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The Effects of Arbuscular Mycorrhiza Trees on the Diversity of Forest Communities Worldwide Are Greater than Those of Ectotrophic Mycorrhiza Trees

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Abstract: The interaction between woody plants and mycorrhizal fungi is an important biological interaction; however, the driving factors behind the diversity of mycorrhizal trees formed through the symbiosis of mycorrhizal fungi and woody plants remain unclear. In this study, we collected and compiled the woody plant data of 34 forest dynamic plots containing 3350 species from habitats around the world and divided them into AM and EcM trees. We tested the contribution of AM and EcM trees to tree diversity and its components in forest communities worldwide. Our results showed that AM trees rather than EcM trees affect the tree diversity of forest communities, and that the diversity of AM trees has a significant latitudinal gradient pattern. Climate variables, especially temperature, are strongly correlated with the diversity patterns for AM trees rather than EcM trees. Topography is the most significant factor affecting the diversity of EcM trees. Our findings highlight the importance of AM trees for the tree diversity of forest communities worldwide. Our findings have important implications for understanding the response of complex woody plant communities with different types of mycorrhizal symbiosis to climate change.

Keywords: AM trees; EcM trees; climate; topography; temperature; latitude gradient

1. Introduction

The symbiotic relationship between plant bodies and mycorrhizal fungi has been recognized and widely studied [1–4]. Mutualistic interactions between plants and mycorrhizal fungi may be an important but often overlooked biological interaction [5]. This interaction improves the absorption and accumulation of mineral elements in soil by plants and promotes plant resistance and tolerance to heavy metal stress [6–8]. Although global biodiversity has been known for centuries [9–11], global biodiversity is still a primary issue of concern [12]. The reciprocal interactions of organisms and fungi, such as plants and fungi, affect the diversity of life on Earth. However, the diversity and spatial distribution pattern of mycorrhizal trees, which are the symbionts of mycorrhizal fungi and trees, on a global scale are unclear.

In the course of centuries of research into plant diversity, the latitudinal gradient of plant species richness from the poles to the equator has been widely recognized and confirmed [13–17]. Plant diversity is highest in the tropics, where the rate of species formation is much higher than the rate of species extinction [18]. The link between climate and diversity has been explored in all directions for many years [19–22]. However, the influence of climate on the spatial distribution of the diversity of mycorrhizal trees is unclear.

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Many studies have shown that mycorrhizal fungi play an important role across many terrestrial ecosystems worldwide [23–34]. Among them, arbuscular mycorrhizal fungi (AMF) and ectomycorrhizal fungi (EcMF) form symbioses with more than 80% of the vascular plants globally [35,36]. AMF form specialized structures in plant root cells termed arbuscules, which are the site for the transfer of nutrients between fungus and plant [37]. The hyphae of the EcMF are mainly distributed on the surface of the roots. Some studies have shown that plant litter in AMF-dominated ecosystems is often higher than that in EcMF-dominated ecosystems [38]. EcMF have the genetic capability to degrade litter to some extent [38,39]. Moreover, mycorrhizal diversity, seasonality, and host preference have received extensive attention at different spatial scales [40,41]. A simulated experiment with increasing temperature showed that the diversity and community structure of mycorrhizal fungi could be affected by increasing temperature [38,42,43]. However, some questions still need to be answered: Does temperature have an effect on the diversity of mycorrhizal trees? Is temperature the most important factor influencing the diversity of mycorrhizal trees? Are the spatial patterns and drivers of AM and EcM trees, as symbionts of AMF and EcMF with woody plants, different?

In this study, we examine the influence of mycorrhizal associations and environmental factors (space, climate, and topography) on the latitudinal gradient in forest tree diversity, aiming to identify the driving factors behind diversity changes in AM and EcM trees by analyzing their diversity patterns. Using data from 34 large, stem-mapped forest plots across the globe (Figure 1), we calculate species richness for AM and EcM trees to investigate the contribution of different mycorrhizal tree types to the overall forest community diversity and confirm the significant role of AM tree diversity in forest tree diversity. We hypothesize that the diversity of AM trees increases with latitude. Specifically, we test three hypotheses: (1) the latitudinal gradient pattern of diversity of forest communities is closely related to the mycorrhizal types of host trees; (2) the factors causing the diversity change in different types of trees are distinct and not the same; and (3) the diversity of mycorrhizal trees is primarily determined by temperature rather than precipitation. Given the current complex and variable climate conditions, we hope our findings will provide valuable data for understanding the response mechanisms of different mycorrhizal trees to climate change and offer theoretical references for the maintenance and protection of forest ecosystems.

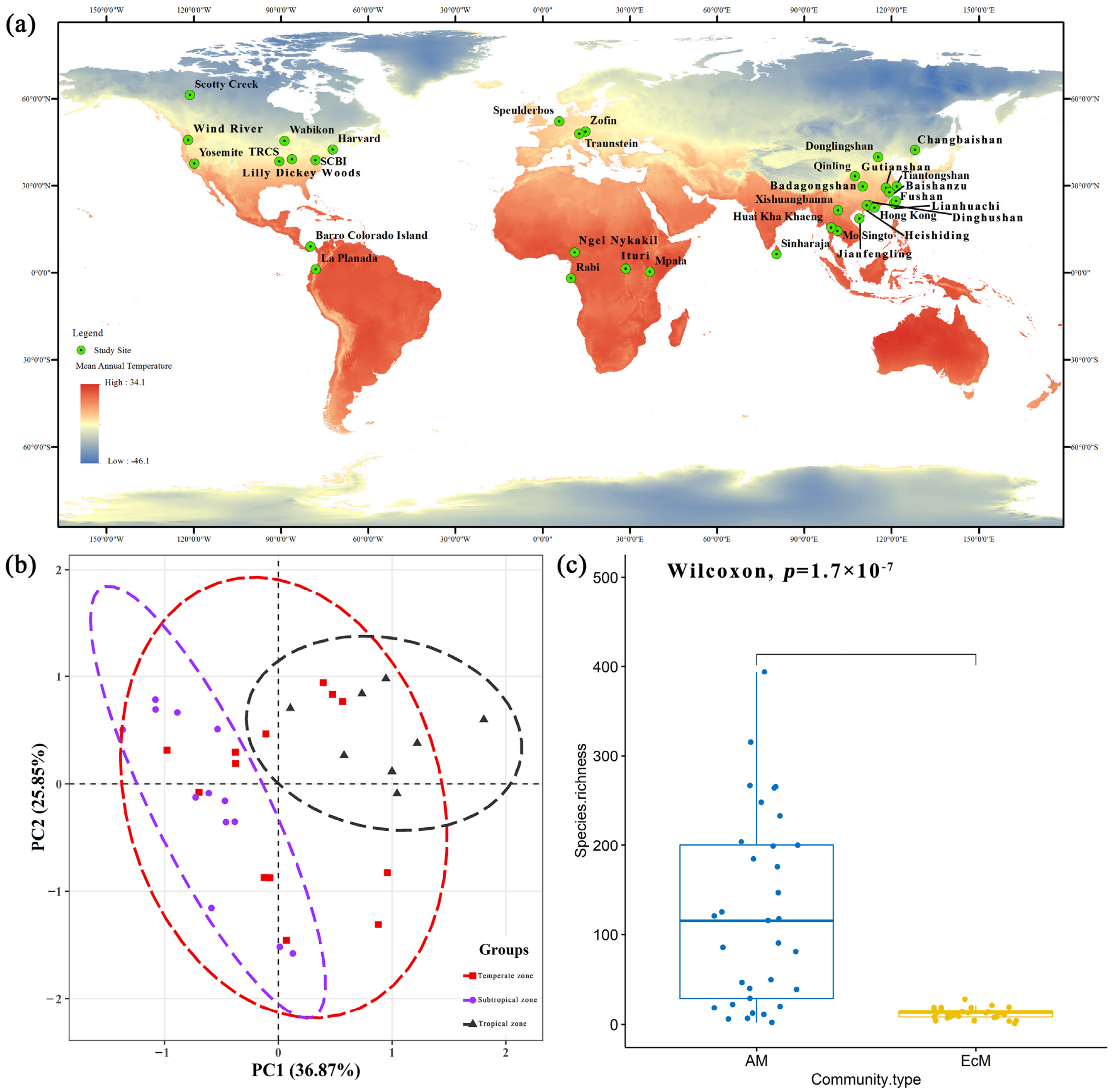

Figure 1. (**a**) Global distribution of 34 forest plots. (**b**) PCA of woody plants in different climatic zones (Red dashed lines represent temperate zone, blue dashed subtropical zone and black dashed tropical zone). (**c**) Diversity of AM and EcM trees.

2. Material and Methods

2.1. Study Sites

We used data from 34 forest dynamic plots around the world from the Forest Global Earth Observatory network (ForestGEO, http://www.ForestGEO.si.edu/ (accessed on 13 April 2023)) and the Chinese Forest Biodiversity Monitoring Network (https://geobon.org/downloads/PDF/2016-CForBio-EN.pdf (accessed on 20 May 2023)) [44]. In 34 plots, all the freestanding woody plants with DBH ≥ 1 cm were counted in accordance with a standardized census program [45]. The 34 dynamic forest dynamic plots were divided into three climatic zones: tropical, subtropical, and temperate according to latitude (Table S1A). The size of the plots ranges from 20 ha (Xishuangbanna) to 120 ha (Mpala), and these plots encompass a broad latitudinal gradient from 1.9246 S° (Rabi) to 61.30 N° (Scotty Creek, Canada). The plots extend across 63.2246 degrees latitude, and they cover all the continents with forests (i.e., Asia, Africa, Europe, South America, North America, and Oceania). The plots are located in forest types ranging from temperate forests to subtropical and tropical forests and are composed of tree diversities from 11 to 511 woody species.

2.2. Classification of Mycorrhizal Plants

We collected and sorted mycorrhizal datasets from 34 forest dynamic plots and extracted woody plants for analysis. Based on anatomy and partner identity, four principal types of mycorrhizae are recognized: arbuscular mycorrhizae (AM), ectomycorrhizae (EcM), ericoid mycorrhizae, and orchid mycorrhizae [46]. In this study, we assigned mycorrhizal type at the genus level (Table S1B). AM and EcM associations are the most common mycorrhizal types for trees. Thus, we focused predominantly on AM and EcM trees in the present study. The classification of mycorrhizal trees was referenced by the global database FungalRoot published on the GBIF (Global Biodiversity Information Facility) platform [47] (https://www.gbif.org/dataset/744edc21-8dd2-474e-8a0b-b8c3d56a3c2d (accessed on 30 May 2023)).

2.3. Environmental Data

ForestGEO sites cover a wide diversity of physical and biotic environments. We collected data for 12 environmental variables. The spatial factors included latitude (°) and longitude (°); topographic factors included maximum altitude (HA, m), minimum altitude (LE, m), mean altitude (ME, m), and mean slope (MS, °); and climatic factors included warmest month temperature (MTWM, °C), coldest month temperature (MTCM, °C), annual mean temperature (MAT, °C), driest month precipitation (PDM, mm), wettest month precipitation (PWM, mm), and annual mean precipitation (MAP, mm). The topographic and climatic factors were selected from ForestGEO, among which the climatic factors were also referred to in the literature [48,49].

2.4. Statistical Analyses

Based on the AM and EcM tree data of 34 forest plots, the similarities and differences in communities in different climatic zones were analyzed by principal component analysis (PCA). The Kruskal–Wallis test was used to examine the differences in diversity between AM and EcM trees. We used the “ggplot2” package in the R software platform (R version 3.6.1) to visualize the results of the PCA and Kruskal–Wallis.

The species composition of the woody plants under different climatic zones was analyzed by ordination using NMDS with Bray–Curtis dissimilarity, and the environmental factors (space, climate, and topography) were fitted into the NMDS ranking of species abundance by the ENVFIT function. Permutational multivariate ANOVA was applied to explore the significant differences on the basis of 999 permutations. NMDS was conducted using the metaMDS command in the R vegan package (R version 3.6.1) [50].

Linear models were fitted for each region with the richness of AM and EcM trees as the response and the environmental factors (space, climate, and topography) as predictors to analyze diversity changes with environmental factors. The linear regression models were performed with the R software and visualized using “ggplot2” [51].

The direct and indirect effects of the environmental factors (space, climate, and topography) on the diversity of AM and EcM trees were further investigated. SEM was used to evaluate the causal relationship between the diversity of two types of mycorrhizal (AM and EcM) trees and the different environmental factors. We used the “lavaan” package in the R software platform to parameterize the SEM.

3. Results

3.1. Diversity of AM and EcM Trees

The PCA showed that the environmental interpretations of PC1 and PC2 were 36.87% and 25.85%, respectively, and the total interpretation amount was 62.72% (Figure 1b). The

Kruskal–Wallis test showed that the diversity of AM trees was significantly higher than that of EcM trees (Figure 1c).

3.2. Pattern of AM and EcM Diversity

For AM trees, the diversity pattern displayed pronounced latitudinal gradients. In particular, the richness of AM trees increased with the decrease in absolute latitude at a rate of 5.255 species per degree. The diversity of AM trees increased with longitude ($p < 0.05$), MAT ($p < 0.01$), MAP ($p < 0.05$), PWM ($p < 0.05$), MTWM ($p < 0.01$), and MTCM ($p < 0.01$). By contrast, it decreased with latitude ($p < 0.01$) and PDM. Temperature is an important affecting factor in determining the diversity of AM trees. The amount of variance (R2) explained was highest with MAT and MTCM (≥50%), followed by MTWM. For EcM trees, the spatial (longitude and latitude) and climatic factors (MAT, MAP, MTCM, MTWM, PWM, and PDM) had no significant effect on diversity. The diversity of EcM trees did not have pronounced latitudinal gradients (Figure 2).

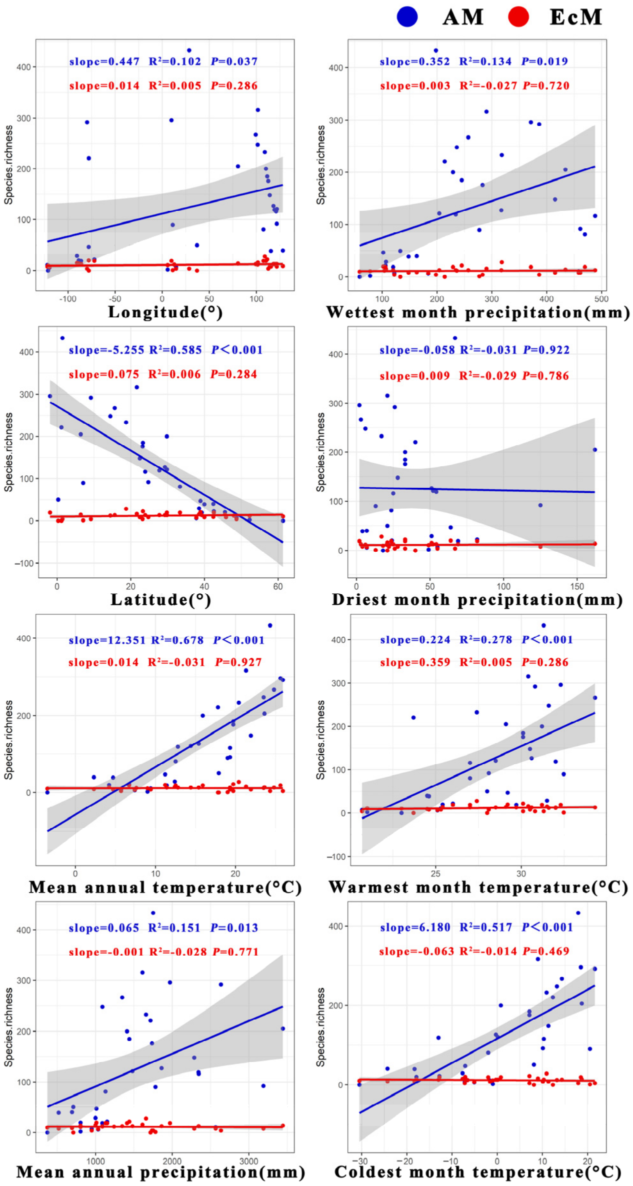

Figure 2. Effects of environment on the richness of the different types of mycorrhizal trees. The blue line represents AM trees, and the red line represents EcM trees.

3.3. Effects of Environmental Variables on the Diversity of AM and EcM Trees

We found that the climate factors MAT and MTCM were only significantly correlated with AM trees, while PDM was only significantly correlated with EcM trees. MAP and PWM significantly affected AM and EcM trees. The topographic factors (mean slope and mass fraction) were significantly correlated only with trees. The spatial factors (longitude) significantly affected AM and EcM trees (Figure 3).

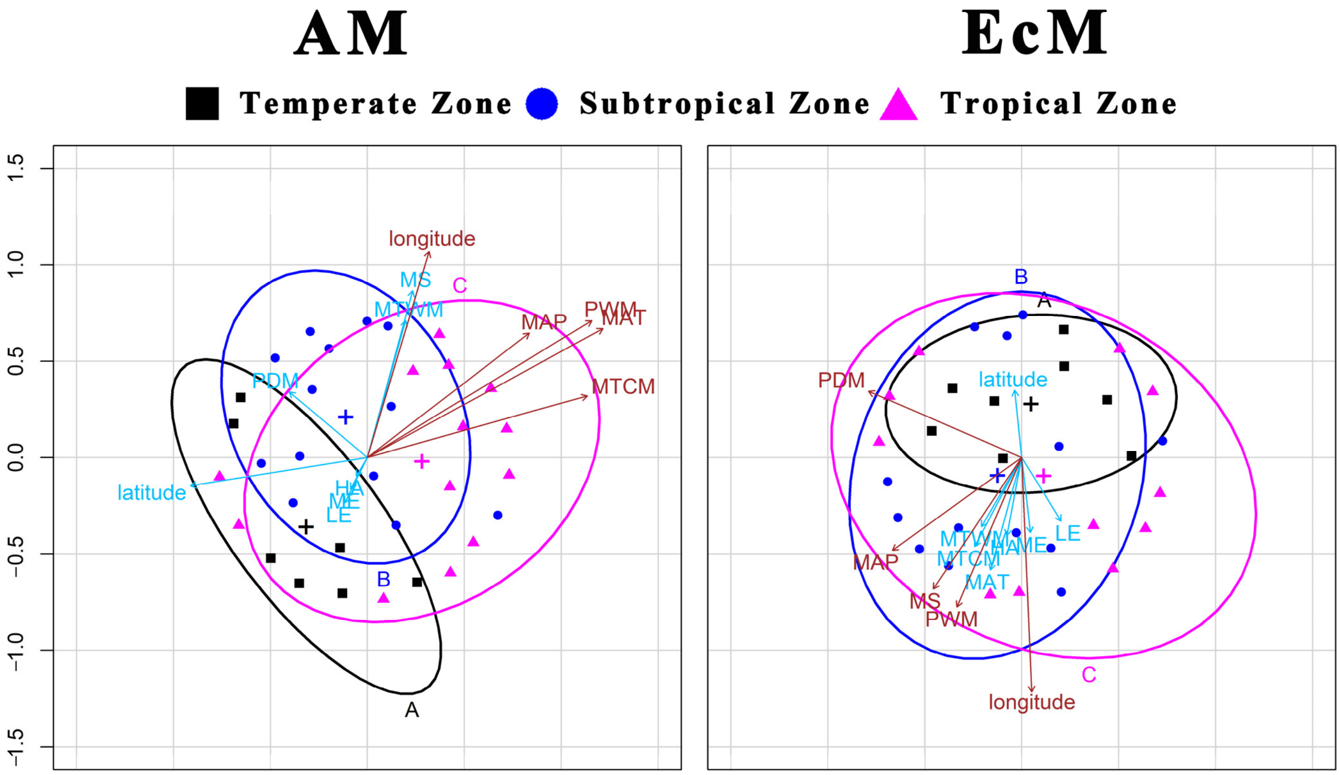

Figure 3. NMDS of the species composition of woody plants with different mycorrhizae. The black circles represent tropical zones, blue circles represent tropical zones, and purple circles represent tropical zones. The brown arrows represent insignificance, and blue arrows represent significance. HA (maximum altitude, m), LE (minimum altitude, m), ME (mean altitude, m), MS (mean slope, °), MTWM (the warmest month temperature, °C), MTCM (the coldest month temperature, °C), MAT (the annual mean temperature, °C), PDM (the driest month precipitation, mm), PWM (the wettest month precipitation, mm), and MAP (the annual mean precipitation, mm). The same below.

The effects of the environmental factors on the abundance of AM trees (R2 = 0.62) were much higher than those on the abundance of EcM trees (R2 = 0.21). Climate is the most important affecting factor for the diversity of AM trees. The influence of the climatic factors (R2 = 0.71, $p \leq 0.05$) on the richness of AM trees was much greater than that of the spatial (R2 = 0.19, $p > 0.1$) and topographic (R2 = −0.03, $p > 0.1$) factors. The topographic factors are the most important affecting factors for the species richness of EcM trees. The influence of the topographic factors (R2 = −0.33, $p \leq 0.05$) on the richness of EcM trees was greater than that of the spatial (R2 = 0.3, $p > 0.1$) and environmental (R2 = −0.23, $p > 0.1$) factors. The influence of the climate factors on the richness of AM trees was greater than that on the richness of EcM trees. The effects of the topographic and spatial factors on the species richness of EcM trees were higher than those of AM trees. The climate factors had opposite effects on the species richness of AM and EcM trees (Figure 4).

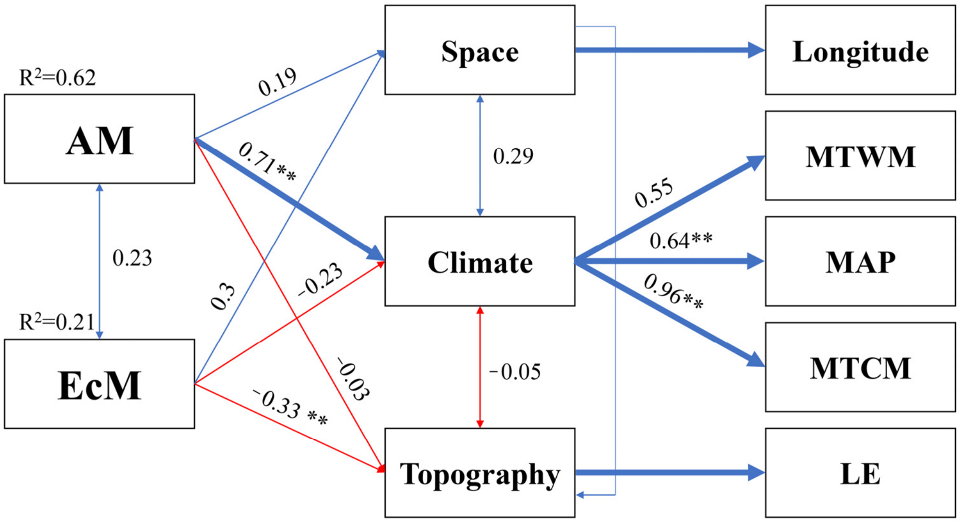

Figure 4. Results of the best-fitted piecewise structural equation model (SEM) showing the linkages among space, climate, topography, and mycorrhizal tree diversity. The blue and red lines indicate the positive and negative pathways, respectively. Statistical significance is indicated by asterisks. (** $p < 0.01$). MTWM (the warmest month temperature, °C), MTCM (the coldest month temperature, °C), MAP (the annual mean precipitation, mm), and LE (minimum altitude, m).

4. Discussion

4.1. The Diversity of AM Trees Rather than EcM Trees Affects the TREE Diversity of the Forest Community

The diversity of AM trees had a significant latitudinal gradient pattern, while the diversity of EcM trees had no significant change along the latitudinal gradient. In general, the tropics contain more diverse and abundant species because lower latitudes have higher material energy and productivity to sustain more species [18,52–54]. Higher rates of speciation, DNA evolution, and ecological interactions (e.g., competition, herbivory, predation, and parasitism) at lower latitudes produce more species [14,18,55,56]. In this study, the diversity of AM trees followed the same rule. We found that the diversity of AM trees has a significant latitudinal gradient, and the diversity decreases with the increase in latitude. By contrast, for EcM trees, diversity generally lacks significant latitudinal patterns. This result is probably due to the fact that the wide distributions of EcM trees do not generate strong differences in diversity among localities.

Despite the widespread interest in climate change for forest diversity patterns [57,58], more attention needs to be paid to the impact of climate on the diversity of mycorrhizal symbionts. Climate has long been an important affecting factor for diversity, and climate change directly or indirectly affects species richness and community stability [59]. Climate can also affect the species composition of communities by affecting the control of succession by plant–soil feedback (PSF) [60]. Climate, such as extreme temperature, is an important abiotic factor that affects PSFs and may undermine the stabilizing forces of negative PSFs [61]. In this study, we found that the diversity of AM trees was regulated by climate factors and had a certain regularity. The diversity of AM trees increased with the rise in temperature (MAP, MTCM, and MTWM). In the SEM, we found significant differences in diversity between AM and EcM trees as influenced by environmental factors. Climate is the most important affecting factor for the diversity of AM trees and has the least influence on the diversity of EcM trees. However, topographic factors are the most important affecting factors for the diversity of EcM trees and have the least influence on the diversity of AM trees. The diversity of AM trees increases with the rise in temperature and decreases with the increment in latitude. Therefore, AM trees are the predominant contributors to forest communities in tree diversity.

4.2. Temperature, Not Precipitation, Is the Most Important Affecting Factor for the Diversity of AM Trees

Temperature and precipitation have been key factors in the study of the effects of climate on the diversity of forest communities [62–64]. Species richness is strongly temperature dependent, as Wang [54] elucidated in his study of trees in eastern Asia and North America. Some studies have shown that AM trees are dominant in warm, humid, and seasonal tropical areas with high decomposition rates, while EcM trees are dominant in dry, cold, and seasonal temperate areas [5,65,66]. In this study, we found that three temperature variables (MAT, MTWM, and MTCM) significantly affected the diversity of AM trees. The diversity of AM trees increased significantly with the increase in temperature. Studies have shown that AMF symbionts exhibit a more active growth response to warm environments [67]. Therefore, higher temperature is beneficial to the better development of AMF symbionts, and temperature may affect the diversity of AMF symbionts by affecting the symbiosis of AMF. In addition, the AMF community composition is significantly affected by increased precipitation via soil moisture rather than by warming [68]. PSFs affect diversity by regulating the intensity of interspecific competition, the local distribution of species, and even niche division [5,69–71]. Changes in precipitation patterns can change the intensity of PSFs and affect the stability of biological communities [72]. However, we found that the influence of precipitation on the diversity of AM trees was limited, which may be due to the low utilization rate of AMF to precipitation, and the soil water content may have a more direct effect on AMF. It may also be that AMF play a role in promoting drought resistance in the host [73], which attenuates the effect of water on it.

Some studies have shown that topography is an important affecting factor for the diversity of EcM communities and fruiting bodies, as well as the distribution of EcM [74,75]. In this study, topography replaced climate as the most significant affecting factor for the diversity of EcM trees. Complex topography constitutes a complex ecological environment. Complex topography creates small-scale variations in microclimate [75]. Topography influences the distribution of EcMF groups by mediating changes in environmental conditions [75]. Topography may affect the diversity of EcM trees by mediating microclimate change. Compared with the change in climate conditions, the change in environmental conditions mediated by topography had a more significant effect on the diversity of EcM trees.

5. Conclusions

Unlike previous studies, our research encompasses sample sites from three different climatic regions (tropical, subtropical, and temperate). Based on this, we tested the effects of three different environmental factors (spatial, climatic, and topographical) on the diversity of different types of mycorrhizal trees (AM trees and EcM trees). We found that the diversity of AM trees rather than EcM trees affects the tree diversity of forest communities worldwide. The diversity of AM trees significantly decreased with increasing latitude. The diversity of AM trees has a significant latitudinal gradient pattern. Climate factors are generally much more important than spatial and topographic factors in diversity and its components of AM trees. In particular, temperature is the most important environmental affecting factor for the diversity of AM trees. Compared with AM trees, topography is the most important affecting factor for the diversity of EcM trees. AM tree diversity and EcM tree diversity are driven by different environmental variables, suggesting that environmental variables likely drive species diversity by affecting the mycorrhizal associations of trees. Our study affirms the contribution of AM trees to forest communities and demonstrates that the driving factors for diversity changes in AM trees and EcM trees are different. The primary factor driving EcM tree diversity is not climate but topography. Future research is also needed to discover the mycorrhizal associations of more trees and the specific selection of mycorrhizal species to tree hosts under the circumstances of global warming. As the global climate changes rapidly, we should pay more attention to the effects of climate (especially temperature) on mycorrhizal associations and the diversity of mycorrhizal trees (and even global trees).

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d16090587/s1, Figure S1: Effects of topography on the richness of different types of mycorrhizal trees. The blue line represents AM trees, and the red line represents EcM trees; Table S1: Sample land data. File S1: Plant List; File S2: Ecoregion.

Author Contributions: Conceptualization: Z.L. and Z.Y.; methodology: Z.L. and Y.S.; software: Z.L., W.L. and R.Q.; investigation: W.L., F.L. and Z.L.; data curation: Z.L., R.Q. and N.X.; formal analysis: Z.L., W.L. and X.X.; visualization: Z.L. and R.Q.; writing—original draft: Z.L.; validation: W.L, F.L., Y.Y. and Y.C.; writing—review and editing: X.X. and D.W.; resources: X.L. and Q.L.; supervision: F.L. and Y.S.; funding acquisition: Z.Y. and D.W.; project administration: Z.Y. and D.W. All authors have read and agreed to the published version of the manuscript.

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