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The Increased Environmental Niche of Dual-Mycorrhizal Woody Species

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ABSTRACT

The presence and distribution of mycorrhizal symbionts can influence plant distribution through specific host-mycorrhiza symbiosis interactions. However, generalist hosts also exist, such as dual-mycorrhizal plants that form symbiotic associations with both ectomycorrhizal fungi (EM) and arbuscular mycorrhizal fungi (AM). Little is known about the effect of dual mycorrhization status on the hosts' global distribution and acclimation to specific environments. This study investigates the potential advantage of dual associations of more than 400 woody genera spread at a global scale. We found that dual-host woody species occupy a broader geographical range and environmental niche space compared to those associating exclusively with either AM or EM. We show that the increased geographic range and expanded environmental niche space are independent of the phylogenetic architecture and evolutionary history of the woody genera. Our results highlight the advantage of generalist host-microbe symbioses between woody species and fungi to expand their range, and their potential role in colonising dry climates.

1 | Introduction

In natural environments, it is common that soil nutrients or water availability limit plant growth. One of the leading adaptation mechanisms for most plants to cope with these challenges is the formation of symbiotic interactions with mycorrhizal fungi (Martin and van der Heijden 2024). Mycorrhizal fungi form associations with the majority of land plants and supply plants with nutrients in return for photoassimilates. The two most dominant types of mycorrhizal associations with plants are ectomycorrhizal (EM) fungi and

arbuscular mycorrhiza (AM) fungi (Smith and Read 2010). Although ubiquitously distributed, it has been shown that the abundance and diversity of AM and EM host communities are strongly influenced by both abiotic (i.e., climatic and edaphic conditions) and biotic factors (i.e., competition and facilitation of fungi) (Read 1991; Tedersoo et al. 2014; Steidinger et al. 2019). Notably, at large macroecological scales, there is an almost clear-cut distinction between the distribution of EM and AM-host trees, as the former are located mostly in higher latitudes, characterised by seasonally cold climates, whilst the latter prevail in lower latitudes (e.g., the tropics), where

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warm, wet, stable climates prevail (Soudzilovskaia et al. 2015; Steidinger et al. 2019; Mikryukov et al. 2023). At more local ecological scales, such as the transition in temperate regions, a more gradual shift is observed. Interestingly, a large geographical scale analysis in the USA reported that forest plots with mixed mycorrhiza hosts produce more biomass and have higher species diversity than plots dominated by either AM or EM hosts (Carteron et al. 2022; Luo et al. 2023).

It was originally thought that plants uniquely associate with either one of the functional types of mycorrhizal fungi, EM or AM. However, the occurrence of plants that form dual mycorrhizal associations is increasingly being recognised as a viable phenomenon in natural environments (Chilvers et al. 1987; Moyersoen and Fitter 1999; van der Heijden 2001; Teste et al. 2020). Dual colonisation can occur within the same root system (Lapeyrie and Chilvers 1985; Chen et al. 2000), with the colonisation ratio varying by species, life stage and environment (Teste et al. 2020). For example, *Eucalyptus* seedlings are initially colonised by AM fungi, shifting to EM associations later (Chen et al. 2000; Teste et al. 2020). EM fungi can also inhibit AM colonisation in the early stages (Santos et al. 2001), and soil properties further influence this balance (Teste et al. 2020). EM fungi often outcompete AM fungi, though the mechanisms behind this 'priority effect' are unclear.

Host-mycorrhizal associations are key drivers in the evolution of host species by increasing the fitness of the plant individuals as well as the overall plant community fitness (Osborne et al. 2018; Cosme 2023). Host mycorrhizal type has been shown to be phylogenetically conserved, indicating the tendency of species to retain their ancestral mycorrhizal association patterns (Meng et al. 2023). Interestingly, the mycorrhizal status can be best explained by environmental variables (e.g., soil texture and climatic factors) (Meng et al. 2023). Overall, based on a meta-analysis of dual colonisation status, using data from pot/field experiments that investigate the effects of dual symbiosis versus single symbiont status on plant growth, dual mycorrhization usually results in a positive or neutral effect on plant host responses compared to a single type of colonisation (Teste et al. 2020). On the contrary, few studies have also identified the potential inhibitory effects of dual-mycorrhizal associations (Egerton-Warburton and Allen 2001; Kariman et al. 2012). Despite their potential importance, the global distribution and ecological niche of woody species able to form dual mycorrhization has not been described yet.

There is growing interest in understanding two key aspects of dual mycorrhizal interactions: first, the specific conditions that determine the formation of these interactions over exclusive AM or exclusive EM associations; and second, the advantages of dual mycorrhizal associations in responding to biotic or abiotic challenges. Whilst past research has predominantly examined the relationships of trees and their exclusive mycorrhizal fungi associations, there is still limited understanding of how a dual colonisation directly affects the host's niche breadth and adaptation to novel environments. In this study, we analyse the geographical and climatic distribution of >400 host genera, summing to 1012 species, proposed to form dual mycorrhizal associations against those with exclusive AM or

EM associations. Such a comparative approach can allow us to make informed assumptions and foster a better understanding of the potential role dual-mycorrhizal interactions might play in influencing the ecological range and potential adaptability of their host plants (Lerner et al. 2023). We hypothesise that plants forming dual mycorrhizal interactions are likely located at the geographical and environmental intersections between EM and AM-associated species' distributions, extending both the single AM and EM environmental niches, particularly in harsher environments where exclusive AM or EM hosts may not succeed (Steidinger et al. 2019).

In order to understand the biogeographical and environmental uniqueness of dual mycorrhizal host species, we mapped their geographical distributions, obtained from the confirmed list of genera forming dual associations (Teste et al. 2020) against genera shown to have exclusive EM or AM associations, based on the FungalRoot database (Soudzilovskaia et al. 2020). We matched the genera from these lists to the woody species within these genera with known species' distributions (Lerner et al. 2023). These datasets were subsequently combined with a comprehensive phylogeny database (Segovia et al. 2020), with the goal of examining how geographical and ecological niches are partitioned among species with different mycorrhizal associations and phylogeny. The integration of phylogenetic distances with phenotypic and geographic data can enhance our understanding of the relative importance of mycorrhizal influence versus evolutionary constraints on species distribution (Blomberg et al. 2003; Meng et al. 2023). Here we (1) examine phylogenetic clustering throughout different types of mycorrhizal associations in woody species', specifically in dual hosts; (2) Assess the impacts of various mycorrhizal association types on the geographic range of woody species globally and within predefined ecoregions; and (3) understand whether dual hosts have a broader environmental niche space in comparison to exclusive AM or EM hosts. We hypothesise that dual-host woody species occupy a broader geographical range and environmental niche space compared to those associating exclusively with a single mycorrhizal type, even when accounting for evolutionary distances between different association groups.

2 | Materials and Methods

2.1 | Dataset Collection

We gathered a list of woody genera confirmed to host dual-mycorrhiza based on the confirmed dual mycorrhiza hosts list published (Teste et al. 2020). 'Confirmed dual-mycorrhizal plants' are only cases where specific fungal structures such as arbuscules/coils (for AM fungi) and hartig net/transfer (for EM fungi) were detected on the fine roots of the plant. Additionally, we obtained separate lists of species that exclusively host either EM or AM associations (Soudzilovskaia et al. 2020). To ensure clarity in our data, we excluded any species from the exclusive EM or AM lists that appeared in the dual-host list, thus maintaining distinct categories for species with solely dual-mycorrhiza associations and those with only single-mycorrhiza associations. While Teste et al. (2020) assessed dual mycorrhizal hosts at the genus level, they did

not link these data with the distribution of these host species. Hence, this dataset was matched to a dataset containing species distributions, obtained from Lerner et al. (2023) in order to test whether the mycorrhizal host strategy (exclusive AM, exclusive EM or dual host) influences the global distribution of woody species. A phylogeny of the investigated woody species was obtained from Sanchez-Martinez et al. (2020). This complete phylogeny is in collaboration with previous datasets (Dexter et al. 2017; Neves et al. 2020; Segovia et al. 2020), resolved to the genus level. All three datasets: phylogenetic, species distribution and mycorrhizal associations were integrated by matching the distribution of species to their respective genus, producing a final phylogeny of 438 genera tips, with a total of 1012 species distributions of both gymnosperms and angiosperms. The genera included in the combined dataset are not evenly distributed across woody species' families and orders (Figures S1 and S2), compared to the complete woody genera representation in the phylogeny by (Sanchez-Martinez et al. 2020). Some families, such as Fagaceae (order Fagales), are highly represented, while others, such as Ericaceae, are underrepresented. This uneven coverage reflects differences in sampling effort or ecological dominance and may introduce potential biases in the analyses.

2.2 | Phylogenetic Niche Conservatism

We assessed the phylogenetic niche conservatism of dual mycorrhizal hosts – the tendency of species to retain their ancestral association patterns – by quantifying the phylogenetic signal of mycorrhizal association traits using two distinct analytical methods. Initially, we applied the delta statistics (Borges et al. 2019), which evaluate the phylogenetic signal across the entire span of a phylogenetic tree for a set of discrete trait variables. This method uses a Bayesian approach similar to Shannon entropy, where a higher delta statistic (δ) indicates a stronger phylogenetic signal (e.g., a high tendency of closely related species to share the same mycorrhizal type associations). To determine the significance of this signal, we compared the observed delta statistic to a bootstrap null distribution, created by shuffling the trait vector at the tips of the phylogeny, thus obtaining a p -value.

Furthermore, we assessed each trait independently for a phylogenetic signal using the mean phylogenetic distance (MPD) approach (Webb et al. 2002). This metric calculates the average pairwise phylogenetic distance between all taxa sharing a particular trait. We normalised this distance by comparing it against a null model that assumes an equal-sized community under the same phylogenetic constraints. The normalisation process involved shuffling the trait vector at the tips of the phylogenetic tree to generate a standardised effect size of the mean phylogenetic distance (SES-MPD). A community structure yielding an SES-MPD value > 1.96 suggests phylogenetic overdispersion, whereas an SES-MPD value < -1.96 indicates phylogenetic clustering.

All analyses were carried out in R (version 4.4.2) (R Core Team 2018), using the libraries ape (5.8.1) (Paradis et al. 2004), phytools (2.4.4) (Revell 2012) and picante (1.8.2) (Kembel et al. 2010).

2.3 | Community Distribution Maps and Statistical Evaluation

We categorised each species' distribution across the 14 biomes defined by the World Wildlife Fund (WWF, <http://www.worldwildlife.org/>) and grouped them into four defined ecoregions: tropics, temperate, deserts and boreal/tundra. We used the biomes classification system as a proxy for ecological niche given its foundational role as a biodiversity delineator, particularly for woody species (Prentice et al. 1992; Olson et al. 2001). These ecoregions were delineated based on clusters derived from the extent of the WWF biomes.

To investigate the occupancy differences among mycorrhizal associating communities across various biomes and ecoregions, we systematically recorded the presence or absence of each genus within the 14 defined biomes. We conducted binomial regression models where the dependent variable was the mycorrhizal type classification for each genus (AM, EM or dual), and the independent variable was the presence (1) or absence (0) in a specific biome. This analysis allowed us to assess the relative likelihood of each community being present in a biome compared to the dual-association group, which served as the reference category in these models.

For the analyses concerning ecoregions, which aggregate multiple biomes, we employed Poisson regression models. These models were used to handle the count data, representing the total occurrences of each mycorrhizal type across all biomes constituting an ecoregion. In both the binomial and Poisson models, a positive regression coefficient for a community signifies a higher likelihood of presence in the biome or ecoregion relative to the dual-association group, whereas a negative coefficient indicates a lower likelihood. By utilising these regression frameworks, we aimed to quantify the distinct presence patterns of mycorrhizal associations, adjusting for the overarching influence of mycorrhizal type in structuring genus distribution across ecological landscapes.

To account for the non-independence of data points due to shared evolutionary histories amongst genera, the regression models were carried out using phylogenetic generalised least squares (PGLS) using the R package 'phylolm' (2.5.6) (Ho et al. 2016). This approach corrects for the phylogenetic signal, ensuring that our estimates of community differences in biome or ecoregion occupancy are not biased by phylogenetic relatedness. The inclusion of phylogenetic corrections enhances the robustness and ecological validity of our findings, providing insights that are phylogenetically informed.

In addition, we employed binomial generalised linear models (GLMs) and PGLMs to model the presence of each mycorrhizal association type within individual biomes (Figure S4). For each model, the dependent variable was the binary outcome representing the presence (1) or absence (0) of a mycorrhizal type in a particular biome. The independent variable for each model was the presence or absence of the same type across all other biomes, serving as a predictor of presence in the target biome. This relationship was captured using the regression formula $\text{presence}_{\text{biome}} \sim \text{type}_x$, where $\text{presence}_{\text{biome}}$ is the binary response for a specific biome, and type_x indicates the overall presence of the group across the biomes.

2.4 | Sensitivity Analysis to Data Uncertainty and Availability

To assess the impact of missing and unconfirmed data in our results, we conducted sensitivity analyses focusing on the pool of unidentified dual mycorrhizal-associating genera (Figures S1 and S2) (Werner et al. 2018; Teste et al. 2020). Given the likelihood that many dual mycorrhizal-associating species remain unidentified (Teste et al. 2020), we expanded the pool of the dual mycorrhizal type by including a dataset of unconfirmed dual-associating genera from Teste et al. (2020) and compared the results using this extended dataset with the original dataset. To investigate whether the observed effects of the extended dataset were driven by the mere increase in the dataset size or if they might reflect actual biological relevance, we performed a re-simulation analysis (Werner et al. 2018) (Appendix S1, Figures S1 and S2).

2.5 | Extent of Environmental Niches Between Mycorrhizal Types

To identify the climatic niche space of each mycorrhizal associated type, we utilised key bioclimatic attributes sourced from the WorldClim Global Climate Data. These variables, known to differentiate ecoregions (Whittaker 1970), particularly the latitudinal differences between tropical and temperate regions (O'Donnell and Ignizio 2012) include: mean annual temperature (MAT), mean annual precipitation (MAP), isothermality (ISO), mean diurnal range (MDR) and temperature annual range (TAR). These were accessed at a resolution of 5 arcminutes (Hijmans et al. 2005) and extracted using the 'raster' R package (3.6.31) (Hijmans et al. 2015). Additionally, we incorporated the most recent global dataset on plant-available phosphorus (McDowell et al. 2023), along with data on soil pH, soil organic carbon (SOC) and nitrogen (Poggio et al. 2021).

We determined the extent of each group's environmental niche space by extracting the set of environmental variables from global raster layers and overlapping these with the species distribution within each group, assessed using the species distribution polygons obtained from Lerner et al. (2023) (Figure 3b,c, Figures S4 and S5). A *t*-test was used to identify the significant difference in climate experienced by species within each mycorrhizal type.

In order to account for phylogenetic structure and assess the influence of phylogenetic signal on the distribution and extent of mycorrhizal types, we calculated the mean environmental variables experienced by each genus independently, based on the distribution of all species within that genus. These genus-specific environmental means were then utilised in simulation-based phylogenetic ANOVA models (Garland Jr. et al. 1993), implemented using the R package 'phytools' (2.4.4) (Revell 2012). This approach ensures that phylogenetic distances between genera are considered, effectively correcting for any phylogenetic signal and providing a more accurate representation of niche differentiation among the types.

3 | Results

From our unified dataset of phylogeny, geographic distributions and mycorrhizal strategies, 62% were associated with AM fungi,

10% with EM fungi and 28% had associations with both, AM and EM fungi (Figure 1a). We detected a significant phylogenetic signal for the mycorrhizal states across all genera using the delta statistic, ($\delta=25.7$, *p*-value < 0.05), suggesting that species have conserved their mycorrhizal associations throughout evolution. However, this strong phylogenetic clustering was predominantly attributed to genera with AM associations (Figure 1b). The distribution of genera with dual or EM mycorrhizal associations exhibited non-random patterns and significant over-dispersion, respectively, as assessed by the Mean Pairwise Distance (MPD) within each group type. These results suggest that while a general phylogenetic signal is present in relation to the mycorrhizal association strategy, it is specifically driven by the AM-associated genera, implying the weak evolutionary bound strategy of EM or dual associations.

We confirmed a pronounced latitudinal partitioning of EM and AM host species, characterised by the low presence of EM species in lower-latitude tropical regions and a scarcity of AM host species in the highest-latitude temperate regions, particularly in Eurasia (Figure 2a). Dual mycorrhizal host woody species showed a more extensive distribution than either AM or EM hosts, given their presence in lower and higher latitudes, as well as a strong notable presence in Australia. Typical examples of dual trees in Australia are species from the genera *Eucalyptus* and *Acacia* (Teste et al. 2020). We found that species with dual mycorrhiza associations have a broader geographic range than those associated exclusively with AM or EM, given the significantly greater presence across multiple biomes (Figure 2b). We identified the global distribution of dual-species more closely resembles that of AM species (Figure 2a). However, these species also exhibit a higher congruence with EM species in the desert ecoregion, which is the only ecoregion where EM species do not exhibit a significantly lower presence compared to dual species (Figure 2b). In addition, dual mycorrhizal species were the only type to show a notable likelihood of presence in the desert biomes, as indicated by the positive odds ratio (Figure S3), although this finding was not statistically significant.

We used a more extensive list of woody species suspected as dual mycorrhizal hosts and simulations to test the sensitivity of our findings. The inclusion of an unconfirmed dataset of dual mycorrhizal genera (Figures S1 and S2) yielded highly consistent results in comparison to the confirmed dataset analysis (Figure 2b)—dual mycorrhizal species exhibited a broader geographic range compared to both AM and EM species globally and across most ecoregions. Notable exceptions included a significantly higher presence of dual-species in desert ecoregions, contrasting with a significantly lower presence in boreal ecoregions. To validate these findings, we conducted bootstrap simulations that tested the robustness of the original dataset. In addition, we assessed whether differences between the original and unconfirmed datasets were driven solely by increased species pool size or by meaningful dual associations. The output from the simulations closely matched the original dataset results (Figure S3), indicating the robustness of our conclusions to the uncertainty of missing data of dual types. However, there were notable differences between the simulations and the extended unconfirmed datasets. For example, adding unconfirmed genera significantly increased the presence of dual-associating species in the desert ecoregion, while simulations reduced this pattern (Figure S3), particularly in comparison to EM-associating species. This suggests that the addition of the unconfirmed dataset

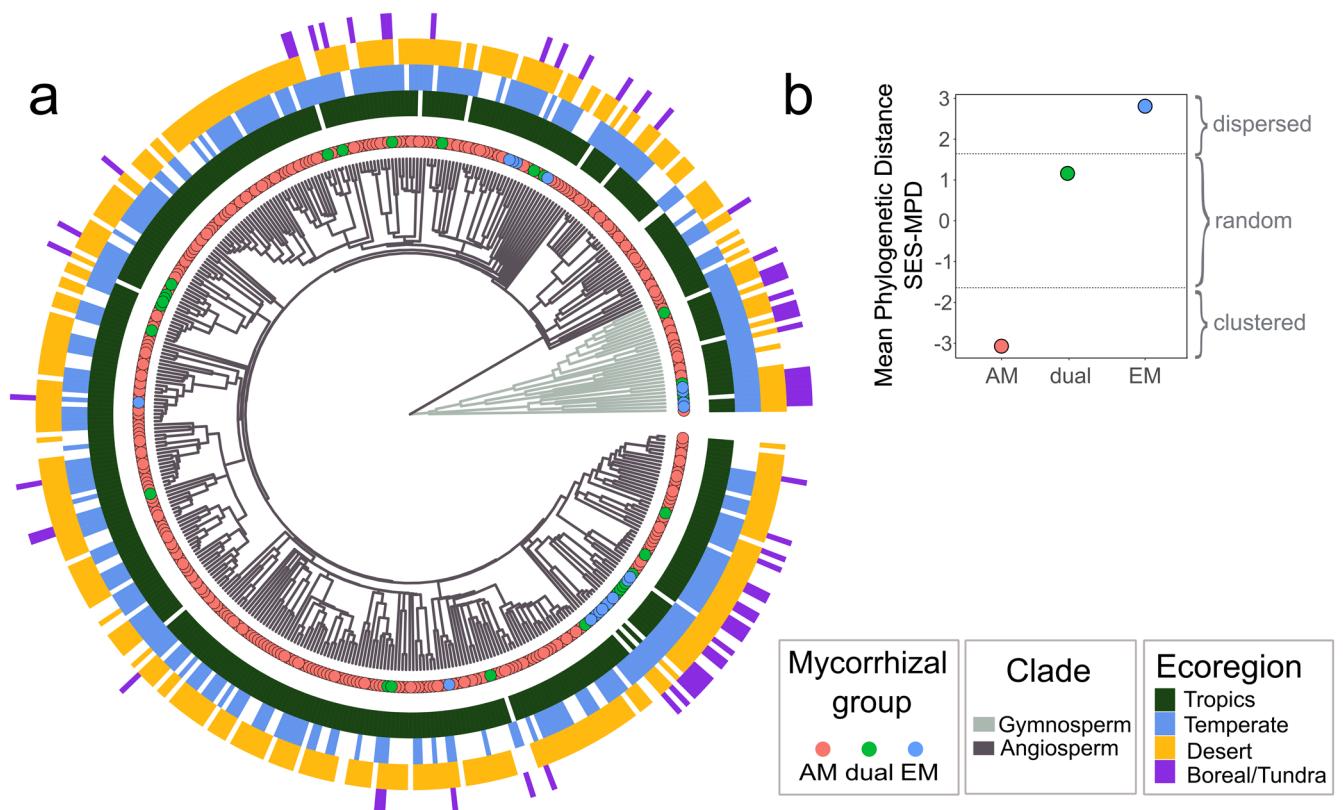


FIGURE 1 | Phylogenetic, geographical and mycorrhizal relation of 413 woody genera. (a) The phylogenetic tree nodes are shaded to differentiate between the gymnosperm and angiosperm clades. The tips are coloured to represent the mycorrhizal association types (EM, AM and dual). The outer rings indicate the presence or absence (colour or white) of each genus tip on each of the four defined ecoregions; Tropics, Temperate, Desert and Boreal/Tundra. These ecoregions were obtained by combining the 14 biomes defined by the World Wildlife Fund into one of the four categories. (b) A scatter plot showing the SES-Mean Phylogenetic Distance (MPD) Z-scores (Webb et al. 2002), a metric used for measuring phylogenetic signal between a trait of interest (association to mycorrhizal type) and the phylogeny. SES-MPD Z-scores < -1.96 have a significant phylogenetic clustering and SES-MPD Z-score > 1.96 have significant phylogenetic over-dispersal. Tropical ecoregion included: (1) Tropical and subtropical moist broadleaf forest, (2) Tropical and subtropical dry broadleaf forest, (3) Tropical and subtropical coniferous forest, (4) Tropical and subtropical grasslands, savannas and shrublands, (5) Flooded grasslands and savannas and, (6) Mangrove biomes. Temperate ecoregion included: (1) Temperate broadleaf and mixed forests, (2) Temperate coniferous forests, (3) Temperate grasslands, savannas and shrublands, (4) Montane grasslands and shrublands, (5) Mediterranean forests, woodlands and scrub. Desert ecoregion is constituted uniquely of the Desert biome. Boreal/Tundra ecoregion included: (1) Boreal forests/taiga and (2) Tundra biome.

produces results that are not merely statistical artefacts caused by altered sample size, but instead, reflect the inclusion of genera that possibly form dual mycorrhization.

Dual mycorrhiza species experience a broader range of climates and edaphic factors in comparison to species associated with single mycorrhiza types, as shown by the calculated environmental range, which reflects the breadth of individual climatic and edaphic variables experienced across species' distributions (Figure 3a, Figure S4). This expanded environmental range of dual-species is independent of phylogenetic relationships (Figure S5). To examine how climatic and edaphic variables collectively shape the environmental space of each mycorrhizal type, we plotted their environmental niche space using PCA. Dual species exhibited an evident expanded niche space relative to EM species, with greater overlap with the niche space of AM species compared to the overlap between EM and AM species (Figure 3b). This positions dual species at an interface between AM and EM niche spaces. This interface was further supported by the extent of environmental variables associated

with the different mycorrhizal types, calculated as the mean of the climatic and edaphic conditions experienced across species' distributions. The extent of environmental variables of dual-species consistently fell between those of AM and EM species (Figure S6). This pattern was consistent across all climatic variables except for MAP and MDR, where dual species exhibited lower MAP and higher MDR extents compared to both AM and EM species. The MAP and MAT values for each genus exhibited signs of evolutionary convergence, as reflected by a Blomberg's K value < 1 ($K = 0.69$ for temperature and $K = 0.14$ for precipitation), indicating that the niche expansion of dual-species is not led by evolutionary conservatism, but rather, by the ecological effects of mycorrhizal associations. The edaphic factors phosphorus availability, SOC and nitrogen levels were intermediate between those observed in single type associations, while soil pH was higher in dual-species compared to both AM and EM species (Figure S6, Figure 3b). This trend likely reflects the predominant presence of dual-species in desert biomes, which are characterised by alkaline soil conditions compared to the acidic soils typical of tropical and temperate regions (Figure 3c).

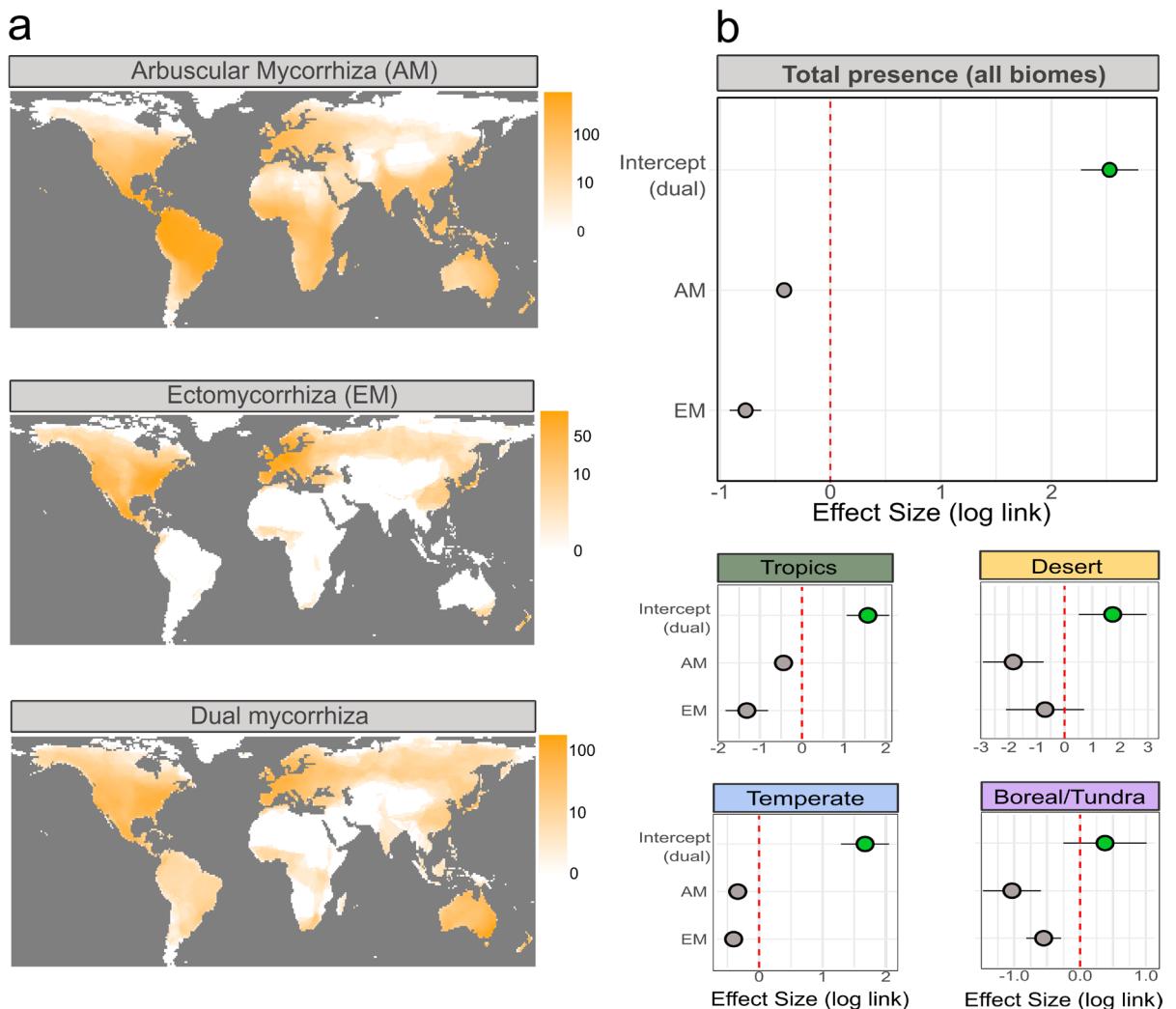


FIGURE 2 | Global distribution of different mycorrhiza host types. (a) Geographical distribution of the species confirmed to associate with either arbuscular mycorrhizal fungi (AM), ectomycorrhizal fungi (EM) or both with AM and EM fungi (Dual). The intensity of the colour represents the number of species present in each of the pixels. (b) Forest plots showing the relative presence of each mycorrhiza-associating type globally and within each ecoregion independently, obtained from a phylogenetically corrected Poisson regression (phylogenetically corrected binomial regression for Desert Ecoregion). The effect size measures the likelihood of the presence of a mycorrhizal association type in an ecoregion. The dual mycorrhizal (intercept) effect size represents the baseline presence, whilst AM and EM effect sizes are relative to the reference group. 95% confidence intervals are shown. Tropical ecoregion included: (1) Tropical and subtropical moist broadleaf forest, (2) Tropical and subtropical dry broadleaf forest, (3) Tropical and subtropical coniferous forest, (4) Tropical and subtropical grasslands, savannas and shrublands, (5) Flooded grasslands and savannas and, (6) Mangrove biomes. Temperate ecoregion included: (1) Temperate broadleaf and mixed forests, (2) Temperate coniferous forests, (3) Temperate grasslands, savannas and shrublands, (4) Montane grasslands and shrublands, (5) Mediterranean forests, woodlands and scrub. Desert ecoregion is constituted uniquely of the Desert biome. Boreal/Tundra ecoregion included: (1) Boreal forests/taiga and (2) Tundra biome.

4 | Discussion

Abiotic factors influence the global distribution of mycorrhizal host plants (AM and EM) (Steidinger et al. 2019), raising the possibility that dual associations with both mycorrhizal types may enhance species' distribution range and environmental niche space. Using global datasets on mycorrhizal types, plant phylogeny and species distributions, we show an increased geographical range and environmental niche space of woody genera associating with dual mycorrhizal types compared to those with single associations. Despite traditional views of mycorrhizal specialisation, this study suggests that dual associations serve as an adaptive strategy to diverse environmental conditions.

The strong phylogenetic clustering of mycorrhizal associations at the genus level was primarily driven by evolutionary relationships among AM-associating genera (Figure 1). Even after accounting for phylogenetic distances, dual associations were more prevalent than either AM or EM species across most ecoregions (except for the boreal/tundra ecoregion) (Figure 2b) and had a greater environmental niche space than AM and EM species (Figure 3a,b, Figure S5), suggesting that the dual mycorrhiza associations could represent an adaptive mechanism for woody species to an increased geographical and environmental space. The presence of dual-species was particularly characteristic in desert regions, which lie in the interface between AM-dominated tropical ecoregions and EM-dominated

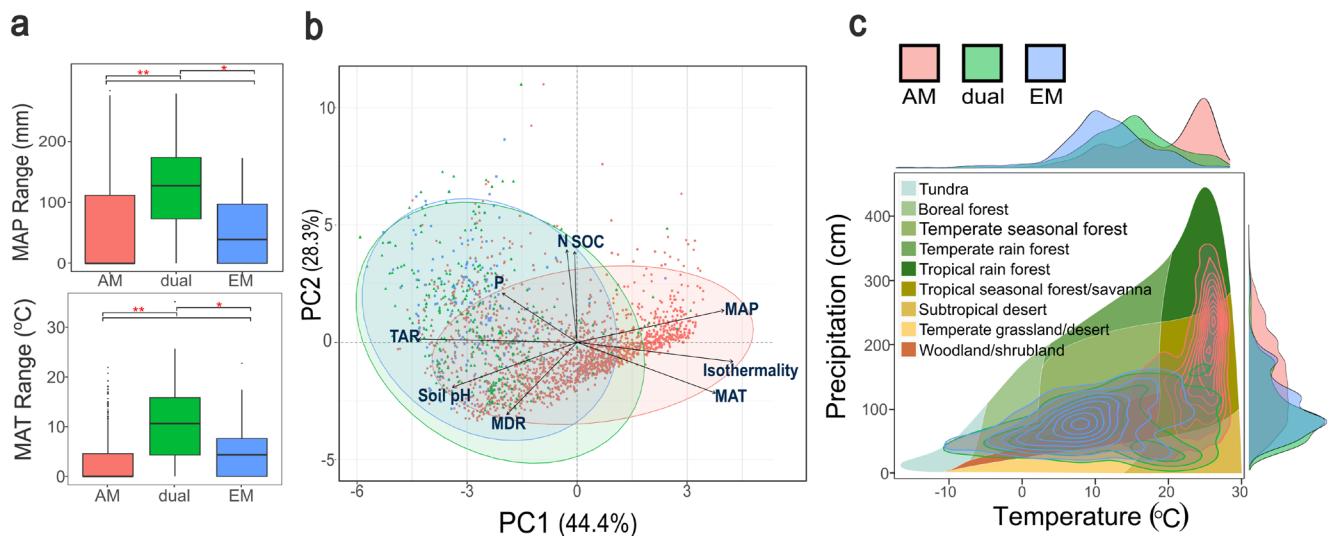


FIGURE 3 | Environmental space of EM, AM and dual mycorrhizal hosts. (a) Boxplot showing the climatic range of genera given their mycorrhizal associations. Post hoc significant differences from a phylogenetically-corrected, simulation-based ANOVA analysis (Garland Jr. et al. 1993) are shown with an asterisk (** for $p < 0.01$ and * for $p < 0.05$). (b) Principle component analysis (PCA) to represent the environmental niche of EM, AM and dual hosts. Climatic and edaphic variables: MAP, Mean Annual Precipitation; MAT, Mean Annual Temperature; MDR, Mean Diurnal Range; N, Soil Nitrogen; P, Olsen Phosphorous; SOC, Soil Organic Carbon; TAR, Temperature Annual Range. Host types are colour coded red blue and green for AM, EM and dual-hosts, respectively. (c) 2-dimensional kernel density plots of the mean annual temperatures (MAT) and mean annual precipitations (MAP) experienced by the different host species, overlayed onto a Whittaker Biome plot. Distribution of confirmed dual-mycorrhizal hosts woody genera have a significant preference to lower mean annual precipitations area compared to arbuscular host (AM) ($p < 0.001$) and ectomycorrhizal host (EM) ($p = 0.04$), and intermediate mean annual temperatures, between AM-host ($p < 0.001$) and EM-host ($p < 0.001$).

temperate regions (Figure 2a, Figure S3). Thus, dual-species experience lower mean MAPs than AM and EM-associating species (Figure 2c and Figure S6).

The low phylogenetic clustering of EM and dual mycorrhiza associating genera contrasts with previous findings (Meng et al. 2023). The discrepancy may stem from differences in the resolution of the phylogenetic analyses used: our study employed a phylogenetic tree at the genus level, exclusively focusing on woody species, rather than encompassing all the flora at the species resolution. This suggests that while species within the same genus may have evolved with similar mycorrhizal associations, it remains possible that these associations evolved independently (Brundrett and Tedersoo 2018). Such a phenomenon is suggestive of fast adaptations, a mechanism developed mainly by woody species due to their longer life cycle compared to annuals (Xie et al. 2023). This can also be explained by the evolutionary succession of EM associations from the previously evolved AM, as EM mycorrhizal species could have undergone specific evolutionary changes with particular hosts to enable expansion to novel conditions (Hoeksema and Thompson 2007). This model could thus explain dual mycorrhization to be an intermediate status in the evolution towards EM from AM host specificity. Therefore, it makes sense that dual species are the result of a transition phase from AM to EM associations. The retention of such a transition phase could be more pronounced at the interface between regions dominated by either AM or EM species, such as in poor-phosphorus, arid regions—i.e., deserts, rather than high latitude N-limited soils—i.e., boreal regions (Figure 2b, Figure S3) (Brundrett and Tedersoo 2018). Dual associations may therefore serve as an adaptive strategy enabling hosts to colonise nutrient-limited niches and endure harsher climates.

Both EM and AM colonisation of plant roots have been shown to increase host nutrient uptake (Smith and Read 2010). However, the beneficial effect of simultaneous colonisation by the two mycorrhizal types is not well understood. Analysing the available edaphic factors for the plants (i.e., plant-available phosphorus) (McDowell et al. 2023), reveals that woody species capable of dual colonisation are distributed in areas with lower phosphorus availability compared to woody species that have exclusive associations with EM mycorrhiza (Figure S6). The possible benefits of dual-mycorrhizal status are the complementarity in nutrient acquisition and a greater ability to take over a more extensive soil depth profile and soil properties (Teste et al. 2020; Luo et al. 2023). While AM hyphae uptake nutrients predominantly in mineral form, i.e., ‘scavenging’ (Lambers et al. 2008), EM hyphae are also able to exudate enzymes and organic acids that enable the alteration of nutrients to their mineral form (Plassard and Dell 2010). In addition, other factors, such as mycorrhizal-associated microbes (Zhang et al. 2016, 2024), nitrogen availability and soil pH might influence the dual mycorrhization interaction and nutrient uptake (Teste et al. 2020). Overall, our findings support the role of mycorrhiza association in plant nutrient uptake strategies (Crowther et al. 2019; Anthony et al. 2022) and indicate that dual mycorrhizal woody species have an expanded niche space.

Trees can also benefit from dual-mycorrhizal associations along a soil moisture gradient. Trees with dual mycorrhiza association benefit from spatial partitioning of roots in different soil depths and improved water uptake (Neville et al. 2002). We show that the distribution of dual hosts is significantly more pronounced in drier areas than AM and EM host species, given the lower MAP of dual species (Figure 3, Figure S5). Our conclusions are in agreement with studies at regional scales, where

water availability appeared to explain well the association of the known dual-mycorrhizal hosts, *Populus*, with EM rather than AM species (Karst et al. 2021). Likewise, Rog et al. (2021) suggested that, given the deeper root system of EM-hosts in Mediterranean forests, the unexpected dual host associations of the shallower AM-hosts could benefit from connecting to the EM network, and by doing so, enlarging their niche space. This trend is nonetheless bound to exceptions, given cases where AM associating plants have been shown to colonise drier biomes as well (Worochel et al. 2013). Other studies testing dual hosts under post-drought conditions found that AM fungal spores are more tolerant than EM, leading to the higher presence of AM mycorrhiza species in drier regions (Kilpeläinen et al. 2017). Our findings at a global scale, together with regional-scale evidence, indicate a higher prevalence of dual host species in arid regions.

The observations from this study are based on a large, but still limited list of confirmed dual host species (Teste et al. 2020). Overall, our mycorrhizal association data include genera representing more than 70% of the families and 80% of the orders in the woody phylogenetic tree database (Figures S1 and S2). Approximately 40 woody species' families and 10 orders are entirely absent from both the confirmed and unconfirmed lists (Teste et al. 2020), highlighting a significant gap that warrants attention in global surveys. Furthermore, another possible limitation could arise as a result of conducting the study at the genus level, as we assume that all species within a genus are capable of forming these interactions, which may increase the potential for false positives. Nonetheless, the strong phylogenetic niche conservatism observed for mycorrhizal association types in plant species (especially for EM and dual associations) suggests that species from the same genera will tend to share the same mycorrhizal type. The level of misclassification errors has shown to be lower at the genera level in comparison to the family level (Bueno et al. 2019). This generalisation from the species to the genus has been used for individual groups of mycorrhizal association and non-mycorrhizal hosts (Soudzilovskaia et al. 2020; Teste et al. 2020). However, more research is required to confirm the strong phylogenetic conservatism of dual hosts for species from the same genera.

Identifying mycorrhizal associations, specifically dual associations, requires complex diagnostic criteria, which can sometimes lead to misidentifications. The interaction between roots and fungi is not limited to symbiotic nutrient exchange, as fungal hyphae can access the roots without forming a classical mycorrhizal interaction (Wang et al. 2021), or can even develop parasitic interactions (Johnson et al. 1997; Hoeksema et al. 2010). Moreover, not all nutrient exchange takes place at typical and recognised structures, such as arbuscules for AM associations (Dickson 2004; Manjarrez et al. 2010), and the Hartig net for EM associations (Sa et al. 2019). In addition, the degree of nutrient exchange and the symbiotic relationship may fluctuate independently of the structures used for mycorrhizal trait criteria (Bueno et al. 2019). Therefore, these associations require a more nuanced categorisation strategy than the simplistic binary system of single versus dual statuses used here. As a result of the high variability and complexity, part of the mycorrhizal association dataset used here may contain misdiagnosis of the morphological fungal criteria and misinterpretation of the plant

mycorrhizal status (Brundrett and Tedersoo 2019). However, our analysis shows that the unconfirmed group of dual mycorrhizal types reported in Teste et al. (2020), which did not meet all the criteria in their study, exhibits similar geographical patterns and trends to the confirmed group when compared to a random group (Figure S4). Thus, the conclusions of our study are also valid when a more stringent dataset is used to test our hypotheses.

While global data analyses have inherent limitations, they enable us to identify broad trends. Our results highlight the unique niche expansion of dual mycorrhizal hosts compared to single mycorrhizal types (AM and EM) by focusing on their direct comparison. Specifically, dual mycorrhizal associations appear to facilitate the colonisation of low-nutrient and dry environments, such as deserts, expanding the geographic and environmental range of woody species. Plant species may associate exclusively with AM or EM in one region but develop dual-mycorrhizal relationships in another. However, our dataset lacks the spatial resolution needed to make such distinctions. These findings challenge the traditional view that dual-mycorrhizal species are uncommon (Lodge 2000) and suggest an adaptive strategy that allows plants to thrive in resource-limited and harsh climates.

Understanding the ecological role of dual mycorrhizal associations is especially important in the context of global climate change (Terrer et al. 2016; Hawkins et al. 2023). Future studies should explore other plant-microbe interactions, such as those involving N-fixing plants, ericoid or orchid mycorrhiza and non-mycorrhizal hosts, to better understand adaptations in resource-limited environments. Additionally, higher-resolution research is needed to investigate regional distribution patterns and classify dual species into functional types, as well as to uncover the mechanisms driving their environmental niche expansion. Upon an expanded and better-characterised dataset of dual-mycorrhizal hosts, further analyses of the evolutionary pathways leading to the emergence of dual mycorrhizal associations should be conducted.

Author Contributions

Ido Rog conceived the research further developed with David Lerner. David Lerner performed the analyses. Ido Rog and David Lerner drafted the manuscript, with contributions from all co-authors.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in Zenodo at <https://zenodo.org/records/15193559>, reference number 15193559.

Peer Review

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.