




## RESEARCH ARTICLE

## Mycorrhizal Networks

# Organic management shapes AM fungal community structure and function, partially mitigating the negative effects of conventional agriculture

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**Abstract**

1. Arbuscular mycorrhizal (AM) fungi are important plant symbionts that provide plants with nutrients and water as well as support plant defences against pests and disease. Consequently, they present a promising alternative to using environmentally damaging and costly fertilisers and pesticides in agricultural systems. However, our limited understanding of how agricultural practices impact AM fungal diversity and functions is a key impediment to using them effectively in agriculture.
2. We assessed how organic and conventional agricultural management systems shaped AM fungal communities. We also investigated how AM fungal communities derived from these agricultural management systems affected crop biomass and development. Six soil samples from five organically and five conventionally managed agricultural sites were used to cultivate *Sorghum bicolor*. Plant growth, plant nutrient concentrations and AM fungal colonisation rates were analysed alongside DNA metabarcoding of community composition.
3. We observed that soil from conventional agricultural fields resulted in a pronounced reduction in sorghum biomass (−53.6%) and a significant delay in flowering compared to plants grown without AM fungi. Sorghum biomass was also reduced with soil from the organic system, but to a lesser extent (−30%) and without a delay in flowering. Organic systems were associated with a large proportion of AM fungal taxa (50.5% of VTs) not found in conventional systems, including *Diversispora* ( $r^2=0.09$ ,  $p<0.001$ ), *Archaeospora* ( $r^2=0.07$ ,  $p<0.001$ ) and *Glomus* ( $r^2=0.25$ ,  $p<0.001$ ) spp., but also shared a large proportion of taxa with conventional systems (42.3% of VTs). Conventional systems had relatively few unique taxa (7.2% of VTs).
4. Our results suggest that conventional agricultural practices selected against AM fungi that were, in this context, more beneficial for host plants. In contrast, organic management practices mitigate this negative effect, likely due to the

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presence of specific key AM fungal taxa. However, this mitigation is only partial, as less beneficial AM fungal taxa still persist, probably due to abiotic factors associated with agricultural management and the sensitivity of AM fungi to these factors. This persistence explains why the effect is not entirely eradicated.

#### KEYWORDS

arbuscular mycorrhizal fungi, biological soil fertility, community composition, food security, sustainable agriculture

## 1 | INTRODUCTION

Arbuscular mycorrhizal (AM) fungi, forming symbiotic relationships with the majority of terrestrial plants, are commonly present in agricultural environments (Brundrett & Tedersoo, 2018). Within this symbiosis, plants provide the fungi with carbon (C) in the form of lipids and sugars, while the fungi reciprocate by improving the plants' access to essential nutrients, particularly phosphorus (P), and water (Smith & Read, 2008). Beyond nutrient provision, AM fungi play pivotal roles in nutrient cycling (Zhang & Powell, 2021), the reduction of soil nutrient losses (Cavagnaro et al., 2015) and indirect influences on decomposition processes (Taylor et al., 2016). Additionally, they possess the capacity to enhance plant resistance against biotic stressors such as insect herbivores and pathogens (Frew et al., 2021). Consequently, they have the potential to support soil health and crop productivity, offering a pathway to reduce reliance on fertilisers and pesticides, thus fostering more sustainable agricultural practices.

Conventional agricultural practices reduce AM fungal network complexity and connectivity as well as the abundance of keystone taxa (Banerjee et al., 2019). For example, tilling or ploughing of the soil physically disrupts the hyphal network (Kabir, 2005), while the absence of a symbiotic partner in fallow areas post-tillage further diminishes colonisation rates and can lower AM fungal diversity in some cases (Bowles et al., 2017; Vahter et al., 2024). Furthermore, high nutrient availability through fertilisation can cause the AM fungal community to become less diverse, leading to a greater degree of genetic relatedness amongst its members (Frew et al., 2023). However, different results exist (Liu et al., 2015). As such, farming techniques place selective pressure on AM fungi as they can create unstable environments associated with, for example, the removal of host plants or high nutrient fluctuations. Lastly, pesticide use can decrease AM fungal species richness and colonisation rates (Riedo et al., 2021; Vahter et al., 2022) and seems to have especially an effect on a few rare species within the community (Karpouzias et al., 2014; Vahter et al., 2022). Overall, agricultural systems are anticipated to favour AM fungi that demonstrate rapid reproductive capabilities, for example Glomeraceae (Horsch et al., 2023), and result in diminished functional diversity within AM fungal communities when compared to natural environments (Verbruggen & Kiers, 2010).

Thus, agricultural management selects for certain AM fungi that can persist in agricultural environments (Johnson et al., 1997).

The number of fungicide applications was, for example, shown to correlate with decreased AM fungal mediated phosphorus uptake (Edlinger et al., 2021). On the other hand, a high nutrient availability through fertilisation can reduce plant dependence on the fungi for nutrients and are thought to simultaneously select for AM fungi that are more aggressive competitors for plant carbohydrates (Chagnon et al., 2013). However, this does not necessarily go hand in hand with a high C cost to the plant (Corrêa et al., 2012, 2024; Horning et al., 2023). Furthermore, evidence suggests that high nutrient availability can result in selection of AM fungal communities offering less benefits in regard to plant growth or nutrient uptake, but may still offer benefits associated with plant defence (Frew et al., 2023). Ultimately, soil tillage has been hypothesised to favour the selection of AM fungi with short life cycles and the ability to rapidly repair damaged hyphae (Chagnon et al., 2013; Verbruggen & Kiers, 2010).

However, our understanding on how agricultural practices affect AM fungi and the functional outcome for plants remains constrained. Currently, the majority of research aimed at addressing these challenges tends to concentrate solely on a limited number of commonly utilised AM fungal taxa (Berruti et al., 2016; Malik, 2018). This presents a concern considering the functional diversity inherent within AM fungi (Powell & Rillig, 2018), suggesting a need to focus on the functional outcomes of whole agricultural AM fungal communities rather than just a few overrepresented taxa. Thus, comparing how conventional and organic agricultural practices shape whole AM fungal communities offers a promising way to better understand which practices are damaging to AM fungal communities with respect to the functions they can offer to the plant. This approach also has the potential to help develop guidelines that could support beneficial AM fungal communities.

In order to assess the structure and functional potential of AM fungal communities associated with different management intensities, we grew *Sorghum bicolor* with soil from 10 agricultural fields containing, amongst other soil biota, AM fungi, half of them organically managed, half of them conventionally managed. Conventional agricultural management was predominantly associated with monocultures, the application of synthetic pesticides and fertilisers and tractor-based tillage, whereas organic farming was associated with a broader variety of crops, sometimes even within the same field patch, the application of organic certified fertilisers and pesticides and tillage with light machinery. Our study aimed to investigate the impact of these management systems on taxonomic diversity and

the functionality of the AM symbiosis in regard to nutrient uptake, plant growth and development stage benefits. Using DNA metabarcoding, we identified the AM fungal communities, evaluated their taxonomic diversity and structure, and interpreted these findings in the context of plant growth, nutrient levels, flowering status and root colonisation.

We hypothesise that (i) plants grown with soil containing AM fungi exhibit greater growth, nutrient uptake and more accelerated development than plants grown without AM fungi ('No AM fungi' treatment). Additionally, (ii) AM fungal communities from organically managed fields have a distinct community structure. Consequently, (iii) AM fungal communities derived from organic farming practices will offer greater functional benefits for the host plant than AM fungal communities sourced from conventional fields.

## 2 | METHODS

### 2.1 | Experimental design

We conducted a factorial glasshouse experiment with five soils from organically managed fields and five soils from conventionally managed fields using 110 *Sorghum bicolor* L. Moench cv. 'Acclaim' plants. Farms from which the soil was sourced followed their management system for  $\geq 5$  years and organically managed farms were certified (Table S2). Thus, the experiment consisted of 11 treatments, including a 'No AM fungi' treatment. Each treatment was replicated 10 times. Plants were grown from seeds that were surface-sterilised using 0.5% sodium hypochlorite solution. The seeds were germinated in Petri dishes for 6 days, after which individual seedlings were transplanted into 3.7 L pots.

All plants were grown in gamma-irradiated (50kGray) 50:50 sand: soil mixture (Table S1). Plants which were grown with soil containing AM fungi had 250g of the appropriate field soil inoculum added. The field soil for this experiment was collected from each of the 10 agricultural fields from the top 0–10 cm layer where six sampling points were evenly distributed within a 25 × 25 m plot in January 2023. Field soil inoculum from each of the six sampling points per site was mixed in a bucket, sieved through a 2 mm sieve, dried at 38°C and then kept at 4°C until the start of the experiment. Field soil inoculum was stored and used in the experiment separated by the field sites. Pots without an AM fungal treatment received 250g autoclaved field soil inoculum, which was mixed across the fields. In addition, all pots received 300 mL microbial filtrate obtained from washed field soil, which was filtered through a 38- $\mu$ m sieve to standardise the non-AM fungal microbial community (Koide & Li, 1989). Throughout the experiment, plants were watered approximately every second day with tap water and were grown in the glasshouse for 9 weeks with 11 h day length, a mean maximum light level of 260  $\mu$ mol m<sup>-2</sup> s<sup>-1</sup> and day/night temperatures of 27°C/17°C. To minimise any spatial or edge effects, the pots were fully randomised within the glasshouse chamber every week.

At the time of the harvest, plants were removed from pots, and the roots and above-ground tissues were separated. Roots were washed and from each plant, a 1 g subsample of fresh roots was taken to assess mycorrhizal fungal colonisation. The above-ground biomass and the remaining below-ground biomass were oven dried at 38°C for 72 h. Once dried to constant weight, the weights were recorded. To enable nutrient analyses, the above-ground plant tissue was ground to powder, and dried roots samples were obtained for molecular analyses.

After harvest, a subset of the pots which received a combination of all five soil inocula from conventionally managed fields and all five inocula from organically managed fields were checked for nematodes following the Baermann funnel method (Baermann, 1917). In total, 20 pots were checked. These pots were exclusively used for checking for nematodes. Plant and fungal data were not collected from these pots or analysed.

### 2.2 | Soil analysis

To determine soil nutrients, four out of 10 subsamples from the pots per treatment were analysed for total nitrogen (TN), total carbon (TC), plant-available nitrogen (N) and phosphorus (P) as well as pH following the methods described by Rayment and Lyons (2011). Plant-available N and P were determined by the Environmental Analysis Laboratory by the Southern Cross University using the Colwell method for P and potassium chloride (KCl) for N.

### 2.3 | Plant nutrient analysis and DNA metabarcoding of AM fungi

To determine the plant nutrient concentrations, the ground plant samples were analysed with X-ray fluorescence spectrometry (Epsilon 3x, PANalytical, EA Almelo, The Netherlands) according to the methodology described by Reidinger et al. (2012).

DNA extraction from 70 mg of dried root samples was conducted using the DNeasy Powersoil Pro Kit (Qiagen, GmBH, Hilden, Germany) following the manufacturer's instructions. A modification was made where dried root material, cut into small 0.5 mm fragments, was added to the extraction tubes. Subsequently, sequencing was carried out through the liquid handling pipeline at Western Sydney University's Next-Generation Sequencing Facility (Richmond, NSW, Australia), utilising in-house optimised protocols. The extracted DNA underwent purification using Agencourt AMPure XP Beads (Beckman Coulter), followed by quality assessment using the Qubit-iT™ PicoGreen fluorescence-based analysis (ThermoFisher Scientific, North Ryde, NSW, Australia). For amplification, the purified DNA underwent polymerase chain reaction targeting the small-subunit ribosomal RNA gene. The AM fungal-specific primers WANDA (Dumbrell et al., 2011) and AML2 (Lee et al., 2008) were used. The subsequent sequencing procedures were performed on the Illumina MiSeq platform using the Illumina MiSeq reagent kit v3

with 2×300bp paired-end chemistry, following the manufacturer's instructions.

The graphical downstream analysis tool (gDAT), as described by Vasar et al. (2021), was employed for the bioinformatic analysis and processing of rDNA sequences. A total of 2×3,504,908 raw reads underwent demultiplexing and cleaning through a sequence of bioinformatic steps (Vasar et al., 2017, 2021). Briefly, demultiplexing involved checking double barcodes, permitting one mismatch for both reads. Retention criteria included correct primer sequences (WANDA and AML2) with allowance for one mismatch each, an average quality of at least 30, and the removal of orphan reads, resulting in 2×3,333,787 cleaned reads. Putative chimeric sequences (3.4% of cleaned reads; total count of 119,061) were identified and subsequently eliminated using vsearch v2.15.0 (Rognes et al., 2016) in reference database mode against the MaarjAM database (Öpik et al., 2010) with the default parameters. The cleaned and chimera-free sequences were then assigned to virtual taxa (VT) using BLAST+ (v2.7.1, Camacho et al., 2009) by referencing the MaarjAM database (Öpik et al., 2010) with a minimum of 97% identity and 95% alignment thresholds. The representative sequences of each VT were selected by choosing those with the highest scores, following the methodology outlined in Vasar et al. (2021), for subsequent phylogenetic analysis. These selected sequences were aligned using ClustalW (Thompson et al., 2003), and a neighbour-joining phylogenetic tree (Figure S3) was constructed from the representative sequences using the maximum composite likelihood method in MEGA11 (Tamura et al., 2021).

## 2.4 | AM fungal colonisation

To verify root colonisation in plants inoculated with AM fungi and the absence of colonisation in the 'No AM fungi' treatment, 1g fresh root subsamples were taken at harvest. The subsample was cleared with 10% potassium hydroxide at 90°C for 10min in a water bath, followed by staining with 5% ink vinegar solution (Vierheilig et al., 1998). For each plant, five cleared and stained 3cm long root fragments were placed on glass slides with glycerine under a cover slip and scored to assess the presence of AM fungi using the intersect method, counting at least 100 intersections per slide at 200× magnification (McGonigle et al., 1990). To be conservative in quantifying colonisation, only hyphae visibly connected to AM fungal structures, such as arbuscules, vesicles or spores, were counted.

## 2.5 | Statistical analyses

All analyses were carried out using R v4.0.5 and RStudio v2023.12.0, 'Ocean Storm' (R Core Team, 2023).

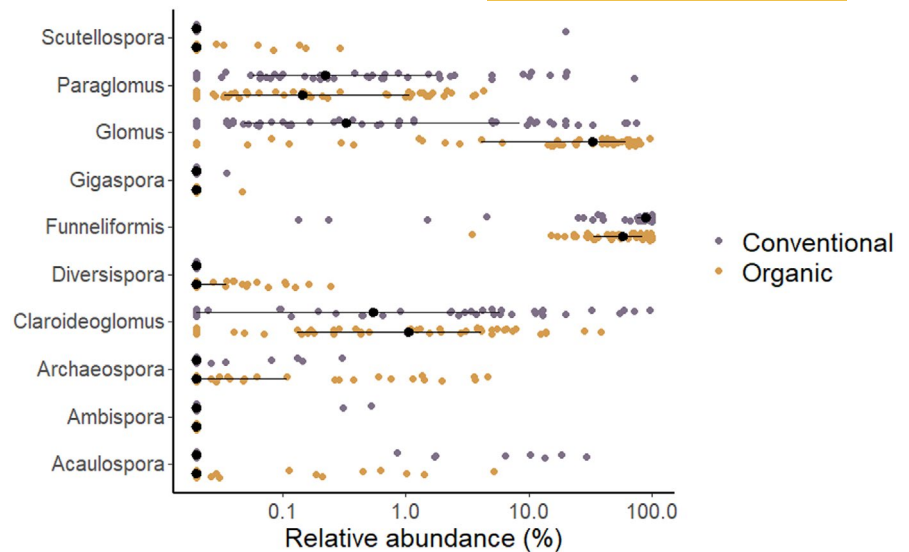
To counteract bias from differences in sequencing depth, all samples were rarefied to the minimum number of sequences per sample (100 sequences) using the *avgdist* function from the R package 'vegan' (Oksanen et al., 2022).

The effects of the management practices on alpha diversity indices (Observed VT richness, Shannon diversity, Pielou's evenness) were analysed using the 'vegan' package. Dissimilarity in community composition and structure of the root-colonising AM fungal communities were visualised using non-metric multidimensional scaling (NMDS, package 'vegan') based on Bray–Curtis dissimilarity. To statistically test the effects of the management practices on the observed changes in community dissimilarity, we used permutational multivariate ANOVA (perMANOVA) using the *adonis* function from the R package 'vegan' (Oksanen et al., 2022). To investigate preferential management–taxa associations, we tested for significance on individual taxa using the *wilcox.test* from base R (R Core Team, 2023). The related  $r^2$  value was calculated using a combination of the *summary* and *lm* functions from base R. We also performed an indicator species analysis using the R package 'indicspecies'. This package offers an association index that indicates the degree of association between a taxon and a specific level within a grouping variable (Cáceres & Legendre, 2009) and we used this to identify potential indicator species for the conventional and organic systems we investigated.

To investigate the community assembly process associated with the management systems, we assessed phylogenetic diversity and structure by calculating Faith's phylogenetic diversity (Faith, 1992) using the *pd* function from the 'picante' package (Kembel et al., 2010), mean pairwise distance using the *mpd* function from 'picante' and mean nearest taxon distance using the *mntd* function from 'picante' (Webb et al., 2002). Additionally, we calculated standardised effect sizes (SES) using *ses.mpd* and *ses.mntd* functions from 'picante' (Kembel et al., 2010).

To determine how management practices shifted the outcome of the AM symbiosis between nutritional and growth benefits, we fitted linear mixed-effects models using *lmer* from the 'lme4' package (Bates et al., 2015) and the *Anova* function from the 'car' package (Fox & Weisberg, 2019) to assess significance based on the likelihood ratio test. We fitted four separate models to assess how difference in management affected different plant responses we measured. The response variables were (1) plant total biomass, (2) nutrient concentrations, (3) photosynthesis rate and (4) flowering stage. In each case, the response variables were normally distributed and so fit using a Gaussian distribution. In each of the models, management type was the fixed effects and to account for repeat measures from each farm, the individual farm level was a random effect (Fox & Weisberg, 2011; Kuznetsova et al., 2017) (Table S4). We also calculated the mycorrhizal growth response (MGR) and the mycorrhizal P response (MPR) under each of the management practices. These plant mycorrhizal responses (%) were calculated as ((plant response – mean plant responses with No AM fungi)/mean plant responses with No AM fungi)×100, where the plant response was either the total biomass or P concentration of plants with soil containing AM fungi. Linear mixed-effects models with a Gaussian/normal distribution were also used to determine the effects of the management practices on plant mycorrhizal responses, phylogenetic metrics and alpha diversity indices. Generalised mixed-effects models with a beta distribution for percentage data were used to

**FIGURE 1** Preferential management-taxa analysis with *Diversispora*, *Aracheospora* and *Glomus* as closely related genera ( $p < 0.001$ ) for the organic treatment. Black points represent the median values and the bars represent the 50% confidence interval around the median values.



determine the effects of management practices on the total, vesicular and arbuscular colonisation of plant roots using *glimmTBM* and the *Anova* function from the 'glimmTMB' (Brooks et al., 2017) and 'car' (Fox & Weisberg, 2019) packages (Table S4). Additionally, we used the 'emmeans' (Lenth, 2023) package to calculate the estimated marginal means for the different levels of management system and performed pairwise comparisons between the estimated marginal means for each level (Tables S3 and S4).

### 3 | RESULTS

Across all AM fungal samples, 98 VTs were detected (Table S5). The top five abundant taxa in the dataset constituted 88.7% of all AM fungal sequences, belonging to the genera *Funneliformis* (VTX00067: 69.7%), *Glomus* (VTX00114: 5.5%, VTX00113: 4.7%, VTX00143: 3.7%), and *Claroideoglossum* (VTX00193: 5.1%). Across the two management systems, 91 VTs were identified in the organic and 49 VTs were identified in the conventional system (Table S5).

*Diversispora* spp. were with 5 VT, 89 sequences especially associated with the organic system, whereas no VT was found in the conventional system ( $r^2 = 0.09$ ,  $p < 0.001$ ). The same trend was true for *Aracheospora* spp. with 6 VT, 1350 sequences in the organic system and 4 VT, 18 sequences in the conventional system ( $r^2 = 0.07$ ,  $p < 0.001$ ) and *Glomus* spp. with 57 VT, 131.441 sequences associated with the organic system and 28 VT, 12.282 sequences associated with the conventional system ( $r^2 = 0.25$ ,  $p < 0.001$ ) (Figure 1). Thus, the presence of *Diversispora* was unique for the organic system. *Aracheospora* and *Glomus*, while present in the conventional system, were considerably reduced (Table 1; Table S5).

AM fungal diversity, represented by observed VT richness, Shannon diversity and Pielou's evenness, was reduced under the conventional management system (Figure 2). Observed VT richness was 103.5% higher in the organic system than in the conventional one. Meanwhile, Shannon diversity was 87.2% higher in the organic system. This pattern was also true for Pielou's evenness with a

31.9% increase in the organic system compared to the conventional one. Additionally, the AM fungal communities between the two management systems were particularly distinct based on non-metric multidimensional scaling (NMDS) of beta diversity (Bray-Curtis dissimilarity) ( $p < 0.001$ ) and the Venn diagram (Figure 3). The organic systems were not only associated with a large proportion of unique taxa (50.5% of VTs) but also shared a large proportion of taxa with the conventional systems (42.3% of VTs). Conversely, conventional systems had relatively few unique taxa (7.2% of VTs). Further, Faith's phylogenetic diversity was affected by the management systems where phylogenetic diversity was on average by 59% increased under the organic treatment. The mean pairwise distances (SES) and mean nearest taxon distances (SES) were not significantly different between the conventional and organic systems (Figure S2).

Plant biomass was reduced when grown on soil containing agricultural AM fungi (Figure 4a) relative to plants grown without AM fungi, although the magnitude of reduction depended on the management system. Soil from conventional agricultural fields resulted in a pronounced reduction in sorghum biomass (−53.6%) whereas the reduction was less for soil from organically managed fields (−30%) (Figure 4a; Figure S1). Plant phosphorus concentrations were higher with soil containing AM fungi, represented by the MPR but were not significantly different between the conventional (+45.1%) and the organic (+39.7%) system. Furthermore, silicon (Si) was lowest in plants with soil from organic fields and highest in plants with soil from conventional fields. We also observed considerably higher potassium (K) concentrations for plants with soil from conventionally managed fields. The N:P ratio was highest for the 'No AM fungi' treatment (average: 17.2; standard deviation:  $\pm 2.86$ ) and plants with soil from conventional systems (average: 15.8; standard deviation:  $\pm 2.82$ ) and lowest for plants with soil from organic systems (average: 14.4; standard deviation:  $\pm 6.11$ ) (Table S3). The photosynthesis rate was increased for plants receiving soil from organic agriculture (+18%) compared to plants with soil from conventional agriculture. However, photosynthesis rates from the 'No AM fungi' treatment and the organic system were almost identical with just 1% increase

**TABLE 1** Relative sequence abundances (%) and numbers of VT of arbuscular mycorrhizal (AM) fungal genera (families) in roots of *Sorghum bicolor* from conventional and organic management.

Management system	Acaulospora (Acaulo-sporaceae)	Ambispora (Ambi-sporaceae)	Archaeospora (Archaeo-sporaceae)	Claroideoglossum (Claroideo-glomeraceae)	Diversispora (Diversi-sporaceae)	Gigaspora (Gigaspo-raceae)	Scutellospora (Gigasporaceae)	Glomus (Glomeraceae)	Funnellifor-mis (Glomeraceae)	Paraglossum (Paraglo-meraceae)
Conventional	1.65	0.02	0.01	9	0	<0.01	0.4	7.97	77.27	3.69
Organic	0.19	0	0.41	3.78	0.02	<0.01	0.01	34.29	60.63	0.67
Genus (family)										
Number of VTs per genus										
Conventional	1	1	4	4	0	1	1	28	2	7
Organic	3	0	6	6	5	1	5	57	2	7

for the organic system (Figure 4b). Besides differences in growth and nutrient responses, we detected noticeable effects on the development stage, reflected by the number of plants reaching the flowering stage. After 9 weeks of growth, 85.7% of the plants with soil from organically managed fields reached the flowering stage. In comparison, 70% of the 'No AM fungi' treatment and only 22% of the plants with soil from conventionally managed fields reached the flowering stage (Figure 4d).

The total colonisation of roots by AM fungi was affected ( $p=0.003$ ) by the different management systems and was 58.1% greater for the organic system (Figure 4c). The same trend was true for vesicular colonisation with an average colonisation of 5.2% for the organic system and 2.1% for the conventional system. Arbuscular colonisation alone showed no significant differences (Table S4).

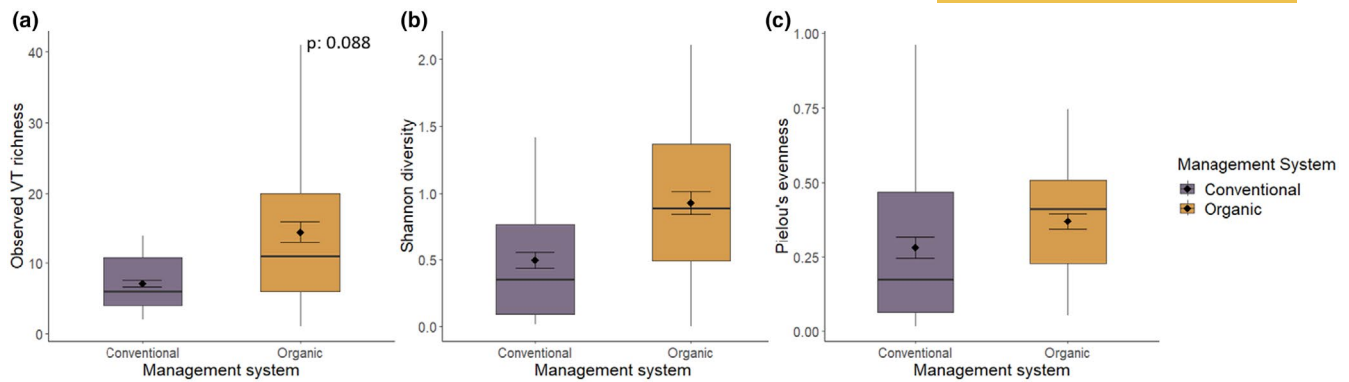
A subset of the pots which received a combination of all five soil inocula from conventional managed farms and all five inocula from organically managed fields were checked for nematodes and no nematodes were found.

## 4 | DISCUSSION

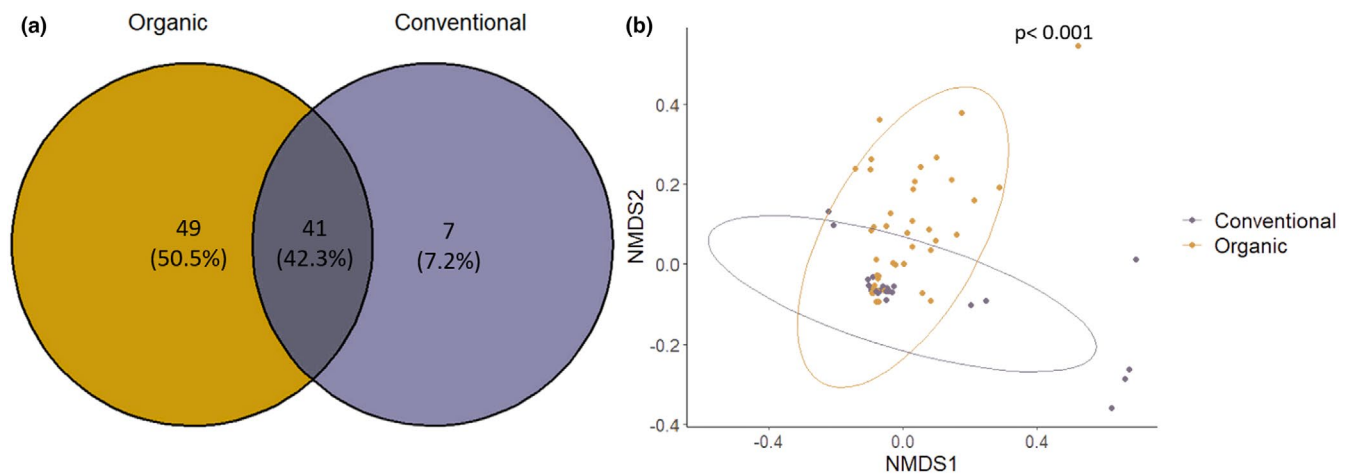
Our study found that soil from agricultural sites had detrimental effects on plant growth, suggesting that agricultural practices select for less beneficial fungal symbionts. However, the strength of these effects depended on whether the soil was from organic or conventionally managed agricultural systems. This distinction was associated with a high diversity of root-colonising AM fungi in plants grown with soil from organic sites, the presence of particular AM fungal taxa (*Diversispora*, *Archaeospora* and *Glomus*) and higher colonisation of roots. At the same time, we observed significantly more plants with soil from organically managed fields reaching the flowering stage. These patterns suggest, that in our studied system, agricultural practices select against AM fungi that offer more functional benefits for the host plant in comparison with the 'No AM fungi' treatment. However, the effect is partially mitigated, but not fully eliminated under organic practices.

Agricultural soil containing AM fungal communities had negative impacts on plant growth compared with the 'No AM fungi' treatment. This suggests agricultural management can select for AM fungi that offer limited or no benefits to their hosts in terms of biomass, which challenges our first hypothesis (i) that plants grown with soil containing AM fungi would have higher growth, nutrient uptake, and developmental rates. Focusing on the measured N:P ratios, the observed negative growth response does not appear to result from increased N limitation due to competition from the fungi (Riley et al., 2019). Instead, it suggests that plants grown with soil containing AM fungi were not limited by either N or P (Johnson et al., 2015), achieving growth rates commensurate with their maximum potential (Elser et al., 2010). As such, other mechanisms that limited growth potential must have been responsible.

The negative plant responses observed in our study for plants grown with AM fungi could be linked to several factors related to the



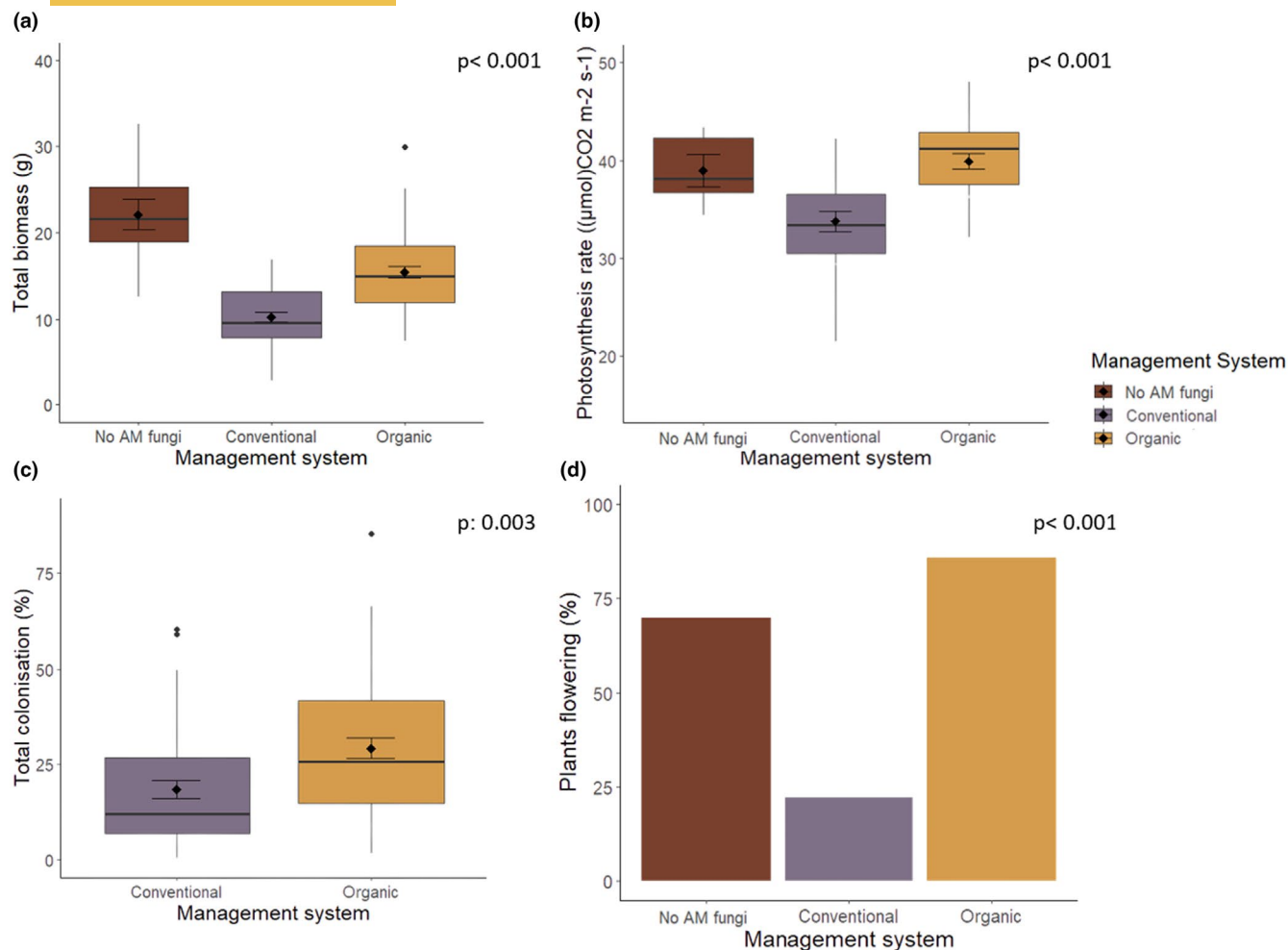
**FIGURE 2** Boxplots showing the distribution (centre horizontal line is the median, lower and upper sections are 25th and 75th percentiles, respectively, whiskers show the full range of the data, excluding outliers) of the effect of conventional and organic farming practices on three alpha diversity indices: (a) Observed VT richness, (b) Shannon diversity, (c) Pielou's evenness of arbuscular mycorrhizal (AM) communities of *Sorghum bicolor* roots. Points overlain on the boxplots represent the mean value and error bars represent the standard error of the mean. Effects with  $p > 0.1$  are not shown based on linear-mixed effects models.



**FIGURE 3** (a) Venn diagram showing the number of arbuscular mycorrhizal (AM) fungal virtual taxa (VT) shared and unique between the conventional and organic farming system. (b) Non-metric multidimensional scaling (NMDS) of beta diversity (Bray-Curtis dissimilarity) comparing the structure of AM fungal communities under the two different management systems. Associated ellipses represent 95% confidence intervals. Effects with  $p > 0.1$  are not shown based on the adonis function.

experimental design. For example, it is important to recognise that the use of soil inoculum does not exclude other soil biota, like bacteria, pathogens, or nematodes, which can influence plant responses (for potential effects of bacteria, see Chai et al., 2024). Although the microbial wash was added to pots to account for the presence of other soil organisms, we acknowledge that the microbial wash does not perfectly represent the entire soil community. Moreover, we examined pots that received a combination of soil inocula from both conventionally and organically managed fields to assess whether differences in the abundance of nematodes existed and found no nematodes in these samples. While this, along with the observed differences in AM fungal responses, suggests that observed plant responses are likely to be due to AM fungi, the potential influence of other soil biota cannot be definitely ruled out, which should be considered.

Furthermore, it was shown that the effectiveness of the AM symbiosis can be dependent on plant growth stage as AM fungi might suppress early plant growth but enhance seed P content and grain yield (Li et al., 2005). These plant growth depressions can be attributed to an imbalance between P uptake through the fungal pathway and direct uptake via the roots and mitigated with increasing plant density (Li et al., 2008). This suggests that the MGRs observed in plants grown singly in pots may not be directly translatable to field conditions (Li et al., 2008), a limitation that likely applies to our experimental set-up as well. Additionally, while AM fungi may impose a cost on the plant during early growth stages due to the investment required for symbiosis, they can provide long-term benefits at later growth stages (Johnson et al., 1997). This dynamic could have influenced the outcomes of our study, especially considering that the effect can further intensify when using annual plants (here: sorghum) as they



**FIGURE 4** Boxplots showing the distribution (centre horizontal line is the median, lower and upper sections are 25th and 75th percentiles, respectively, whiskers show the full range of the data, except for outliers which are shown as points) of (a) the total amount of biomass (g), (b) the photosynthesis rate ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) measured using a LiCor 6400, (c) the total root AM fungal colonisation (%) of *Sorghum bicolor* plants under each management system after 9 weeks of growth. Points overlain on the boxplots represent the mean value and error bars represent the standard error of the mean. (d) Percentage of sorghum plants per management system that have reached the flowering stage (where flowering is the presence of one flower) after 9 weeks of growth. Effects with  $p > 0.1$  are not shown based on linear mixed-effects models.

have short lifespans (Primieri et al., 2022). However, the idea of C costs to the plant is challenged by work from Corrêa et al. (2024) who demonstrated that C allocation to AM fungi had no impact on the MGR.

Additionally, plant-AM fungi interactions are species-specific (Li et al., 2019), meaning that the variation in crop species at our sampling sites, none of which included sorghum (Table S2), may have influenced the composition of AM fungal communities and, consequently, plant responses. This is especially relevant since it was shown that plant identity can shape root AM fungal communities (Li et al., 2019).

Despite the common experimental limitations mentioned above, a lot of studies have demonstrated positive impacts of AM fungi on plant growth (Kaur et al., 2020; Thirkell et al., 2017; Watts-Williams et al., 2022). However, there are also many examples where AM fungi have resulted in a plant growth depression (Johnson et al., 1997;

Klironomos, 2003; Ng et al., 2023), a trend also evident in our study. Ryan and Graham (2018) also argued that the benefits of AM fungi on crop yields have not been conclusively demonstrated, especially at the field scale, suggesting that the active management of AM fungi by farmers is currently unjustified. Our results support this statement, though they also provide evidence that organic management systems exert less of a negative effect on sorghum growth and development compared to conventional systems. While additional (field) studies are certainly needed, our findings offer a step towards identifying management practices that reduce the prevalence of AM fungal taxa causing strong negative plant responses.

In an agricultural context, negative effects of the AM symbiosis on crop growth can be related to abiotic factors associated with intensive agricultural management that can influence mycorrhizal networks. In our study, conventional farming sites relied on tillage, and on the application of synthetic pesticides and fertilisers



several times a year. The rate and type of fertiliser that is applied to a system can determine whether crops are likely to benefit from AM symbiosis or not (Johnson, 2010). In line with this, high fertilisation can reduce the plant's reliance on AM fungal symbiosis as the plant's nutrient requirements are met through fertilisation (Mäder et al., 2000). This could favour AM fungi, which offer fewer benefits for the plant, potentially explaining the reduction in total plant biomass we observed in response to AM fungi, especially for those with AM fungi from conventional systems. In addition to fertiliser effects, synthetic pesticide use can also disrupt the functioning of mycorrhizal networks in agroecosystems by disrupting key physiological processes such as the uptake and transport of metabolites and nutrients resulting in a decreased abundance of AM fungi (Riedo et al., 2021). Although pesticides can have such negative outcomes, there is also evidence to suggest that the effects of pesticide use on AM fungi are not only negative but can also be neutral or even positive (Karpouzias et al., 2014). Lastly, the tillage regime can physically disrupt the hyphal network, which reduces hyphal survival and expansion (Bowles et al., 2017; Kabir, 2005). Consequently, intensive agricultural management techniques could select for AM fungal communities which are less diverse, reflected by lower alpha diversity values for conventionally derived AM fungi in this study, and may be not specialised to offer plant growth benefits (Frew et al., 2023). However, different study results exist which highlights the need for more detailed and long-term studies (Vahter et al., 2024).

Although soil containing AM fungi had negative impacts, this was significantly less so for the fungal communities derived from organic compared to conventional systems. This difference in functional outcomes is associated with the differences observed in the phylogeny, diversity and composition of the AM fungi within plant roots. We found that roots of plants grown with soil from conventionally managed fields exhibited higher proportions of specific AM fungal families in some cases than those in the organic treatment. For instance, this was evident in the relative abundance of Claroideoglomeraceae. This particular group of AM fungi has been observed to colonise newly exposed substrates first (Nielsen et al., 2016) and has been identified as an indicator of disturbed habitats (Moora et al., 2014). This pattern held also true for Paraglomerales which was previously found in conventional systems (Harkes et al., 2019). At the genus level, the relative abundance for *Funneliformis* increased, aligning with the findings of Schneider et al. (2015), who observed higher *Funneliformis* abundance in conventional fields. At the VT level, VTX00065, which belongs to *Funneliformis*, is, amongst others, an indicator VT for the conventional system. This result is supported by other studies showing that VT00065 is frequently found in agricultural contexts (Öpik et al., 2006; Peng et al., 2023).

In contrast, organically sourced AM fungi had higher taxonomic diversity and harboured unique taxa. Taxa from the genera *Diversispora* were unique to organically derived communities, which was also partially true for taxa from the genera *Archaeospora* and *Glomus*. Despite the overall negative impacts of soil containing AM fungi, these unique taxa could be the driver of the observed

benefits in sorghum biomass and development stage compared to plants which received soil inocula from conventional fields. While Liu et al. (2015) found that Diversisporaceae relative abundance increased with fertilisation, a different study observed Diversisporaceae richness to increase in response to organic farming within a large experimental site, the Global Change Experimental Facility (Wahdan et al., 2021). Members of Diversisporaceae have been previously described as efficient in resource use (Hart & Reader, 2002; Maherali & Klironomos, 2007) and characterised as edaphophilic, which would enable them to increase plant access to water and nutrients (Phillips et al., 2019; Weber et al., 2019). Members of the family Archaeosporaceae were found to be present in organic but almost absent in conventional systems (Peltoniemi et al., 2021). We acknowledge that different study results exist, as a member of this family was also suggested to be an indicator for disturbed environments (Moora et al., 2014). This inconsistency clearly underpins the need for more studies to fully understand the factors that determine the distribution of AM fungi and how this related to their characteristics and functions. Lastly, we found *Glomus* spp. to be more associated with the organic system, which contradicts results from other studies (Chen et al., 2022; Oehl et al., 2004; Verbruggen & Kiers, 2010). This might be due to the latest reclassification within this group (Wijayawardene et al., 2022) and it remains to be seen whether this reclassification will impact future study outcomes.

Organic and conventional farming also shaped the phylogenetic diversity of AM fungi with AM fungi from organically managed fields leading to a slightly higher Faith's phylogenetic diversity. Thus, organic management techniques seem to select for AM fungi with a diverse set of evolutionary lineages which may enable them to offer functional benefits for the plant. In this context, Säle et al. (2021) found in their greenhouse study that especially more recently developed AM fungal families, such as Diversisporaceae (in our study unique to the organic system) and Glomeraceae (in our study with a higher mean relative abundance than the conventional system), stimulate leek growth and nutrient uptake more than species from ancient families. The comparisons with other studies throughout our discussion show that the observed differences are global patterns rather than unique to Australia. Overall, we found support for our hypothesis (ii) and further hypothesise that within the context of this experiment, which used soil collected from varied agricultural systems, a reduction or potential absence of specific AM fungal taxa in conventionally managed systems could negatively impact sorghum production. This indicates that certain AM fungi may play a functionally important role in supporting sorghum growth and development. However, this hypothesis needs to be tested in field experiments, as our study was restricted to controlled glasshouse conditions.

In line with this, the differences between AM fungal communities from organic and conventionally managed farms do not only manifest in their taxonomic diversity, as described above, but also in their functional diversity. However, potential effects from other soil biota have to be taken into account as well. In addition to

biomass and nutritional benefits, plants with soil from organically managed fields had a higher photosynthesis rate and considerable benefits with respect to their development stage than plants with soil from conventionally managed fields, which aligns with our hypothesis (iii). These functional benefits for the host plant suggest that, in our system, particular taxon groups such as *Diversispora*, *Archaeospora* and *Glomus* may hold importance for organic farming. Whether this remains true under field conditions, as well as different biotic and abiotic conditions, needs to be tested in further studies.

Interestingly, higher Si and K concentrations were associated with the conventional system. K is known to play a key role in activating enzymes and contributes to the detoxification of reactive oxygen species (ROS) (Sardans & Peñuelas, 2015; Wang et al., 2013), which is important under herbivore attacks as ROS signalling pathways are closely linked to hormone signalling pathways in plant-insect interactions (Kerchev et al., 2012). In addition, Si accumulation in plants reduces herbivore performance directly and indirectly by reducing nutritional quality (Frew et al., 2019). The accumulation of Si can further be accelerated by AM fungi which absorb Si through their hyphae and spores (Etesami et al., 2022). Thus, while AM fungi from conventional systems might be less beneficial for plant growth or nutrient uptake, they may provide benefits with respect to plant defence (Barber et al., 2013; Frew et al., 2023), although we did not assess this here.

Furthermore, we found an effect of soil from organically managed fields on plant flowering stage. A faster development of flowers for plants with soil containing AM fungi was also observed by Liu et al. (2018). Interestingly, other studies have reported effects on various aspects of plant reproduction extending flowering time and have proposed related hypotheses (Bennett & Meek, 2020). In line with this, a recently published study shows a correlation between mycorrhizas and improved floral traits such as floral display size or pollinator visitation (Hyjazie & Sargent, 2024). Although we did not measure specific floral traits, the faster development of flowers for plants with soil from organic farms could support the assumption of a mycorrhizal role in plant-pollinator interactions, but this needs to be tested further.

Alongside differences in flowering, photosynthesis rates in plants with soil from organic farms were not lower than those in the 'No AM fungi' treatment. However, photosynthesis rates were depressed in plants with soil from conventional fields. Since the carbon source for AM fungi is the photosynthetically fixed carbon (Drigo et al., 2010) and AM fungi are known to have the ability to enhance photosynthesis rates (Chen et al., 2017), we speculate that within the conventional treatment, the effectiveness of the AM symbiosis was limited, reflected by low photosynthesis rates. Further, because AM fungi present in the conventional treatment were not particularly beneficial in respect of photosynthesis, plants did not associate with them as extensively, reflected by lower colonisation rates. Conversely, an example of a functioning symbiosis with high photosynthesis rates and consequently more available carbon for the fungi could be reflected by the organic treatment.

Again, the selection for AM fungal communities offering more benefits to the plant could be mirrored by higher colonisation rates of AM fungi from organic systems. The assumption that plants may select for AM fungi with certain benefits was already stated in a previous paper (see Frew et al., 2023). Overall, it appears that in our study system, conventional farming selected against AM fungi that have more benefits for the host plant. Under organic farming, this effect is mitigated, but not fully eliminated. The positive functional outcomes for the plant may be due to the organic management-related taxa we have found, with some being unique to the organic system. However, less benefits observed for agricultural AM fungal communities compared to the 'No AM fungi' treatment are possibly driven by the fact that less beneficial taxa which thrive under agricultural practices are, in our study, still present in organic systems. This underpins the role agricultural management can play in fostering the effectiveness of AM symbiosis (Rillig et al., 2019).

The application frequency of, especially, fertilisers varied in the examined organic and conventional management systems. However, certain aspects were consistent within each system that may have influenced the presence or absence of, in our case, beneficial AM fungi. Organic systems adhered strictly to regulations, using only organic fertilisers, while conventional systems relied on synthetic products. Additionally, organic farms utilised low-impact machinery for tilling. Therefore, we speculate that tilling practices and the types of fertilisers used could significantly impact the AM fungal community (see also Edlinger et al., 2021; Säle et al., 2015; Thirkell et al., 2017) and support the proliferation of non-beneficial AM fungi (Kiers et al., 2002). Therefore, transitioning to certified organic products, reducing the use of heavy machinery, and applying fertilisers less frequently may be essential for fostering beneficial AM fungi (Verbruggen et al., 2010). Lastly, under the conditions of our study, the presence of less beneficial fungi in organic systems may be from the irregular application of fertilisers, where some farms were applying organic fertilisers each time before planting. If crops with high turnover rates are planted, fertilisers would still be applied every couple of weeks, probably leading to competition and the proliferation of more aggressive strains (Johnson et al., 1992; Kiers et al., 2002). Thus, reducing fertiliser use could potentially decrease the prevalence of less beneficial fungi in organic systems. However, it needs to be highlighted that more studies including varying abiotic and biotic factors, different host plants and types of experimental designs (glasshouse study vs. field experiment) are necessary to verify the general assumptions made here.

## 5 | CONCLUSIONS

As we begin to enhance our understanding of how agricultural practices influence AM fungal communities and their functional value for plant hosts, we still face challenges in terms of understanding which aspects of the AM fungal community structure best explain plant outcomes. Our study found that soil containing agricultural

AM fungal communities have negative effects on plant biomass compared to the 'No AM fungi' treatment, which may be due to factors like plant life history, weeks of plant growth or type of experimental design. However, this effect was stronger for soil inoculum from conventionally managed fields and less for soil inoculum from organically managed fields. AM fungal communities from organic systems were more diverse and consisted of potential key taxa, especially within the families Diversisporaceae, Archaeosporaceae and within the genus *Glomus*. In general, conventional agricultural practices tend to select against AM fungal communities that are, in our study system, more beneficial to host plants. In the organic systems studied, this trend is mitigated, likely because of the presence of specific key AM fungal taxa. Nevertheless, less beneficial AM fungal taxa still persist in the specific organic systems studied likely due to abiotic factors associated with agricultural management and the susceptibility of AM fungi to these factors. This persistence explains why the effect is not entirely eradicated.

#### AUTHOR CONTRIBUTIONS

Meike K. Heuck designed the study and collected the data. Meike K. Heuck, Adam Frew and Jeff R. Powell analysed the data. Meike K. Heuck, Adam Frew, Jeff R. Powell, Jarrod Kath and Christina Birnbaum interpreted the data and outcomes. Meike K. Heuck wrote the first draft of the article, Adam Frew, Jeff R. Powell, Jarrod Kath and Christina Birnbaum revised the article, and all authors contributed critically to final draft and provided approval for publication.

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#### CONFLICT OF INTEREST STATEMENT

Adam Frew is an associate editor of *Functional Ecology* but took no part in the peer review and decision-making processes for this paper. Apart from that, the authors have no conflict of interests to declare.

#### DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available on FigShare: <https://figshare.com/account/projects/229608/articles/27949431> (Heuck et al., 2024). Raw DNA sequencing data are available under the NCBI accession number PRJNA1193215 (<http://www.ncbi.nlm.nih.gov/bioproject/1193215>).

#### STATEMENT ON INCLUSION

Our study involved scientists based in the country where the research was conducted. All authors were actively involved early on with the research and study design to ensure that a diverse range of perspectives was considered from the start. Additionally, our study

included collaboration with local farmers, who were provided with a concise report summarising the main findings of the study.

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#### REFERENCES

- Baermann, G. (1917). Eine einfache Methode zur Auffindung von Ancylostomum (Nematode) Larven in Erdproben. *Nederlands Tijdschrift Voor Geneeskunde*, 57, 131–137.
- Banerjee, S., Walder, F., Büchi, L., Meyer, M., Held, A. Y., Gattinger, A., Keller, T., Charles, R., & Van Der Heijden, M. G. A. (2019). Agricultural intensification reduces microbial network complexity and the abundance of keystone taxa in roots. *The ISME Journal*, 13(7), 1722–1736. <https://doi.org/10.1038/s41396-019-0383-2>
- Barber, N. A., Kiers, E. T., Theis, N., Hazzard, R. V., & Adler, L. S. (2013). Linking agricultural practices, mycorrhizal fungi, and traits mediating plant–insect interactions. *Ecological Applications*, 23(7), 1519–1530. <https://doi.org/10.1890/13-0156.1>
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67(1), 1–48. <https://doi.org/10.18637/jss.v067.i01>
- Bennett, A. E., & Meek, H. C. (2020). The influence of arbuscular mycorrhizal fungi on plant reproduction. *Journal of Chemical Ecology*, 46(8), 707–721. <https://doi.org/10.1007/s10886-020-01192-4>
- Berruti, A., Lumini, E., Balestrini, R., & Bianciotto, V. (2016). Arbuscular mycorrhizal fungi as natural biofertilizers: Let's benefit from past successes. *Frontiers in Microbiology*, 6, 1559. <https://doi.org/10.3389/fmicb.2015.01559>
- Bowles, T. M., Jackson, L. E., Loeher, M., & Cavagnaro, T. R. (2017). Ecological intensification and arbuscular mycorrhizas: A meta-analysis of tillage and cover crop effects. *Journal of Applied Ecology*, 54(6), 1785–1793. <https://doi.org/10.1111/1365-2664.12815>
- Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Maechler, M., & Bolker, B. M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, 9(2), 378–400. <https://doi.org/10.32614/RJ-2017-066>
- Brundrett, M. C., & Tedersoo, L. (2018). Evolutionary history of mycorrhizal symbioses and global host plant diversity. *New Phytologist*, 220(4), 1108–1115. <https://doi.org/10.1111/nph.14976>
- Camacho, C., Coulouris, G., Avagyan, V., Ma, N., Papadopoulos, J., Bealer, K., & Madden, T. L. (2009). BLAST+: Architecture and applications. *BMC Bioinformatics*, 10, 421. <https://doi.org/10.1186/1471-2105-10-421>
- Cáceres, M. D., & Legendre, P. (2009). Associations between species and groups of sites: Indices and statistical inference. *Ecology*, 90(12), 3566–3574. <https://doi.org/10.1890/08-1823.1>
- Cavagnaro, T. R., Bender, S. F., Asghari, H. R., & Heijden, M. G. A. V. D. (2015). The role of arbuscular mycorrhizas in reducing soil nutrient loss. *Trends in Plant Science*, 20(5), 283–290. <https://doi.org/10.1016/j.tplants.2015.03.004>
- Chagnon, P.-L., Bradley, R. L., Maherali, H., & Klironomos, J. N. (2013). A trait-based framework to understand life history of mycorrhizal fungi. *Trends in Plant Science*, 18(9), 484–491. <https://doi.org/10.1016/j.tplants.2013.05.001>
- Chai, Y. N., Qi, Y., Goren, E., Schiniquy, D., Sheflin, A. M., Tringe, S. G., Prenni, J. E., Liu, P., & Schachtman, D. P. (2024). Root-associated bacterial communities and root metabolite composition are linked

- to nitrogen use efficiency in sorghum. *mSystems*, 9(1), e01190-23. <https://doi.org/10.1128/msystems.01190-23>
- Chen, J., Li, J., Yang, Y., Wang, Y., Zhang, Y., & Wang, P. (2022). Effects of conventional and organic agriculture on soil arbuscular mycorrhizal fungal community in low-quality farmland. *Frontiers in Microbiology*, 13, 914627. <https://doi.org/10.3389/fmicb.2022.914627>
- Chen, S., Zhao, H., Zou, C., Li, Y., Chen, Y., Wang, Z., Jiang, Y., Liu, A., Zhao, P., Wang, M., & Ahammed, G. J. (2017). Combined inoculation with multiple arbuscular mycorrhizal fungi improves growth, nutrient uptake and photosynthesis in cucumber seedlings. *Frontiers in Microbiology*, 8, 2516. <https://doi.org/10.3389/fmicb.2017.02516>
- Corrêa, A., Ferrol, N., & Cruz, C. (2024). Testing the trade-balance model: Resource stoichiometry does not sufficiently explain AM effects. *New Phytologist*, 242(4), 1561–1575. <https://doi.org/10.1111/nph.19432>
- Corrêa, A., Gurevitch, J., Martins-Loução, M. A., & Cruz, C. (2012). C allocation to the fungus is not a cost to the plant in ectomycorrhizae. *Oikos*, 121(3), 449–463. <https://doi.org/10.1111/j.1600-0706.2011.19406.x>
- Drigo, B., Pijl, A. S., Duyts, H., Kielak, A. M., Gamper, H. A., Houtekamer, M. J., Boschker, H. T. S., Bodelier, P. L. E., Whiteley, A. S., Veen, J. A. V., & Kowalchuk, G. A. (2010). Shifting carbon flow from roots into associated microbial communities in response to elevated atmospheric CO<sub>2</sub>. *Proceedings of the National Academy of Sciences of the United States of America*, 107(24), 10938–10942. <https://doi.org/10.1073/pnas.0912421107>
- Dumbrell, A. J., Ashton, P. D., Aziz, N., Feng, G., Nelson, M., Dytham, C., Fitter, A. H., & Helgason, T. (2011). Distinct seasonal assemblages of arbuscular mycorrhizal fungi revealed by massively parallel pyrosequencing. *New Phytologist*, 190(3), 794–804. <https://doi.org/10.1111/j.1469-8137.2010.03636.x>
- Edlinger, A., Garland, G., Banerjee, S., Degrune, F., García-Palacios, P., Hallin, S., Herzog, C., Jansa, J., Kost, E., Maestre, F., Pescador, D. S., Philippot, L., Rillig, M., Romdhane, S., Saghāi, A., Spor, A., Frossard, E., & Heijden, M. V. D. (2021). *Agricultural management and pesticide use reduce the phosphorus uptake capability of beneficial plant symbionts* [preprint]. In Review. <https://doi.org/10.21203/rs.3.rs-827966/v1>
- Elsner, J. J., Fagan, W. F., Kerkhoff, A. J., Swenson, N. G., & Enquist, B. J. (2010). Biological stoichiometry of plant production: Metabolism, scaling and ecological response to global change. *New Phytologist*, 186(3), 593–608. <https://doi.org/10.1111/j.1469-8137.2010.03214.x>
- Etesami, H., Shokri, E., & Jeong, B. R. (2022). The combined use of silicon/nanosilicon and arbuscular mycorrhiza for effective management of stressed agriculture: Action mechanisms and future prospects. In *Silicon and nano-silicon in environmental stress management and crop quality improvement* (pp. 241–264). Elsevier. <https://doi.org/10.1016/B978-0-323-91225-9.00008-X>
- Faith, D. P. (1992). Conservation evaluation and phylogenetic diversity. *Biological Conservation*, 61(1), 1–10. [https://doi.org/10.1016/0006-3207\(92\)91201-3](https://doi.org/10.1016/0006-3207(92)91201-3)
- Fox, J., & Weisberg, S. (2011). *An R companion to applied regression* (2nd ed.). Sage Publications.
- Fox, J., & Weisberg, S. (2019). *An R companion to applied regression* (3rd ed.). Sage. <https://socialsciences.mcmaster.ca/jfox/Books/Companion/>
- Frew, A., Heuck, M. K., & Aguilar-Trigueros, C. A. (2023). Host filtering, not competitive exclusion, may be the main driver of arbuscular mycorrhizal fungal community assembly under high phosphorus. *Functional Ecology*, 37, 1856–1869. <https://doi.org/10.1111/1365-2435.14349>
- Frew, A., Price, J. N., Oja, J., Vasar, M., & Öpik, M. (2021). Impacts of elevated atmospheric CO<sub>2</sub> on arbuscular mycorrhizal fungi and their role in moderating plant allometric partitioning. *Mycorrhiza*, 31(3), 423–430. <https://doi.org/10.1007/s00572-021-01025-6>
- Frew, A., Weston, L. A., & Gurr, G. M. (2019). Silicon reduces herbivore performance via different mechanisms, depending on host-plant species. *Austral Ecology*, 44(6), 1092–1097. <https://doi.org/10.1111/aec.12767>
- Harkes, P., Suleiman, A. K. A., Van Den Elsen, S. J. J., De Haan, J. J., Holterman, M., Kuramae, E. E., & Helder, J. (2019). Conventional and organic soil management as divergent drivers of resident and active fractions of major soil food web constituents. *Scientific Reports*, 9(1), 13521. <https://doi.org/10.1038/s41598-019-49854-y>
- Hart, M. M., & Reader, R. J. (2002). Taxonomic basis for variation in the colonization strategy of arbuscular mycorrhizal fungi. *New Phytologist*, 153(2), 335–344. <https://doi.org/10.1046/j.0028-646X.2001.00312.x>
- Heuck, M. K., Powell, J., Kath, J., Birnbaum, C., & Frew, A. (2024). Supporting data 'Organic management shapes AM fungal community structure and function, partially mitigating the negative effects of conventional agriculture'. figshare. Dataset. <https://figshare.com/account/projects/229608/articles/27949431>
- Horning, A. L., Koury, S. S., Meachum, M., Kuehn, K. A., & Hoeksema, J. D. (2023). Dirt cheap: An experimental test of controls on resource exchange in an ectomycorrhizal symbiosis. *New Phytologist*, 237(3), 987–998. <https://doi.org/10.1111/nph.18603>
- Horsch, C. C. A., Antunes, P. M., & Kallenbach, C. M. (2023). Arbuscular mycorrhizal fungal communities with contrasting life-history traits influence host nutrient acquisition. *Mycorrhiza*, 33(1–2), 1–14. <https://doi.org/10.1007/s00572-022-01098-x>
- Hyjazie, B. F., & Sargent, R. D. (2024). Manipulation of soil mycorrhizal fungi influences floral traits. *New Phytologist*, 242, 675–686. <https://doi.org/10.1111/nph.19625>
- Johnson, N. C. (2010). Resource stoichiometry elucidates the structure and function of arbuscular mycorrhizas across scales. *New Phytologist*, 185(3), 631–647. <https://doi.org/10.1111/j.1469-8137.2009.03110.x>
- Johnson, N. C., Copeland, P. J., Crookston, R. K., & Pflieger, F. L. (1992). Mycorrhizae: possible explanation for yield decline with continuous corn and soybean. *Agronomy Journal*, 84(3), 387–390. <https://doi.org/10.2134/agronj1992.00021962008400030007x>
- Johnson, N. C., Graham, J. H., & Smith, F. A. (1997). Functioning of mycorrhizal associations along the mutualism-parasitism continuum. *New Phytologist*, 135(4), 575–585. <https://doi.org/10.1046/j.1469-8137.1997.00729.x>
- 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(4), 1473–1484. <https://doi.org/10.1111/nph.13172>
- Kabir, Z. (2005). Tillage or no-tillage: Impact on mycorrhizae. *Canadian Journal of Plant Science*, 85(1), 23–29. <https://doi.org/10.4141/P03-160>
- Karpouzias, D. G., Papadopoulou, E., Ipsilantis, I., Friedel, I., Petric, I., Udikovic-Kolic, N., Djuric, S., Kandeler, E., Menkissoglu-Spiroudi, U., & Martin-Laurent, F. (2014). Effects of nicosulfuron on the abundance and diversity of arbuscular mycorrhizal fungi used as indicators of pesticide soil microbial toxicity. *Ecological Indicators*, 39, 44–53. <https://doi.org/10.1016/j.ecolind.2013.12.004>
- Kaur, J., Chavana, J., Soti, P., Racelis, A., & Kariyat, R. (2020). Arbuscular mycorrhizal fungi (AMF) influences growth and insect community dynamics in Sorghum-sudangrass (*Sorghum × drummondii*). *Arthropod-Plant Interactions*, 14(3), 301–315. <https://doi.org/10.1007/s11829-020-09747-8>
- Kembel, S. W., Cowan, P. D., Helmus, M. R., Cornwell, W. K., Morlon, H., Ackerly, D. D., Blomberg, S. P., & Webb, C. O. (2010). Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*, 26(11), 1463–1464. <https://doi.org/10.1093/bioinformatics/btq166>
- Kerchev, P. I., Fenton, B., Foyer, C. H., & Hancock, R. D. (2012). Plant responses to insect herbivory: Interactions between photosynthesis, reactive oxygen species and hormonal signalling pathways.

- Plant, Cell & Environment*, 35(2), 441–453. <https://doi.org/10.1111/j.1365-3040.2011.02399.x>
- Kiers, E. T., West, S. A., & Denison, R. F. (2002). Mediating mutualisms: Farm management practices and evolutionary changes in symbiont co-operation. *Journal of Applied Ecology*, 39(5), 745–754. <https://doi.org/10.1046/j.1365-2664.2002.00755.x>
- Klironomos, J. N. (2003). Variation in plant response to native and exotic arbuscular mycorrhizal fungi. *Ecology*, 84(9), 2292–2301. <https://doi.org/10.1890/02-0413>
- Koide, R. T., & Li, M. (1989). Appropriate controls for vesicular–arbuscular mycorrhiza research. *New Phytologist*, 111(1), 35–44. <https://doi.org/10.1111/j.1469-8137.1989.tb04215.x>
- Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). lmerTest package: Tests in linear mixed effects models. *Journal of Statistical Software*, 82(13), 1–26. <https://doi.org/10.18637/jss.v082.i13>
- Lee, J., Lee, S., & Young, J. P. W. (2008). Improved PCR primers for the detection and identification of arbuscular mycorrhizal fungi: PCR primers for arbuscular mycorrhizal fungi. *FEMS Microbiology Ecology*, 65(2), 339–349. <https://doi.org/10.1111/j.1574-6941.2008.00531.x>
- Lenth, R. V. (2023). *emmeans: Estimated marginal means, aka least-squares means*. <https://CRAN.R-project.org/package=emmeans>
- Li, H., Smith, F. A., Dickson, S., Holloway, R. E., & Smith, S. E. (2008). Plant growth depressions in arbuscular mycorrhizal symbioses: Not just caused by carbon drain? *New Phytologist*, 178(4), 852–862. <https://doi.org/10.1111/j.1469-8137.2008.02410.x>
- Li, H. Y., Zhu, Y. G., Marschner, P., Smith, F. A., & Smith, S. E. (2005). Wheat responses to arbuscular mycorrhizal fungi in a highly calcareous soil differ from those of clover, and change with plant development and P supply. *Plant and Soil*, 277(1–2), 221–232. <https://doi.org/10.1007/s11104-005-7082-7>
- Li, M., Jordan, N. R., Koide, R. T., Yannarell, A. C., & Davis, A. S. (2019). Interspecific variation in crop and weed responses to arbuscular mycorrhizal fungal community highlights opportunities for weed biocontrol. *Applied Soil Ecology*, 142, 34–42. <https://doi.org/10.1016/j.apsoil.2019.05.016>
- Liu, S., Guo, H., Xu, J., Song, Z., Song, S., Tang, J., & Chen, X. (2018). Arbuscular mycorrhizal fungi differ in affecting the flowering of a host plant under two soil phosphorus conditions. *Journal of Plant Ecology*, 11(4), 623–631. <https://doi.org/10.1093/jpe/rtx038>
- Liu, Y., Johnson, N. C., Mao, L., Shi, G., Jiang, S., Ma, X., Du, G., An, L., & Feng, H. (2015). Phylogenetic structure of arbuscular mycorrhizal community shifts in response to increasing soil fertility. *Soil Biology and Biochemistry*, 89, 196–205. <https://doi.org/10.1016/j.soilbio.2015.07.007>
- Mäder, P., Edenhofer, S., Boller, T., Wiemken, A., & Niggli, U. (2000). Arbuscular mycorrhizae in a long-term field trial comparing low-input (organic, biological) and high-input (conventional) farming systems in a crop rotation. *Biology and Fertility of Soils*, 31(2), 150–156. <https://doi.org/10.1007/s003740050638>
- Maherali, H., & Klironomos, J. N. (2007). Influence of phylogeny on fungal community assembly and ecosystem functioning. *Science*, 316(5832), 1746–1748. <https://doi.org/10.1126/science.1143082>
- Malik, R. J. (2018). Recent trend: Is the role of arbuscular mycorrhizal fungi in plant-enemies performance biased by taxon usage? *The American Midland Naturalist*, 180(2), 306–311. <https://doi.org/10.1674/0003-0031-180.2.306>
- McGonigle, T. P., Miller, M. H., Evans, D. G., Fairchild, G. L., & Swan, J. A. (1990). A new method which gives an objective measure of colonization of roots by vesicular–Arbuscular mycorrhizal fungi. *New Phytologist*, 115(3), 495–501. <https://doi.org/10.1111/j.1469-8137.1990.tb00476.x>
- Moora, M., Davison, J., Öpik, M., Metsis, M., Saks, Ü., Jairus, T., Vasar, M., & Zobel, M. (2014). Anthropogenic land use shapes the composition and phylogenetic structure of soil arbuscular mycorrhizal fungal communities. *FEMS Microbiology Ecology*, 90(3), 609–621. <https://doi.org/10.1111/1574-6941.12420>
- Ng, A., Wilson, B. A. L., & Frew, A. (2023). Belowground crop responses to root herbivory are associated with the community structure of native arbuscular mycorrhizal fungi. *Applied Soil Ecology*, 185, 104797. <https://doi.org/10.1016/j.apsoil.2022.104797>
- Nielsen, K. B., Kjølter, R., Bruun, H. H., Schnoor, T. K., & Rosendahl, S. (2016). Colonization of new land by arbuscular mycorrhizal fungi. *Fungal Ecology*, 20, 22–29. <https://doi.org/10.1016/j.funeco.2015.10.004>
- Oehl, F., Sieverding, E., Mäder, P., Dubois, D., Ineichen, K., Boller, T., & Wiemken, A. (2004). Impact of long-term conventional and organic farming on the diversity of arbuscular mycorrhizal fungi. *Oecologia*, 138(4), 574–583. <https://doi.org/10.1007/s00442-003-1458-2>
- Oksanen, J., Simpson, G. L., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Solymos, P., Stevens, M. H. H., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., Caceres, M. D., Durand, S., ... Weedon, J. (2022). *Vegan: Community ecology package*. <https://CRAN.R-project.org/package=vegan>
- Öpik, M., Moora, M., Liira, J., & Zobel, M. (2006). Composition of root-colonizing arbuscular mycorrhizal fungal communities in different ecosystems around the globe. *Journal of Ecology*, 94(4), 778–790. <https://doi.org/10.1111/j.1365-2745.2006.01136.x>
- Öpik, M., Vanatoa, A., Vanatoa, E., Moora, M., Davison, J., Kalwij, J. M., Reier, Ü., & Zobel, M. (2010). The online database Maarj AM reveals global and ecosystemic distribution patterns in arbuscular mycorrhizal fungi (Glomeromycota). *New Phytologist*, 188(1), 223–241. <https://doi.org/10.1111/j.1469-8137.2010.03334.x>
- Peltoniemi, K., Velmala, S., Fritze, H., Lemola, R., & Pennanen, T. (2021). Long-term impacts of organic and conventional farming on the soil microbiome in boreal arable soil. *European Journal of Soil Biology*, 104, 103314. <https://doi.org/10.1016/j.ejsobi.2021.103314>
- Peng, Z., Johnson, N. C., Jansa, J., Han, J., Fang, Z., Zhang, Y., Jiang, S., Xi, H., Mao, L., Pan, J., Zhang, Q., Feng, H., Fan, T., Zhang, J., & Liu, Y. (2023). Mycorrhizal effects on crop yield and soil ecosystem functions in a long-term tillage and fertilization experiment. *New Phytologist*, 242, 1798–1813. <https://doi.org/10.1111/nph.19493>
- Phillips, M. L., Weber, S. E., Andrews, L. V., Aronson, E. L., Allen, M. F., & Allen, E. B. (2019). Fungal community assembly in soils and roots under plant invasion and nitrogen deposition. *Fungal Ecology*, 40, 107–117. <https://doi.org/10.1016/j.funeco.2019.01.002>
- Powell, J. R., & Rillig, M. C. (2018). Biodiversity of arbuscular mycorrhizal fungi and ecosystem function. *New Phytologist*, 220(4), 1059–1075. <https://doi.org/10.1111/nph.15119>
- Primieri, S., Magnoli, S. M., Koffel, T., Stürmer, S. L., & Bever, J. D. (2022). Perennial, but not annual legumes synergistically benefit from infection with arbuscular mycorrhizal fungi and rhizobia: A meta-analysis. *New Phytologist*, 233(1), 505–514. <https://doi.org/10.1111/nph.17787>
- R Core Team. (2023). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. <https://www.R-project.org/>
- Reidinger, S., Ramsey, M. H., & Hartley, S. E. (2012). Rapid and accurate analyses of silicon and phosphorus in plants using a portable X-ray fluorescence spectrometer. *New Phytologist*, 195(3), 699–706. <https://doi.org/10.1111/j.1469-8137.2012.04179.x>
- Riedo, J., Wettstein, F. E., Rösch, A., Herzog, C., Banerjee, S., Büchi, L., Charles, R., Wächter, D., Martin-Laurent, F., Bucheli, T. D., Walder, F., & Van Der Heijden, M. G. A. (2021). Widespread occurrence of pesticides in organically managed agricultural soils—The ghost of a conventional agricultural past? *Environmental Science & Technology*, 55(5), 2919–2928. <https://doi.org/10.1021/acs.est.0c06405>
- Riley, R. C., Cavagnaro, T. R., Brien, C., Smith, F. A., Smith, S. E., Berger, B., Garnett, T., Stonor, R., Schilling, R. K., Chen, Z., & Powell, J. R. (2019). Resource allocation to growth or luxury consumption drives

- mycorrhizal responses. *Ecology Letters*, 22(11), 1757–1766. <https://doi.org/10.1111/ele.13353>
- Rillig, M. C., Aguilar-Trigueros, C. A., Camenzind, T., Cavagnaro, T. R., Degrune, F., Hohmann, P., Lammel, D. R., Mansour, I., Roy, J., Van Der Heijden, M. G. A., & Yang, G. (2019). Why farmers should manage the arbuscular mycorrhizal symbiosis. *New Phytologist*, 222(3), 1171–1175. <https://doi.org/10.1111/nph.15602>
- Rognes, T., Flouri, T., Nichols, B., Quince, C., & Mahé, F. (2016). VSEARCH: A versatile open source tool for metagenomics. *PeerJ*, 4, e2584. <https://doi.org/10.7717/peerj.2584>
- Ryan, M. H., & Graham, J. H. (2018). Little evidence that farmers should consider abundance or diversity of arbuscular mycorrhizal fungi when managing crops. *New Phytologist*, 220(4), 1092–1107. <https://doi.org/10.1111/nph.15308>
- Säle, V., Aguilera, P., Laczko, E., Mäder, P., Berner, A., Zihlmann, U., Van Der Heijden, M. G. A., & Oehl, F. (2015). Impact of conservation tillage and organic farming on the diversity of arbuscular mycorrhizal fungi. *Soil Biology and Biochemistry*, 84, 38–52. <https://doi.org/10.1016/j.soilbio.2015.02.005>
- Säle, V., Palenzuela, J., Azcón-Aguilar, C., Sánchez-Castro, I., Da Silva, G. A., Seitz, B., Sieverding, E., Van Der Heijden, M. G. A., & Oehl, F. (2021). Ancient lineages of arbuscular mycorrhizal fungi provide little plant benefit. *Mycorrhiza*, 31(5), 559–576. <https://doi.org/10.1007/s00572-021-01042-5>
- Sardans, J., & Peñuelas, J. (2015). Potassium: A neglected nutrient in global change. *Global Ecology and Biogeography*, 24(3), 261–275. <https://doi.org/10.1111/geb.12259>
- Schneider, K. D., Lynch, D. H., Dunfield, K., Khosla, K., Jansa, J., & Voroney, R. P. (2015). Farm system management affects community structure of arbuscular mycorrhizal fungi. *Applied Soil Ecology*, 96, 192–200. <https://doi.org/10.1016/j.apsoil.2015.07.015>
- Smith, S. E., & Read, D. J. (2008). *Mycorrhizal symbiosis* (3rd ed.). Academic Press.
- Tamura, K., Stecher, G., & Kumar, S. (2021). MEGA11: Molecular evolutionary genetics analysis version 11. *Molecular Biology and Evolution*, 38(7), 3022–3027. <https://doi.org/10.1093/molbev/msab120>
- Taylor, M. K., Lankau, R. A., & Wurzbarger, N. (2016). Mycorrhizal associations of trees have different indirect effects on organic matter decomposition. *Journal of Ecology*, 104(6), 1576–1584. <https://doi.org/10.1111/1365-2745.12629>
- Thirkell, T. J., Charters, M. D., Elliott, A. J., Sait, S. M., & Field, K. J. (2017). Are mycorrhizal fungi our sustainable saviours? Considerations for achieving food security. *Journal of Ecology*, 105(4), 921–929. <https://doi.org/10.1111/1365-2745.12788>
- Thompson, J. D., Gibson, T. J., & Higgins, D. G. (2003). Multiple sequence alignment using ClustalW and ClustalX. *Current Protocols in Bioinformatics*. <https://doi.org/10.1002/0471250953.bi0203s00>
- Vahter, T., Sepp, S.-K., Astover, A., Helm, A., Kikas, T., Liu, S., Oja, J., Öpik, M., Penu, P., Vasar, M., Veromann, E., Zobel, M., & Hiiesalu, I. (2022). Landscapes, management practices and their interactions shape soil fungal diversity in arable fields—Evidence from a nationwide farmers' network. *Soil Biology and Biochemistry*, 168, 108652. <https://doi.org/10.1016/j.soilbio.2022.108652>
- Vahter, T., Taylor, A. R., Landa, B. B., Linsler, D., Rodriguez, E. M. M., Moreno, F. G., Pérès, G., Engell, I., Hiiesalu, I., Bengtsson, J., Oja, J., Torppa, K. A., Arias-Giraldo, L. F., Guzmán, G., Potthoff, M., Vasar, M., Sandor, M., Sepp, S., Stoian, V., & Öpik, M. (2024). Reduced tillage intensity does not increase arbuscular mycorrhizal fungal diversity in European long-term experiments. *European Journal of Soil Science*, 75(4), e13546. <https://doi.org/10.1111/ejss.13546>
- 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(8), 761–773. <https://doi.org/10.1007/s00572-017-0791-y>
- Vasar, M., Davison, J., Neuenkamp, L., Sepp, S., Young, J. P. W., Moora, M., & Öpik, M. (2021). User-friendly bioinformatics pipeline gDAT (graphical downstream analysis tool) for analysing rDNA sequences. *Molecular Ecology Resources*, 21(4), 1380–1392. <https://doi.org/10.1111/1755-0998.13340>
- Verbruggen, E., & Kiers, T. (2010). Evolutionary ecology of mycorrhizal functional diversity in agricultural systems: AMF in agriculture. *Evolutionary Applications*, 3(5–6), 547–560. <https://doi.org/10.1111/j.1752-4571.2010.00145.x>
- Verbruggen, E., Röhling, W. F. M., Gamper, H. A., Kowalchuk, G. A., Verhoef, H. A., & Van Der Heijden, M. G. A. (2010). Positive effects of organic farming on below-ground mutualists: Large-scale comparison of mycorrhizal fungal communities in agricultural soils. *New Phytologist*, 186(4), 968–979. <https://doi.org/10.1111/j.1469-8137.2010.03230.x>
- Vierheilig, H., Coughlan, A. P., Wyss, U., & Piché, Y. (1998). Ink and vinegar, a simple staining technique for arbuscular-mycorrhizal fungi. *Applied and Environmental Microbiology*, 64(12), 5004–5007. <https://doi.org/10.1128/AEM.64.12.5004-5007.1998>
- Wahdan, S. F. M., Reitz, T., Heintz-Buschart, A., Schädler, M., Roscher, C., Breitzkreuz, C., Schnabel, B., PuraHong, W., & Buscot, F. (2021). Organic agricultural practice enhances arbuscular mycorrhizal symbiosis in correspondence to soil warming and altered precipitation patterns. *Environmental Microbiology*, 23(10), 6163–6176. <https://doi.org/10.1111/1462-2920.15492>
- Wang, M., Zheng, Q., Shen, Q., & Guo, S. (2013). The critical role of potassium in plant stress response. *International Journal of Molecular Sciences*, 14(4), 7370–7390. <https://doi.org/10.3390/ijms14047370>
- Watts-Williams, S. J., Gill, A. R., Jewell, N., Brien, C. J., Berger, B., Tran, B. T. T., Mace, E., Cruickshank, A. W., Jordan, D. R., Garnett, T., & Cavagnaro, T. R. (2022). Enhancement of sorghum grain yield and nutrition: A role for arbuscular mycorrhizal fungi regardless of soil phosphorus availability. *Plants, People, Planet*, 4(2), 143–156. <https://doi.org/10.1002/ppp3.10224>
- Webb, C. O., Ackerly, D. D., McPeck, M. A., & Donoghue, M. J. (2002). Phylogenies and community ecology. *Annual Review of Ecology and Systematics*, 33(1), 475–505. <https://doi.org/10.1146/annurev.ecolsys.33.010802.150448>
- Weber, S. E., Diez, J. M., Andrews, L. V., Goulden, M. L., Aronson, E. L., & Allen, M. F. (2019). Responses of arbuscular mycorrhizal fungi to multiple coinciding global change drivers. *Fungal Ecology*, 40, 62–71. <https://doi.org/10.1016/j.funeco.2018.11.008>
- Wijayawardene, N., Hyde, K., Dai, D., Sánchez-García, M., Goto, B., Saxena, R., Erdoğan, M., Selçuk, F., Rajeshkumar, K., Aptroot, A., Błaszczowski, J., Boonyuen, N., Da Silva, G., De Souza, F., Dong, W., Ertz, D., Haelewaters, D., Jones, E., Karunarathna, S., ... Thines, M. (2022). Outline of fungi and fungus-like taxa—2021. *Mycosphere*, 13(1), 53–453. <https://doi.org/10.5943/mycosphere/13/1/2>
- Zhang, H., & Powell, J. R. (2021). Advances in understanding arbuscular mycorrhizal fungal effects on soil nutrient cycling. In *Understanding and improving crop root function*, Burleigh Dodds series in agricultural science (pp. 195–212). Burleigh Dodds Science Publishing. <https://doi.org/10.19103/AS.2020.0075.10>

## SUPPORTING INFORMATION

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

**Figure S1:** Boxplots showing (a) the arbuscular mycorrhizal (AM) phosphorus response (MPR) and (b) AM growth response (MGR) (center horizontal line is the median, lower and upper sections are

25th and 75th percentiles, respectively, whiskers show the full range of the data, except for outliers which are shown as points) of *Sorghum bicolor* plants under each management system.

**Figure S2:** Boxplots showing the effects of the management systems on the (a) phylogenetic diversity (Faith's), (b) mean pairwise distance (standardised effect sizes), and (c) mean nearest taxon distance (standardised effect sizes) of arbuscular mycorrhizal (AM) fungal communities of *Sorghum bicolor* roots.

**Figure S3:** Neighbour-joining phylogenetic tree of arbuscular mycorrhizal (AM) fungal virtual taxa (VT) detected in roots across the different management types. Bootstrap support values are shown.

**Table S1:** Nutrient analysis of source soil/sand substrate including the live soil inoculum. Analysis by EAL Environmental Analysis Laboratory, Southern Cross University, NSW, Australia.

**Table S2:** Metadata per farm. Farms are anonymised.

**Table S3:** Average plant nutrient concentrations and ratios for plants grown either without or with AM fungi from conventional or organic managed fields including the standard deviation and p-values obtained from a post-hoc test.

**Table S4:** Linear mixed-effects model results for the effects of the management system on plant total biomass, plant height, plant nutrient concentrations, photosynthesis rate, chlorophyll content (SPAD) and flowering stage.

**Table S5:** List of virtual taxa (VT) of arbuscular mycorrhizal (AM) fungi showing total sequence abundance (after rarefaction) of each VT across treatments.

**Table S6:** Indicator virtual taxa (VT) of arbuscular mycorrhizal (AM) fungi in plants under either conventional or organic agricultural management.

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