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Spatiotemporal gradients are principal architects of arbuscular mycorrhizal fungal assemblages

Liyuan Wang [a], Stavros D. Veresoglou [a,b,*]

[a] State Key Laboratory of Biocontrol, School of Ecology, Sun Yat-sen University, Shenzhen, 518107, China
[b] Laboratory of Ecology and Environmental Sciences, Department of Crop Science, Agricultural University of Athens, Iera Odos 75, Athens, 11855, Greece

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ABSTRACT

We maintain a good understanding of the drivers of arbuscular mycorrhizal (AM) fungal communities in the roots and the soil, but we underappreciate their relative ecological importance. As a result, we likely understand the structuring forces of AM fungal communities less well than we realize. We conducted a meta-analysis of 140 articles investigating AM fungal community structure with AM fungal-specific primers under field settings and had exercised two or more experimental manipulations. Based on ordination graphs from these studies, we assessed the relative importance of each experimental manipulation as well as quantified how context dependent these metrics have been to other manipulations. We found that spatiotemporal variables explained a major part of ordination variance, that site differences induced more context dependent effects than time (but only after using an alternative definition of site differences), and that long-vs short-term changes differed between root but not soil communities. Moreover, high precipitation and evapotranspiration led to a homogenization of AM fungal communities. We demonstrate that space and time govern AM fungal community assemblies, with site properties generating strong context-dependences; we noticed just a minor role for plant identity, but specific metadata analysis, including provisions for variation in AMF species identification precision, is needed to evaluate robustness of this observation. This spatiotemporal framework can help us map how AM fungal communities vary globally.

1. Introduction

An overwhelming majority of terrestrial plants engage in arbuscular mycorrhizal nutritional mutualisms with fungi of the phylum Glomeromycota (Brundrett and Tedersoo, 2018): The delivery of nutrients from the fungus to the plant is reciprocated with the transport of photoassimilates to the fungus, resulting in mutual benefits (Smith and Read, 2008; Kiers et al., 2011). Studies, where the mycorrhizal state of the plant has been manipulated, revealed that the community structure of the plants depends strongly on arbuscular mycorrhiza, with the effect sizes exceeding parallel practices such as fertilization, disturbances and grazing (Klironomos et al., 2011). We understand less well how strongly the changes in the mycorrhizal fungal community respond to common manipulations. The drivers of the plant and the fungal communities in the mutualism could, however, differ considerably. This is an apparent gap in the literature, which we wanted to address here through a synthesis.

An environmental filter of arbuscular mycorrhizal (AM) fungal communities, that has fascinated the community of mycorrhizal ecologists for a long time, is host selectivity (Öpik et al., 2009; Veresoglou and Rillig, 2014). Even though it has been possible to pair any arbuscular mycorrhizal fungus with any host under controlled settings, the degree to which we observe a host selectivity in AM fungal communities remains under debate (Perez-Lamarque et al., 2018; Sepp et al., 2019; Tsiknia et al., 2021 but see Kivlin et al., 2011; Chagnon et al., 2013; Vályi et al., 2015). Compared with other mutualisms with higher specificity, such as orchid mycorrhizae and pollination networks, it is less clear to what extent the plant host affects the community structure of AM fungi (Bascompte et al., 2003; Thébault and Fontaine, 2010; Chagnon et al., 2012; Dearnaley et al., 2012). Most of the literature indicates that host selectivity constitutes a key driver of AM fungal communities (e.g. Sepp et al., 2019; Chagnon et al., 2012; Veresoglou and Rillig, 2014), which is coupled with extensive evidence that AM fungi present weak biogeographic patterns (Davison et al., 2015). We thus hypothesized that host selectivity is a major driver of AM fungal community assembly (*Hypothesis One*).

* Corresponding author. State Key Laboratory of Biocontrol, School of Ecology, Sun Yat-sen University, Shenzhen, 518107, China.
E-mail address: veresoglou@aua.gr (S.D. Veresoglou).

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Many responses in mycorrhizal ecology are context dependent, in that the directionality of the changes induced by a parameter often depends on another (Hoeksema et al., 2010). For example, nitrogen (N) fertilization commonly reduces AM fungal root colonization, but only if plant growth is not limited by phosphorus (P) (Egerton-Warburton et al., 2007). Context dependency could be even more pronounced in relation to the structure of AM fungal communities (Johnson et al., 2015). It is clear that abiotic factors such as soil composition and climate strongly shape AM fungal communities (Kivlin et al., 2011; Davison et al., 2015). Community shifts resulting from abiotic drivers, however, could depend on unreported soil properties. Despite pronounced seasonal variation (Vályi et al., 2015; Tsiknia et al., 2021), there is a smaller pool of likely confounding factors affecting mycorrhizal fungal community dynamics over time, likely resulting in a smaller context dependency of AM fungal communities in relation to time. Thus, we hypothesized that temporal changes in AM fungal communities are less context dependent than spatial changes are (*Hypothesis Two*).

Arbuscular mycorrhizal communities change considerably over time, which we refer to as temporal turnover. Temporal turnover captures diverse drivers of AM fungal community structure: Seasonal responses are driven not only by changes in the phenology of the two partners in the symbiosis over the growth season but also by changes in climatic conditions within the growth season (Fu et al., 2022). AM fungal communities sampled at the same phenological stage across different years are often less different than those sampled across different phenological stages (Dumbrell et al., 2011; Vályi et al., 2015). Drivers of cross-year variation should include priority effects (Hausmann and Hawkes, 2010), phenological synchrony (Wang et al., 2016) and climatic settings (Jafarian et al., 2024). The relative strength of seasonal vs annual changes in mycorrhizal ecology has not been studied sufficiently (but see Dumbrell et al., 2011; Grunfeld et al., 2021), which is what motivated our second hypothesis. We crudely clustered temporal changes into short- and long-term, and hypothesized that AM fungal communities respond disproportionally to long-term temporal changes compared to short-term changes (*Hypothesis Three*).

An influential, but heavily debated, idea in biogeography is the *Latitudinal gradient hypothesis*, which postulates that biodiversity increases from the poles towards the tropics, with species richness, community complexity, and ecological interactions generally peaking in tropical regions and declining with higher latitudes (Vázquez and Stevens, 2004). Mittelbach et al. (2007) discuss some of the possible underlying mechanisms for the *Latitudinal gradient hypothesis* and group them into three categories, related to (i) history, (ii) speciation, and (iii) extinctions. The latitudinal gradient hypothesis makes the prediction that niche breadth increases with absolute latitude. Several studies have demonstrated that AM fungal diversity peaks in the tropics (Davison et al., 2015 but see Veresoglou et al., 2019 on the possibility that those changes are constrained by variability in host diversity). One possibility is that AM fungi experience, as a result, a narrower ecological niche (resulting in weaker interspecific competition across AM fungi: Engelmoer et al., 2014) in tropical systems (Thébault and Fontaine, 2010) and a relatively wider (and thus more intense interspecific competition) at high latitudes (Bascompte et al., 2003; Chagnon et al., 2013; Tsiknia et al., 2021). Alternatively, low latitude systems might have disproportionally promoted compared to latitudinal habitats a differentiation of the niche of competing species, facilitating coexistence (Davison et al., 2023). This latitudinal pattern prompted us to also examine how effect sizes scale directly with continuous climate variables. We expected that the relative differences that manipulations induce to AM fungal communities scale with climatic variables (*Hypothesis Four*).

We carried out a meta-analysis of the existing literature to address the abovementioned four hypotheses.

2. Materials and methods

2.1. Sources of data

On 17 September 2024 we carried out a systematic literature search at the Web of Science Core Collection using the search string *(arbuscul* OR glomerom* OR AMF) (Title) AND sequencing (Topic)*, yielding 1596 preliminary hits (Fig. 1).

Studies were screened based on the following inclusion criteria:

(a) Use of AM fungal-specific primers: The studies had used PCR primers targeting AM fungal-specific genomic regions were included to ensure taxonomic resolution and avoid nontarget amplification (eligible primers are listed in Table S1).
(b) Availability of ordination graphs: Studies contained a multivariate ordination capturing how the AM fungal community structure responded to two or more ecological factors.
(c) The study described was a field study (i.e. we did not consider studies using artificial soil substrates or sterilized soil).
(d) There were at minimum two distinct experimental parameters.

Upon careful examination of the articles, we were left with 140 eligible studies. A PRISMA diagram of the selection process is presented in Fig. 1.

For those 140 articles we recorded information on the following variables:

(1) Species (categorical): Describing the identity of the plant host.
(2) Site (categorical): Ecological and geographical context of the study location.
(3) Time (categorical): Covers temporal variables. Classified into long-term (observations spanning a full year or more) and short-term (observations spanning less than one year, usually over the growth season).
(4) Fertilization (categorical): Refers to the nutrient input regimes which we observed mostly in agricultural studies.
(5) Land management (categorical): Agricultural practices altering soil structure and microbial habitats.
(6) Water (continuous): Hydrological parameters.
(7) Cultivar (categorical): Genetic variants of the host plant, classified by traits relevant to AM fungal symbiosis (i.e. intraspecific variation).
(8) DNA source (categorical): Specifies the origin of AM fungal DNA samples and had two levels (roots and soil).

Ordination data were extracted from ordination plots according to Komatsu et al. (2019). For each observation in the ordination graph (i.e. site) we extracted the coordinates in the two principal ordination axes (i.e. sites), as well as information on the treatment it belonged. We worked exclusively on ordination graphs containing the two principal axes (i.e. two most significant axes). Information on sites was extracted with Plot Digitizer (v.3.1.6).

Traditional meta-analytical approaches integrating ordination graphs quantify and cross-compare the absolute shift in the centroid between treatments. The absolute shift, however, could be biased by considerations such as the sequencing depth (i.e. smaller changes for studies with a shallower sequencing depth) but also the complexity of the experimental system (e.g. community differences could be smaller across plants in an ephemeral grassland assayed regularly than at a global scale study assayed annually). To address such idiosyncrasies, we focused in our analysis on the relative changes when two or more experimental factors had been co-assessed within the same study, using unitless log response ratios of community distances. This approach standardises comparisons across studies by quantifying the magnitude of community shifts between paired treatments rather than absolute community states.

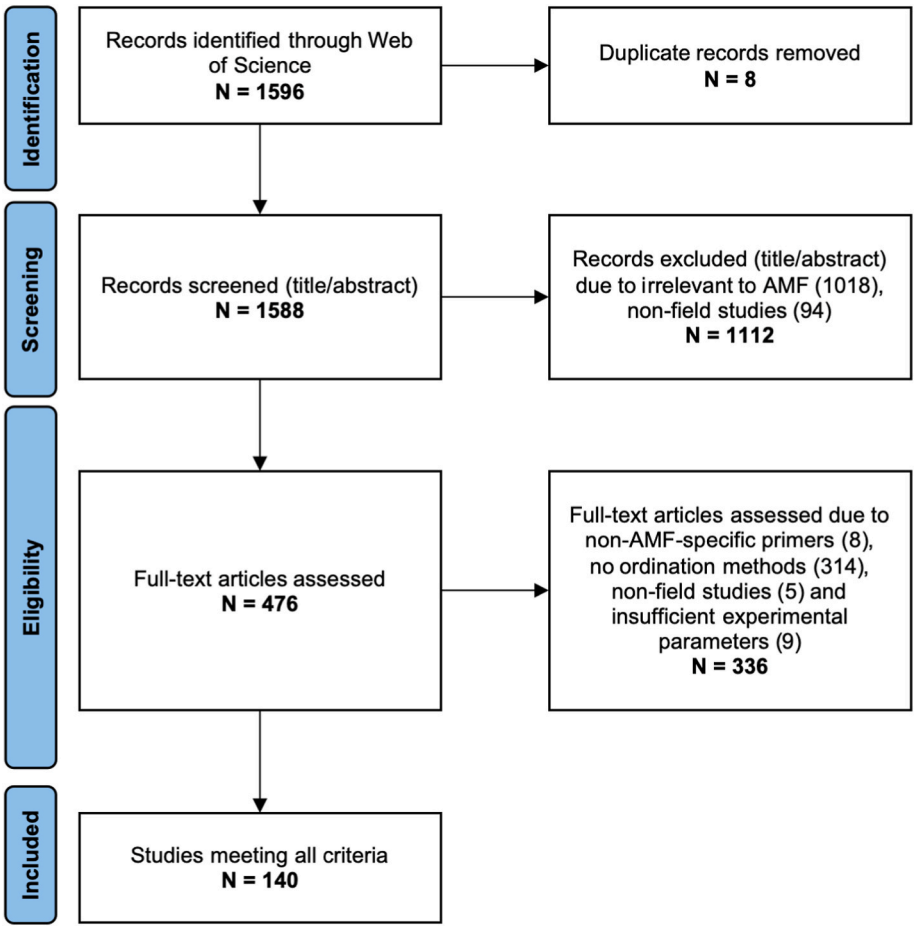

Fig. 1. PRISMA flow diagram outlining the literature search and screening process for inclusion in the meta-analysis. Initial query returned 1596 articles; inclusion criteria involved use of AMF-specific primers, field-based experiments, availability of ordination results, and presence of at least two distinct experimental parameters. After full-text assessment, 140 studies met eligibility and were retained for quantitative synthesis.

We obtained climatic variables for the study coordinates using WorldClim v 2.1 (Fick and Hijmans, 2017) with a 30 arc-second spatial resolution. From this spatial database, we extracted two key bioclimatic indicators: mean annual temperature (MAT) and mean annual precipitation (MAP). We also extracted information on the aridity index and evaporotranspiration from Zomer et al. (2022). The experimental manipulations were then classified into the following crude classification groups: (1) species: biotic factors encompassing comparisons across two or more plant species identity and cultivar genetic traits; (2) site: experimentation over two or more locations; (3) time: harvests over two or more distinct time points; (4) fertilization: addition of nutrients in the form of fertilization practices; (5) land use change: manipulations such as tillage and plowing that could not be classified as fertilization; and (6) water: manipulation of irrigation regime. We report how our meta-analysis conforms with the PRISMA guidelines in Notes S1. We note that the reliability of centroid distances depends on the proportion of total community variation captured by the first two ordination axes. This is a limitation of our approach, and readers should interpret effect sizes with caution when the ordination had low explanatory power.

2.2. Hypothesis One: host selectivity is a major driver of AM fungal community assembly

For each possible pair of experimental factors per study we calculated a log-response ratio of centroid distances (i.e. $\log RR(d_{param1}/d_{param2})$). Distances per experimental parameter described mean changes with vs without the experimental parameter per level of other listed experimental parameters. To assess the meta-analytical variance of each statistic we used the cumulative variance in the two axes of the points per experimental treatment in the ordination graph with each individual site as a replicate. We based our variance estimate on replicate observations across the two ordination axes. We worked independently per axis and calculated the variance of the observations. We subsequently pooled the two variance estimates, through their mean (i.e. they originated from an equal number of observations). We used standardized approaches on log ratios and their weighting to pool the variance statistics (which we describe above) and used them for weighting purposes in our meta-analysis (Lajeunesse, 2011). In our analytical procedure each point represented the effect size from a single study, so that there was no violation of the criterion of independence of individual studies.

For *Hypothesis One* we only analyzed combinations of experimental manipulations that had been replicated at minimum across three experimental studies. The meta-analytical model was a method of moments using a random-effects model with a Hedges (Cochran) estimator (Hedges, 1992).

Our effect sizes (i.e. log-response ratio of centroid distances) are sensitive to the distance metric used and the ordination approach. First, we replicated the analyses with ordination type (i.e. Bray-Curtis based, Hellinger based or other as a moderator (Notes S1). Second, we used the *vegan* dataset mites to conduct a sensitivity analysis (Notes S1).

2.3. Hypothesis Two: Temporal changes in AM fungal communities are less context dependent than spatial changes

We here assessed interactive terms per study. Interactive terms

captured the ratio of community distances (i.e. larger over smaller Euclidean distances) with vs without the treatment over all possible combinations of two or more experimental settings. As an example, in a bifactorial experiment with time and site as factors, each containing two levels, the interaction term for time was the ratio of the time distance at site A over site B (i.e. the largest distance was the denominator, resulting in interactive terms above 1). Interactive terms close to zero manifested a smaller context dependency of the effects of a specific manipulation.

To address this hypothesis, we exclusively analyzed data from root samples. Contrary to soil data, root data had yielded sufficient statistical signal, which we attempted to explain here. We excluded treatments for which we had data from less than three samples. For this hypothesis we did not merge studies that addressed species differences with those addressing cultivar differences. First, we carried out a Kruskal-Wallis test to assess if the interaction terms differed across manipulations. We compared the interaction terms for site vs. time using a *t*-test (i.e. both were categorical variables with two levels).

2.4. Hypothesis Three: Long term temporal changes induce stronger shifts to AM fungi than short-term ones

We tested whether AM fungal communities respond more strongly to long-term temporal variation than to short-term fluctuations. We classified temporal comparisons into short-term (intra-annual; e.g., within a growth season) and long-term (cross-year; e.g., either cross-season or cross-year studies). The model we fitted was a general linear model with the differences in the effect size as a predictor and the predictors time span (i.e. short-vs long-term) and the origin of DNA (i.e. roots vs soil) as well as their interaction.

2.5. Hypothesis Four: The relative differences that manipulations induce to AM fungal communities scale with climatic variables

We tested whether biogeographic predictors explained part of the variation in experimental-induced changes of AM fungal communities. We tested separately community data from root and soil samples. Per combination pair in *Hypothesis One* we assessed the residuals (for latitude we also used the actual effect sizes as covariates) of the effect size compared to the mean effect size. Second, we modelled the absolute value of those residuals (i.e. expressing the degree to which we observed heteroscedasticity; distance to the mean effect size) in relation to our environmental predictors, comprising, absolute latitude, mean annual temperature, mean annual precipitation, aridity index, evapotranspiration, total N deposition, dry N deposition and wet N deposition. We used for this reason correlation tests (either Pearson or Spearman).

2.6. Sensitivity analyses

To assess the robustness of our conclusions, we conducted two types of sensitivity analyses:

(a) Sample Source: We repeated the analyses separately for root- and soil-derived AM fungal data. We compared the resulting effect sizes to assess whether DNA source biased our findings. Root-based studies tended to yield more conservative effect sizes, possibly due to host filtering.
(b) Unweighted Averaging: We repeated the meta-analysis without variance-based weighting to test if results depended on study precision. The results remained consistent in direction, though effect sizes were slightly attenuated. This confirms the robustness of our conclusions.

We further used for the root samples the type of ordination as a covariate to assess the degree to which our results were sensitive to it. We note that most species comparisons came from field studies where plant species co-occurred naturally. Although site and time were held constant, we cannot entirely exclude the possibility of unmeasured micro-environmental variation associated with different host plant patches. However, a sensitivity analysis restricted to experimentally controlled studies confirmed the same qualitative ranking of drivers.

2.7. P values

Because the scope of meta-analyses lies mainly on the estimation of effect sizes, manifesting the strength of a phenomenon, rather than per se hypothesis testing, it is unusual that they integrate corrections for *P* value inflation. This is what we did here,as well. We present all comparisons in full, and we encourage readers to interpret the effect sizes and confidence intervals as the primary evidence. In some cases, such as when addressing *Hypothesis Two*, we reclassified variables to balance between good reporting practices and effectively addressing the research questions. In these cases, we both report on the original statistics and the statistics after the reclassification.

Extracting information on AM fungal community structure from ordination graphs propagated biases inherent to the original studies. As an example, in some studies the sequencing depth was relatively shallow, whereas several primer pairs, and in particular those targeting the small subunit or relied on alignments with existing virtual taxa, maintained a low resolution for species. We here, through log response ratios of community distances, evaluated relative changes in community structure, which might have been less sensitive to metabarcoding biases than the original estimates. The possibility, however, remains, that metabarcoding biases (i.e. sequencing depth and low taxonomic resolution) introduced artifacts into our analysis and possibly biased our conclusions.

3. Results

In our dataset, there were 63 studies addressing AM fungal-community data from roots and 136 from soil. 58 of the studies compared different species and 11 different isolates. In many of these studies, AM fungal community data were available for both the roots and the soil. 49 out of 140 studies used matches to virtual taxa from the MaarjAM database (Öpik et al., 2010). We present a detailed table with study attributes in Notes S2.

3.1. Hypothesis One: host selectivity is a major driver of AM fungal community assembly

In root-associated AM fungal communities, site ($ES_{species\text{-}site} = -0.629$, $P < 0.001$, with CIs: −0.86, −0.40 and a $Q_h = 13.6$, $P = 0.03$) and land use ($ES_{species\text{-}landuse} = -0.466$, $P = 0.014$, with CIs: −0.84, −0.09 and a $Q_h = 7.5$, $P = 0.12$) over performed (i.e. had a higher relative importance) compared with species (Fig. 2a; Table S2). This pattern should be interpreted cautiously, as the dataset was not specifically assembled to estimate host-identity effects and taxonomic resolution varied across studies (see Section 4.1). We therefore refrain from drawing firm conclusions about the relative importance of host selectivity versus spatiotemporal drivers based on this comparison alone. There were also non-zero effect sizes for the contrast time vs site ($ES_{time\text{-}site} = 0.396$, $P < 0.001$, with CIs: 0.19, 0.60 and a $Q_h = 5.9$, $P = 0.21$). Soil-based studies contained less conspicuous differences and there were only two non-zero effect sizes: the contrast between species and site (ES = −0.588, $P = 0.002$, with CIs: −0.95, −0.23 and a $Q_h = 4.2$, $P = 0.12$) and that between time and land use (ES = −0.561, $P < 0.001$, with CIs: −0.86, −0.26 and a $Q_h = 14.6$, $P = <0.01$; Fig. 2b; Table S3).

3.2. Hypothesis Two: Temporal changes in AM fungal communities are less context dependent than spatial changes

Interaction terms differed across the drivers (Kruskal–Wallis

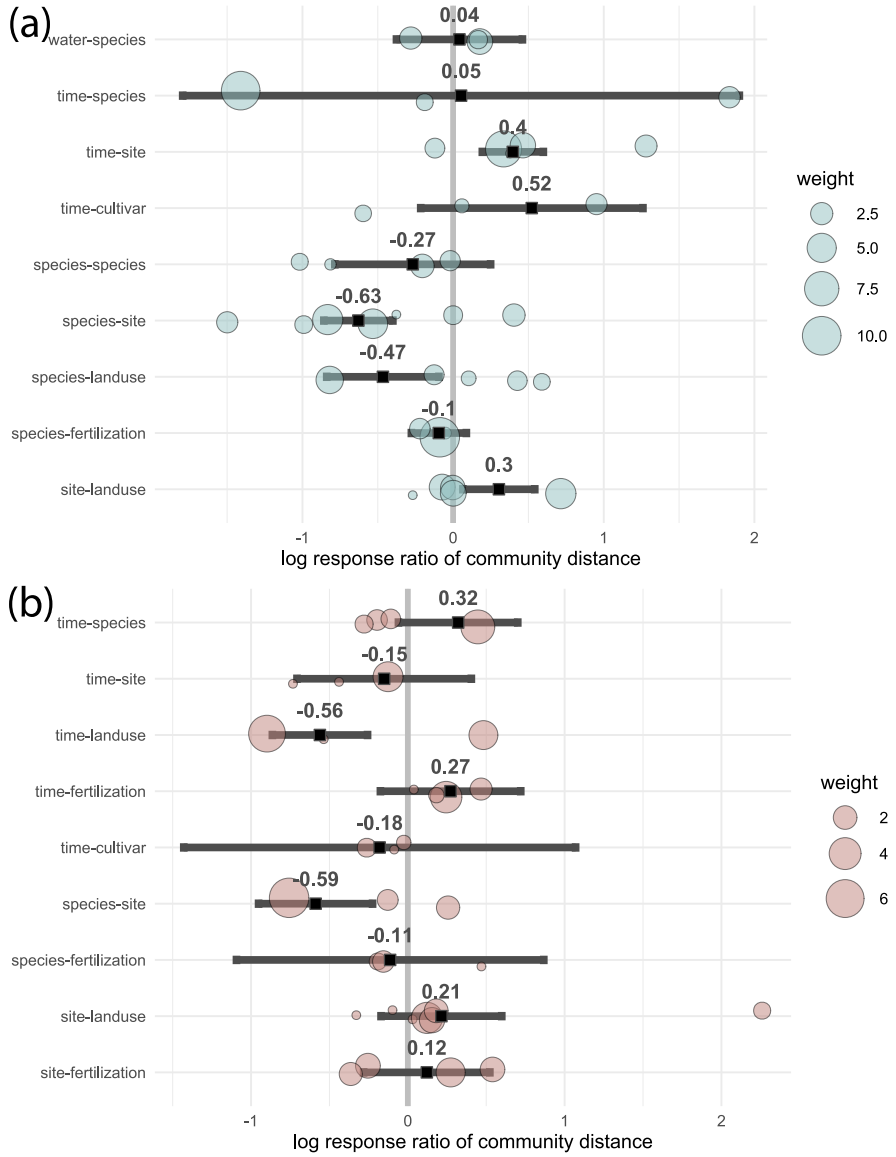

Fig. 2. Means (black squares) and 95% CIs (black bars) of all combinations of (a) root- (light blue) and (b) soil- (red) based studies exploring simultaneously at minimum two experimental manipulations. Each colored balloon represents an observation from a single study with the weight being proportional to the size of the balloon. We present specific model Q statistics in Table S2 and Table S3 and retained only combinations that were represented with a minimum of three independent studies. Values above 0 manifest that the first manipulation from the two listed on the left had a bigger change to the AM fungal community than the second one, and vice versa. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

$\chi^2 = 13.5$, $P = 0.035$; Fig. 3a), but these were mainly driven by the very low interaction terms that we observed for DNA source. There was a non-significant trend for interaction terms describing time to be smaller than those for site (W = 89, $P = 0.096$). When we combined together *land use change* and *site* into a single factor (i.e. collectively describing experimental sites where the abiotic settings differed between treatments) and compared the interaction term with that for *time* (this time with a *t*-test) these were different (i.e. smaller for time: t = 2.06, $P = 0.048$; Fig. 3b).

3.3. Hypothesis Three: Long term temporal changes induce stronger shifts to AM fungi than short-term ones

In our model containing effect sizes as a response variable and time (i.e. short vs long term) and DNA source as predictors the interactive term of the two predictors was significant with more pronounced time differences across root samples ($F_{time:DNA} = 5.01$, $P = 0.035$; Fig. 4). Given the significance of the interaction term we flattened the design to an one-way ANOVA (Marini, 2003) and used a least-significance difference posthoc test, which identified the two root treatments as different.

3.4. Hypothesis Four: The relative differences that manipulations induce to AM fungal communities scale with climatic variables

There were no relationships with latitude in root samples ($rho_{absolute\ latitude\ -\ residuals} = -0.11$, P = 0.49; $rho_{absolute\ latitude\ -\ effect\ sizes} = -0.05$, $P = 0.77$). There were relationships by contrast for soil samples ($rho_{absolute\ latitude\ -\ effect\ sizes} = 0.51$, $P = 0.002$; Fig. 5a; with a trend for a relationship with absolute residuals: r = 0.3, $P = 0.081$). The relationship of effect sizes with absolute latitude across soil samples was subject to the hierarchy we used in calculating effect sizes (i.e. time > species > site > other parameters). For this reason, we assessed respective relationships of the residuals from the mean value (absolute

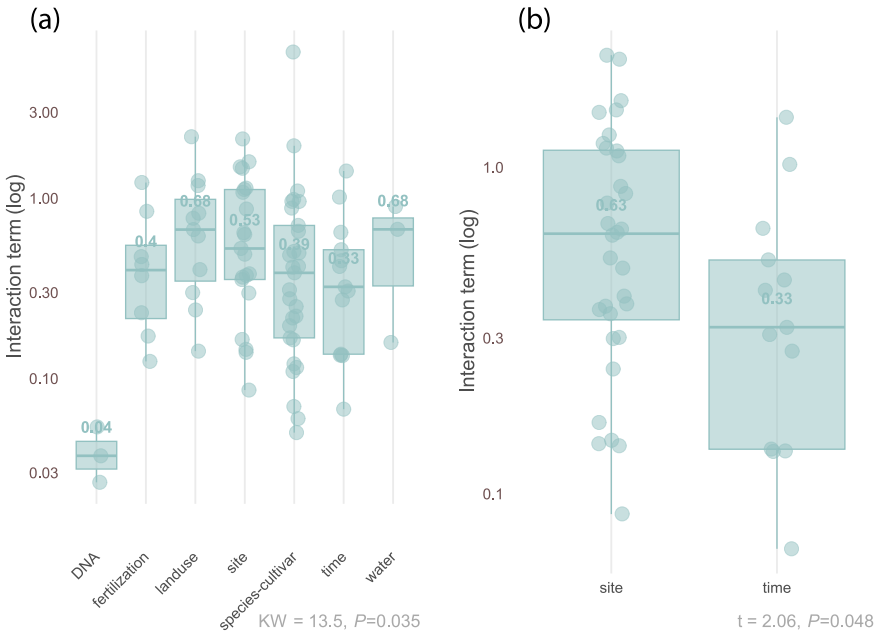

Fig. 3. Relative contributions of different environmental factors to AM fungal community variation, shown as interaction terms in root samples: (a) differences across all manipulation factors; (b) statistics for the contrast site vs time. In (b) we integrated in the manipulation factor site the manipulation landuse. Interactions were defined as the ratio of larger over smaller Euclidean distances of the experimental manipulation over the levels of the other manipulations.

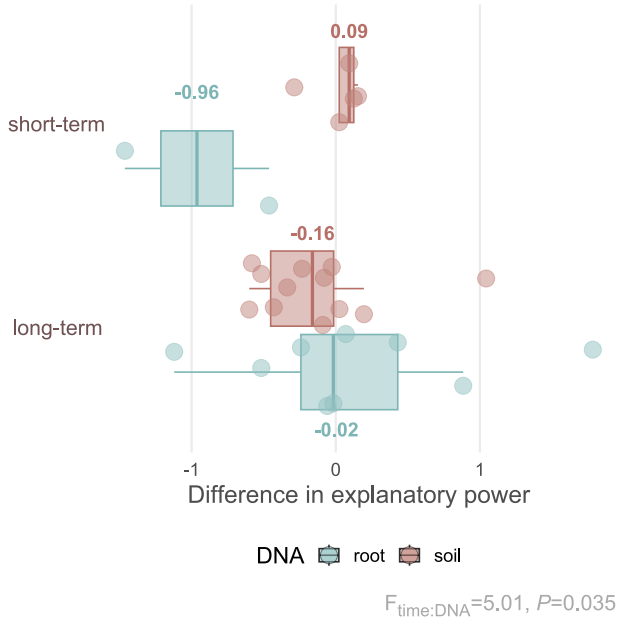

Fig. 4. Short-term vs. long-term temporal effects on AM fungal community explanatory power: Comparison of effect sizes between root- (light blue) and soil-derived (red) DNA samples. Values represent log-response ratios (negative values indicate reduced explanatory power). Statistical interaction between time and DNA source is shown ($F_{time:DNA} = 5.01$, $P = 0.035$). Differences are categorized as short-term (within-season) and long-term (cross-year) observations. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

values) and bioclimatic variables. We observed two relationships in the absolute residuals (in both cases the latitudinal gradient had a negative slope), first with precipitation ($r = -0.49$, $P = 0.041$; Fig. 5b) and second evapotranspiration (rho = −0.35, P = 0.004; Fig. 5c).

3.5. Sensitivity analysis

There were pronounced differences between soil and root samples (e.g. Fig. 2) and we uncovered statistical interactions between DNA source and time (Fig. 4). Upon using an unweighted averaging approach, the differences between time and site, as well as species and site, species and landuse and site and land use in the roots remained significant, and the same happened for the differences between time and site and species and site in the soil (Fig. S1).

The choice of ordination type was significant in two cases (i.e. the species – land use contrast and the species – site contrast), but this did not alter the overall significance of the results (Notes S1). In the species - site contrast the moderator distance:Hellinger had an estimate of −1.15 (CIs −2.09 to −20.6, $P = 0.017$) and the moderator distance:other had an estimate of −0.42 (CIs −0.90 – 0.06, $P = 0.082$). In the species – landuse contrast the moderator distance:Hellinger had an estimate of −0.55 (CIs −1.86 – 0.75, $P = 0.41$) and the moderator distance:other had an estimate of −1.23 (CIs −2.17 to −0.31, $P = 0.009$).

4. Discussion

Our global meta-analysis addresses common biotic and abiotic drivers, which shape AM fungal communities. Some of our results, such as the low relative importance of host selectivity in structuring AM fungi and that the relative importance of the drivers depends on biogeographic drivers, such as evapotranspiration and precipitation are at first glance counterintuitive. We structure our discussion into four sections addressing how well each of our hypotheses got supported.

4.1. Hypothesis One: host selectivity is a major driver of AM fungal community assembly

Host selectivity was detectable as a driver of AMF community assembly in our analysis, though effect sizes were generally smaller than those for *site* and *landuse* descriptors (Fig. 2). Two of the largest effect sizes in absolute value concerned host selectivity, indicating that plant identity does structure AMF communities. While it is widely recognized that arbuscular mycorrhizal systems exhibit a certain degree of host

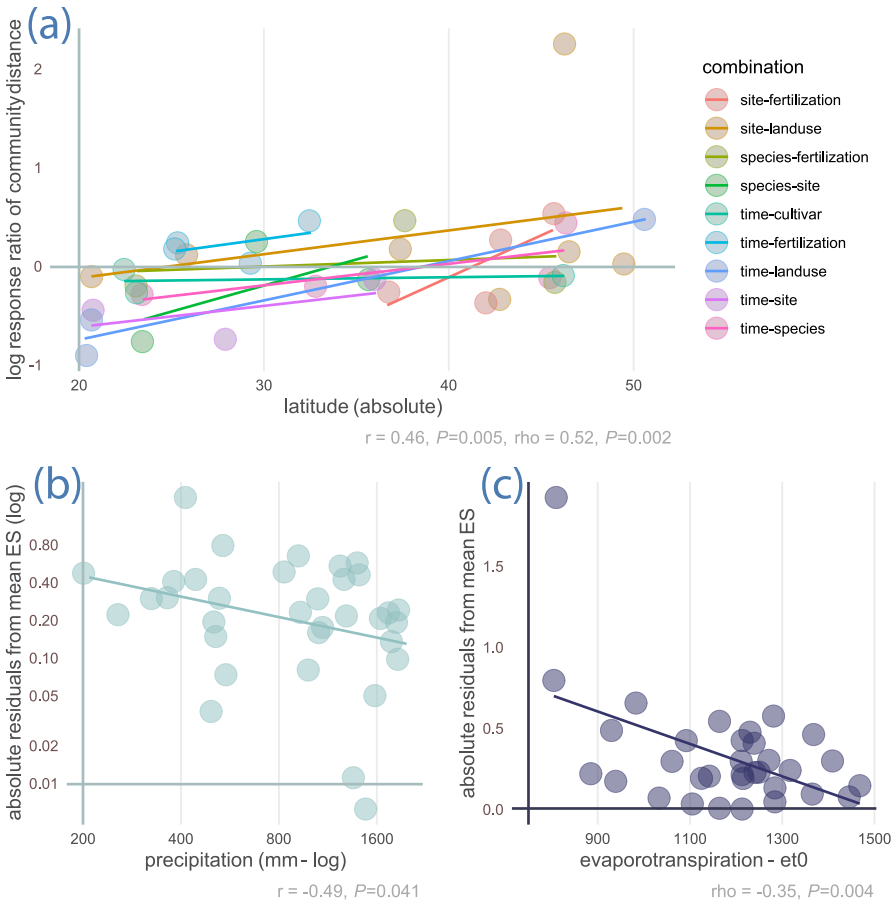

Fig. 5. Biogeographic scaling of manipulation-induced effects on AM fungal communities. (a) Effect sizes (log-response ratios of centroid distances) in relation to absolute latitude. Points represent individual studies, with colors indicating the specific combination of experimental factors compared. (b, c) The absolute residuals of the effect sizes from their global (b) mean annual precipitation and (c) evapotranspiration. Solid lines capture best-fit relationships. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

selectivity (Sepp et al., 2019), the extent of this host selectivity is considerably weaker than that observed in other mycorrhizal types, such as ectomycorrhizas and ericoid mycorrhizas (Smith and Read, 2008). There are many ways to partition pairwise host effects, such as total variation across all hosts, average pairwise host effects, max pairwise host effects (Sepp et al., 2019), which we could however not integrate into our analysis here. Several abiotic properties, such as pH (Veresoglou et al., 2013; Davison et al., 2021) and soil texture (Lekberg et al., 2007), may pose stronger environmental filters for arbuscular mycorrhizal fungi than host specificity, contributing to the observed pattern in studies where both factors were simultaneously assessed (Fig. 2). Host selectivity, nonetheless, still explains a considerable fraction of community variation, as has been demonstrated in comparable meta-analyses (e.g. Hoeksema et al., 2018).

Our sensitivity analysis revealed that ordination method significantly moderated effect sizes for two comparisons: species versus site ($QM = 7.06$, $P = 0.029$) and species versus land use ($QM = 7.27$, $P = 0.026$). For both comparisons, eigenvalue-based methods (PCA, CA, RDA) yielded larger pooled effect sizes than distance-based methods (NMDS, PCoA on dissimilarity matrices). Importantly, however, both classes of methods showed the same directional pattern: spatiotemporal drivers consistently had larger effect sizes than host species effects. This consistency supports the robustness of the finding that host selectivity, while detectable, operates alongside stronger spatiotemporal and environmental filters. Nevertheless, the difference in magnitude raises two concerns. First, distance-based and eigenvalue-based ordination spaces are not mathematically equivalent: NMDS preserves rank orders but not Euclidean distances, whereas PCA produces Euclidean distances but assumes linearity. Pooling centroid distances across these methods implicitly assumes commensurability that may not hold. We therefore caution readers that absolute effect sizes should be interpreted with care. Second, the moderation effect itself suggests that some variation in our dataset may be attributable to methodological choices of primary study authors. We have provided stratified estimates in Notes S1 so that readers can evaluate the robustness of each comparison independently. Future meta-analyses should develop standardised effect size metrics that are invariant to ordination algorithm, or conduct multi-method sensitivity analyses as we have done here.

A limitation of our host-selectivity analyses concerns taxonomic resolution. Approximately half of the relevant studies relied on virtual taxa from the MaarjAM database (Öpik et al., 2010). The VT system has been instrumental in advancing mycorrhizal ecology by providing a standardized framework for AMF identification and enabling cross-study comparisons that would otherwise be impossible. This has driven considerable progress in our understanding of AMF biogeography and community ecology. Nevertheless, VTs group sequence-similarity-based operational units that may encompass multiple cryptic lineages. These lineages can differ in their host preferences. Fine-scale host-specific associations operating below the VT level are therefore systematically obscured. This biases analyses toward apparent generalism. The apparent weakness of host-selectivity effects in our analysis may thus partly reflect a methodological ceiling on detectability rather than a true biological pattern. Our analysis likely represents a conservative estimate of host selectivity's importance. Future

meta-analyses leveraging higher-resolution taxonomy will be needed to resolve this question more fully. Such approaches might include amplicon sequence variants from the ITS region, long-read sequencing, or multi-locus methods. Until then, we caution against overinterpreting the magnitude of host-selectivity effects derived from VT-based classifications.

4.2. Hypothesis Two: Temporal changes in AM fungal communities are less context dependent than spatial changes

Our ability to predict AM fungal community structure hinges upon factoring in likely sources of context dependency (Hoeksema et al., 2010;Wang et al., 2023). These were captured in our analysis through the interaction terms. In agreement with our hypothesis, interaction terms for time were amongst the smallest whereas those for site among the largest. Even though abiotic settings stay relatively invariable over time, seasonality shifts AM fungal community structure in predictable but also profound ways (e.g. Dumbrell et al., 2011). Community shifts should however be of comparable intensity across experimental observations, resulting to relatively small interaction terms in relation to time. Soil properties, by contrast, interfere with the environmental conditions on broad scales that are relevant to understanding coarse-scale ecological and geographic properties of a species, which Soberon (2007) terms as the Hutchinsonian ecological niche, of the organisms in remarkably different ways. For nutrient availability for example, we observe a zone of sufficiency and minimum/maximum tolerance zones with changes within the zone of sufficiency having much less of an impact that changes close to the limits. Because the structure of the ecological niche differs across organisms, and in this case AM fungi, a change in location (and thus abiotic settings) could prevent some of the species in the original local pool from establishing while leaving others unaffected. As a result, observations across different sites can foster asymmetric responses of the AM fungal community, which we captured in the form of big interaction terms.

4.3. Hypothesis Three: Long term temporal changes induce stronger shifts to AM fungi than short-term ones

Biotic interactions stabilize communities on the short term (e.g. Hallett et al., 2014), but on the longer term senescence, community turnover and recruitment modify biotic interactions so that their relative importance declines (HilleRisLambers et al., 2012). In our analysis we observed that the interactive term of time (intra-annual vs. cross-year) and DNA source (root vs. soil) was significant, implying that root and soil communities change at a different pace. In particular, there were minimal temporal changes in relation to soil AM fungal communities but pronounced differences in the roots. AM fungal communities from roots tend to be dynamic in nature and change considerably even within a single growth season (e.g. Schalamuk and Cabello, 2010), which matches our findings. Respective soil communities, by contrast, reflect to a large degree the relative abundance of asexual spores in soil and change considerably less, which is what we uncovered with our analysis. Asexual spores have a high DNA content and bias metabarcoding estimates from soil (Gamper et al., 2008), while being considerably less dynamic than the respective AM fungal communities in the roots. Soil propagules of AM fungi thus often act as a reservoir of AM fungal species for the next growth season (Schalamuk and Cabello, 2010). This consideration triggers a clear dichotomy on the utility of studies addressing root and soil communities, which we used to our advantage when addressing *Hypothesis Four*.

4.4. Hypothesis Four: The relative differences that manipulations induce to AM fungal communities scale with climatic variables

The relative differences in the predictive power of manipulations (i.e. which we assessed in the form of the absolute difference from the mean of the effect sizes) decreased with precipitation and evapotranspiration (Fig. 5b and c) and there were scaling relationships between our hierarchy of manipulations and absolute latitude (Fig. 5a). These observations support our hypothesis but are less straight forward to explain. There is always the possibility, for example, that sampling protocols have been different in temperate regions and in the tropics, which we captured through our analysis. To a certain degree low-latitude tropical habitats, which typically experience high precipitation and show high evapotranspiration are the least ephemeral. In our scaling relationships (Fig. 5a) it was time that scaled best with latitude, suggesting that our observation is capturing to a large degree the differences in seasonality between tropical (even though we did not explicitly test tropical systems here) and temperate systems. In settings such as high latitudes or areas with low precipitation or evapotranspiration, experimental conditions should trigger larger differences in AM fungal communities compared to humid habitats. At the same time the latitudinal gradient in AM fungal richness might imply that in the tropics environmental settings favor AM fungi the best. The Stress-Dominance Hypothesis, is a widely cite tenet in community ecology, which predicts a high importance of abiotic drivers in stressed habitats, and an increase in the relative importance of biotic interactions in benign environmental settings, and has received mixed support (Pakgohar et al., 2024). In our particular case, the tropics could be classified as benign habitats (i.e. AM fungal diversity peaks), whereas latitudinal habitats as stressful habitats, and in this regards we can approach the Stress-Dominance-Hypothesis as a likely interpretation of our observation. Notwithstanding this point, the fact that we observe such biogeographical relationships in our effect sizes gives evidence of how important it is to extend present investigations on AM fungi beyond the usual experimental settings (i.e. typically the Western world and China; Li et al., 2023) and explore underrepresented habitats.

There exist, however, alternative explanations that justify our patterns without supporting the Stress Dominance hypothesis. First, we could not explicitly (due to the small number of contrasts per combination of drivers) address the role of agriculture. Farmers, particularly in the temperate regions, tend to implement practices, such as irrigation and fertilization, which are often not reported. In particular, irrigation in arid regions – which are more common at lower latitudes – may artificially homogenize soil conditions, reducing effect size heterogeneity independently of natural stress. A large fraction (Notes S2) of our studies originated from agricultural habitats, which could have contributed to the latitudinal gradients we observed. Moreover, to calculate our effect sizes we resorted to analytical approaches that have not been explicitly tested in the literature and could have generated artifacts. We explicitly tried to address biases through sensitivity tests, but the possibility remains that the latitudinal gradient resulted from one or more of these artifacts. We could thus not explicitly assert that the Stress Dominance hypothesis was behind our latitudinal gradients, but we raise it as a possibility. Addressing this possibility could be an interesting follow up to our study.

5. Conclusion

We conclude that space and time are major filters of AM fungal communities. We also observed a detectable role for plant identity, although the taxonomic resolution of available studies limits confidence in the magnitude of this effect. Temporal changes exhibit lower context dependency compared to spatial variations, underscoring the relative predictability of seasonal and annual turnover in AMF assemblages. The magnitude of community responses to experimental manipulations scales with key climatic variables, including precipitation and evapotranspiration, supporting that these factors homogenize AMF communities. Our findings open up opportunities to more effectively design mycorrhizal surveys in the future.

CRediT authorship contribution statement

Liyuan Wang: Data curation, Formal analysis, Writing – original draft, Writing – review & editing. **Stavros D. Veresoglou:** Conceptualization, Formal analysis, Investigation, Supervision, Writing – original draft, Writing – review & editing.

Data availability statement

We make the data available through Notes S2 and Notes S3.

Declaration of generative AI in scientific writing

The authors did not use any AI tools to write the manuscript.

Declaration of competing interests

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Stavros D Veresoglou reports financial support was provided by National Natural Science Foundation of China. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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