a crucial component of all terrestrial ecosystems, among other reasons, because they mediate plant adaptation to the site-specific abiotic conditions (Rodriguez et al., 2008; Bunn et al., 2009; Hausmann and Hawkes, 2009; Lau and Lennon, 2011, 2012; Kivlin et al., 2013; Tomiolo et al., 2015). Symbiotic mycorrhizal fungi stand out among soil microbiota, because they directly interlink plants and soil, supplying their plant hosts with nutrients and protecting them against a range of environmental stresses (Smith and Read, 2008). For these reasons, there have been long-term efforts to include promotion of mycorrhizal fungi into vegetation management, with the purpose of increasing food or biomass production (Barea, 2015; Bender et al., 2016; Zhang et al., 2019a,b) or for more efficient restoration of degraded habitats (Barea et al., 2011; Maltz and Treseder, 2015; Neuenkamp et al., 2019). Furthermore, considering mycorrhizal fungi has been also proposed in measures designed to mitigate the impacts of climate change on vegetation (Johnson et al., 2013; Allsup and Lankau, 2019; Bennett and Classen, 2020).

Solid evidence has been gathered for the functional importance of co-adaptation in plants and their associated soil microorganisms, meaning that the origins of plants and microbiota influence the microbial effects on plant fitness (Johnson et al., 2010; Middleton et al., 2015; Revillini et al., 2016; Rúa et al., 2016; Rekret and Maherali, 2019; Bauer et al., 2020; Remke et al., 2020). Plants profit more from association with their sympatric arbuscular mycorrhizal fungal (AMF) communities as compared to allopatric communities, particularly in their sympatric soil conditions, but also in new soils (Rúa et al., 2016). Inoculation of plant

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material with sympatric soil microorganisms could thus be a means to increase the success of many out-planting activities, including but not limited to ecological restoration or assisted migration (McLachlan et al., 2007). However, sympatric AMF symbionts may produce less mycelia in new soils (Johnson et al., 2010; Ji et al., 2013; Sikes et al., 2014) or climates (Shi et al., 2015; Yang et al., 2018; Zhang et al., 2019a,b). Novel abiotic conditions may also significantly change the composition of AMF communities, because soil chemistry and climate are important determinants of AMF community structure (Dumbrell et al., 2010; Chaudhary et al., 2014, 2018; Van Geel et al., 2018; Stevens et al., 2020). Novel conditions can alter the competitive relationships among the community members (Lekberg et al., 2007), leading to changes in their relative abundances (Li et al., 2015; Deveautour et al., 2018), or even elimination of particular species due to environmental filtering (Islam et al., 2020). Additionally, co-inoculated sympatric fungi may become gradually replaced by mycorrhizal fungal species or genotypes from the new site due to extraradical mycelia radiating from the surrounding vegetation (Janoušková et al., 2017) or through animal or wind dispersal of infective propagules (Egan et al., 2014; Vašutová et al., 2019; Chaudhary et al., 2020).

Responses of mycorrhizal fungal communities to allopatric conditions are much less explored than plant responses (Rúa et al., 2016), and their compositional changes have been rarely studied. Greenhouse experiments indicate that novel soil conditions and distinct climatic conditions may significantly alter the composition of AMF communities (Ji et al., 2013; Zhang et al., 2019a,b). Impacts of changed climatic conditions have also been reported from field trials (Deveautour et al., 2018; Islam et al., 2020). However, no information is available on the relative importance of soil and climate or on how pre-inoculated AMF communities merge with local communities. This is surprising because knowing how sympatric communities respond to novel conditions may be crucial for understanding the context dependency of the benefits of local adaptation or plant-fungal co-adaptation. For example, mycorrhizal fungi tend to confer more benefits to their host plants if all three components of the system (plants, fungi and soil) are sympatric as compared to conditions where only plants and fungi are sympatric, while the soil is allopatric (Rúa et al., 2016). Poorer than expected performance of sympatric mycorrhizal fungi could be also due to compositional changes of the sympatric fungal communities in the novel soil conditions, which may weaken the link of plant-fungal co-adaptation. This aspect, however, remains unexplored in most studies.

The main objective of our study was to evaluate root-associated AMF communities in plants transplanted to new sites, and to determine how inoculum, soil and climate contribute to compositional divergence from the AMF community in the plant's original conditions. For this purpose, we selected blue grama (*Bouteloua gracilis*) as a broadly-distributed North American grass, which associates with AMF forming variable levels of root colonization (Johnson et al., 2003; Porras-Alfaro et al., 2007). The genetic structure of this grass species is partly related to environmental factors, and it is often used in restoration programs (Tso and Allan, 2019). We established a three-year field experiment that transplanted two ecotypes of *B. gracilis* into six sites of different climatic conditions in northern Arizona. Two sites provided two reference treatments and were the source of the host-plant ecotypes, their sympatric soils and microbial inocula. At the other four sites, the plants were grown in their sympatric soils or the allopatric soils of the new sites and inoculated with their sympatric microbiota or the allopatric microbiota of the new sites.

We hypothesized that 1) AMF community composition is mostly determined by the initial inoculation, but also 2) modified by the abiotic conditions. Additionally, we assumed 3) local adaptation of the AMF communities to their original conditions. Consequently, we expected a significant effect of the initial inoculation on the AMF community composition and diversity even after the three seasons at the new sites (corresponding to our first hypothesis), but also significant effects of the abiotic conditions (corresponding to the second hypothesis). Furthermore, we expected to find higher root colonization and/or AMF diversity at the site of origin and in sympatric soil as compared to the new sites' conditions (corresponding to the third hypothesis).

2. Material and methods

2.1. Site description and experimental set up

The experiment was conducted at Northern Arizona University's Southwest Experimental Garden Array (SEGA, https://sega.nau.edu/home), which is a collection of experimental sites situated on a climate and elevation gradient. It was established with two plant-soil-microbiota complexes, each consisting of a *Bouteloua gracilis* ecotype, sympatric ("home") soil and soil microbial inoculum from the same location - the climatically similar "home" sites Blue Chute (BC) and White Pockets Canyon (WPC). Four "new" sites spanned a ~6 °C gradient of mean annual temperature with two warmer sites - Black Point (BP) and Walnut Creek (WAL), and two colder sites - Little Mountain (LM) and Arboretum Flagstaff (ARB). The new sites were the sources of soils and microbial inocula, which were allopatric to the plant ecotypes. The BC and WPC sites are approximately 100 km distant from each other, all the sites are located within a radius of approximately 90 km. Their GPS coordinates, climatic and soil characteristics are summarized in Table 1.

At the new sites, each of the two plant ecotypes (BC and WPC) were grown either in the home soil or in the new site's soil after double sterilization (factor Soil), inoculated either with the home soil microbiota or with the new site's biota (factor Inoculum). Thus, four treatments were established at each of the four new sites with each of the two plant-soil-microbiota complexes (factor Plant). In addition, a reference ("all-home") treatment was established at each of the two home sites, which consisted of the corresponding plant ecotype growing in its home soil and with its home microbiota. Thus, the experiment comprised 34 treatments in total (Fig. 1). The treatments with the home soils and home microbiota were established at all the new sites, while each of the new sites' soil and microbiota were present only at their site of origin. Treatments with matching soil, site and microbiota conditions (i.e., the two all-home treatments and, at each of the new sites, treatments with the new site's soil and new site's microbiota) are subsequently called "site-specific" treatments (see Fig. 1).

Plants were grown in 7.8 L plastic tree pots (Steuwe & Sons TP812), which were buried at the sites to the surface level of the surrounding terrain, i.e., soil level inside and outside of pots was approximately equal, with the rim of the pot protruding ~3–4 cm above the surface. Each experimental treatment was replicated 10 times, resulting in a total of 340 experimental units (pots).

2.2. Establishment and harvest of the experiment

The procedures for the establishment of the experiment are described in detail by (Remke et al., 2022). Briefly, seeds of the two *B. gracilis* ecotypes were collected at the two home sites. Soils for the experiment were collected from the six experimental sites to the depth of 60 cm, homogenized and steam-sterilized at 125 °C for 2 × 24 h. Rhizosphere soil under *B. gracilis* at each site was collected (to the depths of 30 cm) for microbial inocula. At sites where *B. gracilis* was uncommon or absent, Black Point and Little Mountain, rhizosphere soil of other herbaceous vegetation was taken. Pots were filled with 7.5 L of sterilized soil and topped with a 2-cm thick band of living inoculum soil. Twenty seeds of *B. gracilis* were added into each pot, covered with 1 cm of the sterilized soil, and later thinned to one seedling per pot. The seedlings were pre-grown for six months under a standard nursery watering regime, prior to the establishment of the field experiment, i.e. their transfer to the field sites in May 2015.

The experiment was harvested in November 2017. The pots were dug out of the ground and transferred to the laboratory. Root systems were

Table 1
Location and abiotic characteristics of the experimental sites and soils.

	Black Point (BP)	Walnut Creek (WAL)	Blue Chute (BC)	White Pockets (WPC)	Little Mountain (LM)	Arboretum Flagstaff (ARB)
Status	new (warmer)	new (warmer)	home	home	new (colder)	new (colder)
GPS coordinates	35.68 −111.48	34.92 −112.84	35.58 −111.97	36.61 −112.41	36.58 −112.36	35.16 −111.73
Elevation (m a. s. l.)	1566	1567	1930	2057	2276	2179
Precipitation (mm.year^{-1})	152	397	478	443	502	556
Mean annual T_{max} (°C)	21.0	22.0	18.6	19.0	16.0	16.0
Mean annual T_{min} (°C)	5.0	3.0	0.9	4.0	1.0	−1.0
Soil type	orthent	argid	ulstalf	argid	ustoll	ustoll
Clay (%)	5.2	6.4	30.1	24.2	26.7	28.7
Silt (%)	9.9	18.3	56.1	53.3	47.2	70.3
Sand (%)	84.8	75.3	13.8	22.5	26.1	1.0
pH	8.9	8.24	8.51	8.13	7.36	7.35
C_{org} (%)	0.083	1.505	0.803	4.929	1.670	1.238
C_{carb} (%)	0.658	1.151	1.171	1.098	0.419	0.299
N_{tot} (%)	0.024	0.159	0.105	0.476	0.107	0.091
P_{avail} (mg.kg^{-1})	4.71	30.72	20.56	70.65	41.69	19.10
Ca_{avail} (mg.kg^{-1})	2223	5622	5983	3439	2836	3584
Mg_{avail} (mg.kg^{-1})	259	265	378	490	577	809
K_{avail} (mg.kg^{-1})	340	274	399	483	227	107
CEC (mmol.kg^{-1})	74.6	303.1	286.4	279.5	237.5	306.6

The geographical location, climatic parameters and soil type are given according to the Southwest Experimental Garden Array, https://sega.nau.edu/. Soil pH was measured in deionized H_2O (1:5 w/v sample/liquid ratio). Organic C (C_{org}) was determined after digestion of carbonate C (C_{carb}) with HCl on a Flash 2000 analyzer. C_{carb} was calculated as the difference between total C and C_{org}. Total nitrogen (N_{tot}) concentration was determined on a Flash 2000 analyzer. Available P (P_{avail}) was extracted from the soil samples according to (Olsen SR and Sommers LE, 1982) and measured spectrophotometrically as phosphomolybdenum blue at 750 nm (Unicam UV-400). Available calcium (Ca_{avail}), magnesium (Mg_{avail}) and potassium (K_{avail}) were determined after extraction with ammonium acetate by atomic absorption spectroscopy (AAS, ContrAA 700, Analytik Jena). Cation exchange capacity (CEC) was determined after extraction with 0.1 M $BaCl_2$ by AAS (ContrAA 700).

carefully washed, trimmed to the part corresponding to approximately 2–15 cm of depth and randomly subsampled. The root sample from each plant was divided into two parts, one was stored in 60% ethanol (for histochemical staining), the other part transferred into silica gel (for DNA extraction). Only root samples of plants, which displayed green leaves during the previous growing season (i.e. could be considered alive) were further processed (4–10 replicates per treatment).

2.3. Laboratory analyses

Roots stored in ethanol were transferred to 10% KOH and stained with 0.05% Trypan Blue in lactoglycerol (Koske and Gemma, 1989) for the microscopic estimation of root colonization. Root colonization by AMF was estimated using the magnified intersection method, scoring usually 100 intersections within 30 root segments (about 2 cm long) at 200× magnification (Olympus IX51). If the stained root sample did not render enough material due to the small size of the plant (about 20% of all samples), fewer intersections were scored (40 minimum).

Dried root samples of 50 mg were ground in liquid nitrogen and DNA was extracted using DNA Plant Mini Kit (Qiagen, Hilden, Germany) according to the manufacturer's extraction. A part of the small subunit (SSU) of the ribosomal DNA was amplified from the DNA extracts in a nested PCR with the primer pair NS31/AML2 (Vasar et al., 2017) in the first step. In the second step, the PCR product was amplified with the primer pair NS31Glo3 (Kolaříková et al., 2021) and AML2, which rendered a fragment of approx. 500 bp. Both primers used in the second PCR were tagged with sample-specific molecular identifiers of 10–12 bases, which enabled us to pool up to 70 samples into one sequencing library. The libraries were sequenced on an Illumina MiSeq (2 × 300 bp, SEQme company, Dobříš, Czech Republic).

PCR mix was performed in the total volume of 25 ml and contained 0.5 U Taq DNA Polymerase (Fermentas, St. Leon-Rot, Germany), 1× PCR Blue Buffer (without $MgCl_2$) (Top-Bio, Vestec, Czech Republic), 0.25 mM each dNTP, 2.5 mM $MgCl_2$, 20 μg BSA (Thermo Fisher Scientific, Waltham, USA), 0.2 μM each primer and 1 μl of DNA template (in the first step) or 1 μl of 1:9 diluted PCR product (in the second step). Thermocycling conditions for the first PCR step were 94 °C for 5 min, 35 cycles of 94 °C for 30 s, 52 °C for 30 s and 72 °C for 45 s, followed by 20 min at 72 °C; for the second step: 94 °C for 5 min, 20 cycles of 94 °C for 30 s, 52 °C for 30 s, 72 °C for 45 s, followed by 20 min at 72 °C. Each DNA extract was amplified in triplicate. The pooled triplicates were purified through columns with the QIAquick PCR Purification Kit (Qiagen, Hilden, Germany) according to the manufacturer's protocol and eluted into 20 μl of ddH_2O. DNA concentrations of the amplicon pools were quantified using a Qubit 2.0 Fluorometer (Thermo Fisher Scientific) with High Sensitivity Assay Kit and ranged between 2.7 and 34.0 ng μl^{-1}. The purified amplicons were pooled in equimolar ratios. Negative PCR controls (with ddH_2O instead of a template) were processed in the same way as the experimental samples and included into each sequencing library.

2.4. Bioinformatical analysis

In total, Illumina paired end sequencing of 312 samples and 6 negative controls in 6 libraries yielded 14,584,774 raw sequences. The data were processed using the pipeline SEED2 ver. 2.0.4 (Větrovský et al., 2018). Due to the relatively long amplicon size (ca 500 bp), overlap of the R1/R2 reads was achieved only in a very small proportion (<1%) of reads. We therefore used only reads starting with the primer NS31Glo3 from the R1 file, as the majority of the taxonomically informative characters occur between the positions 70–300 of the NS31/AML2 amplicon (Vasar et al., 2017). First, low-quality sequences were discarded (mean < 30 for R1 file reads and mean < 20 for R2 file reads due to overall worse quality of the R2 reads). The reads were demultiplexed (no mismatch allowed in the tag sequences) and in order to detect tag switches, the read titles from the R2 file were searched for in the R1 file. Tag switches (i.e. reads with non-matching tags) were discarded and subsequently, only sequences starting with the primer NS31Glo3 from the R1 file were kept for further analyses.

After removal of the tags and the primer, all sequences shorter than 250 bp were discarded. From this point on, sequences from all six libraries were analyzed together: They were subsampled to 9000 reads per sample (93 samples with lower read numbers were kept as they were), reads were trimmed to the sequence length 264 bp and clustered

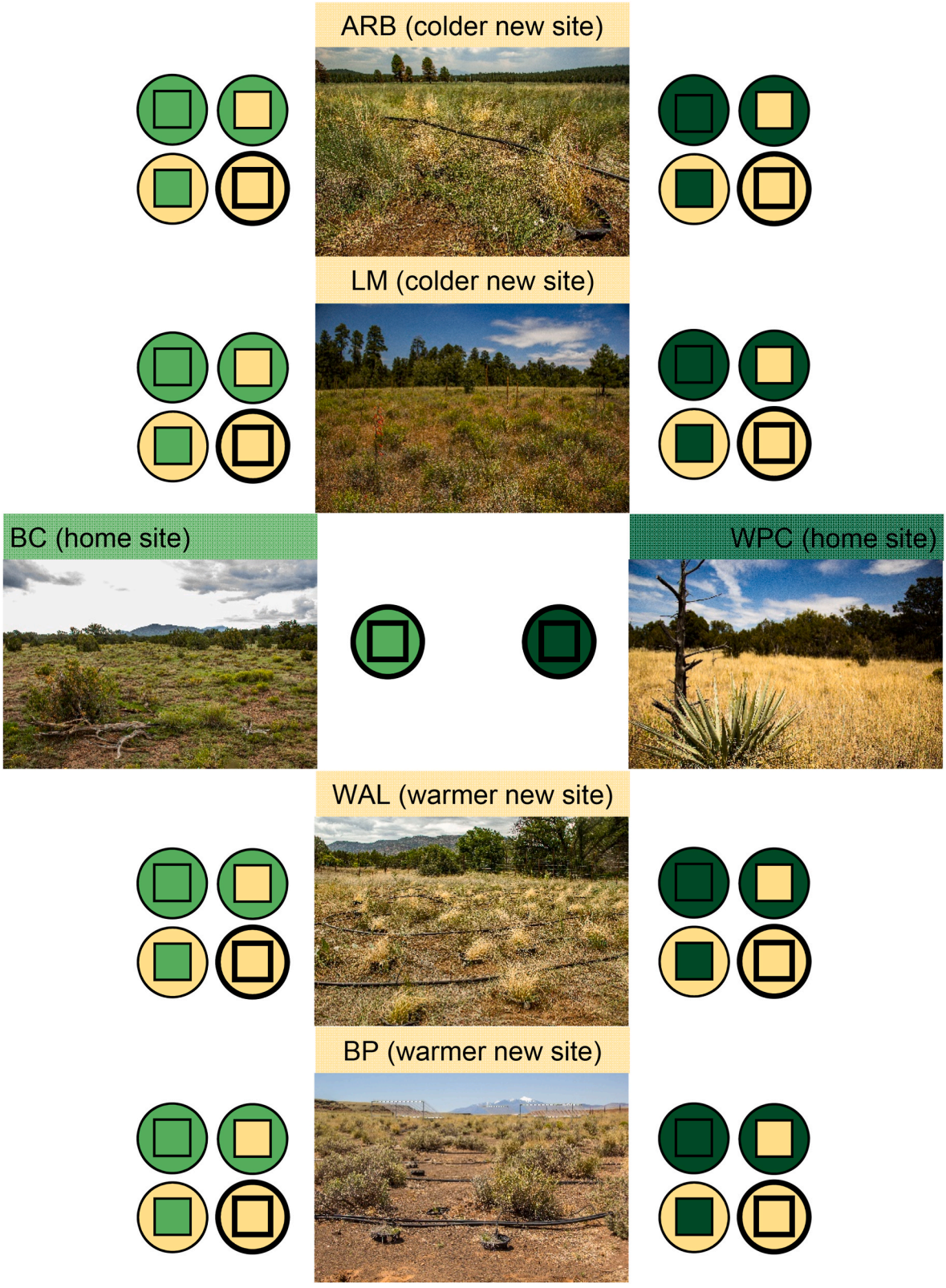

Fig. 1. Diagram of the experimental design. Each square in circle represents one treatment with 10 replicates. At the home sites (Blue Chute – BC or White Pockets – WPC), plants of the corresponding ecotype were grown only in their sympatric (home) soil (green circle) inoculated with their home soil microbiota (green square) as the "all-home" reference treatment. At the new sites, each plant ecotype was grown in four combinations of home soil, home microbiota, the new site's soil (orange circle) and the new site's microbiota (orange square). Thicker outlines mark the "site-specific" treatments, i.e. treatments with matching site, soil and microbiota, which includes also the "all-home" reference treatments. Photos by M. Remke.

to operational taxonomic units (OTUs) using UPARSE implementation in USEARCH ver. 8.11861 (Edgar, 2013), with 97% similarity threshold. 132,878 chimeric sequences detected in this step were discarded. All global single-, double- and tripletons (187,857) were removed from the data set, which resulted in 2,311,162 reads corresponding to 5293 OTUs. The most abundant sequences from the OTUs were checked for their closest hits using a BLAST search against the GenBank. To reduce the number of erroneous OTUs and obtain more realistic richness estimates, the OTUs were then processed using the post-clustering algorithm LULU (Frøslev et al., 2017), settings: coverage 95, identity 98.5%, minimum match 97, minimum relative occurrence 0.95), which resulted in 4676 OTUs. All non-Glomeromycotina sequences (642 OTUs, 175,037 reads) were then excluded from further analyses, leaving finally 4034 OTUs represented by 2,134,850 reads. Read numbers of the 31 OTUs detected in the negative controls were subtracted from the read numbers of these particular OTUs in samples from the corresponding libraries, 329 singletons and doubletons were removed, resulting in 3684 OTUs (1,460,780 reads). The sequences and the associated metadata are available in the PlutoF repository (https://dx.doi.org/10.15156/BIO/2483936).

2.5. Statistical analyses

The dataset with 3684 OTUs was subsampled to the lowest read number within the sample set (1208), resulting in 2901 OTUs with at least 1 read. The subsampled dataset was used for the calculation of Shannon diversity index (H′) according to (Hill, 1973) using the 'vegan' package (Oksanen et al., 2019) as well as for all the community analysis. All analysis were conducted in R (R Core Team, 2020).

1) To characterize the system, principal differences among the AMF communities of the six sites were determined by comparing the communities of the site-specific treatments (see Fig. 1 for their specification), as these treatments represent the original conditions of the communities (home site in combination with home soil). Compositional differences between these communities were determined by PERMANOVA on Hellinger-transformed data as implemented in the Adonis routine of the 'vegan' package, and pairwise Adonis with Bonferroni correction. The similarity of the fungal communities in individual samples was visualized with non-metric multi-dimensional scaling (NMDS) plots using Bray-Curtis dissimilarity. Likewise, differences between the communities in Shannon diversity (H′) and root colonization (arcsine-transformed) were determined by ANOVA followed by Tukey's test for the pairwise comparison of means.
2) In order to address our first hypothesis on significant effect of initial inoculation on the AMF communities, drivers of community divergence at the new sites were determined using dissimilarity from the reference all-home community as the response variable. To create this response variable, we calculated the Bray-Curtis dissimilarity between each replicate sample and the average reference community as established in the corresponding all-home treatment (BC or WPC, depending on the plant ecotype). We analyzed the community divergence using linear models with two sets of predictors. The first set of predictors comprised the experimental factors Site, Soil, Inoculum and Plant. The Soil and Inoculum factors had five levels: the four new sites' identities (BP, WAL, LM, ARB) and the level "home" for BC and WPC soil/biota. The factor Site had four levels (BP, WAL, LM, ARB). In the second set of predictors, the experimental factors Site, Soil and Inoculum were coded as dissimilarities of climate, soil and inoculum (i.e. of the inoculated AMF community) from the all-home reference conditions. They were calculated as Euclidean distances of climatic/soil conditions and as Bray-Curtis dissimilarities of the inoculated AMF communities as detailed in Supplementary Text S1. An overview on the values is given in Supplementary Fig. S1. Community divergence was analyzed with the two sets of predictors, because each set was optimized to reveal a different kind of response to experimental treatments, and it was not possible to know which type of response to expect on apriori grounds. The first set of predictors was ideal to detect differences explainable by differing factor levels, regardless of the shape of the response. The second set of predictors was ideal to detect linear relationships between dissimilarity in the AMF communities and that of their environment. With both sets of predictors, the initial model included the four main effects as well as interactions of Plant with each of the other three predictors. This model was reduced in a backward stepwise fashion, and the final model was selected according to Akaike information criterion (AIC). The original models and their stepwise reduction are given in Tables S1–S17. Variation partitioning (the varpart function in 'vegan' package (Oksanen et al., 2019),) was used to determine the relative importance of the predictors in driving the community divergence from the reference conditions.

Drivers of divergence from the all-home reference conditions were also determined for root colonization and H'. In order to maintain the direction of the divergence (increase or decrease) it was calculated as response ratio R=N/Ref, where N is the value in the new-site replicate, and Ref is the mean value in the corresponding all-home reference treatment (Lekberg and Koide, 2005). Likewise, the dissimilarities of the inoculated AMF communities were calculated specifically for each response parameter (H′ or root colonization) based on the same parameter (i.e. H′ or root colonization), as detailed in Text S1. Otherwise, the analyses were performed as described above for the compositional divergence.

3) Our second hypothesis predicting a significant effect of abiotic conditions on the AMF communities was addressed on a subset of the data that comprised only the home-inoculated communities, i.e. communities established after inoculation with the sympatric BC or WPC microbiota. As with the whole data set, drivers of the divergence of community composition, diversity and root colonization from the all-home reference conditions were analyzed using two sets of predictors. The first set comprised the three experimental factors Plant, Site and Soil; the second set of predictors comprised the factor Plant and the dissimilarities of soil and site conditions from the reference conditions. Thereby, dissimilarity of site conditions was split into two predictors: 1) dissimilarity of climate and 2) dissimilarity of the new site's AMF communities. This separated two site-related factors, which may impact on the divergence of the home-inoculated communities - climate and local AMF communities as source of new fungal genotypes. See Text S1 for details on the calculation. Linear models and variation partitioning models were constructed as described above in point 2).
4) Specific pairwise comparisons of AMF community composition were performed using pairwise Adonis ('vegan' package) with Bonferroni correction in order to determine whether new site, new soil, or the combined effect of both significantly affected the composition of the home-inoculated communities as compared to the all-home conditions. Within each combination of plant ecotype and new site, the home-inoculated treatment in home soil and the home-inoculated treatment in the new site's soil were compared to each other and to the corresponding all-home treatment.
5) In order to address the hypothesis on local adaptation, AMF diversity and root colonization values were analyzed directly using linear models with the factors Site, Soil and Inoculum coded by two levels only, denoting their provenance with respect to the site of origin of the plant ecotype: "home" (the BC/WPC site, the sympatric inocula and soils from these sites) and "away" (comprising all the new sites, the allopatric soils and inocula from these sites). These analyses were performed across all the experimental communities or across the

home-inoculated communities only. The linear models were constructed and reduced as described above in point 2).

3. Results

3.1. Main characteristics of the AM fungal communities

Despite the high number of OTUs determined, the phylogenetic diversity of the AM fungal communities was low. Out of the 161 closest hits delimited in GenBank, 42 were annotated as 'Glomeromycota' (without further taxonomic specification), while the remaining 119 were assigned exclusively to the order Glomerales, the majority to the family Glomeraceae (112). Within Glomeraceae, the most abundant species (according to the closest hit) was *Rhizophagus irregularis*, which accounted for 39.8% of all reads (comprising 1020 of the OTUs delimited at 97% similarity). The second most abundant species was *Dominikia iranica* (7.3% of all reads). An overview on the identity of all OTUs and their distribution in samples is available in the PlutoF repository (https://dx.doi.org/10.15156/BIO/2483936).

The site-specific AMF communities (i.e. those developing at their home sites and in their home soils) differed in their composition in all pairwise comparisons according to PERMANOVA ($F = 8.306$, $P < 0.001$) and pairwise Adonis (at $P = 0.05$) (Fig. 2a). They also significantly differed in diversity ($F = 22.901$, $P < 0.001$), whereby the BC home community was significantly more diverse than the WPC home community, and the BP community was the least diverse (Fig. 2b). The site-specific communities of the new sites (BP, WAL, LM and ARB) did not differ between the two plant ecotypes in composition or diversity (analyses not shown).

AMF root colonization of the experimental plants was highly variable, ranging between <1% and 98%. Unlike diversity and community composition, it did not significantly differ among the site-specific AMF communities ($F = 1.542$, $P = 0.192$). However, the AMF communities of the new sites produced significantly higher root colonization in WPC plants than in BC plants ($F = 8.810$, $P = 0.005$, Fig. 2c).

3.2. Initial inoculation and other experimental factors as drivers of divergence of AMF communities

Focusing on all communities that developed in the experiment, the compositional divergence from the all-home reference community was significantly affected by the experimental factors Inoculum, Soil and Site, as well as by the interaction of Plant and Inoculum, meaning that the effect of Inoculum depended on the plant ecotype (Table 2).

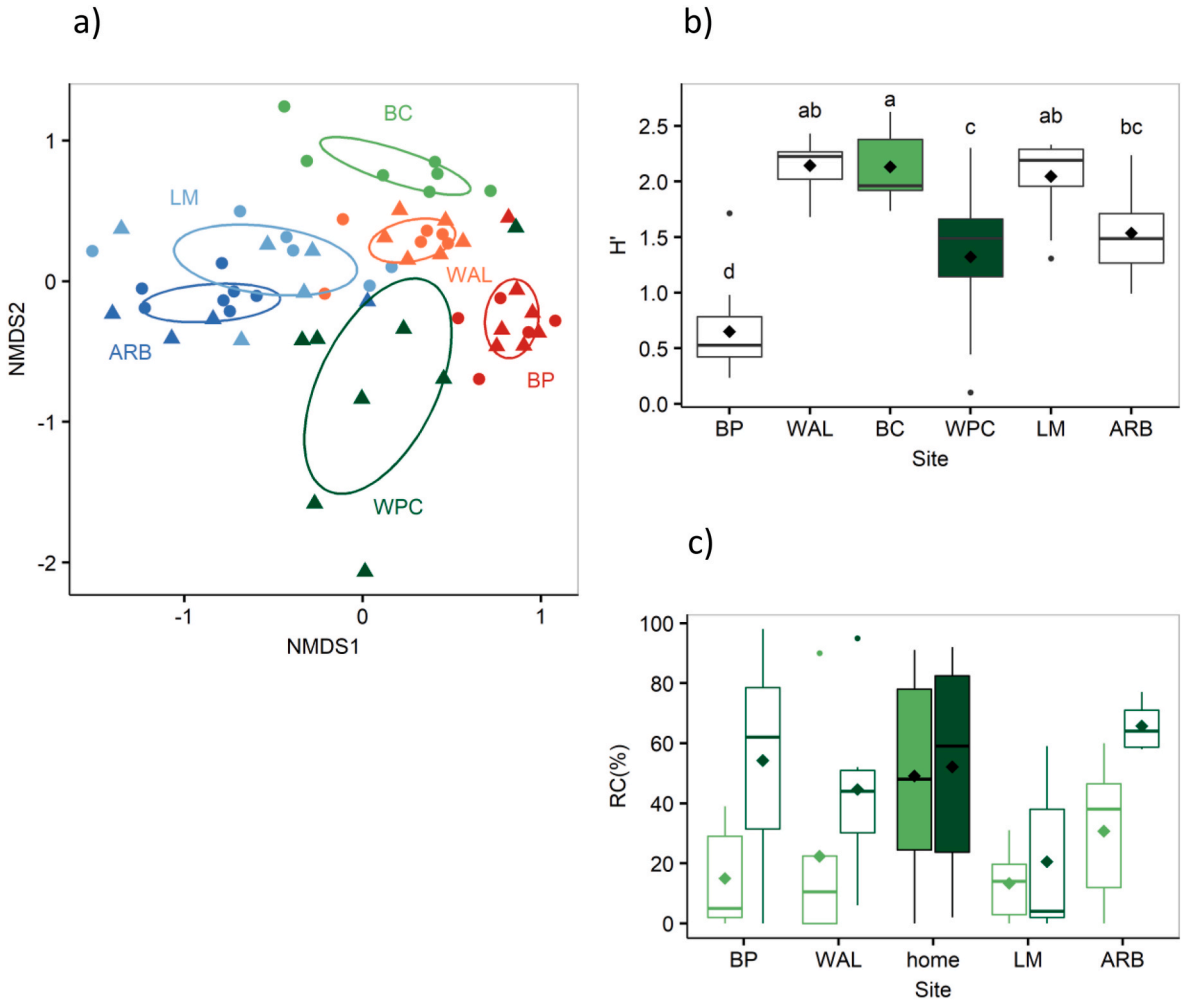

Fig. 2. Characteristics of the site-specific arbuscular mycorrhizal fungal (AMF) communities. These are communities that developed at each of the sites (BP, WAL, BC, WPC, LM, ARB) in the site's soil after inoculation with the site's microbiota: (a) Plot of non-metric multidimensional scaling (stress = 0.199) showing differences in their compositions. Each symbol is one replicate community in the roots of the BC (circle) or WPC (triangle) plant ecotype. Ellipses show standard deviations of points within site. (b) Diversity (Shannon index H′). Diamonds show means, the new sites' (BP, WAL, LM, ARB) values are pooled for the two plant ecotypes. Letters denote significant differences between sites (those marked with the same latter are not statistically different). (c) Frequency of root colonization by AMF (RC%) in the BC (light green) and WPC (dark green) plant ecotype, diamonds show means.

Table 2
Effects of the experimental factors on divergence of arbuscular mycorrhizal fungal (AMF) communities from the reference all-home community. Divergence in community composition, diversity (Shannon index) and root colonization were analyzed for all AMF communities established at the new sites.

		Composition		Diversity		Root colonization	
	df	F	P	F	P	F	P
Plant	1	*0.018*	*0.892*	9.596	0.002	*3.624*	*0.058*
Inoculum	4	35.839	<0.001	4.547	0.002	–	–
Soil	4	7.785	<0.001	*1.921*	*0.109*	*2.049*	*0.089*
Site	3	5.903	<0.001	7.065	<0.001	6.050	<0.001
Plant × Inoculum	4	7.401	<0.001	*1.984*	*0.099*	–	–
Plant × Soil	4	*2.032*	*0.092*	–	–	–	–
Plant × Site	3	–	–	–	–	–	–
AdjR^2		0.549		0.507		0.124	
AIC		−253.672		67.441		291.135	

AdjR^2, F and P values are given according to models, which were selected based on Akaike information criterion (AIC) after step-wise reduction of an initial model including all main effects (Plant, Inoculum, Soil and Site) and the interactions of Plant with the other predictors. The initial and intermediate reduced models are shown in Supplementary Tables S2–S4. Total df = 198. Hyphen - term not included into the final model; italics - term non-significant within the final model at P = 0.05.

According to variation partitioning, Inoculum explained the highest proportion of variability (30%), followed by Plant (14%), while only low proportions were explained by Site and Soil (3% and 5%, respectively) (Fig. 3a).

When Inoculum, Site and Soil were coded as dissimilarities from the home conditions, the explained variability in community divergence remained similarly high and similarly distributed (Supplementary Table S18, Supplementary Fig. S2a). Divergence of AMF communities was largely driven by dissimilarity of inoculum, but also related to the dissimilarities of soil and climate. Their relationship was always direct, i.e. community divergence increased with the predictive dissimilarities.

Divergence of AMF diversity from the all-home reference conditions was significantly explained by the experimental factors Inoculum, Plant and Site, while Soil had no significant effect (Table 2). Together, these experimental factors explained 50% of the variation in diversity divergence according to variation partitioning, but a large proportion of the explained variation could not be attributed to one particular factor alone (Fig. 3b).

When Inoculum, Site and Soil were coded as dissimilarities from the all-home conditions, divergence of AMF diversity was significantly affected by Plant and dissimilarity of inoculum, marginally by dissimilarity of climate (Supplementary Table S18). Dissimilarity of inoculum accounted for most of the variation in diversity changes (23% out of 41% of total explained variation) according to variation partitioning (Supplementary Fig. S2b). More diverse inocula lead to the establishment of more diverse communities and less diverse inocula to less diverse communities (Fig. 4a), the former being the case only in the WPC plant ecotype (with a less diverse home community), the latter mainly the BC plant ecotype (with a more diverse home community). The effect of climate was driven by a significant decrease of diversity at the driest site (BP; highly dissimilar climate) as compared to the other sites (Fig. 4b).

Divergence of root colonization from the all-home reference conditions significantly depended on Site, while plant ecotypes and Soil had only marginally significant effect (Table 2). The R^2 of the model was distinctly lower than the R^2 of analogous models for the divergences of community composition and diversity (compare within Table 2), consistently with variation partitioning, which revealed only small proportion of explained variation in total and by the factors Plant and Site (Supplementary Fig. S3a). Dissimilarities of community composition, soil and climate as predictors rendered a model with low R^2 of 0.061 (Supplementary Table S18, which was inconsistent with the model based on the categorical predictors (see also Supplementary Fig. S3b for variation partitioning results).

3.3. Drivers of divergence of the sympatric AMF communities

Focusing only on the communities established after inoculation with the plants' sympatric (home) microbiota, divergence from the all-home reference community only depended on Plant (Table 3, Supplementary Fig. S4a), being overall higher in the WPC than in the BC system. In the models with dissimilarities from all-home conditions as predictors, the

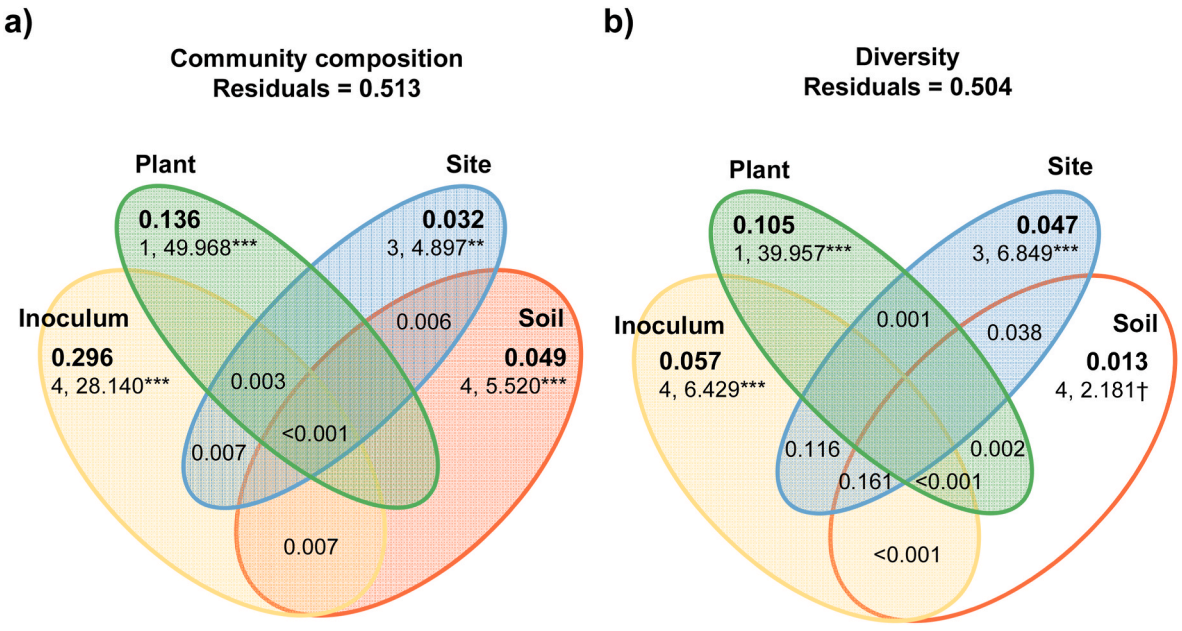

Fig. 3. Variation partitioning diagrams showing pure effects (explained by each factor alone) and shared effects of the experimental factors on divergence of arbuscular mycorrhizal fungal (AMF) communities from the reference all-home community. Divergence in community composition (a) and Shannon diversity (b) were analyzed for all AMF communities established at the new sites. Numbers give the proportion of explained variation (if > 0), df and F statistics for the pure effects. P-values are indicated by symbols (***P < 0.001, **P < 0.01, *P < 0.05, †P < 0.1). Shared effects are indicated as explained variation if > 0.

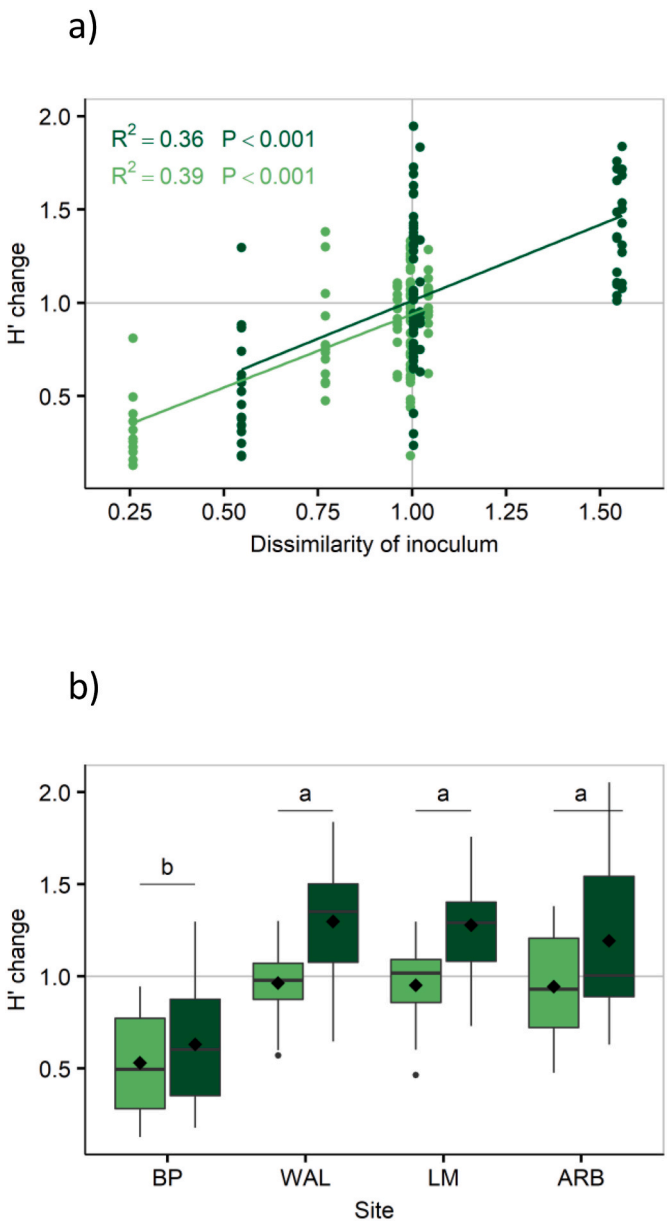

Fig. 4. Divergence of Shannon diversity (H′ change) of the arbuscular mycorrhizal fungal communities established at the new sites from the all-home conditions. H′ change is related to the dissimilarity of inoculum from the all-home community (a) and shown for the different sites (b). Light green color corresponds to BC plants, dark green to WPC plants. In (a), each dot represents one community, grey lines mark no divergence, R^2 and P are given according to simple linear regression; in (b), diamonds visualize means and letters denote significant differences between the sites (those, marked with the same latter are not statistically different).

dissimilarities of soil and local communities were significant predictors, in addition to plant ecotype (Supplementary Table S19). According to variation partitioning, however, their contribution to the total explained variability of 41% were only 2% and 4%, respectively (Supplementary Fig. S4b). The community divergence increased with increasing dissimilarity of soil conditions and, counterintuitively, with decreasing dissimilarity of the surrounding communities.

The small contribution of the new sites' climatic and soil conditions to the compositional divergence was consistent with only a few significant differences between the all-home community and the communities initiated with the home inocula at the new sites. These new-site communities never significantly differed from the all-home community

Table 3
Effects of the experimental factors on divergence of arbuscular mycorrhizal fungal (AMF) communities from the reference all-home community. Divergence in community composition, diversity (Shannon index) and root colonization were analyzed for those AMF communities established at the new sites, which were initiated with the plants' sympatric (home) microbiota.

		Composition		Diversity		Root colonization	
	df	F	P	F	P	F	P
Plant	1	53.926	<0.001	7.194	0.009	*1.379*	*0.243*
Soil	4	–	–	-	-	–	–
Site	3	*2.415*	*0.072*	11.126	<0.001	4.115	0.009
Plant × Soil	4	–	–	–	–	–	–
Plant × Site	3	–	–	–	–	3.468	0.020
AdjR^2		0.377		0.283		0.178	
AIC		−95.808		38.826		128.001	

AdjR^2, F and P values are given according to models, which were selected based on Akaike information criterion (AIC) after step-wise reduction of an initial model including all main effects (Plant, Soil and Site) and the interactions of Plant with the other two predictors. The initial and intermediate reduced models are shown in: Supplementary Tables S8–S10. Total df = 94. Hyphen - term not included into the final model; italics - term non-significant within the final model at P = 0.05.

when developing in their original soils, meaning that the new climate alone never significantly changed the composition of the BC or WPC community. They also never significantly differed between the home soil and the new-site soil within the specific climatic conditions of a site, meaning that none of the new soils significantly affected the community composition. Although climate or soil alone did not significantly change the communities, combined effects of soil and climate did lead to significant compositional difference from the all-home reference in the BC community at BP ($R^2 = 0.195$, P = 0.016) and at WAL ($R^2 = 0.242$, P = 0.041). No significant combined effect was found for the WPC community (Table 4).

Diversity changes in the home-inoculated communities were affected by the factors Plant and Site (Table 3), with Site explaining 8% of the variation (Supplementary Fig. S4c). Dissimilarities of conditions as predictors revealed dissimilarity of the local community as the only significant factor (Supplementary Fig. S4d). Diversity mainly decreased at the BP site with less diverse local community, similarly to the pattern determined for the complete data set (as reported in section 3.3 and shown in Fig. 4 a, b).

Divergence of root colonization from the all-home reference conditions displayed the same pattern as in the complete data set. It was significantly affected by Site in the model with the experimental factors as predictors (Table 3), while the model with dissimilarities of conditions had low R^2 and was inconsistent with the former (Supplementary

Table 4
Specific pairwise comparisons of the compositions of arbuscular mycorrhizal fungal communities initiated with the plants' sympatric (home) soil microbiota. Within each combination of Plant and Site, the home-inoculated communities were compared between the home soil and the new site's soil (Soil effect), between the home soil and the all-home reference (Site effect), and between the new site's soil and the all-home reference (Combined effect).

Plant	Site	Soil effect		Site effect		Combined effect	
		R^2	P	R^2	P	R^2	P
BC	BP	0.115	0.806	0.114	1.000	**0.195**	**0.016**
	WAL	0.160	0.488	0.073	1.000	**0.242**	**0.041**
	LM	0.124	1.000	0.068	1.000	0.147	0.353
	ARB	0.086	1.000	0.069	1.000	0.148	1.000
WPC	BP	0.059	1.000	0.098	1.000	0.093	1.000
	WAL	0.171	0.508	0.123	0.794	0.138	0.503
	LM	0.139	1.000	0.099	1.000	0.100	1.000
	ARB	0.078	1.000	0.116	0.212	0.154	0.370

R^2 values are given according to pairwise Adonis, P values are after Bonferroni correction for the number of comparisons within Plant.

Table S19).

3.4. Local adaptation of the mycorrhizas?

Diversity was unaffected by the provenance of soil or site consistently across all communities and across the home-inoculated communities only (Table 5). Further significant factors of the models were Plant and Inoculum (across all communities), in line with principal differences among the site-specific communities as described in section 3.1. Root colonization was significantly higher in the home soils than in the new sites' soils (Table 5, Fig. 5) and significantly higher in WPC plants than in BC plants. The provenance of inoculum or site, in contrast, had no significant effect (Table 5). However, root colonization did significantly differ between some of the new sites (Fig. 5). The difference in root colonization between the home and new sites' soils was significant for the subset of the home-inoculated communities, too (Table 5).

4. Discussion

The main result of our study is the surprisingly stable composition of AMF communities following their transfer to novel soil and climatic conditions. To the best of our knowledge, long-term persistence of complex AMF communities after co-transfer with their host plants to new abiotic conditions has not been addressed before.

4.1. Drivers of community divergence

In accordance with our first hypothesis, the identity of inoculum strongly influenced AMF community composition and diversity: the dissimilarity of the inoculated community explained a high proportion of divergence from the all-home conditions. On the other hand, dissimilar soil or climate played a much smaller role than expected by our second hypothesis, which was based on well-documented relevance of soil conditions (e.g. Lekberg et al., 2007; Dumbrell et al., 2010; Chaudhary et al., 2014; Antoninka et al., 2015; Van Geel et al., 2018) and climate (Chaudhary et al., 2018; Stevens et al., 2020) as determinants of AMF community composition. In our study, the contribution of the abiotic factors to compositional divergence was an order of magnitude smaller than that of initial inoculation, and the new soil or climatic conditions alone never significantly altered the composition of the sympatric community as compared to the all-home reference (see Table 4). This discrepancy points to the need to distinguish long-term evolution of AMF communities in specific abiotic contexts (the focus of most studies) from their responses to changed abiotic conditions (the focus of our study). Climatic factors may take time to significantly alter the composition of AMF communities in field conditions. Similar to our study, Deveautour et al. (2020) reported that reduced rainfall became consistently significant as a factor only after two years and even then, explained only a low proportion of the variability in community composition. Resistance of AMF community composition to altered climatic factors within two to three seasons has been shown also by other recent studies (Wei et al., 2021; Emery et al., 2022; Xu et al., 2022). The magnitude and time-scale of the fungal community responses probably also depends on the specific abiotic factors. For example, the compositional response of AMF communities to new soil conditions was strongly related to acidic vs. slightly basic soil pH in the study of (Ji et al., 2013), while the soils in our study were less variable in pH (all basic) and differed considerably in other parameters such as texture, P availability and organic matter content.

In addition to potential effects of climatic or soil conditions, transplanted AMF communities are likely to change due to invasion by local AMF. In our experiment, this confounding factor was intentionally constrained by the buried tree pots in order to highlight the response of the inoculated communities to the new environmental factors. The pots shielded the transplanted mycorrhizas against networks of AMF

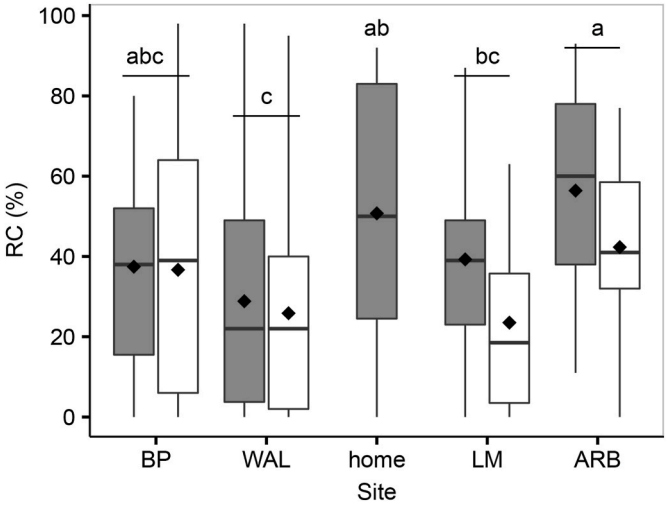

Fig. 5. Frequency of root colonization (RC%) by the arbuscular mycorrhizal fungal communities at the different sites. They were growing either in the sympatric ("home") soils of the plant ecotypes (BC or WPC, grey boxes) or in the "away" soils of each site (white boxes). Diamonds show means, the data are pooled for the two plant ecotypes and both inoculation treatment at the "away" sites. Diamonds show means, letters denote significant differences between sites (those, marked with the same latter are not statistically different).

Table 5
Effects of the experimental factors on root colonization by arbuscular mycorrhizal fungal (AMF) communities and their diversity (Shannon index). They were determined either for all communities (All microbiota) or only for those communities, which were initiated with the plants' sympatric (home) microbiota (Home microbiota).

		Root colonization				Diversity			
		All microbiota		Home microbiota		All microbiota		Home microbiota	
	df	F	P	F	P	F	P	F	P
Plant	1	6.252	0.013	–	–	28.349	<0.001	28.764	<0.001
Inoculum	1	–	–	n.i.		4.466	0.036	n.i.	
Soil	1	6.785	0.010	5.746	0.018	–	–	–	–
Site	1	–	–	–	–	–	–	–	–
AdjR^2		0.049		0.042		0.125		0.203	
AIC		2017.680		1034.989		402.030		184.103	

The factors Inoculum, Soil and Site were coded as provenance with respect to the site of origin of the plant ecotype, with two levels: "home" (the BC or WPC inocula, soils and sites) and "away" (comprising all the other sites, the corresponding inocula and soils). AdjR^2, F and P values are given according to models, which were selected based on Akaike information criterion (AIC) after step-wise reduction of an initial model including all main effects (Plant, Inoculum, Soil and Site) and the interactions of Plant with the other predictors. The initial and intermediate reduced models are shown in Appendix S2Supplementary Tables S14–S17. Total df = 213/109 for the All/Home microbiota data sets. Hyphen - term not included into the final model; n.i. - the factor was not included into the initial model; the interaction terms are omitted from the table, because they were not included in any of the models presented.

extraradical mycelia radiating from the surrounding vegetation, considered more competitive invasive agents than isolated propagules (Johnson, 2015). This is probably the main reason why we didn't find any convincing evidence for merging of the sympatric communities with AMF communities from the new sites. Additionally, negative priority effects may have contributed against the spread of infection from isolated propagules arriving at the soil surface by animal, wind or water dispersal, because priority in the occupancy of the root niche constitutes an important competitive advantage (Pearson et al., 1993; Mummey et al., 2009; Hausmann and Hawkes, 2010; Werner and Kiers, 2015). Surprisingly, the merging of pre-established fungal communities and those of outplant sites remains little explored despite the importance of this process for the formation of the root mycobiome of inoculated plants in field conditions. Sýkorová et al. (2016) described dominance of ectomycorrhizal fungal taxa of nursery origin in the roots of various tree species one season after their transplanting to a field site, which suggests, for ectomycorrhizal symbionts, important priority effects even in seedlings planted directly into local soils.

Interestingly, the clear hierarchy of drivers that determined the divergence in AMF community composition and diversity did not apply to the degree to which roots became colonized i.e. the ability of the communities to associate with the host plant. Percent root length colonized depended on the site rather than on soil or inoculum. As demonstrated by Soudzilovskaia et al. (2015), climate is a strong predictor of root colonization by AMF at the global scale. Our results demonstrate consistent differences between the climatic conditions independent of the origin of the inoculated AMF community, which strongly suggests that we observed immediate responses of the mycorrhizas to the climatic conditions. The model presented in the meta-analysis of Soudzilovskaia et al. (2015) is consistent with the trend for highest root colonization at the coldest site (ARB, mean temperature of the warmest month approx. 18 °C) as compared to the other new sites. However, the pattern of differences between the combinations of plant ecotype, soil and climate certainly also reflect interactions of the factors (Frater et al., 2018), which all impact the needs of host plants for mycorrhiza-derived services (Johnson et al., 2010; Grman, 2012). For example, the soil of the BP site – one of the warmest sites – is highly P-deficient (Table 1), which may explain higher root colonization values than would be expected based on the climatic gradient.

4.2. Indications for local adaptation?

Local adaptation of AMF communities, assumed in our third hypothesis, has been previously documented as higher proliferation of mycelia in the original abiotic conditions than in new conditions (Johnson et al., 2010; Ji et al., 2013; Sikes et al., 2014; Shi et al., 2015; Yang et al., 2018; Zhang et al., 2019a,b). The diversity of AMF communities may also decrease in new climatic conditions, possibly due to adaptation of some AMF taxa to their local climatic conditions (Islam et al., 2020).

We did not find any indication for overall diversity losses of the sympatric communities due to transfer into novel conditions. Their diversity was unaffected by the provenance of soil (Table 5) and diversity changes from the all-home conditions were consistent with the differences in diversity encountered among the local communities. This suggests that the lower diversity of the sympatric communities at some of the new sites was due to the same factors that shape the long-term diversity of the sites' local communities. The most pronounced change in diversity was the decrease at the warmer and driest BP site, where extreme climatic conditions likely represent a strong environmental filter to AMF genotypes arriving by natural dispersal (Kivlin et al., 2014) as well as to those introduced by inoculation in our experiment.

The root colonization pattern, however, does indicate adaptation of the plants' mycorrhizal interaction to their original abiotic environments. Higher root colonization in the sympatric soils than in the allopatric soils as well as high root colonization levels at the climatically intermediate home sites (Fig. 5) suggest that plants supported higher root colonization by AMF in their original abiotic conditions than in the new soils and possibly also than in the new climates. Root colonization by AMF depends on the amount of photosynthates, which the plant can allocate to the fungal symbiont and on the plant's need for nutrients, which are provided by the fungi (Treseder, 2004; Johnson et al., 2015). Plant adaptation to a specific abiotic context may fine-tune its photosynthetic capacity to the sympatric climatic conditions (Aspinwall et al., 2013; Carlson et al., 2016; Florence et al., 2019) and optimize the nutrient uptake via mycorrhizal symbionts to the sympatric soil conditions (Schultz et al., 2001; Sherrard and Maherali, 2012; Pánková et al., 2014), leading to higher support of fungal proliferation in the original abiotic contexts as compared to divergent conditions.

As hyphal root colonization can be directly related to the mycorrhizal contribution to plant growth and P uptake (Treseder, 2004; Soudzilovskaia et al., 2015; Remke et al., 2020), the encountered difference in root colonization between the sympatric soil and the allopatric soils corroborates the importance of sympatry of plant and soil for mycorrhiza functioning within the plant-soil-AMF triangle (Rúa et al., 2016). However, plant performance was influenced by the experimental factors in a much more complex pattern as described in detail by Remke et al. (2022). Interestingly, better performance of plants in sympatric soil was most pronounced with sympatric microbiota and in the stressful conditions of the warmer sites. At the colder sites, in contrast, soil and inoculum provenance had little influence on plant performance. Additionally, the role of sympatry in plant performance depended on the plant genotypes, i.e. differed between the two plant-soil-microbiota complexes (Remke et al., 2022). It suggests that while mycorrhiza formation (the extent to which AMF can colonize roots) is favored by plant-soil sympatry regardless of the fungal identities, the functioning of mycorrhizas may be partly influenced by soil sympatry, but also by a range of other factors related to the provenance and/or characteristics of the root-colonizing AMF community.

4.3. Phylogenetic diversity of the AMF communities

An interesting feature of the experimental communities was their extremely low phylogenetic diversity. Root-associated communities of AMF are usually dominated by Glomeraceae (e.g. (Hempel et al., 2007; Mickan et al., 2017; Li et al., 2020) and some plant species filter out only a small subset out of the available AMF pool in soil as their symbionts (Helgason et al., 2002; Öpik et al., 2016). Previously, Porras-Alfaro et al. (2007) described relatively low AMF diversity in the roots of *B. gracilis* from field sites. Even so, the complete absence of other glomeromycotan fungi than Glomerales and large proportion of reads assigned to one species only (*Rhizophagus irregularis*) is remarkable and possibly not attributable to biotic filtering by *B. gracilis* only.

Preparation of inocula from field soils, which involves homogenization and drying, inevitably means disturbance of the microbial communities. The original site-specific communities may thus have been reduced to disturbance-tolerant taxa mainly by the inoculation process including also a period of greenhouse cultivation (Jansa et al., 2002; Sýkorová et al., 2007; Schnoor et al., 2011; Chung et al., 2019). As demonstrated by Sýkorová et al. (2007), the 'cultivation bias' associated with greenhouse cultivation reduces the richness of root-associated AMF communities and alters the species' relative abundances. Disturbance usually favors members of Glomeraceae family and reduces representatives of other phylogenetic lineages of AMF (Jansa et al., 2002). These had been previously shown to be part of the AMF pool in the studied region (Beauchamp et al., 2006; Chaudhary et al., 2014).

May the selection of disturbance and cultivation tolerant taxa have underestimated the community responses to abiotic factors as compared to more intact communities? A shift of the species spectrum towards disturbance-tolerant taxa is expected to decrease the responsiveness of the community to abiotic conditions (Southwood, 1988; Marvier et al., 2004). On the other hand, specifically for AMF, preferences for certain

soil conditions are found also in typical r-strategists (Oehl et al., 2010; Jansa et al., 2014). Unfortunately, disturbance of microbial communities is an inherent factor of all inoculation trials, unless intact soil monoliths are used (Yang et al., 2018; Islam et al., 2020), while the concomitant functional shifts in the resulting communities remain little understood.

4.4. Conclusions

Our experiment demonstrates that transferred AMF communities largely retain their composition across a broad range of soil and climatic conditions for at least three seasons. This finding is practically important, as it testifies that seedlings can remain associated with sympatric communities in dissimilar abiotic contexts, at least in the first seasons of establishment. It also shows that longer time scales are necessary to evaluate potential effects of global change on AMF communities in similar experimental setups. Further research should focus on the merging of the inoculated AMF communities with the local communities, with respect to AMF community succession in the target plant roots, but also to potential spread of the inoculated fungi at the new sites (Janoušková et al., 2017).

The surprisingly stable community composition may also have drawbacks. Not only co-adaptation of plants and their fungi, but also adaptation of the fungal symbionts to the local conditions may be important for the functioning of the symbiosis, particularly if the local conditions are harsh (Weissenhorn et al., 1993; Estrada et al., 2013; Symanczik et al., 2015). It is conceivable that shifted relative abundances according to the species symbiotic performance in the new conditions (Kiers et al., 2011; Werner et al., 2018) may lead to more beneficial mycorrhizas than the original AMF community established by pre-inoculation. The results of our study, however, do not support this assumption. The extent of root colonization by the transferred sympatric communities responded to the novel abiotic conditions and possibly also to the ability of the plant to sustain the fungi, which indicates functional flexibility of the sympatric AMF communities in the novel conditions. Plants associated with sympatric microbiota consistently performed as well or better than plants associated with allopatric microbiota at the warmer sites of this experiment (Remke et al., 2022). This is in line with better performance of sympatric than allopatric AMF in *B. gracilis* grown in a greenhouse experiment (Remke et al., 2020). Thus, we show that considering functional benefits of sympatric mycorrhizal inocula in vegetation management is legitimate, as the sympatric AMF communities retain their composition on one hand while reacting to the new abiotic conditions in mycorrhiza formation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The link to my data is given as in the manuscript (doi referring to PlutoF repository).

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.soilbio.2023.109190.

References

Allsup, C., Lankau, R., 2019. Migration of soil microbes may promote tree seedling tolerance to drying conditions. Ecology 100, e02729. https://doi.org/10.1002/ecy.2729.

Antoninka, A.J., Ritchie, M.E., Johnson, N.C., 2015. The hidden Serengeti-Mycorrhizal fungi respond to environmental gradients. Pedobiologia 58, 165–176. https://doi.org/10.1016/j.pedobi.2015.08.001.

Aspinwall, M.J., Lowry, D.B., Taylor, S.H., Juenger, T.E., Hawkes, C.V., Johnson, M.V.V., Kiniry, J.R., Fay, P.A., 2013. Genotypic variation in traits linked to climate and aboveground productivity in a widespread C4 grass: evidence for a functional trait syndrome. New Phytologist 199, 966–980. https://doi.org/10.1111/nph.12341.

Barea, J.M., 2015. Future challenges and perspectives for applying microbial biotechnology in sustainable agriculture based on a better understanding of plant-microbiome interactions. Journal of Soil Science and Plant Nutrition 15, 261–282.

Barea, J.M., Palenzuela, J., Cornejo, P., Sánchez-Castro, I., Navarro-Fernández, C., López-García, A., Estrada, B., Azcón, R., Ferrol, N., Azcón-Aguilar, C., 2011. Ecological and functional roles of mycorrhizas in semi-arid ecosystems of Southeast Spain. Journal of Arid Environments 75, 1292–1301. https://doi.org/10.1016/j.jaridenv.2011.06.001.

Bauer, J.T., Koziol, L., Bever, J.D., 2020. Local adaptation of mycorrhizae communities changes plant community composition and increases aboveground productivity. Oecologia 192, 735–744. https://doi.org/10.1007/s00442-020-04598-9.

Beauchamp, V.B., Stromberg, J.C., Stutz, J.C., 2006. Arbuscular mycorrhizal fungi associated with *Populus-Salix* stands in a semiarid riparian ecosystem. New Phytologist 170, 369–380. https://doi.org/10.1111/j.1469-8137.2006.01668.x.

Bender, S.F., Wagg, C., van der Heijden, M.G.A., 2016. An underground revolution: biodiversity and soil ecological engineering for agricultural sustainability. Trends in Ecology & Evolution 31, 440–452. https://doi.org/10.1016/j.tree.2016.02.016.

Bennett, A.E., Classen, A.T., 2020. Climate change influences mycorrhizal fungal–plant interactions, but conclusions are limited by geographical study bias. Ecology 101, e02978. https://doi.org/10.1002/ecy.2978.

Bunn, R., Lekberg, Y., Zabinski, C., 2009. Arbuscular mycorrhizal fungi ameliorate temperature stress in thermophilic plants. Ecology 90, 1378–1388. https://doi.org/10.1890/07-2080.1.

Carlson, J.E., Adams, C.A., Holsinger, K.E., 2016. Intraspecific variation in stomatal traits, leaf traits and physiology reflects adaptation along aridity gradients in a South African shrub. Annals of Botany 117, 195–207. https://doi.org/10.1093/aob/mcv146.

Chaudhary, V.B., Cuenca, G., Johnson, N.C., 2018. Tropical-temperate comparison of landscape-scale arbuscular mycorrhizal fungal species distributions. Diversity and Distributions 24, 116–128. https://doi.org/10.1111/ddi.12664.

Chaudhary, V.B., Nolimal, S., Sosa-Hernández, M.A., Egan, C., Kastens, J., 2020. Trait-based aerial dispersal of arbuscular mycorrhizal fungi. New Phytologist 228, 238–252. https://doi.org/10.1111/nph.16667.

Chaudhary, V.B., O'Dell, T.E., Rillig, M.C., Johnson, N.C., 2014. Multiscale patterns of arbuscular mycorrhizal fungal abundance and diversity in semiarid shrublands. Fungal Ecology 12, 32–43. https://doi.org/10.1016/j.funeco.2014.06.003.

Chung, Y.A., Jumpponen, A., Rudgers, J.A., 2019. Divergence in diversity and composition of root-associated fungi between greenhouse and field studies in a

semiarid grassland. Microbial Ecology 78, 122–135. https://doi.org/10.1007/s00248-018-1277-y.
Deveautour, C., Donn, S., Power, S.A., Bennett, A.E., Powell, J.R., 2018. Experimentally altered rainfall regimes and host root traits affect grassland arbuscular mycorrhizal fungal communities. Molecular Ecology 27, 2152–2163. https://doi.org/10.1111/mec.14536.
Deveautour, C., Power, S.A., Barnett, K.L., Ochoa-Hueso, R., Donn, S., Bennett, A.E., Powell, J.R., 2020. Temporal dynamics of mycorrhizal fungal communities and co-associations with grassland plant communities following experimental manipulation of rainfall. Journal of Ecology 108, 515–527. https://doi.org/10.1111/1365-2745.13267.
Dumbrell, A.J., Nelson, M., Helgason, T., Dytham, C., Fitter, A.H., 2010. Relative roles of niche and neutral processes in structuring a soil microbial community. The ISME Journal 4, 337–345. https://doi.org/10.1038/ismej.2009.122.
Edgar, R.C., 2013. UPARSE: highly accurate OTU sequences from microbial amplicon reads. Nature Methods 10, 996–998. https://doi.org/10.1038/nmeth.2604.
Egan, C., Li, D.W., Klironomos, J., 2014. Detection of arbuscular mycorrhizal fungal spores in the air across different biomes and ecoregions. Fungal Ecology 12, 26–31. https://doi.org/10.1016/j.funeco.2014.06.004.
Emery, S.M., Bell-Dereske, L., Stahlheber, K.A., Gross, K.L., 2022. Arbuscular mycorrhizal fungal community responses to drought and nitrogen fertilization in switchgrass stands. Applied Soil Ecology 169, 104218. https://doi.org/10.1016/J.APSOIL.2021.104218.
Estrada, B., Barea, J.M., Aroca, R., Ruiz-Lozano, J.M., 2013. A native *Glomus intraradices* strain from a Mediterranean saline area exhibits salt tolerance and enhanced symbiotic efficiency with maize plants under salt stress conditions. Plant and Soil 366, 333–349. https://doi.org/10.1007/s11104-012-1409-y.
Florence, A., Ennos, R.A., Hoad, S.P., Hoebe, P.N., 2019. Variation in light interception traits in European spring barley landraces. Field Crops Research 241, 107549. https://doi.org/10.1016/j.fcr.2019.06.006.
Frater, P.N., Borer, E.T., Fay, P.A., Jin, V., Knaeble, B., Seabloom, E., Sullivan, L., Wedin, D.A., Harpole, W.S., 2018. Nutrients and environment influence arbuscular mycorrhizal colonization both independently and interactively in *Schizachyrium scoparium*. Plant and Soil 425, 493–506. https://doi.org/10.1007/s11104-018-3597-6.
Frøslev, T.G., Kjøller, R., Bruun, H.H., Ejrnæs, R., Brunbjerg, A.K., Pietroni, C., Hansen, A. J., 2017. Algorithm for post-clustering curation of DNA amplicon data yields reliable biodiversity estimates. Nature Communications 8, 1188. https://doi.org/10.1038/s41467-017-01312-x.
Grman, E., 2012. Plant species differ in their ability to reduce allocation to non-beneficial arbuscular mycorrhizal fungi. Ecology 93, 711–718. https://doi.org/10.1890/11-1358.1.
Hausmann, N.T., Hawkes, C.V., 2010. Order of plant host establishment alters the composition of arbuscular mycorrhizal communities. Ecology 91, 2333–2343. https://doi.org/10.1890/09-0924.1.
Hausmann, N.T., Hawkes, C.V., 2009. Plant neighborhood control of arbuscular mycorrhizal community composition. New Phytologist 183, 1188–1200. https://doi.org/10.1111/j.1469-8137.2009.02882.x.
Helgason, T., Merryweather, J.W., Denison, J., Wilson, P., Young, J.P.W., Fitter, A.H., 2002. Selectivity and functional diversity in arbuscular mycorrhizas of co-occurring fungi and plants from a temperate deciduous woodland. Journal of Ecology 90, 371–384. https://doi.org/10.1046/j.1365-2745.2001.00674.x.
Hempel, S., Renker, C., Buscot, F., 2007. Differences in the species composition of arbuscular mycorrhizal fungi in spore, root and soil communities in a grassland ecosystem. Environmental Microbiology 9, 1930–1938. https://doi.org/10.1111/j.1462-2920.2007.01309.x.
Hill, M.O., 1973. Diversity and evenness: a unifying notation and its consequences. Ecology 54, 427–432. https://doi.org/10.2307/1934352.
Islam, M.N., Germida, J.J., Walley, F.L., 2020. Responses of arbuscular mycorrhizal fungal communities to soil core transplantation across saskatchewan prairie climatic regions. Canadian Journal of Soil Science 100, 81–96. https://doi.org/10.1139/cjss-2019-0053.
Janoušková, M., Krak, K., Vosátka, M., Püschel, D., Štorchová, H., 2017. Inoculation effects on root-colonizing arbuscular mycorrhizal fungal communities spread beyond directly inoculated plants. PLoS One 12, e0181525. https://doi.org/10.1371/journal.pone.0181525.
Jansa, J., Erb, A., Oberholzer, H.R., Šmilauer, P., Egli, S., 2014. Soil and geography are more important determinants of indigenous arbuscular mycorrhizal communities than management practices in Swiss agricultural soils. Molecular Ecology 23, 2118–2135. https://doi.org/10.1111/mec.12706.
Jansa, J., Mozafar, A., Anken, T., Ruh, R., Sanders, I.R., Frossard, E., 2002. Diversity and structure of AMF communities as affected by tillage in a temperate soil. Mycorrhiza 12, 225–234. https://doi.org/10.1007/s00572-002-0163-z.
Ji, B., Gehring, C.A., Wilson, G.W.T., Miller, R.M., Flores-Renteria, L., Johnson, N.C., 2013. Patterns of diversity and adaptation in Glomeromycota from three prairie grasslands. Molecular Ecology 22, 2573–2587. https://doi.org/10.1111/mec.12268.
Johnson, D., 2015. Priorities for research on priority effects. New Phytologist 205, 1375–1377. https://doi.org/10.1111/nph.13143.
Johnson, N.C., Angelard, C., Sanders, I.R., Kiers, E.T., 2013. Predicting community and ecosystem outcomes of mycorrhizal responses to global change. Ecology Letters 16, 140–153. https://doi.org/10.1111/ele.12085.
Johnson, N.C., Rowland, D.L., Corkidi, L., Egerton-Warburton, L.M., Allen, E.B., 2003. Nitrogen enrichment alters mycorrhizal allocation at five mesic to semiarid grasslands. Ecology 84, 1895–1908. https://doi.org/10.1890/0012-9658(2003)084[1895:NEAMAA]2.0.CO;2.
Johnson, N.C., Wilson, G.W.T.T., Bowker, M.A., Wilson, J.A., Miller, R.M., 2010. Resource limitation is a driver of local adaptation in mycorrhizal symbioses. Proceedings of the National Academy of Sciences of the United States of America 107, 2093–2098. https://doi.org/10.1073/pnas.0906710107.
Johnson, N.C., Wilson, G.W.T., Wilson, J.A., Miller, R.M., Bowker, M.A., 2015. Mycorrhizal phenotypes and the law of the minimum. New Phytologist 205, 1473–1484. https://doi.org/10.1111/nph.13172.
Kiers, E.T., Duhamel, M., Beesetty, Y., Mensah, J.A., Franken, O., Verbruggen, E., Fellbaum, C.R., Kowalchuk, G.A., Hart, M.M., Bago, A., Palmer, T.M., West, S.A., Vandenkoornhuyse, P., Jansa, J., Bücking, H., 2011. Reciprocal rewards stabilize cooperation in the mycorrhizal symbiosis. Science 333, 880–882. https://doi.org/10.1126/science.1208473.
Kivlin, S.N., Emery, S.M., Rudgers, J.A., 2013. Fungal symbionts alter plant responses to global change. American Journal of Botany 100, 1445–1457. https://doi.org/10.3732/ajb.1200558.
Kivlin, S.N., Winston, G.C., Goulden, M.L., Treseder, K.K., 2014. Environmental filtering affects soil fungal community composition more than dispersal limitation at regional scales. Fungal Ecology 12, 14–25. https://doi.org/10.1016/j.funeco.2014.04.004.
Kolaříková, Z., Slavíková, R., Krüger, C., Krüger, M., Kohout, P., 2021. PacBio sequencing of Glomeromycota rDNA: a novel amplicon covering all widely used ribosomal barcoding regions and its applicability in taxonomy and ecology of arbuscular mycorrhizal fungi. New Phytologist 231, 490–499. https://doi.org/10.1111/NPH.17372.
Koske, R.E., Gemma, J.N., 1989. A modified procedure for staining roots to detect VA mycorrhizas. Mycological Research 92, 486–505. https://doi.org/10.1016/S0953-7562(89)80195-9.
Lau, J.A., Lennon, J.T., 2012. Rapid responses of soil microorganisms improve plant fitness in novel environments. Proceedings of the National Academy of Sciences of the United States of America 109, 14058–14062. https://doi.org/10.1073/pnas.1202319109.
Lau, J.A., Lennon, J.T., 2011. Evolutionary ecology of plant-microbe interactions: soil microbial structure alters selection on plant traits. New Phytologist 192, 215–224. https://doi.org/10.1111/j.1469-8137.2011.03790.x.
Lekberg, Y., Koide, R.T., 2005. Is plant performance limited by abundance of arbuscular mycorrhizal fungi ? A meta-analysis of studies published between 1988 and 2003. New Phytologist 168, 189–204. https://doi.org/10.1111/j.1469-8137.2005.01490.x.
Lekberg, Y., Koide, R.T., Rohr, J.R., Aldrich-Wolfe, L., Morton, J.B., 2007. Role of niche restrictions and dispersal in the composition of arbuscular mycorrhizal fungal communities. Journal of Ecology 95, 95–105. https://doi.org/10.1111/j.1365-2745.2006.01193.x.
Li, X., Zhu, T., Peng, F., Chen, Q., Lin, S., Christie, P., Zhang, J., 2015. Inner Mongolian steppe arbuscular mycorrhizal fungal communities respond more strongly to water availability than to nitrogen fertilization. Environmental Microbiology 17, 3051–3068. https://doi.org/10.1111/1462-2920.12931.
Li, Z.F., Lü, P.P., Wang, Y.L., Yao, H., Maitra, P., Sun, X., Zheng, Y., Guo, L.D., 2020. Response of arbuscular mycorrhizal fungal community in soil and roots to grazing differs in a wetland on the Qinghai-Tibet plateau. PeerJ 19, e9375. https://doi.org/10.7717/peerj.9375.
Maltz, M.R., Treseder, K.K., 2015. Sources of inocula influence mycorrhizal colonization of plants in restoration projects: a meta-analysis. Restoration Ecology 23, 625–634. https://doi.org/10.1111/rec.12231.
Marvier, M., Kareiva, P., Neubert, M.G., 2004. Habitat destruction, fragmentation, and disturbance promote invasion by habitat generalists in a multispecies metapopulation. Risk Analysis 24, 869–878. https://doi.org/10.1111/j.0272-4332.2004.00485.x.
McLachlan, J.S., Hellmann, J.J., Schwartz, M.W., 2007. A framework for debate of assisted migration in an era of climate change. Conservation Biology 21, 297–302. https://doi.org/10.1111/j.1523-1739.2007.00676.x.
Mickan, B.S., Hart, M.M., Solaiman, Z.M., Jenkins, S., Siddique, K.H.M., Abbott, L.K., 2017. Molecular divergence of fungal communities in soil, roots and hyphae highlight the importance of sampling strategies. Rhizosphere 4, 104–111. https://doi.org/10.1016/j.rhisph.2017.09.003.
Middleton, E.L., Richardson, S., Koziol, L., Palmer, C.E., Yermakov, Z., Henning, J.A., Schultz, P.A., Bever, J.D., 2015. Locally adapted arbuscular mycorrhizal fungi improve vigor and resistance to herbivory of native prairie plant species. Ecosphere 6, 1–16. :27610.1890/es15-00152.1.
Mummey, D.L., Antunes, P.M., Rillig, M.C., 2009. Arbuscular mycorrhizal fungi pre-inoculant identity determines community composition in roots. Soil Biology and Biochemistry 41, 1173–1179. https://doi.org/10.1016/j.soilbio.2009.02.027.
Neuenkamp, L., Prober, S.M., Price, J.N., Zobel, M., Standish, R.J., 2019. Benefits of mycorrhizal inoculation to ecological restoration depend on plant functional type, restoration context and time. Fungal Ecology 40, 140–149. https://doi.org/10.1016/j.funeco.2018.05.004.
Oehl, F., Laczko, E., Bogenrieder, A., Stahr, K., Bösch, R., van der Heijden, M., Sieverding, E., 2010. Soil type and land use intensity determine the composition of arbuscular mycorrhizal fungal communities. Soil Biology and Biochemistry 42, 724–738. https://doi.org/10.1016/j.soilbio.2010.01.006.
Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.M., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., 2019. vegan: Community Ecology Package. R package version 2.5-6 [WWW Document]. URL. https://cran.r-project.org/package=vegan.
Olsen, S.R., Sommers, L.E., 1982. Phosphorus. In: Page, A., Miller, R., Keeney, D. (Eds.), Methods of Soil Analysis, Part 2, Chemical and Microbiological Properties. American Society of Agronomy, Madison, pp. 403–430.

Öpik, A.M., Metsis, M., Daniell, T.J., Zobel, M., Moora, M., 2016. Large-scale parallel 454 sequencing reveals host ecological group specificity of arbuscular mycorrhizal fungi in a boreonemoral forest. New Phytologist 184, 424–437. https://doi.org/10.1111/j.1469-8137.2009.02920.x.

Pánková, H., Münzbergová, Z., Rydlová, J., Vosátka, M., 2014. Co-adaptation of plants and communities of arbuscular mycorrhizal fungi to their soil conditions. Folia Geobotanica 49, 521–540. https://doi.org/10.1007/s12224-013-9183-z.

Pearson, J.N., Abbott, L.K., Jasper, D.A., 1993. Mediation of competition between two colonizing VA mycorrhizal fungi by the host plant. New Phytologist 123, 93–98. https://doi.org/10.1111/j.1469-8137.1993.tb04534.x.

Porras-Alfaro, A., Herrera, J., Natvig, D.O., Sinsabaugh, R.L., 2007. Effect of long-term nitrogen fertilization on mycorrhizal fungi associated with a dominant grass in a semiarid grassland. Plant and Soil 296, 65–75. https://doi.org/10.1007/s11104-007-9290-9.

R Core Team, 2020. R: A Language and Environment for Statistical Computing. WWW Document]. R Foundation for Statistical Computing, Vienna, Austria. URL. https://www.r-project.org/.

Rekret, P., Maherali, H., 2019. Local adaptation to mycorrhizal fungi in geographically close *Lobelia siphilitica* populations. Oecologia 190, 127–138. https://doi.org/10.1007/s00442-019-04412-1.

Remke, M.J., Johnson, N.C., Bowker, M.A., 2022. Sympatric soil biota mitigate a warmer drier climate for *Bouteloua gracilis*. Global Change Biology 28, 6280–6292. https://doi.org/10.1111/gcb.16369.

Remke, M.J., Johnson, N.C., Wright, J., Williamson, M., Bowker, M.A., 2020. Sympatric pairings of dryland grass populations, mycorrhizal fungi and associated soil biota enhance mutualism and ameliorate drought stress. Journal of Ecology 109, 1210–1233. https://doi.org/10.1111/1365-2745.13546.

Revillini, D., Gehring, C.A., Johnson, N.C., 2016. The role of locally adapted mycorrhizas and rhizobacteria in plant–soil feedback systems. Functional Ecology 30, 1086–1098. https://doi.org/10.1111/1365-2435.12668.

Rodriguez, R.J., Henson, J., Van Volkenburgh, E., Hoy, M., Wright, L., Beckwith, F., Kim, Y.O., Redman, R.S., 2008. Stress tolerance in plants via habitat-adapted symbiosis. The ISME Journal 2, 404–416. https://doi.org/10.1038/ismej.2007.106.

Rúa, M.A., Antoninka, A., Antunes, P.M., Chaudhary, V.B., Gehring, C., Lamit, L.J., Piculell, B.J., Bever, J.D., Zabinski, C., Meadow, J.F., Lajeunesse, M.J., Milligan, B. G., Karst, J., Hoeksema, J.D., 2016. Home-field advantage? evidence of local adaptation among plants, soil, and arbuscular mycorrhizal fungi through meta-analysis. BMC Evolutionary Biology 16, 122. https://doi.org/10.1186/s12862-016-0698-9.

Schnoor, T.K., Lekberg, Y., Rosendahl, S., Olsson, P.A., 2011. Mechanical soil disturbance as a determinant of arbuscular mycorrhizal fungal communities in semi-natural grassland. Mycorrhiza 21, 211–220. https://doi.org/10.1007/s00572-010-0325-3.

Schultz, P.A., Michael Miller, R., Jastrow, J.D., Rivetta, C.V., Bever, J.D., 2001. Evidence of a mycorrhizal mechanism for the adaptation of *Andropogon gerardii* (Poaceae) to high- and low-nutrient prairies. American Journal of Botany 88, 1650–1656. https://doi.org/10.2307/3558410.

Sherrard, M.E., Maherali, H., 2012. Local adaptation across a fertility gradient is influenced by soil biota in the invasive grass, *Bromus inermis*. Evolutionary Ecology 26, 529–544. https://doi.org/10.1007/s10682-011-9518-2.

Shi, L., Yang, R., Zhang, J., Cai, X., Christie, P., Li, X., Gai, J., 2015. Evidence for functional divergence in AM fungal communities from different montane altitudes. Fungal Ecology 16, 19–25. https://doi.org/10.1016/j.funeco.2015.03.009.

Sikes, B.A., Maherali, H., Klironomos, J.N., 2014. Mycorrhizal fungal growth responds to soil characteristics, but not host plant identity, during a primary lacustrine dune succession. Mycorrhiza 24, 219–226. https://doi.org/10.1007/s00572-013-0531-x.

Smith, S.E., Read, D.J., 2008. Mycorrhizal Symbiosis, third ed., third ed. Academic Press, London.

Soudzilovskaia, N.A., Douma, J.C., Akhmetzhanova, A.A., van Bodegom, P.M., Cornwell, W.K., Moens, E.J., Treseder, K.K., Tibbett, M., Wang, Y.P., Cornelissen, J. H.C., 2015. Global patterns of plant root colonization intensity by mycorrhizal fungi explained by climate and soil chemistry. Global Ecology and Biogeography 24, 371–382. https://doi.org/10.1111/geb.12272.

Southwood, A.T.R.E., 1988. Tactics , strategies and templets. Oikos 52, 3–18. https://doi.org/10.2307/3565974.

Stevens, B.M., Propster, J.R., Öpik, M., Wilson, G.W.T., Alloway, S.L., Mayemba, E., Johnson, N.C., 2020. Arbuscular mycorrhizal fungi in roots and soil respond differently to biotic and abiotic factors in the Serengeti. Mycorrhiza 30, 79–95. https://doi.org/10.1007/s00572-020-00931-5.

Sýkorová, Z., Ineichen, K., Wiemken, A., Redecker, D., 2007. The cultivation bias: different communities of arbuscular mycorrhizal fungi detected in roots from the field, from bait plants transplanted to the field, and from a greenhouse trap experiment. Mycorrhiza 18, 1–14. https://doi.org/10.1007/s00572-007-0147-0.

Sýkorová, Z., Rydlová, J., Slavíková, R., Ness, T., Kohout, P., Püschel, D., 2016. Forest reclamation of fly ash deposit: a field study on appraisal of mycorrhizal inoculation. Restoration Ecology 24, 184–193. https://doi.org/10.1111/rec.12301.

Symanczik, S., Courty, P.E., Boller, T., Wiemken, A., Al-Yahya'ei, M.N., 2015. Impact of water regimes on an experimental community of four desert arbuscular mycorrhizal fungal (AMF) species, as affected by the introduction of a non-native AMF species. Mycorrhiza 25, 639–647. https://doi.org/10.1007/s00572-015-0638-3.

Tomiolo, S., Van Der Putten, W.H., Tielborger, K., Allison, S.D., 2015. Separating the role of biotic interactions and climate in determining adaptive response of plants to climate change. Ecology 96, 1298–1308. https://doi.org/10.1890/14-1445.1.

Treseder, K.K., 2004. A meta-analysis of mycorrhizal responses to nitrogen, phosphorus, and atmospheric CO2 in field studies. New Phytologist 164, 347–355. https://doi.org/10.1111/j.1469-8137.2004.01159.x.

Tso, K.L., Allan, G.J., 2019. Environmental variation shapes genetic variation in *Bouteloua gracilis*: implications for restoration management of natural populations and cultivated varieties in the southwestern United States. Ecology and Evolution 9, 482–499. https://doi.org/10.1002/ece3.4767.

Van Geel, M., Jacquemyn, H., Plue, J., Saar, L., Kasari, L., Peeters, G., van Acker, K., Honnay, O., Ceulemans, T., 2018. Abiotic rather than biotic filtering shapes the arbuscular mycorrhizal fungal communities of European seminatural grasslands. New Phytologist 220, 1262–1272. https://doi.org/10.1111/nph.14947.

Vasar, M., Andreson, R., Davison, J., Jairus, T., Moora, M., Remm, M., Young, J.P.W., Zobel, M., Öpik, M., 2017. Increased sequencing depth does not increase captured diversity of arbuscular mycorrhizal fungi. Mycorrhiza 27, 761–773. https://doi.org/10.1007/s00572-017-0791-y.

Vašutová, M., Mleczko, P., López-García, A., Maček, I., Boros, G., Ševčík, J., Fujii, S., Hackenberger, D., Tuf, I.H., Hornung, E., Páll-Gergely, B., Kjøller, R., 2019. Taxi drivers: the role of animals in transporting mycorrhizal fungi. Mycorrhiza 29, 413–434. https://doi.org/10.1007/s00572-019-00906-1.

Větrovský, T., Baldrian, P., Morais, D., 2018. Seed 2: a user-friendly platform for amplicon high-throughput sequencing data analyses. Bioinformatics 34, 2292–2294. https://doi.org/10.1093/bioinformatics/bty071.

Wei, X., Shi, Y., Qin, F., Zhou, H., Shao, X., 2021. Effects of experimental warming, precipitation increase and their interaction on AM fungal community in an alpine grassland of the Qinghai-Tibetan Plateau. European Journal of Soil Biology 102, 103272. https://doi.org/10.1016/J.EJSOBI.2020.103272.

Weissenhorn, I., Leyval, C., Berthelin, J., 1993. Cd-tolerant arbuscular mycorrhizal (AM) fungi from heavy-metal polluted soils. Plant and Soil 157, 247–256. https://doi.org/10.1007/BF00011053.

Werner, G.D.A., Zhou, Y., Pieterse, C.M.J., Kiers, E.T., 2018. Tracking plant preference for higher-quality mycorrhizal symbionts under varying CO^2 conditions over multiple generations. Ecology and Evolution 8, 78–87. https://doi.org/10.1002/ece3.3635.

Werner, G.D.A., Kiers, E.T., 2015. Order of arrival structures arbuscular mycorrhizal colonization of plants. New Phytologist 205, 1515–1524. https://doi.org/10.1111/nph.13092.

Xu, X., Qiu, Y., Zhang, K., Yang, F., Chen, M., Luo, X., Yan, X., Wang, P., Zhang, Y., Chen, H., Guo, H., Jiang, L., Hu, S., 2022. Climate warming promotes deterministic assembly of arbuscular mycorrhizal fungal communities. Global Change Biology 28, 1147–1161. https://doi.org/10.1111/GCB.15945.

Yang, R., Li, S., Qin, Z., Cai, X., Li, X., Christie, P., Zhang, J., Feng, G., Gai, J., 2018. Importance of AM fungi and local adaptation in plant response to environmental change: field evidence at contrasting elevations. Fungal Ecology 34, 59–66. https://doi.org/10.1016/j.funeco.2018.04.006.

Zhang, H., Cai, Y., Li, X., Christie, P., Zhang, J., Gai, J., 2019a. Temperature-mediated phylogenetic assemblage of fungal communities and local adaptation in mycorrhizal symbioses. Environmental Microbiology Reports 11, 215–226. https://doi.org/10.1111/1758-2229.12729.

Zhang, S., Lehmann, A., Zheng, W., You, Z., Rillig, M.C., 2019b. Arbuscular mycorrhizal fungi increase grain yields: a meta-analysis. New Phytologist 222, 543–555. https://doi.org/10.1111/nph.15570.