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ORIGINAL PAPER

Common soil history is more important than plant history for arbuscular mycorrhizal community assembly in an experimental grassland diversity gradient

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Abstract

The relationship between biodiversity and ecosystem functioning strengthens with ecosystem age. However, the interplay between the plant diversity - ecosystem functioning relationship and Glomeromycotinian arbuscular mycorrhizal fungi (AMF) community assembly has not yet been scrutinized in this context, despite AMF's role in plant survival and niche exploration. We study the development of AMF communities by disentangling soil- and plant-driven effects from calendar year effects. Within a long-term grassland biodiversity experiment, the pre-existing plant communities of varying plant diversity were re-established as split plots with combinations of common plant and soil histories: split plots with neither common plant nor soil history, with only soil but no plant history, and with both common plant and soil history. We found that bulk soil AMF communities were primarily shaped by common soil history, and additional common plant history had little effect. Further, the steepness of AMF diversity and plant diversity relationship did not strengthen over time, but AMF community evenness increased with common history. Specialisation of AMF towards plant species was low throughout, giving no indication of AMF communities specialising or diversifying over time. The potential of bulk soil AMF as mediators of variation in plant and microbial biomass over time and hence as drivers of biodiversity and ecosystem relationships was low. Our results suggest that soil processes may be key for the build-up of plant community-specific mycorrhizal communities with likely feedback effects on ecosystem productivity, but the plant-available mycorrhizal pool in bulk soil itself does not explain the strengthening of biodiversity and ecosystem relationships over time.

Keywords Biodiversity and ecosystem functioning relationships · Arbuscular mycorrhizal fungi (AMF) · Jena experiment · Ecosystem age · Plant diversity

Introduction

The relationship between biodiversity and ecosystem functioning (BEF) has been established through manipulation of plant diversity in field experiments (Cardinale et al. 2007; Weisser et al. 2017; Eisenhauer et al. 2019; Hong et al. 2022). Especially in temperate grasslands, aboveground plant biomass has been well studied as a proxy for ecosystem functioning (Cardinale 2011; Eisenhauer 2012; Tilman et al. 2014). The increasing plant productivity in more diverse plant communities is commonly observed as overyielding in mixtures in comparison to monocultures (Steudel et al. 2016; Weisser et al. 2017), of which a large proportion of variation in community biomass is explained by functional

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diversity (Hector et al. 1999; Roscher et al. 2012). Plant communities' adaptations to soil conditions and their interactions with soil biota have been shown to play a central role for plant productivity (Zuppinger-Dingley et al. 2016). In consequence, soil biota have been suggested as main drivers causing the overyielding in more diverse plant communities (Schnitzer et al. 2011; Wagg et al. 2014; Weisser et al. 2017; Eisenhauer et al. 2019) and driving belowground facilitation through mutualistic associations (Wagg et al. 2015; Wright et al. 2017).

Among soil biota, Glomeromycotinian arbuscular mycorrhizal fungi (AMF) are the most promising candidates for drivers of ecosystem functioning. As root endosymbionts, they provide vital nutrients and enable water uptake for ~ 80% of all terrestrial plants, they shift competition and adaptation dynamics, enable less competitive plant species to find their niches and withstand adverse environmental conditions (Smith and Read 2008; Chowdhury et al. 2022; Kuyper and Jansa 2023). The mostly positive correlation between plant and AMF diversities has repeatedly been shown (Burrows and Pfleger 2002; Antoninka et al. 2011; Guzman et al. 2021; Wang et al. 2022). Organic matter input by the plant community and increased soil carbon storage over time drive interactions between plants and fungi including non-mycorrhizal interactions (Lange et al. 2014, 2015), with fungi responding to both plant species richness and plant functional diversity (Eisenhauer et al. 2017; Lange et al. 2023). Vice versa, nutrient uptake through AMF enables different plant species to access different nutrient pools (Wagg et al. 2011; Weisser et al. 2017). However, the dynamics of concurrent plant and AM fungal community assembly in the context of biodiversity and ecosystem functioning relationships remain unresolved.

Prior research has shown that biodiversity and ecosystem functioning relationships strengthen over time, as a result of complementarity effects (Cardinale et al. 2007; Fargione et al. 2007; Eisenhauer 2012; Reich et al. 2012; Wagg et al. 2022). Complementarity is based on resource partitioning, abiotic and biotic facilitation that lead to selection for specific phenotypes and therefore niche differentiation, which is more pronounced in diverse communities (Tilman and Snell-Rood 2014; Zuppinger-Dingley et al. 2014; Barry et al. 2018, 2019). Plant diversity effects on soil microbial biomass likewise develop over time, but with a time-lag as a result of plant-soil feedbacks with accumulation of mutualists in more diverse and antagonists in low diverse communities over time (Habekost et al. 2008; Eisenhauer et al. 2010; Eisenhauer 2012; Thakur et al. 2015; Strecker et al. 2016). This plant-soil feedback is further driven by resource availability like soil carbon and soil nitrogen storage, which is increased at increased root biomass and microbial activity in more diverse communities (Fornara and Tilman 2008; Lange et al. 2015).

AM symbiosis is a result of its ecological context shaped by host biotic factors like plant root architecture, plant nutrient demand and growth stage (Corrêa et al. 2006, 2024; Berger and Gutjahr 2021). Also fungal biotic factors like the efficiency of nutrient turnover (Ji and Bever 2016), as well as abiotic factors like soil properties (Rudgers et al. 2020), play important roles in the formation and extent of mycorrhizal symbiosis. As all of these factors are dynamic, we would expect that AM symbiosis and consequently AM fungal communities are also a product of temporal dynamics. In fact, the long-term biodiversity research platform of the Jena Experiment, started in 2002, has provided a moving image of these relationships. In the Jena Experiment, plant species richness (1–60 native species) and functional richness (4 functional groups) are as independently as possible manipulated in the 80 maintained grassland plots. AMF soil communities analysed in 2007 were significantly affected by both plant species richness and plant functional richness (König et al. 2010). However, in 2010, plant species richness only marginally positively affected total fungal community diversity and had no significant impact on fungal community composition in soil (Dassen et al. 2017). In 2017, a weak positive relationship between plant and total fungal, but not AMF diversity was observed (Albracht et al. 2023), while plant functional group composition significantly affected AMF and total fungal community composition in both soil and roots (Albracht et al. 2023; Maciá-Vicente et al. 2023).

As shown by this plant and fungal diversity relationship alone, effects change with calendar year and it is difficult to separate actual age effects from short-term variations caused by e.g. community assembly as well as weather conditions or general trends of climate change. Climate events such as droughts or floods have been shown to influence both plant productivity and biodiversity and ecosystem functioning relationships (Vogel et al. 2012; Wright et al. 2015; García-Valdés et al. 2018). An experiment on temporal changes in biodiversity and ecosystem functioning relationships ("ΔBEF", Fig. 1) was nested within the Jena Experiment in 2016 to disentangle year effects from history effects by re-establishment of the original biodiversity experiment 14 years after the initial establishment of the experimental communities (Vogel et al. 2019). ΔBEF contains three treatments of (1) re-established split plots with no common plant and soil history (NH), (2) split plots with new plants of the original composition on maintained soil with community-specific history (SH), and (3) the maintained plots with common plant and soil history (PSH). By maintaining the common plant and soil histories of these 14-year-old grassland communities or re-establishing plants or plants and soil, the ΔBEF experiment not only separates

biodiversity and ecosystem relationships from the respective calendar years with their conditions, but also allows to test the individual part of plant and soil history in the age effect. Note that we use the term 'common history' rather than 'legacy' throughout, because 'common history' makes no assumption on whether the newly applied plant community signifies a regime shift while the term 'legacy' indicates that we observe remnants of previous plant communities despite the effects of a new community.

In this setup, Macía-Vicente et al. (2023) could show that while the relationship of fungal diversity and plant diversity was weaker in split plots sharing 15 years compared to 1 year of common plant history, the fungal community composition showed an increasing association with plant diversity over time. The same analysis found that the relative abundance of AMF among the fungal community decreased over time, but AMF diversity was more strongly related to plant diversity after 15 years compared to 1 year of common soil history, suggesting a gradual shift towards specific AMF assemblages (Maciá-Vicente et al. 2023). However, because of the use of universal fungal primers, the resolution of AMF in this study was limited. In addition, the comparison was restricted to split plots with the original plant community and re-established plant communities, and no experimental re-establishment of the soil community was analysed.

With the present study, we investigated how species-rich and -poor plant communities with common plant and soil histories affect AMF communities and vice versa. Thereby, we explored whether plant or soil histories are more important drivers of AMF community composition and diversity. Continuing from the work of Macía-Vicente et al. (2023), we sampled bulk soil at a later stage of the ΔBEF experiment with focus on AMF using specific primers. We further expanded the analysis to all combinations of grassland communities of 19 vs. 5 years of common plant and soil history, therefore also included the soil history as a factor of developing biodiversity and ecosystem relationships.

Given the steeper biodiversity and ecosystem relationship in plant communities with established soil history, we expected (H1a) plant communities with long-term common soil history to have stronger effects on AMF community composition (comparison SH vs. NH). In this context, AMF community composition should respond to plant community diversity and composition. Given the tight interaction between AMF and plants, and in contrast to previous results on other fungal guilds (Maciá-Vicente et al. 2023), we further expected (H1b) common plant history to lead to additional strong effects on AMF community composition (comparison PSH vs. SH). We anticipated AMF diversity to increase with increasing plant diversity in accordance with the abovementioned previous results and hypothesised that (H2) this relationship strengthens with common soil history and – to a lesser extent – additional common plant history. Complementary to (H2), we expected (H3a) AMF to shift from mainly generalists to more specialists in grasslands with common history, therefore diversifying and exploring more niches after the grassland communities have been established. At the AMF community level, this would lead to (H3b) more divergence in contrasting plant communities in split plots with common history. And finally, with AMF being potential drivers of biodiversity and ecosystem relationships, we expected (H4) AMF communities to drive plant productivity more in grasslands with common history.

Materials and methods

Field Experimental Design

As the basic setting, we used the existing long-time biodiversity experimental platform of The Jena Experiment in Jena, Germany (50°55'N, 11°35'E, 130 a.s.l.). The field site is set up on an Eutric Fluvisol soil (IUSS Working Group WRB, 2015) from loamy fluvial sediments alongside the Saale river and consists of 80 grassland plots of differing plant diversity (1, 2, 4, 8, 16, or 60 grassland species) and functional composition (4 functional groups: small and tall herbs, legumes, and grasses; Roscher et al. (2004)). These 80 plots of varying composition out of a 60 grassland species pool (Online Resource: Table S1) have been maintained since 2002.

In 2016, the ΔBEF experiment was established with a setup of three history treatments with varying age of the plant and soil communities, as described in detail in Vogel et al. (2019) (Fig. 1). In the first treatment, main root zones (30 cm depth) were excavated from 1.5 × 3 m split plots and refilled with arable soil from an adjacent crop field, and the plot-specific plant communities were sown from unrelated seeds (Vogel et al. 2019). This treatment is hereafter called NH (no history) as plants and soil have no common history. The soil does however resemble the Jena Experiment soil at the beginning of the original experiment, being used as highly fertilized arable land for at least 40 years and having soil properties falling within the range of the experimental plots (pH 7.3; C_{org} 20.5_{gkg-1};N_{tot} 2.3_{gkg-1} compared with pH 7.1–8.4; C_{org} $5–33_{gkg-1}$; N_{tot} $1–2.7_{gkg-1}$ in 2002 (Roscher et al. 2004; Vogel et al. 2019)). For the second treatment, the soils from the pre-existing experiment plots were kept, but the plant sod was removed from split plots and roots removed by mixing and homogenizing soil up to 30 cm depth with a digger (Vogel et al. 2019), and new plants were sown (again from unrelated seeds). The split plots of this second treatment, hereafter called SH (only soil history)

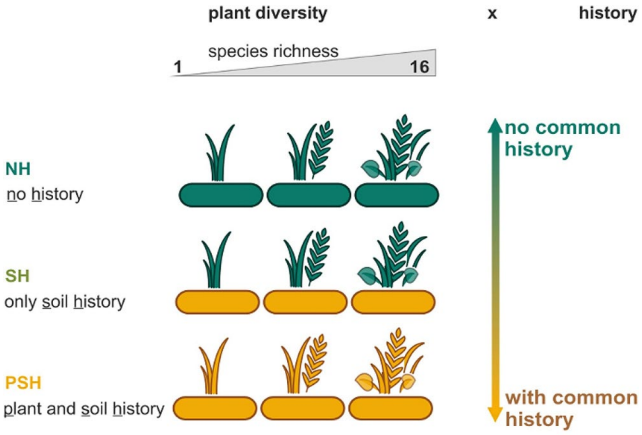

Fig. 1 Simplified design of the ΔBEF experiment sampled here: Plant communities with sown diversity ranging from monocultures, over 2, 4, 8, to 16 species mixtures, varying in composition and functional diversity (14–16 communities per diversity level). In split plots with no common history (NH) plant material and topsoil were removed and split plots were re-sown 5 years prior to sampling; SH split plots kept original soil and only had the plant communities re-sown 5 years before sampling; the split plots with common plant community and soil history (PSH) remained from the main Jena Experiment established 19 years prior to sampling

therefore contained soils that has had a long time to adapt to its specific plant community, but the newly sown plants had no history with the soil. The third treatment was formed by the pre-existing plots of the Jena Experiment with old soil and plant communities (PSH, with plant community history and with soil history).

Soil of all 76 plots with monocultures or 2- to 16-species mixtures (i.e., 14–16 plots per diversity level) and all treatments (i.e., 3 split plots per plot) was collected on one sampling date between May 31st and June 12th 2021. At this point, the newly established plant communities and soil had existed for 5 years, and the original soil and communities for 19 years. The 5 years passed should have allowed the NH split plots to recover from the disturbance (Schmid et al. 2021). For AMF community analysis on plot level, 4 soil cores (5 cm depth, 4 cm in diameter) were taken from the centre of each split plot. One combined sample of bulk soil per split plot was frozen at -20 °C until further processing.

AMF marker gene sequencing and data processing

Genomic DNA was extracted from 300 mg bulk soil samples using the Quick-DNA™ Fecal/Soil Microbe Miniprep Kit (Zymo Research). Quantity and purity of DNA isolated from bulk soil samples were assessed using a NanoDrop 8000 spectrophotometer (Thermo Fisher Scientific). The DNA was then amplified in triplicates. We targeted the SSU rRNA region of AMF with primer pairs Glomer1536 and WT0 (AATARTTGCAATGCTCTATCCCA / CGAGDWTCATTCAAATTTCTGCCC (Wubet et al. 2006; Morgan and Egerton-Warburton 2017) for the first and NS31 and AML2 (TTGGAGGGCAAGTCTGGTGCC / GAACCCAAACAC TTTGGTTTCC (Simon et al. 1992; Lee et al. 2008) for the second PCR step following the protocol of Wahdan et al. (2021). The samples were prepared for Illumina sequencing by purifying amplicons, followed by barcoding and quality checking per the protocol of Wahdan et al. (2021). The sequencing was performed at the Illumina MiSeq platform at the Department of Soil Ecology of the Helmholtz Centre for Environmental Research – UFZ, Halle (Saale), Germany as paired-end sequencing of 2 × 300 bp.

The sequencing output was processed with the *snakemake* implementation of *DADA2* (Callahan et al. 2016) *dadasnake* (Weißbecker et al. 2020): primers were trimmed and sequences filtered to a minimum length of 260 bp (fwd) / 210 bp (rvs); reads with expected error higher than 2 were discarded; amplicon sequencing variants (ASVs) were determined with 'pooled' settings and forward and reverse ASVs were merged with a minimum overlap of 12 bp and 0 mismatches and filtered for chimaeras. Taxonomic classification was done with *mothur* (Schloss et al. 2009) against the SILVA v138 SSUref database (Quast et al. 2013) to then discard non-Glomeromycotinian ASVs.

The remaining fungal ASV were blasted against the MaarjAM database (Öpik et al. 2010) to be assigned to virtual taxa (VTX). All ASVs that could not be assigned to a virtual taxon were extracted, filtered for singletons and used to construct a maximum likelihood phylogenetic tree based on a general time-reversible, discrete gamma (GTR + G) model using raxML (Stamatakis 2014) and FasttreeMP (Price et al. 2010). Thus, these ASVs were assigned custom virtual taxa (VTC) with cophenetic distances below 0.03 (Albracht et al. 2023).

Soil and plant data

Aboveground plant biomass was harvested from May 31st to June 8th 2021 and measured in two 0.1 m^2 (20 × 50 cm) frames per split plot as described in Vogel et al. (2019). Briefly, plants were cut with scissors at around 3 cm above soil surface and stored in plastic bags at 4 °C until they were sorted into target (sown) species, weeds (not sown), rest (unidentifiable plant material), and litter (dead plant material). The sorted samples were weighed after drying at 70 °C for at least 48 h. Final biomass is given in g/m^2 based on the sampled area minus bare ground area.

From May 31st to June 11th 2021, an additional 4 soil cores of 5 cm depth and 3.5 cm diameter were taken in a strip of 1 m in the centre of each split plot. These were bulked together per split plot and all roots washed and

separated into coarse (> 2 mm) and fine (< 2 mm) roots to determine root biomass. All roots were dried at 70 °C for at least 48 h and then weighed. The final root biomass is given in g/m^2 based on the calculated sampled area: *number of cores * (1.75 cm)^2 * π*.

For soil P (P), about ¼ of the soil cores used for root biomass determination was combined, sieved to < 2 mm and dry-weight equivalents of 1 g sample material were extracted with a 0.5 M $NaHCO_3$ solution (Carl Roth) at pH 8.5 for 30 min following Olsen (1954). Phosphate concentrations were analysed after filtering extraction solution (Mn 619 G1/4, Macherey-Nagel) using continuous flow analyser (Seal Analytical) with molybdenum-blue method (Murphy and Riley 1962). Soil water content (SWC) was analysed gravimetrically from the same soil samples with a halogen moisture analyzer (HB43-S Halogen, Mettler Toledo).

Samples for soil microbial respiration were taken at the end of June 2021, pooling 4 soil cores per split plot of 10 cm depth and a diameter of 2 cm which were stored at 4 °C until analysis. The soil was sieved (< 2 mm) and visible plant material and animals removed. The analyses were performed with an O_2 micro-compensation apparatus measuring basal respiration (BR), maximum initial respiratory response (MRR), soil microbial biomass C (Cmic) and specific respiratory quotient (qO2).

Statistical analysis

All statistical analyses were done in *R version 4.1.1* (Ihaka and Gentleman 1996), unless stated otherwise. Virtual taxa (VT, including VTX and VTC) were filtered to at least one count in a minimum 2% of all samples.

We performed an explorative PARAFAC analysis (Harshman 1970; Carroll and Chang 1970; Bro 1997) on filtered and rarefied read count data which was exported to *MATLAB vers. 9.14.0* (The MathWorks Inc. 2022). In MATLAB, the data was cubed, a pseudocount of 1 added, and centre-log transformed. To perform a PARAFAC analysis (Bro 1997) based on the *N-way toolbox* (Bro 2023), the data was centred across VT and scaled within VT (Bro and Smilde 2003), before using bootstrapped initiation of 100 PARAFAC models and selecting the number of valid components based on steady CORCONDIA values (100) across the initiations. The PARAFAC outputs were exported back to R for summarization and averages of bootstrapped models plotted with *ggplot2* (Wickham 2011).

To explore differences in β-diversity across the history treatments, Aitchison distances were calculated with package *robCompositions* (Templ et al. 2011) from the filtered and rarefied abundance matrix after replacing zeros with a pseudo-count of 0.1. All pairwise distances were extracted and compiled for each treatment and plant diversity combination. We used Wilcoxon signed rank tests on the pairwise distances to find significant differences in beta-diversities across the history and diversity gradient.

To quantify history treatment and plant diversity effects on AMF communities, we ran PERMANOVA (*adonis2* function in *vegan*, (Oksanen et al. 2019) on the Aitchison distance matrix (*distances ~ history treatment * plant diversity$_{log}$* (9999 permutations, stratified for block). As we and others have previously observed plant functional group presence to play an additional role in shaping AMF communities (König et al. 2010; Albracht et al. 2023; Maciá-Vicente et al. 2023), we further ran a more complex PERMANOVA on the Aitchison distance matrix to test for effects of plant community compositions:

distances ~ history treatment + plant diversity$_{log}$ + functional diversity + legumes$_{p/a}$ + grasses$_{p/a}$ + herbs$_{p/a}$.

Barplots were based on relative abundances calculated in *phyloseq* (McMurdie and Holmes 2013) on the filtered abundance data. We used *Maaslin2* (Mallick et al. 2021) with a zero-inflated negative binomial (ZINB) model on the count data normalised to trimmed mean of M-values (TMM) to calculate differential abundances. We ran three individual models to find differentially abundant VT between history treatments (plot as random effect), between the plant diversity levels (block and treatment as random effects), and the combined model of history treatment and plant diversity and their interaction (block and plot as random effect). For the second model, we tested both a regression model with VT read counts on the logarithm of plant diversity and, to detect nonlinear plant diversity effects, a categorical model comparing higher diversity levels against the monocultures.

α-diversity indices (Richness, Shannon and Simpson diversity indices, Pielou's evenness) were estimated with *phyloseq* (McMurdie and Holmes 2013) on rarefied data (2400 reads per sample). The α-diversity indices were tested with the linear mixed model:

*α-diversity ~ history treatment * plant diversity$_{log}$*.

As the Jena Experiment field site has a known edaphic variation with *soil P* (P) and *soil water content* (SWC) varying across the 4 blocks the grassland plots are grouped in, the block and plot were carried as a random effect.

We assessed whether AMF VT increase or lose plant partner specificity from younger to older grasslands. The degree of specialisation of AMF VT to plant species was calculated as the phi-coefficient (Chytrý et al. 2002; Weißbecker et al. 2019) per treatment:

$$\varphi = \pm \sqrt{(X^2/N)} = (a \times d - b \times c)/\sqrt{((a+b) \times (c+d) \times (a+c) \times (b+d))}.$$

where a is the number of occurrences of a VT in a split plot where a particular plant species was sown, b the number of occurrences of the VT in split plots without that plant, c the number of times the VT is absent in split plots where the

plant was sown, and *d* the number of times the VT is absent in split plots without the plant. The resulting φ-coefficients range from − 1 to 1 with values above 0 indicating a specificity between the individual VT and plant species. Significance was determined by comparison to null-models. We used 1000 simulations of a *c0* model (preserving VT frequencies) and a *greedyqswap* model (additionally preserving VT richness per sample) in *vegan* (Oksanen et al. 2019) to generate FDR-adjusted p-values for the significance of the φ-coefficients.

We analysed species turnover on filtered and rarefied count data with package *codyn* (Hallett et al. 2016) calculating appearances, disappearances, and the total turnover from treatments NH to SH and SH to PSH.

The edaphic variables were tested with ANOVA against the history treatment and the plant diversity (*env ~ history treatment * plant diversity*$_{log}$) and in a second model against the diversity and presence/absence of functional groups to test how composition and age of the plant communities interact with soil parameters and plant productivity. The edaphic data further was used for mediation analysis with *LDM vers. 5* (Hu and Satten 2022) to analyse which changes in environmental factors are potentially mediated by the AMF communities (base model: *VT_abundance_table | confounder ~ (factors) + (target* e.g. aboveground biomass*)* with *confounder = 1* and three different models in which the factors were (a) *(history treatment + plant diversity*$_{log}$ *+ soil P + SWC)* or only (b) *(history treatment + plant diversity*$_{log}$*)* or (c) *(soil P + SWC)*.

Results

Exploration of the AMF community in plant diversity and history treatments

We obtained a total of 3,967,994 reads (2,450 to 32,249 reads per sample) assigned to *Glomeromycota* ASVs. The ASVs were aggregated to 128 VT, of which 106 were defined by alignment to the MaarjAM database (VTX; Online Resource 1: Table S2) and 22 from a de-novo maximum likelihood phylogenetic tree (VTC; Online Resource 1: Table S3). The majority of AMF in the bulk soil belonged to the genera *Glomus* (46.6%) or *Claroideoglomus* (24.5%), followed by *Diversispora* (overall 18.5%). The custom clusters (VTC) had lower relative abundances ranging from < 1 to 4.3% (Online Resource 1: Fig. S1).

We explored patterns of rarefied AMF abundances across the plant diversity and history treatment using PARAFAC three-way analysis. The best model described a single component with an explained variance of 6.56% (+- 0.15%), demonstrating a weakly reliable relationship between AMF, plant diversity and history treatment. VT abundances responded to the plant diversity gradient with the relationship increasing with plant diversity (Fig. 2a). VT determined as *Claroideoglomus* responded more to high-diverse plots (Fig. 2b), while VT of genus *Glomus* – while showing diverse patterns – displayed the opposite relationship. Out of the history treatments, PSH displayed a slightly more pronounced VT-plant diversity relationship (Fig. 2c).

Plant diversity and identity effects in split plots with different histories

In accordance with the exploratory analysis, a PERMANOVA against the full Aitchison distance matrix revealed that history treatment had a significant, but low, impact on AMF communities ($R^2 = 0.09$, $p < 0.001$). Testing pairs of history treatments with PERMANOVA, we found that the history treatment effect was larger for soil history (history treatment effects NH vs. SH and NH vs. PSH: $R^2 = 0.09$, $p < 0.01$) than for the plant history (SH vs. PSH: $R^2 = 0.02$, $p < 0.01$).

Accordingly, when taking all plant diversity levels together, the AMF communities in PSH split plots were significantly more distant from NH communities than from SH communities (Fig. 3a). NH split plots were as different from PSH as SH split plots. Hence, soil history, which differentiates SH and PSH from NH split plots, seems to be the more important driver shaping AMF communities in this grassland. However, the greater similarity of PSH and SH split plots was only observed in plant communities with 4 or more species (Fig. 3b-f).

Plant diversity ($R^2 = 0.02$, $p < 0.001$) and the interaction of history treatment and plant diversity shaped AMF communities ($R^2 = 0.01$, $p < 0.01$), however both with lower effect sizes. The plant diversity effect was not stronger in NH ($R^2 = 0.03$, p = < 0.01) than SH ($R^2 = 0.02$, $p < 0.01$). The plant diversity effect was however stronger in PSH split plots ($R^2 = 0.06$, $p < 0.001$) than in either split pot without plant community history, indicating that plant diversity effects on AMF communities depend on shared plant community history.

We tested additional potential drivers of AMF community composition among plant community composition. We ran a PERMANOVA on the AMF community composition against the history treatments and plant diversity by adding the number of functional groups and presence/absence of individual plant functional groups. This revealed that the number of different functional groups ($R^2 = 0.01$, $p = 0.37$) was not important, however presence of functional plant groups explained some variation (legumes: $R^2 = 0.01$, $p < 0.001$; grasses: $R^2 = 0.01$, $p = 0.04$; herbs: $R^2 = 0.01$, $p = 0.01$). Relating these findings to edaphic factors, soil P

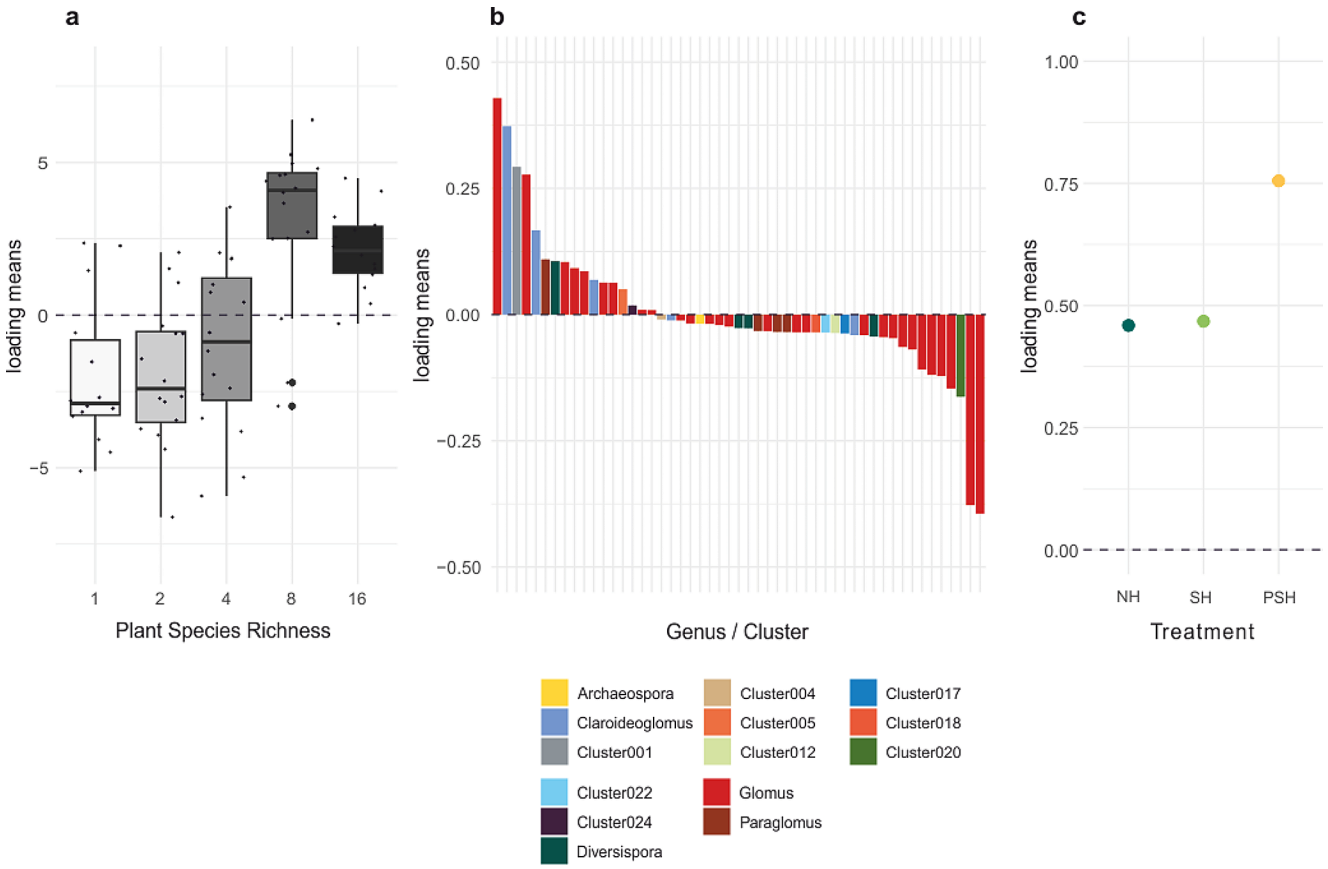

Fig. 2 Three-way exploration of virtual taxa (VT) abundances across plots and history treatments. **(a)** Plot mode: across the data cube, the plant diversity gradient had a strong influence on VT abundance. **(b)** VT mode: in the context of the modes displayed in the other panels, loadings > 0 of VT indicate a higher response of this VT in more diverse plant communities and lower response in low-diverse plant communities; loadings < 0 of VT indicate the opposite trend. **(c)** Treatment mode: the history treatments all follow similar trends (all loadings > 0) with the VT and plant diversity interaction being most pronounced in PSH (with plant community and soil history). Means of loadings from 100 bootstrapped PARAFAC analyses explaining 6.56% of the variance are displayed; NH – no history; SH – soil history; PSH – plant and soil history

was significantly lower when legumes (t = -2.99, $p < 0.01$) were present and significantly higher with grasses (t = 2.23, $p = 0.03$) present. Zooming in on edaphic differences, NH split plots contained significantly higher P (F = 65.22, $p < 0.01$) and had a significantly higher SWC (F = 4.19, $p = 0.02$) than the split plots with soil history. SWC was higher with grasses present (t = 2.12, $p = 0.04$). The presence/absence of herbs had no influence on either soil P (t = -0.84, $p = 0.40$) or SWC (t = 0.00, $p = 0.99$).

Differences in relative abundances of VT across history and plant diversity

As we found AMF communities to shift with soil history and plant diversity, we calculated differential abundances to find which taxa contributed most to these shifts and to discern whether history treatments induced similar or differing changes. Most VT showed the same direction of change in SH and PSH compared to NH (Fig. 4a) and there was no clear trend in PSH having an additional effect to SH. The strongest difference according to soil history was found for VTX00193 (*Claroideoglomus*), which was significantly more abundant in split plots with soil history (Fig. 4a). The same trend could be seen for another *Claroideoglomus* VTX00340. Other *Claroideoglomus* (VTX00056, VTX00357) were only higher in SH split plots, but not in PSH. Among the *Paraglomus*, virtual taxon VTX000281 was less abundant in both SH and PSH than in NH, while VTX00444 and VTX00335 were less abundant in only SH or PSH compared to NH. The genus *Diversispora* had mixed results with VTX00054 being less abundant in SH, while VTX00380 was higher in PSH and VTX00062 higher abundant in both SH and PSH in comparison to the NH split plots. *Cluster 20*, which likely contains *Diversispora*, was more abundant in split plots with soil history, as well. *Glomus* also showed diverse responses to the history treatment with e.g. VTX00214, VTX00130 and VTX00153 being more abundant in split plots with soil history, whereas

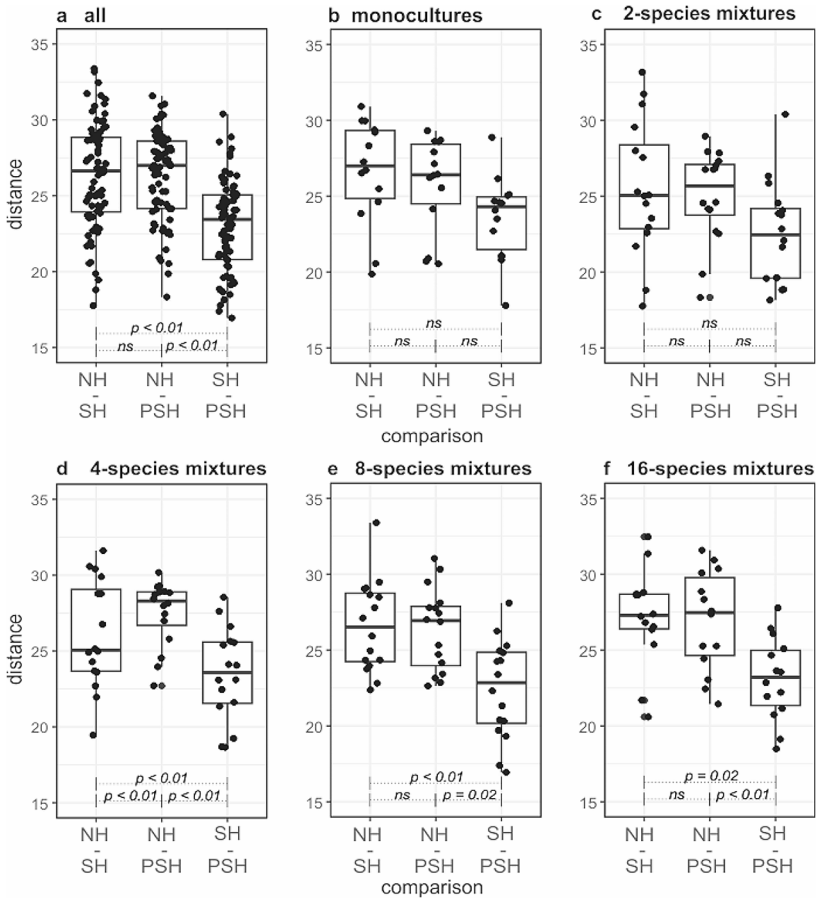

Fig. 3 Comparisons of pairwise Aitchison distances of AMF communities between history treatments in the **(a)** monocultures, **(b)** 2-species plots, **(c)** 4-species plots, **(d)** 8-species plots, and **(e)** 16-species plots. P-values indicate significant differences of the distances between history treatments (Wilcoxon' signed rank test), n.s: not significant at alpha = 0.01; NH – no history; SH – soil history; PSH – plant and soil history

VTX00155, VTX00166 and VTX00064 were significantly less abundant in the split plots with soil history.

Across the plant diversity gradient (Fig. 4b), two *Glomus* taxa (VTX00113, VTX00155) were significantly less abundant in the more diverse plots than in monocultures. However, other *Glomus* (VTX00143, VTX00072, VTX00135) and a *Diversispora* (VTX00060) were significantly more abundant at higher plant diversity. While other VT did not show clear trends along the diversity gradient, some VT were only significantly more abundant in the higher diverse plots with 8 or 16 plant species (*Glomus* VTX00399 and VTX00151; *Diversispora* VTX00054; *Claroideoglomus* VTX00056 and *Cluster 4* (*Archaespora*)).

In summary, a total of 39 VT showed significant differential abundance in response to the history treatments and 28 VT responded to the plant diversity gradient. Of these, 20 VT were responding to both the history treatment and the plant diversity, however we could not find an interactive effect of these two factors on differential abundances.

Plant diversity and history effects on AMF α-diversity and turnover

Next, we analysed whether different components of α-diversity of the AMF communities also responded to history or plant diversity (H2). All calculated α-diversity indices were significantly affected by the block in which the plots were located. When adjusting for block effects, VT richness was not different between the 3 history treatments ($F = 1.00$, $p = 0.37$, Online Resource 1: Fig. S2), but was significantly positively affected by plant diversity ($F = 21.02$, $p < 0.0001$). The effect size of plant diversity on AMF richness differed between the treatments, being highest in PSH and lowest in SH (Online Resource 1: Table S4). Pielou's evenness of AMF communities, on the other hand, was affected by the history treatments only (Online Resource 1: Table S4). Pielous's evenness of PSH was significantly higher than NH ($t = -3.31$, $p = 0.001$) and SH ($t = -2.57$, $p = 0.012$). The history treatments and plant diversity had no significant interactive effect on any of the α-diversity indices.

Species turnover was higher from NH to SH than from SH to PSH (Online Resource 1: Fig. S3), suggesting again that soil history has a bigger impact on AMF presences than

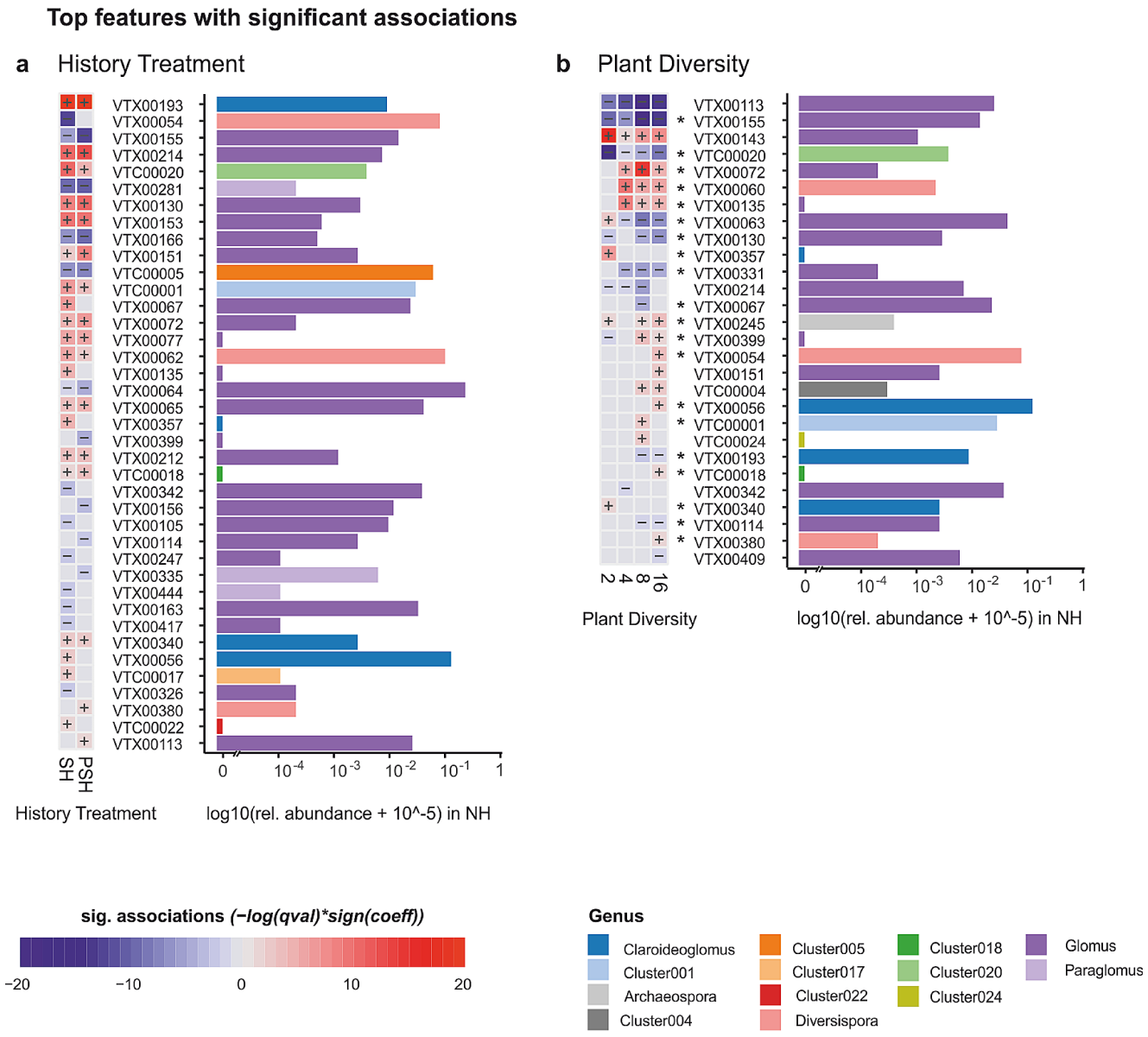

Fig. 4 Significantly differential virtual taxa (VT) showing ***(a)*** differential abundance in history treatments SH (soil history) or PSH (plant and soil history) in comparison to the NH (no history) split plots and ***(b)*** differential abundances of the more diverse plant communities compared to monocultures (factorial comparison) with * indicating significant differences in the linear model. Bar plots indicate relative abundance of VT in NH as base abundance for the differential abundance analysis and colours indicate genus. We found no significant interactions of history treatment and plant diversity. Significance is based on Maaslin2 ZINB model

the plant history. Appearances of species from NH to SH amounted to 40.8% and to 35.4% from SH to PSH. The disappearance was higher from NH to SH with 39.3% than 36.5% from SH to PSH. In addition to history ($F = 21.59$, $p < 0.001$), plant diversity ($F = 4.12$, $p = 0.003$) had a significant effect on species turnover, with the turnover being higher in monocultures than mixtures.

Specificity of AMF communities and effects of plant functional groups

We hypothesised (H3a) that AMF communities specialise over time. To address this, we calculated the φ-coefficient for the frequency of AMF VT co-occurring with specific grassland plant species as measure of specificity per history treatment (Fig. 5). Many VT had positive plant species specificities, but the mode of φ was in the slightly negative range. Comparing φ-values against two null-models which preserve VT frequencies or VT frequencies and VT richness

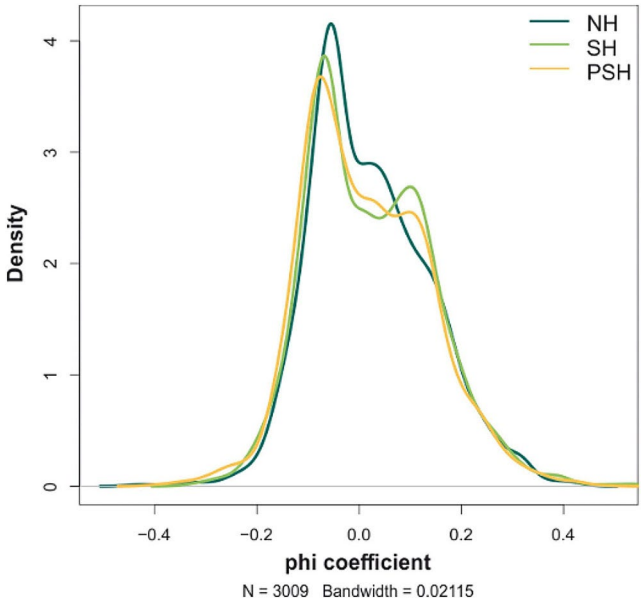

Fig. 5 Density of φ-coefficients for specificity of each AMF virtual taxa (VT) to individual plant species with φ = -1 being non-specific and φ = 1 being highly specific; NH – no history; SH – soil history; PSH – plant and soil history

per sample, we found only few significant specialisations of AMF for plant species: In NH split plots VTX00156 (*Glomus*) co-occurred with *Gallium mollugo* agg., in SH split plots we found VTX00245 (*Archaespora*) with *Poa pratense* and in PSH split plots no VT was specialised on any plant species (Table S5).

The potential mediating role of AMF communities for plant productivity

Lastly, we tested whether AMF communities may explain ecosystem functioning, given the soil properties and treatments (H4). Significant response of aboveground plant biomass, microbial biomass, microbial respiration and other factors to the plant and soil history treatments had been previously shown in Vogel et al. (2019). In accordance with those findings, in 2021 aboveground plant biomass was primarily determined by plant diversity ($F = 28.47$, $p < 0.001$) but also by the history treatment ($F = 10.74$, $p < 0.001$), with the plant diversity slope being steepest in PSH splitplots (Online Resource 1: Fig. S4 and Table S6), but both plant diversity and history effects were weaker at this later time point. Plant biomass of sown species was significantly higher with legumes ($t = 5.52$, $p < 0.01$) or grasses ($t = 3.80$, $p < 0.01$) present and also at higher functional plant diversity ($F = 25.70$, $p < 0.01$). Unlike the aboveground plant biomass, root biomass was not affected by history treatment ($F = 1.39$, $p = 0.25$) but by plant diversity ($F = 15.72$, $p < 0.001$) and presence of legumes ($F = 5.37$, $p = 0.02$) and grasses ($F = 5.03$, $p = 0.03$). We found no interaction of history treatment and plant diversity on plant biomass.

To understand how much of the variation in plant and microbial biomass can be explained through influence of the AMF communities, we performed mediation analysis (Online Resource 1: Table S7). Only 0.84% of variation in soil P ($p = 0.02$), but 2.69% variation in SWC ($p < 0.001$) was potentially mediated by AMF. We found no evidence for significant mediation of history treatment and plant diversity effects on aboveground plant community biomass by AMF communities ($p = 0.24$), but 1.45% of variation in aboveground legume biomass was potentially mediated through AMF communities. None of the variation in grass ($p = 0.26$) or herb ($p = 0.69$) aboveground biomass introduced by history treatment, plant diversity and soil P and SWC were likely mediated through AMF. Belowground, differentiating between coarse and fine root biomass, we found potential mediation effects of AMF on 1.02% variation of fine root biomass ($p < 0.01$). To summarise, the potential for the overall bulk soil AMF community composition to be the mediator of the plant diversity and history effects was found to be limited.

Discussion

Here, we present results of the ΔBEF Experiment (Vogel et al. 2019) to test community age effects as well as plant community-specific soil history effects on AMF communities in grasslands. Our analyses show that AMF communities assemble over time and as a result of plant diversity, but we find no strengthening of plant-AMF diversity relationships over time and limited evidence for the potential of bulk soil AMF communities as lone drivers of biodiversity and ecosystem functioning relationships.

Plant history effects are transient while lack of common soil history has long-lasting effects

The experimental plant diversity gradient has previously been established as a factor shaping AMF communities in bulk soil of the Jena Experiment (König et al. 2010; Dassen et al. 2017). We expected to see recapitulation of plant diversity effects with re-establishment of the experimental grasslands and indeed observed a plant diversity effect on relative abundances of VT and overall AMF community composition in all history treatments. In addition, the identity of the present plant functional groups played a role, as previously described (König et al. 2010; Dassen et al. 2017; Maciá-Vicente et al. 2023). We hypothesised common soil history to lead to strong shaping of AMF communities (H1a), while common plant history would additionally

drive AMF community composition (H1b). Our analyses showed that the plant diversity effect increased with plant history: the plant diversity effect was stronger in split plots with plant community history (PSH) than in the other plots. Plus, divergence of AMF communities with soil history was more pronounced in more diverse plant communities, suggesting convergence or more stability of soil processes at higher diversity.

However, within a plot, NH communities were equally dissimilar from split plots with just soil history (SH) than from split plots with both plant and soil history (PSH). This suggests that soil history was more important for overall AMF community assemblage and additional plant history was less important. Interestingly, comparing our results after 5 years of re-establishment with those of Macía-Vicente et al. (2023) who analysed SH and PSH in the same experiment after 1 year of re-establishment, we see that while plant community and diversity effects did drive AMF community composition after 1 year, these effects seems to have disappeared with time. We did not find significant effects of plant history anymore, indicating potentially saturating effects of plant community age between 1 and 5 years. This would be consistent with the observations that, while plants have been shown to drive AMF colonisation of soil patches (in 't Zandt et al. 2022), plant diversity effects on many soil processes and communities establish after a time lag of ~4 years (Eisenhauer et al. 2010; Eisenhauer 2012). On the other hand, Macía-Vicente et al. (2023) analysed root-associated fungi and the difference in plant history effects may be due to the larger influence of the plant community on those than on bulk soil. In bulk soil, it seems that soil legacy effects take more time to develop than plant community effects, as differences in AMF communities and turnover between NH and SH were still present 5 years after establishment, when the effect of plant history had already vanished. We suspect, however, that plant diversity and plant history effects might be more palpable when observing seasonal dynamics. The experiment was set up in a formerly arable field and, due to discontinuation of fertilisation, showed changes in nutrient availability over time (Oelmann et al. 2007, 2011), which likely continually alters mycorrhizal symbiosis and fungal growth (Antunes et al. 2012; Xiao et al. 2023) with a visible long-term impact. To disentangle these plant and soil history dynamics further, a fourth treatment of common plant history without soil is considered for the design of a follow-up mesocosm experiment.

Even though we were asking questions about fundamental patterns and processes, this apparent difference of temporal effects on plant and soil community assembly needs to be taken into consideration for more applied approaches e.g. restoration and agriculture where mycorrhizal inoculants have gained interest (Baar 2008; Rouphael et al. 2015; Koziol and Bever 2017). Even if mycorrhizal inoculants have been shown to immediately increase plant productivity (Hoeksema et al. 2010; Bi et al. 2018), such approaches might not have the desired positive long-term effects, if soil legacies shift or suppress AMF community assembly or alternatively take years to reach full potential (Wubs et al. 2019).

AM fungal diversity and plant diversity relationship lasts over time

We further tried to answer whether plant diversity positively affects AMF diversity in the different experimental grassland ages and whether this relationship is stronger or weaker with increasing community age (H2). Contrary to early findings by Dassen et al. (2017), we did find a positive effect of plant diversity on AMF diversity in the Jena Experiment field site. In our analysis, this relationship remained but did not strengthen with increased common history.

However, this only held true for AMF VT richness and Shannon diversity, while AMF Simpson diversity, on which VT relative abundance has a stronger effect than on Shannon diversity, and Pielou's evenness of AMF communities never increased with plant diversity. Evenness and evenness-affected diversity measures increased with common soil and plant history. Lower evenness in the newly established grassland split plots could be the result of soil disturbance and new plants having increased nutrient needs for initial growth of the plant communities (Jasper et al. 1991; Hart and Reader 2004; Trejo et al. 2016; Vogel et al. 2019). AMF community compositions are shaped not only by plant diversity, but by dynamic abiotic and biotic factors (Ji and Bever 2016; He et al. 2023; Mansfield et al. 2023) which counteract domination of few AMF and lead to more even AMF community composition over time. With our experimental design, though, we only depict time as age of the communities without taking short-term dynamics into account as we only sampled once. We nevertheless conclude that AMF diversity is governed by multiple factors, as AMF communities are subject to plant diversity driving AMF richness while community age drives AMF evenness.

AMF communities do not become more specialised over time

We expected to see a temporal shift of AMF towards communities with more specialists for plant partners and a changing role in e.g., resource partitioning, with ecosystem age (H3). However, we found that the specificity of AMF was low in all plant communities, independent of history treatments. This result might be related to the sampled bulk soil, which was homogenised to represent the whole split

plots. Bulk soil, though reflecting the available species pool and containing the highest AMF diversity (Hempel et al. 2007), might be less informative on specificity of AMF than what could be found when analysing AMF of the roots or the rhizosphere soil (Ramana et al. 2023), where interactions of AMF and plants are higher. The results of Macía-Vicente et al. (2023) on root fungi were in line with predictions of Buscot (2015) hypothesising older plant communities to favour a smaller species pool of more generalist fungi. The difference could be the result of soil disturbance or input of plant material with increased nutrient needs for initial growth of the plant communities (Jasper et al. 1991; Hart and Reader 2004; Trejo et al. 2016; Vogel et al. 2019). Assuming fungi in bulk soil behave similar to those in roots, after 5 years the initial transition may be over and the selection of a smaller more generalist pool of fungi has been completed, which would explain why we could not find differences between the different plant community ages. Concluding, AMF communities do not gain specialists, but the observed turnover of species showed that both plant diversity and common histories affect AMF assemblage.

Are AMF drivers of biodiversity and ecosystem functioning relationships?

We described how AM fungal communities in grasslands change with time and plant diversity. Since AMFs have been repeatedly proven to enhance plant productivity and resistance (van der Heijden et al. 1998; Hoeksema et al. 2010; Schnitzer et al. 2011; Wagg et al. 2011; Koziol and Bever 2017; Bi et al. 2018; Allsup et al. 2023), but can also stifle productivity at high diversity levels (Klironomos et al. 2000), a central question with regards to biodiversity and ecosystem functioning relationships and its dynamics is, whether AMF are drivers of such relationships (H4). For this to be true, we would expect AMF community composition to plant diversity relationships to change according to shared history. However, across all analyses, the interaction term of history treatment and plant diversity was either not significant or explained less than 1% of the variance. We further showed a limited potential for AMF to mediate plant diversity and history induced variation of plant productivity both above- and belowground.

Can we use any of the results to predict how AMF communities will change in future with more biodiversity loss and increasing soil/plant history and the feedback of these changes to functioning? Plant diversity is easily manipulatable and soil remains a complex, more unpredictable system. Nevertheless, the present field experiment gives us insights into long-term developments and a basis to look more deeply into plant-soil-microbes interplay shaping an ecosystem and its potential in practical application.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00374-024-01821-0.

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Author contributions F.B., N.E., A.W. and A.H.-B. designed the study. C.A., J.H., M.D.S., L.B., and A.W. carried out the soil sampling. M.D.S. performed DNA extraction. C.A. and J.H. prepared and conducted the sequencing. C.A. and A.H.-B. processed the sequence data and C.A. performed the data analysis with support from G.R.vd.P. and A.H.-B. All authors contributed to the interpretation of the data. The manuscript was written by C.A. and A.H.-B. and all authors commented on the manuscript.

Data availability The Illumina sequencing data generated in this study is available in the NCBI Sequence Read Archive (BioProject: PRJNA988299). Further data on biomasses and soil parameters is available for requests through the online data repository of The Jena Experiment (JEXIS: https://jexis.uni-jena.de/) under the following dataset IDs: 315, 319, 240, 318, 321, 379, 303, 304. This data, however, by default falls under the Jena Experiment' data and publication policy and underlies an embargo period of three years from the end of data collection/data assembly to give data owners and collectors time to perform their analysis. These datasets will be made publicly available via JEXIS at a later point of time. The full R script is uploaded to https://github.com/cyn-alb/deltaBEF_AMF.

Declarations

Competing interests A.H.-B. is editorial board member of Biology and Fertility of Soils. The authors have no competing interests to declare that are relevant to the content of this article.

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