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Summary

- It is well-known that the mycorrhizal type of plants correlates with different modes of nutrient cycling and availability. However, the differences in drought tolerance between arbuscular mycorrhizal (AM) and ectomycorrhizal (EcM) plants remains poorly characterized.
- We synthesized a global dataset of four hydraulic traits associated with drought tolerance of 1457 woody species (1139 AM and 318 EcM species) at 308 field sites. We compared these traits between AM and EcM species, with evolutionary history (i.e. angiosperms vs gymnosperms), water availability (i.e. aridity index) and biomes considered as additional factors.
- Overall, we found that evolutionary history and biogeography influenced differences in hydraulic traits between mycorrhizal types. Specifically, we found that (1) AM angiosperms are less drought-tolerant than EcM angiosperms in wet regions or biomes, but AM gymnosperms are more drought-tolerant than EcM gymnosperms in dry regions or biomes, and (2) in both angiosperms and gymnosperms, variation in hydraulic traits as well as their sensitivity to water availability were higher in AM species than in EcM species.
- Our results suggest that global shifts in water availability (especially drought) may alter the biogeographic distribution and abundance of AM and EcM plants, with consequences for ecosystem element cycling and ultimately, the land carbon sink.

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Received: 5 March 2024
Accepted: 14 August 2024

New Phytologist (2024) **244**: 2024–2035
doi: 10.1111/nph.20097

Key words: climate change, drought stress, mycorrhizal associations, plant hydraulics, species distribution.

Introduction

The global distributions of plant mycorrhizal types have long intrigued plant and mycorrhizal ecologists (Read, 1991), yet the factors that give rise to these patterns are incompletely understood. Arbuscular mycorrhizal (AM) trees tend to be dominant in low-latitude regions with high precipitation and high temperature (e.g. tropical rain forests), whereas ectomycorrhizal (EcM) trees tend to be dominant in high-latitude regions with low precipitation and low temperature (e.g. temperate seasonal forests and boreal forests) as well as in tropical savannah and dry forests (Steidinger *et al.*, 2019), such as Asian Dipterocarp forests (Brearley *et al.*, 2017; Primack, 2017). Given observed differences in nutrient use strategies between AM and EcM trees and fungi (Smith & Smith, 2011; Kumar & Atri, 2018; Averill *et al.*, 2019), the disparity in distributions of mycorrhizal types has been attributed to climate-regulated variation in decomposition rates

(Steidinger *et al.*, 2019). In AM-dominated forests, high temperature and high precipitation lead to fast decay of litter and an inorganic nutrient economy where inorganic nutrient assimilation by scavenging AM hyphae and roots predominate (Smith & Smith, 2011). In EcM-dominated forests, low temperature, low precipitation or seasonal drought leads to slow decay of litter and an organic nutrient economy where assimilation of organically bound nutrients occurs via EcM mycelium and roots (Kumar & Atri, 2018). However, higher water stress in EcM-dominated forests than AM-dominated forests suggest that differences in drought tolerance between AM and EcM trees may contribute to the biogeographic patterns. Using forest inventory data from the eastern United States, Jo *et al.* (2019) reported that decadal shifts in the relative abundances of AM and EcM trees depended, in part, on changes in mean annual precipitation over the same time interval supporting the idea that AM and EcM trees may differ in their sensitivities to water stress. Given increases in the frequency

and intensity of droughts globally, mycorrhizal type differences in drought tolerance could affect forest composition, with consequences for regional and global carbon (C) cycling.

Both AM and EcM fungi can access water in soil microsites via their small diameter hyphae, which extend the rooting zone and alter soil structure to increase soil water retention (Auge, 2001; Allen, 2007; Lehto & Zwiazek, 2011). AM fungi can supply substantial amounts of water to their host plants (Kakouridis *et al.*, 2022; Wu *et al.*, 2024) and their hyphae water absorption rates increased several folds under drought stress (Zhang *et al.*, 2018), thus improving plant water status (Abdalla *et al.*, 2023). Ectomycorrhiza fungi can also improve plant water status by developing massive extraradical mycelia that transport water to host plants (Allen, 2007) and by promoting lateral root development that increases fine-root surface area (Nardini *et al.*, 2000; Felten *et al.*, 2009), although the mycelial mantles formed around root tips by EcM fungi were found to reduce the hydraulic conductance of roots (Nardini *et al.*, 2000; Korhonen *et al.*, 2019). Furthermore, AM and EcM fungi could modulate the expression of root aquaporins under drought to improve root water conductivity (Marjanovic *et al.*, 2005; Quiroga *et al.*, 2019) and activate the antioxidant system of plants to reduce damage of plant cells (He *et al.*, 2020; Yin *et al.*, 2021). These adaptations help both AM and EcM plants tolerate and survive drought (Lehto & Zwiazek, 2011; Phillips *et al.*, 2016), and there is also indication that mycorrhizal symbioses played a key role in the evolution of plant adaptation to drought (Cosme, 2023). However, how AM and EcM symbioses differ in enhancing drought tolerance and promoting the evolution of plant adaptation to drought remains unknown. Previous studies suggest that AM and EcM woody plants may differ in their putative drought tolerance (Phillips *et al.*, 2016; Teste *et al.*, 2020), but a limitation is that synthetic assessments spanning broad climatic gradients, biomes or different evolutionary histories (gymnosperms vs angiosperms) are rare.

AM woody plants exhibit higher foliar N and P concentrations and higher photosynthetic rates than EcM woody plants at the global scale (Averill *et al.*, 2019; Shi *et al.*, 2020). Thus, it may be expected that AM woody plants are generally less drought-tolerant than EcM woody plants, as species that are more resource acquisitive (e.g. for nutrients and CO₂) tend to be more water demanding and hence, less tolerant of drought (Zhu *et al.*, 2013; Reich, 2014). However, this pattern may be occurred only in wet regions, as some AM woody plants were also found in severely water-limited areas where few EcM plants occur (Teder-soo, 2017; Teder-soo & Bahram, 2019). For example, in Kuwait, there exist only one native tree species in the desert ecosystem – *Acacia gerrardii* which forms AM associations (Loutfy & Modhi, 1994; Suleiman *et al.*, 2019). This suggests that the drought tolerance of AM woody plants may be comparable to or even surpass that of EcM woody plants in dry regions. Previous studies on the disparity in drought tolerance between AM and EcM woody plants were rare in very wet or dry ecosystems and primarily focused on temperate forests with moderate water availability, yielding inconclusive findings. Ectomycorrhiza-associated oaks (*Quercus*), an ecologically dominant genus across the eastern

United States, were reported to have a better growth performance than other trees during drought (Brzostek *et al.*, 2014; Novick *et al.*, 2022), but have a higher mortality caused by hydraulic failure than other trees in the forests during prolonged drought stresses (Novick *et al.*, 2022). Furthermore, experiments conducted for eight major Central European deciduous tree species revealed that AM trees exhibited higher drought tolerance than EcM trees, that is less drought-induced decreasing in fine-root lifespan (Liese *et al.*, 2019) and less loss of plant photosynthates by root exudation during drought (Liese *et al.*, 2018). Studies of dual-mycorrhizal plants reported that *Alnus incana* seedlings inoculated with AM fungi kept a higher water potential and survived longer than those inoculated with EcM fungi during drought (Kilpelainen *et al.*, 2020). Although most studies support that AM woody plants are more drought-tolerant than EcM plants in temperate regions, it is more likely to be a mixed pattern. To gain a more comprehensive understanding of the disparities in drought tolerance between AM and EcM plants at the global scale, it is imperative to take into account broad climatic gradients and biomes, across which distinct patterns may potentially emerge.

Woody plants are commonly grouped by their evolutionary history (e.g. gymnosperms vs angiosperms), as the two groups evolved opposite strategies. Compared to gymnosperms, angiosperms tend to adopt fast economic strategy with higher leaf nitrogen content (Diaz *et al.*, 2016) and greater photosynthetic rates (Brodrick & Feild, 2010), which promotes the flourish of angiosperms. Thus, the pattern that AM woody plants possess more efficient access to resources with lower drought tolerance than EcM woody plants is more likely to be found in angiosperms rather than in gymnosperms. Gymnosperms possess much higher drought tolerance (i.e. higher xylem resistance to embolism) than angiosperms (Choat *et al.*, 2012; Sanchez-Martinez *et al.*, 2020), and it might have been particularly important for gymnosperms to improve drought tolerance in early terrestrial ecosystems. For example, under Cenozoic climate change, that is the expansion of increasingly arid habitats, most Cupressaceae species (AM-associated) evolved high-drought tolerance (Pittermann *et al.*, 2012). Evolutionary analysis of plant hydraulic traits showed that AM-associated Cupressaceae species generally had higher xylem resistance to embolism than EcM-associated Pinaceae species (Maherali *et al.*, 2004; Sanchez-Martinez *et al.*, 2020). If such pattern holds true for other species of these two families and across other lineages, AM gymnosperms may be more drought-tolerant than EcM gymnosperms.

Another limitation of previous studies of differences between mycorrhizal types is that drought tolerance has been defined by plant growth performance or mortality during drought, but do not take hydraulic failure into consideration. Hydraulic failure, that is functional disruption of the plant water transport system, is a major cause of plant death during drought (McDowell *et al.*, 2008; Powers *et al.*, 2020), and some key hydraulic traits are found to be closely associated with the drought tolerance of plants (Choat *et al.*, 2012; Powell *et al.*, 2017; Blackman *et al.*, 2023). Leaf hydraulic traits are mainly related to leaf physiology, which affect the growth performance of plants during mild

Table 1 Descriptions of four hydraulic traits used in this study.

| Traits | Symbols | Meanings |
|---|------------------|--|
| Leaf water potential at 50% loss of leaf hydraulic conductance | P_{50_leaf} | Plants with a more negative P_{50_leaf} show a higher ability to maintain water transport within leaf, which allows plants to keep stomates open and thus sustain photosynthetic rates during drought (Brodribb & Holbrook, 2003; Bartlett <i>et al.</i> , 2016; Trueba <i>et al.</i> , 2019) |
| Leaf water potential at turgor loss point | TLP | Plants with a more negative TLP are less susceptible to wilt during drought, thus keep the normal physiological functions of the leaves (Bartlett <i>et al.</i> , 2014; Zhu <i>et al.</i> , 2018) |
| Branch water potential at 50% loss of branch hydraulic conductivity | P_{50_branch} | Plants with a more negative P_{50_branch} have higher resistance to embolism in xylem, which reduces the risk of death caused by hydraulic failure during drought (Sperry, 2011; Jacobsen <i>et al.</i> , 2012; Wang <i>et al.</i> , 2023) |
| Xylem vessel/tracheid diameter | D | D is one of the structural traits that reflect the ability of xylem resist embolization, and the narrower D , the less likely it is to be embolized (Sperry, 2011; Jacobsen <i>et al.</i> , 2012; Schuldts <i>et al.</i> , 2016) |

drought, while branch hydraulic traits are mainly related to the risk of plant death caused by hydraulic failure during severe drought (Table 1). Hydraulic traits are thus extensively employed for predicting the drought tolerance of plants, that is drought-induced mortality (Anderegg *et al.*, 2016; Sanchez-Martinez *et al.*, 2023; Torres-Ruiz *et al.*, 2023) or mortality thresholds (Hammond *et al.*, 2019; Liang *et al.*, 2021). Therefore, global pattern of differences in drought tolerance between AM and EcM plants can be understood by comparing their hydraulic traits. Given that no single hydraulic trait captures the many ways that plants can respond to drought, differences in drought tolerance between AM and EcM woody plants are best assessed by considering leaf and branch hydraulic traits simultaneously.

In this study, we compiled a global dataset of leaf and branch hydraulic traits (Table 1) associated with plant drought tolerance of 1457 woody species with a total of 2069 species-by-site combinations (Supporting Information Table S1). First, we tested differences in hydraulic traits between AM and EcM woody species with evolutionary histories (i.e. angiosperms and gymnosperms), water availability (i.e. aridity index) and biomes being considered. Second, we compared ranges, interspecific variation and intraspecific variation of hydraulic traits as well as their sensitivity to water availability between AM and EcM angiosperms and gymnosperms. Phylogenetic patterns in plant hydraulic traits were weak in the tropics (Vargas *et al.*, 2022), but significant at a global scale (Sanchez-Martinez *et al.*, 2020). As mycorrhizal associations are also phylogenetically structured (Averill *et al.*, 2019), we accounted for plant phylogeny as part of our synthesis.

Materials and Methods

Data collection

We compiled a global dataset (Table S1) of four hydraulic traits associated with drought tolerance from original reports and our own measurements, including leaf water potential at 50% loss of leaf hydraulic conductance (P_{50_leaf}), leaf water potential at turgor loss point (TLP), branch water potential at 50% loss of branch hydraulic conductivity (P_{50_branch}) and xylem vessel/tracheid diameter (D). All data were collected from woody plants

(juvenile and adult trees but no seedlings) growing in natural ecosystems (excluding glasshouse and garden experiments). A limitation of this database was the lack of data on leaf related traits for gymnosperms. We focused on woody plants because ectomycorrhiza are rare in herbaceous plants (Brundrett, 2009). We classified woody species as arbuscular mycorrhizal (AM) or ectomycorrhizal (EcM, including dual-mycorrhizal plants, that is AM-EcM) using a taxonomically informed approach (Steidinger *et al.*, 2019) or according to original reports of mycorrhizal identification. The AM-EcM plants were classified as EcM plants as they increasingly form EcM in adult stages (Teste *et al.*, 2020).

An aridity index (AI) was defined as the ratio of annual precipitation to annual potential evapotranspiration, with higher values indicating more humid. AI, mean annual precipitation (MAP) and mean annual temperature (MAT) were extracted from the CGIAR-CSI consortium (<http://www.cgiar-csi.org/data>; Zomer *et al.*, 2008). Sampling sites were assigned to three humidity gradients based on AI: semiarid and arid ($AI < 0.5$), subhumid ($0.5 \leq AI < 1$) and humid ($AI \geq 1$) (Gao & Giorgi, 2008). In addition, sampling sites were assigned to seven biomes according to specific descriptions and previous criteria of each site (Choat *et al.*, 2012): desert (DES), semiarid woodland and shrubland (WDS), temperate seasonal forest (TMS), boreal forest (BOR), tropical/subtropical seasonal forest (TRS, including tropical and subtropical savanna), tropical rainforest (TRR) and temperate rainforest (TMR) with increasing humidity conditions (Fig. S1).

We collected 1457 woody species (1350 angiosperm species and 107 gymnosperm species), including 1139 AM plant species (132 families and 570 genera) and 318 EcM plant species (21 families and 75 genera) at 308 field sites world-wide, with a total of 2069 species-by-site combinations (Table S1). Ectomycorrhiza angiosperms were mainly found in a few families such as Salicaceae, Fabaceae, Rosaceae, Myrtaceae, Dipterocarpaceae, Ericaceae and the Fagales families (i.e. Fagaceae, Betulaceae, and Nothofagaceae) (Fig. 1a). All the primary families associated with EcM fungi (Brundrett & Tedersoo, 2018) were included in our database. AM gymnosperms were mainly found in Cupressaceae, and EcM gymnosperms were mainly found in Pinaceae (Fig. 1a). Thus, there appeared to be a strong phylogenetic signal in mycorrhizal types that needed to be taken into account in subsequent trait

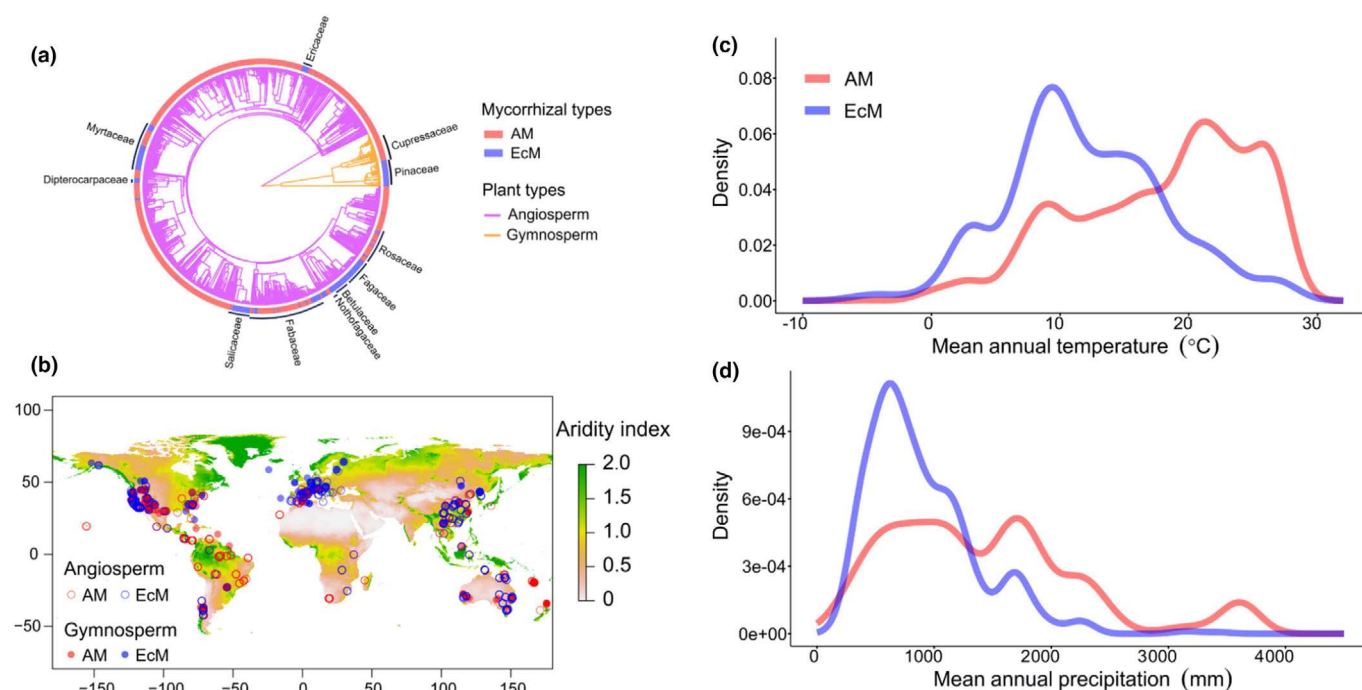


Fig. 1 Phylogeny (a), sample sites (b) and distributions of temperature and precipitation at the sampling sites (c, d) of the plant species used in this study. Mycorrhizal types include arbuscular mycorrhiza (AM) and ectomycorrhiza (EcM). Aridity index (AI) was defined by the ratio of annual precipitation to annual potential evapotranspiration, where higher values indicating more humid. The values of AI > 2 were set to 2.

comparisons. The 308 sample sites were distributed globally with varied humidity conditions across biomes, that is aridity index (AI) ranging from 0.08 to 3.92 (Figs 1b, S1). Most AM plants were distributed in warm areas and over a wide range of precipitation, while EcM plants were mainly distributed in cool and cold areas with less precipitation (Fig. 1c,d), in consistency with previous reports of global distribution pattern (Steidinger *et al.*, 2019).

Data analysis

Mean trait values were calculated for each species at the same site. Before analysis, hydraulic trait values were \log_{10} -transformed to approximate normality. All analyses were performed in R v.4.1.2 (R Development Core Team, 2021). We used a *t*-test to test the significance of trait difference as well as calculated the effect size (Cohen's *D*) using the R package (lsr) to test how different these traits are between AM and EcM woody plants. The larger the value of effect size, the greater the difference was. First, we tested the differences in each of the hydraulic traits between AM and EcM woody plants within angiosperms and gymnosperms separately. Then, we tested the differences in each of the hydraulic traits between AM and EcM plants across three humidity gradients according to the aridity index (AI): semiarid and arid (AI < 0.5), subhumid (0.5 ≤ AI < 1) and humid (AI ≥ 1) and across three biomes: semiarid woodland and shrubland (WDS), temperate seasonal forest (TMS), and tropical/subtropical seasonal forest (TRS). We selected the three biomes because they are the most important biomes where both AM and EcM plants occur, with different water availability (Fig. S1).

To test the sensitivity of hydraulic traits to water availability, we examined correlations between the aridity index (AI) and each of the hydraulic traits for AM and EcM angiosperms and gymnosperms using linear regression analysis. We tested whether the slopes of the correlation differed between AM vs EcM plants by analysis of covariance when the correlations in AM and EcM plants were both significant. We also calculated the range, inter-specific coefficient of variation (CV_{inter}) and intraspecific coefficient of variation (CV_{intra}) in each of the hydraulic traits of AM and EcM angiosperms and gymnosperms. Range is the difference between maximum and minimum trait values. CV_{inter} was used to characterize the variation of hydraulic trait across species within each group (i.e. AM angiosperms or gymnosperms, EcM angiosperms or gymnosperms). First, mean hydraulic trait values were calculated when a species occurred at several sites, thus each species had one value for each hydraulic trait. Then CV_{inter} was calculated as the ratio of the SD to the absolute value of the mean of all species. CV_{intra} was used to characterize the variation of hydraulic trait across sample sites within each species. First, we selected the species that occurred on several sites. Second, CV_{intra} was calculated as the ratio of the SD to the absolute value of the mean of all sample sites. Then, the mean of CV_{intra} ($CV_{intra-mean}$) was calculated for each group. We used a *t*-test to test the differences in $CV_{intra-mean}$ in each of the hydraulic traits between AM vs EcM angiosperms and gymnosperms.

In addition, we constructed a phylogenetic tree for all species in this study using the R package v.PHYLOMAKER2 (Jin & Qian, 2022). The mega-tree GBOTB.extended.tre in this package includes 74 531 species from 479 families, the largest

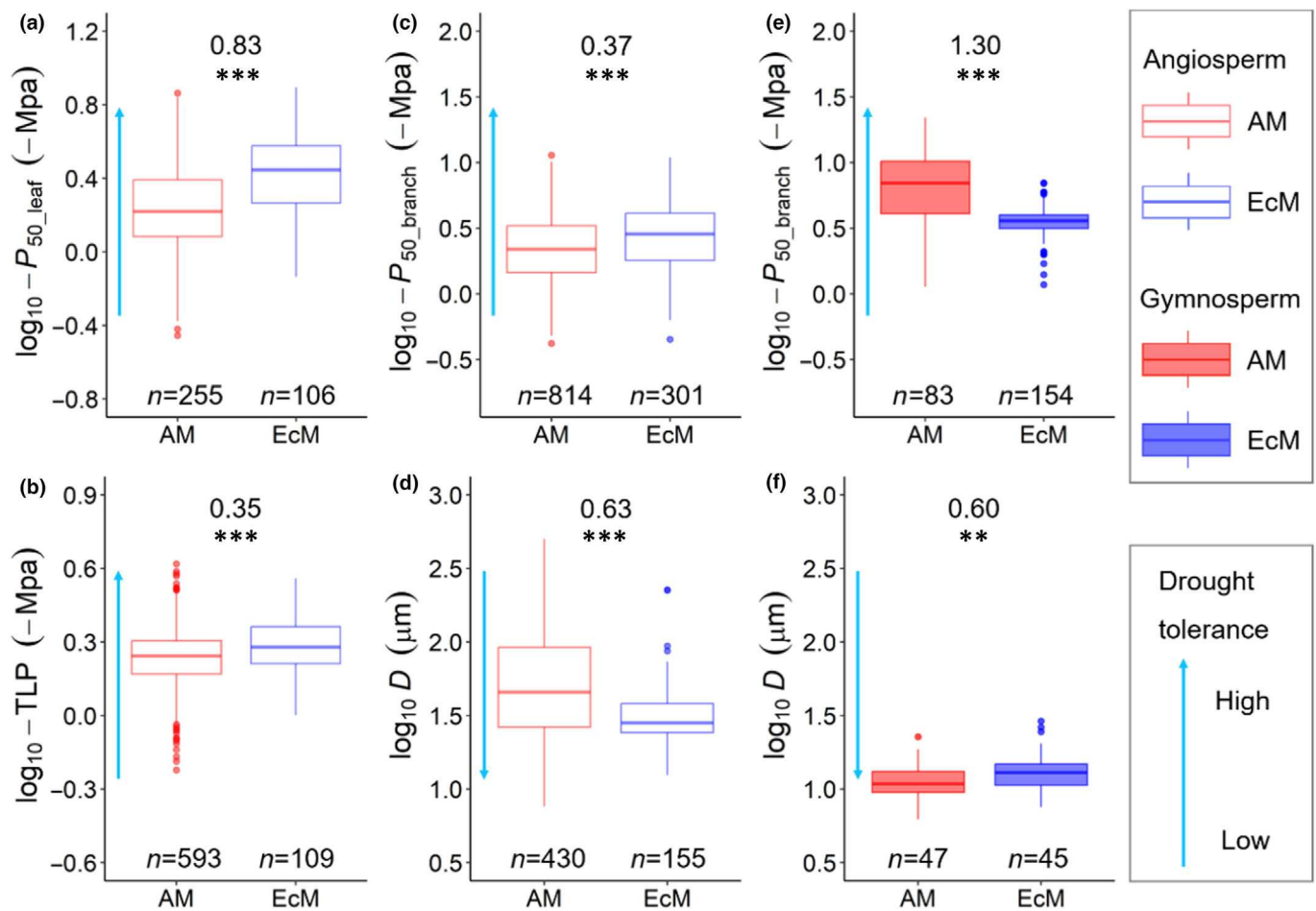


Fig. 2 The differences in each of the hydraulic traits between arbuscular mycorrhizal (AM) and ectomycorrhizal (EcM) woody plants. Hydraulic traits include leaf water potential at 50% loss of leaf hydraulic conductance (P_{50_leaf}) (a), leaf water potential at turgor loss point (TLP) (b), branch water potential at 50% loss of branch hydraulic conductivity (P_{50_branch}) (c, e), and xylem vessel/tracheid diameter (D) (d, f). The light blue line with arrow indicates the direction of higher drought tolerance for each trait. The number of combinations of species-by-site were listed below the box. The box-plots show quartiles for each trait with extreme values as dots. Traits were compared between AM and EcM plants by effect size and t -test. The effect sizes (Cohen's D) were listed above the box. **, $P < 0.01$; ***, $P < 0.001$.

updated plant phylogeny which derived from two mega-trees based on molecular data from NCBI GenBank and phylogenetic data from the Open Tree of Life and fossil records (Zanne *et al.*, 2014; Smith & Brown, 2018). Twenty-four of our species were missing in the mega-tree, so we selected Scenario 3 in V.PHYLOMAKER2 to manually attach them to their close relatives in the mega-tree using the branch length adjuster (BLADJ) method (Webb *et al.*, 2008). In this way, we obtained a time-calibrated tree of 1457-species (Fig. 1a), which we used in subsequent analyses. (1) To test phylogenetic niche conservatism in hydraulic traits, we tested phylogenetic signals in each trait by estimating Pagel's λ for each trait with combined data from AM and EcM species. Pagel's λ indicates the extent to which residual variation in a trait is correlated with phylogeny, using maximum likelihood (Pagel, 1999). There are λ values between zero and one, where $\lambda = 0$ means that there is no phylogenetic signal, while $\lambda = 1$ implies that the distribution of trait values across the phylogeny is as expected under Brownian motion. We constructed phylogenetic generalized least squares (PGLS) models using the *pgls*

function in the R package CAPER (Orme *et al.*, 2018). Strong phylogenetic signals indicate that species retained their ancestral traits, whereas weak phylogenetic signals indicate that traits were more labile among species. (2) To test the extent to which differences in hydraulic traits between AM and EcM plant species are influenced by plant phylogeny, we performed a phylogenetic ANOVA between AM and EcM plant species for each trait using the *phylANOVA* function in the R package PHYTOOLS (Revell, 2012). (3) To test phylogenetic influences on the relationships of hydraulic traits and the aridity index (AI), we tested correlations between AI and each of the hydraulic traits considering evolutionary history (using PGLS models as described for Pagel's λ).

Results

In angiosperms, hydraulic traits indicated higher drought tolerance of EcM species than that of AM species, whereas in gymnosperms the opposite was observed, with higher drought tolerance of AM species relative to EcM species (Fig. 2). The effect size was

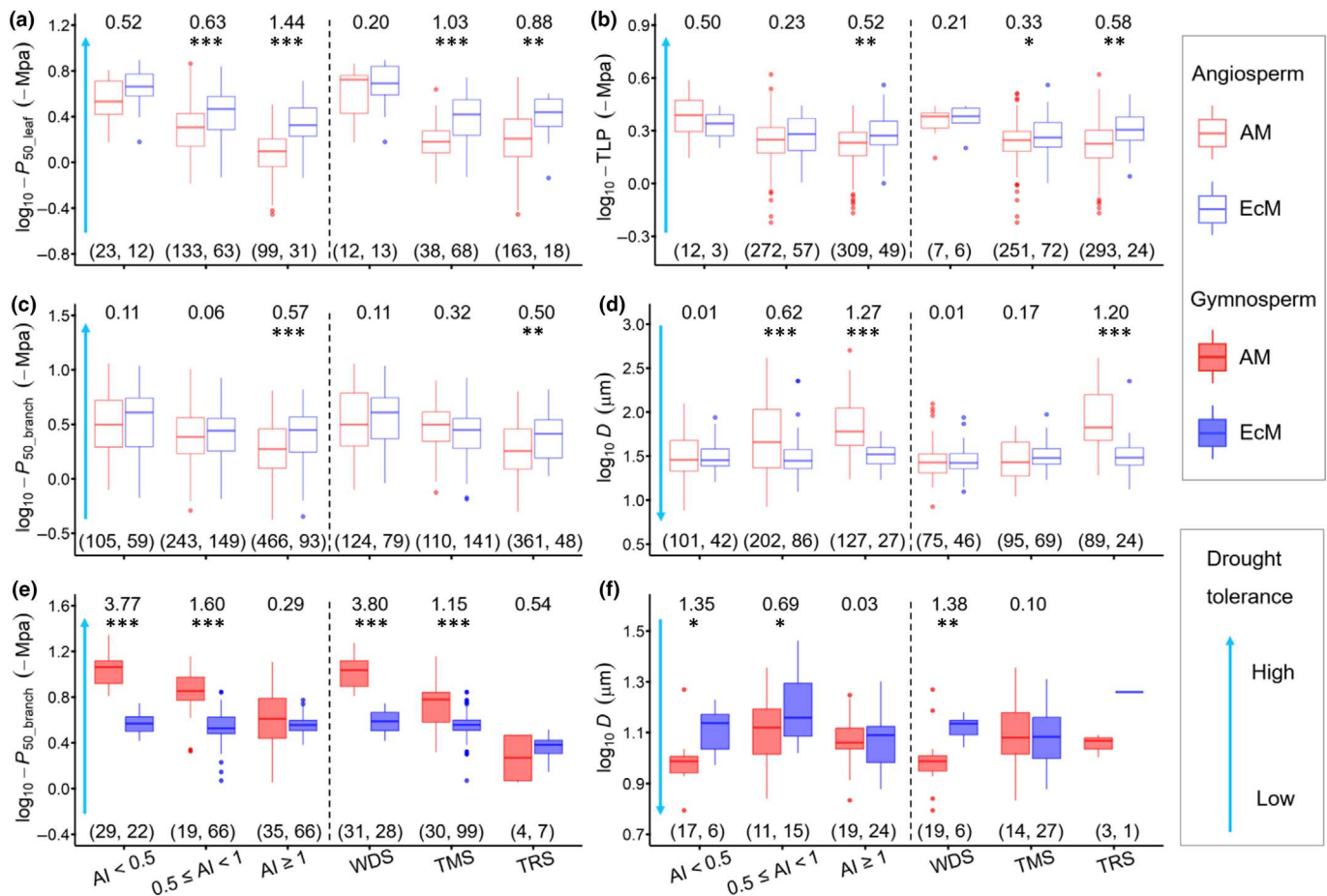


Fig. 3 The differences in each of the hydraulic traits between arbuscular mycorrhiza (AM) and ectomycorrhiza (EcM) plants across humidity gradients and biomes. Hydraulic traits include leaf water potential at 50% loss of leaf hydraulic conductivity (P_{50_leaf}) (a), leaf water potential at turgor loss point (TLP) (b), branch water potential at 50% loss of branch hydraulic conductivity (P_{50_branch}) (c, e) and xylem vessel/tracheid diameter (D) (d, f). Three humidity gradients, divided according to the aridity index (AI), include semiarid and arid ($AI < 0.5$), subhumid ($0.5 \leq AI < 1$) and humid ($AI \geq 1$). Three biomes include semiarid woodland and shrubland (WDS), temperate seasonal forest (TMS) and tropical/subtropical seasonal forest (TRS). The light blue line with arrow indicates the direction of higher drought tolerance for each trait. The number of combinations of species-by-site were listed below the box. The box-plots show quartiles for each trait with extreme values as dots. Traits were compared between AM and EcM plants by effect size and t -test. The effect sizes (Cohen's D) were listed above the box. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

highest in P_{50_leaf} for angiosperms and P_{50_branch} for gymnosperms (Fig. 2). When water availability and biomes were considered, significance and effect sizes of differences in hydraulic traits between AM and EcM plants varied greatly across humidity classes and biomes. Specifically, significant differences between AM and EcM angiosperms were found in wet regions or biomes for angiosperms but in dry regions or biomes for gymnosperms (Fig. 3). It is worth noting that, in temperate seasonal forests (TMS), significant differences were found in leaf hydraulic traits (P_{50_leaf} and TLP) but not in branch hydraulic traits (P_{50_branch} and D) between AM and EcM angiosperms (Fig. 3a–d).

Higher sensitivity and flexibility/variation in hydraulic traits were found in AM woody plants than in EcM species (Fig. 4, Table 2). In AM species (both angiosperms and gymnosperms), hydraulic traits were more sensitive to water availability than in EcM species (Fig. 4). Likewise, most hydraulic traits displayed a wider range, as well as higher interspecific and intraspecific

variation in AM species relative to EcM species (Table 2). In AM angiosperms and gymnosperms, all hydraulic traits were significantly correlated with the aridity index (AI), while only P_{50_leaf} and P_{50_branch} of EcM angiosperms were significantly but weakly correlated with AI (Fig. 4). AM species (both angiosperms and gymnosperms) showed a similar or wider range and higher inter-specific variation than EcM species in all hydraulic traits except for D in gymnosperms (Table 2).

The number of species that could be used to calculate intraspecific variation was small. With limited data, significantly higher intraspecific variation was observed in AM species than in EcM species in P_{50_leaf} ($P \leq 0.05$) of angiosperms and D ($P \leq 0.05$, $P \leq 0.01$) of both angiosperms and gymnosperms (Table 2).

Significant phylogenetic niche conservatism was found in all hydraulic traits for both angiosperms and gymnosperms (Table S2). A subsequent phylogenetic ANOVA showed that differences between AM and EcM plants for most hydraulic traits

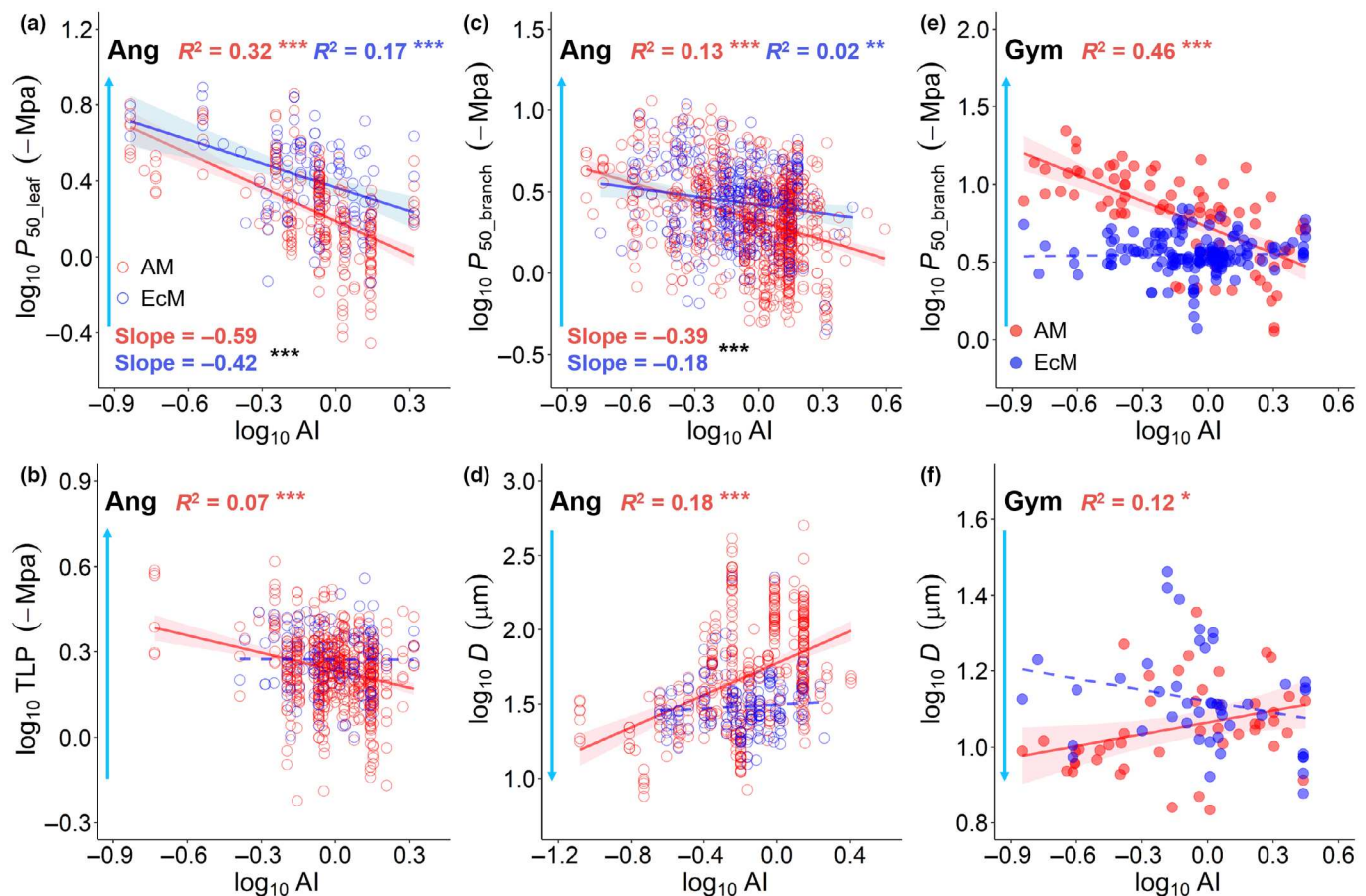


Fig. 4 Different sensitivities of hydraulic traits to water availability between arbuscular mycorrhizal (AM) and ectomycorrhizal (EcM). Red dots, lines and fonts stand for AM; Blue dots, lines and fonts stand for EcM. Hydraulic traits include leaf water potential at 50% loss of leaf hydraulic conductance (P_{50_leaf}) (a), leaf water potential at turgor loss point (TLP) (b), branch water potential at 50% loss of branch hydraulic conductivity (P_{50_branch}) (c, e) and xylem vessel/tracheid diameter (D) (d, f). The light blue line with arrow indicates the direction of higher drought tolerance for each of traits. Correlations of hydraulic traits and aridity index (AI) were calculated by linear regression analysis. The solid lines indicate significant correlations, while the dashed lines indicate insignificant correlations. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

were still significant after phylogeny was taken into account (Table S2). In addition, when plant phylogeny was considered, correlations between AI and hydraulic traits changed little (Fig. S2) compared to the patterns in Fig. 4.

Discussion

We found significant differences in hydraulic traits associated with drought tolerance between AM and EcM woody plants at the global scale. However, the differences between mycorrhizal types depended on other factors such as evolutionary history (gymnosperms vs angiosperms), water availability or biome, in addition to the traits under consideration. Collectively, our results suggest that in addition to well-described differences in nutrient use strategies between AM and EcM woody plants, variation in hydraulic traits may also influence how AM and EcM woody plants are distributed and respond to global changes.

The contrasting hydraulic traits of AM and EcM woody plants may be correlated with the different eco-physiological properties of AM vs EcM fungi. For example, the efficient acquisition of

inorganic nutrients by AM fungi may drive the evolution of resource acquisitive strategies in angiosperms inhabiting wet areas, prioritizing growth over hydraulic safety, thus leading to lower drought tolerance in AM angiosperms than EcM angiosperms in wet regions or biomes. With limited evidence, AM fungi propagules was considered to have higher drought tolerance than EcM fungi propagules (Kilpelainen *et al.*, 2017). If this phenomenon is widespread, drought-tolerant AM fungi may contribute to how AM woody plants (especially gymnosperms) adapt to dry conditions. The effects of different eco-physiological properties of AM and EcM fungi on plant drought tolerance and promotion of the evolutionary plant adaptation to drought, remains to be examined in future studies.

One challenge in drawing inferences from global syntheses is that data sources may have geographical biases. Nutrient use traits collected by predecessors (Averill *et al.*, 2019; Shi *et al.*, 2020) and hydraulic traits collected by us (Figs 1a,b, S1) mainly came from angiosperms in humid and subhumid areas, due to natural factors including the higher woody species diversity in wetter areas and the prevalence of angiosperms over

Table 2 Variation in each of the hydraulic traits of arbuscular mycorrhizal (AM) vs ectomycorrhizal (EcM) angiosperms and gymnosperms.

| Groups | Traits | Mycorrhizal types | Range (min, max) | Interspecific variation | | Intraspecific variation | | P-value |
|------------|------------------------|-------------------|-----------------------|-------------------------|-----|--------------------------|----|---------|
| | | | | CV _{inter} | n | CV _{intra-mean} | n | |
| Angiosperm | P_{50_leaf} (MPa) | AM | 6.95 (−7.30, −0.35) | 0.60 | 244 | 0.28 | 10 | * |
| | | EcM | 7.11 (−7.84, −0.73) | 0.51 | 83 | 0.15 | 11 | |
| | TLP (MPa) | AM | 3.56 (−4.16, −0.60) | 0.28 | 462 | 0.14 | 74 | ns |
| | | EcM | 2.63 (−3.63, −1.00) | 0.26 | 77 | 0.11 | 17 | |
| | P_{50_branch} (MPa) | AM | 10.97 (−11.39, −0.42) | 0.62 | 678 | 0.30 | 84 | ns |
| | | EcM | 10.45 (−10.9, −0.45) | 0.55 | 172 | 0.28 | 44 | |
| Gymnosperm | D (μm) | AM | 496.50 (7.6, 504.10) | 0.94 | 388 | 0.29 | 27 | * |
| | | EcM | 213.8 (12.44, 226.20) | 0.77 | 128 | 0.19 | 18 | |
| | P_{50_branch} (MPa) | AM | 20.87 (−22.00, −1.13) | 0.58 | 57 | 0.18 | 11 | ns |
| | | EcM | 5.82 (−7.00, −1.18) | 0.33 | 49 | 0.15 | 22 | |
| | D (μm) | AM | 16.45 (6.23, 22.68) | 0.24 | 39 | 0.38 | 5 | ** |
| | | EcM | 21.43 (7.55, 28.98) | 0.33 | 25 | 0.14 | 8 | |

Range, interspecific coefficient of variation (CV_{inter}) and the mean value of intraspecific coefficient of variation (CV_{intra-mean}) were used to describe the variation in hydraulic traits which include leaf water potential at 50% loss of leaf hydraulic conductance (P_{50_leaf}), leaf water potential at turgor loss point (TLP), branch water potential at 50% loss of sapwood specific hydraulic conductivity (P_{50_branch}), and xylem vessel/tracheid diameter (D); n, species number; *, $P < 0.05$; **, $P < 0.01$; ns, no significant difference. P values of t-test between AM and EcM groups are only for intraspecific variation, because there was only one CV_{inter} value for each trait of each group.

gymnosperms. As a result, conclusions about trait differences between AM and EcM woody plants at the global scale have been heavily influenced by angiosperms from mesic habitats. In this study, we especially considered potentially different results between angiosperms and gymnosperms and among humidity gradients or biomes, and indeed we found divergent patterns. Our results do offer new insight into survival strategies, biogeographical distributions and responses to climate change of mycorrhizal plants from a hydraulic perspective.

In angiosperms, hydraulic traits indicated higher drought tolerance in EcM species than in AM species (Fig. 2a–d). Thus, besides conservative nutrient strategies by EcM species, higher drought tolerance may serve as an additional factor in contributing to the predominant distribution of EcM woody plants in sub-humid regions (Fig. 1d). We found that significant differences in hydraulic traits between AM and EcM angiosperms mainly occurred in wet areas or biomes (Fig. 3a–d), and that hydraulic traits in EcM angiosperms were less sensitive to water availability than in AM angiosperms (Fig. 4a–d). Ectomycorrhiza angiosperms tend to have high-drought tolerance, even in humid regions where such tolerance is not essential, whereas AM angiosperms with low-drought tolerance and resource acquisitive strategy dominate in humid regions. These results align with the global distribution pattern, that is AM species are mainly distributed at low latitudes with high precipitation and high temperature, while EcM species are mainly distributed at high latitudes with low precipitation and low temperature (Steidinger *et al.*, 2019). Interestingly, in cases where EcM angiosperms are co-dominant in some tropical regions with high precipitation, for example tropical seasonal dipterocarp forests in Asia (Brearley *et al.*, 2017; Primack, 2017), prolonged dry seasons may explain why EcM angiosperms have a survival advantage. Although similar drought tolerances were found in AM and EcM angiosperms

in dry regions (Figs 3a–d, 4a–d), the hydraulic traits associated with exceptional drought tolerance in certain species of AM angiosperms (Table 2) confers them a competitive advantage in extreme drought environments like deserts (Fig. S1) (Shen *et al.*, 2023). Moreover, in AM gymnosperms, *Callitris tuberculata* is known as one of the most drought-tolerant trees in the world, and is widely distributed in extremely dry regions of Western Australia (Larter *et al.*, 2015). Our results indicate that AM gymnosperms possess high-drought tolerance especially in dry regions (Figs 3e,f, 4e,f), which may affect their biogeographical distributions as well.

In wet areas such as tropical/subtropical seasonal forests, hydraulic traits in AM angiosperms were associated with lower drought tolerance than in EcM angiosperms (Figs 3a–d, 4a–d). Consistent with this, it had been reported that the leaves of AM species had higher hydraulic vulnerability than EcM species (Zhao *et al.*, 2021), and that warming decreased the drought tolerance of AM trees but increased the drought tolerance of EcM trees in a subtropical forest (Wu *et al.*, 2023), i.e., warming further increased the difference in drought tolerance between AM and EcM woody plants. Under warming and drying environment, the mortality rate of large trees in this forest has increased significantly (Zhou *et al.*, 2013), and most of the dead trees are AM trees (X. Liu *et al.*, unpublished data). Interestingly, our study found that EcM angiosperms in temperate seasonal forests were more drought-tolerant than AM angiosperms for leaf hydraulic traits but not for branch hydraulic traits (Fig. 3a–d). This suggests that under moderate drought conditions, EcM angiosperms in temperate seasonal forests (e.g. oaks) may be better able to maintain leaf water transport, stomatal aperture and photosynthetic rates, resulting in better growth performance (Brzostek *et al.*, 2014). However, amidst enduring drought conditions, the water potential of EcM angiosperms may decrease

severely due to the maintenance of the stomatal aperture. Without stronger branch resistance to embolism, decreased water potential would increase risk of dying from hydraulic failure, which may explain particularly high mortality in EcM-associated oaks during prolonged drought (Novick *et al.*, 2022). This may be one of the primary reasons for the decline in EcM tree dominance during the past three decades in the eastern United States under climate change (Jo *et al.*, 2019). In dry areas such as semi-arid woodland and shrubland, increasing drought may threaten the survival of EcM gymnosperms more than AM gymnosperms, because AM gymnosperms have much higher drought tolerance (Figs 3e,f, 4e,f). Of course, our forecast needs to be considered along with many other global change factors, such as nitrogen deposition, warming and fire frequency (Jo *et al.*, 2019). In addition to hydraulic strategies, plants have evolved many other strategies to use water resources and cope with water stresses, such as taking advantage of the short wet season (i.e. ephemeral plants and deciduous plants), storage of non-structural carbohydrates (O'Brien *et al.*, 2014) and adaptations of root traits, for example deep rooting systems (Phillips *et al.*, 2016). Although mycorrhizal associations may be part of a constellation of factors that drive the adaptation of plants to water availability, more research is required on the differences in these strategies between AM and EcM plants, to further conduct a comprehensive evaluation of their differences in drought tolerance.

AM plants (both angiosperms and gymnosperms) were found to have higher sensitivity in each of the hydraulic traits to water availability (aridity index) than EcM plants (Fig. 4), indicating that AM plants adopt optimal hydraulic strategies to cope with varying water conditions, thus maintaining their advantage in variable moisture environments. Wider range and higher inter-specific variation in most of the hydraulic traits of AM woody plants (Table 2) allow their global distribution to cover greater water gradients, that is from tropical rain forests to deserts (Steidinger *et al.*, 2019; Suleiman *et al.*, 2019; Tedersoo & Bahr, 2019). Higher intraspecific variation in some of the hydraulic traits was found in AM woody plants (Table 2). This demonstrates a higher trait plasticity and better adaptability within species, which may enable AM species to spread over a wider climatic zone and quickly adapt to changing local climates. However, the extent to which the rate of acclimatization can keep pace with climate change remains uncertain, necessitating further research. In addition, the majority of species used for calculating intraspecific variation in this study were typically found only at two or three sites, which may not adequately capture the full extent of their distribution. To predict the divergent responses of AM and EcM woody plants to climate change more accurately, further investigation into intraspecific trait variation of woody plants with enough sample sites covering main distribution areas is warranted (Liang *et al.*, 2019; Shen *et al.*, 2023).

Conclusion

In this study, we revealed the different hydraulic strategies exhibited by AM vs EcM angiosperms and gymnosperms, which are consistent with their current biogeographical distribution, and

may, thus, constitute a pivotal factor in influencing the biogeographical distribution of mycorrhizal types. In a future climate, for example with increasing dry extremes, the differences of drought tolerance between AM and EcM woody plants would affect their survival and, thereby, tree community composition, thus impacting biogeographic patterns of mycorrhizal types. Specifically, the abundance of AM woody plants may decrease in wet habitat and increase in dry habitat under severe droughts. This may further affect ecosystem processes such as carbon sequestration and nutrient cycling. Future studies regarding the mycorrhizal theories of differences in drought tolerance between AM and EcM woody plants, combining with more dynamic monitoring in dominance change of AM and EcM woody plants in various biomes of terrestrial ecosystem, are needed.

Acknowledgements

This work was funded by National Natural Science Foundation of China (32101256 and U23A20156), and Guangdong Science and Technology Plan Project (2023B1212060046). RPP was supported by Department of Energy ESS (Award: DE-SC0021980) and the National Science Foundation IOS (Award: 2006196). We are grateful to the editor and reviewers for their insightful comments and constructive suggestions on earlier versions of this manuscript.














Competing interests

None declared.

Author contributions

XL and QY conceived the idea. XL, KY, HL, PH, WT, MZ, XG, YJ and YW collected and analyzed the data. XL KY, HL, RPP, XL, CT, KAN, EPB and QY wrote and revised the manuscript.

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Data availability

The data that supports the findings of this study are available in the Supporting Information of this article (Table S1).

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 The aridity index (AI) values of the seven biomes in this study.

Fig. S2 Correlations of aridity index (AI) and each of the hydraulic traits with plant phylogeny being considered.

Table S1 Data file including species list and data source for the traits and references to mycorrhizal classification.

Table S2 Phylogenetic signals and phylogenetic ANOVA in each of the hydraulic traits at species level.

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