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Research Article

Associations between mycorrhizal dominance and woody species diversity shift with stand development and climate across subtropical and tropical forests in Taiwan

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Mycorrhizal symbioses influence woody species diversity, but whether this association shifts with forest stand development remains underexplored. Using forest inventory data across subtropical and tropical forests in Taiwan, we found that woody species diversity was lower in ectomycorrhizal (EM)-dominated than in arbuscular mycorrhizal (AM)-dominated forests, while forests with mixed mycorrhizal strategies supported the highest woody species diversity. However, these associations were strongest in early development stands and tended to converge towards high diversity in late development stands despite differences in mycorrhizal dominance. These results are consistent with stronger conspecific negative density dependence in AM-dominated forests and niche partitioning among mycorrhizal strategies at early developmental stages, while alternative recruitment dynamics associated with AM- and EM-dominated canopies may promote high woody species diversity at late developmental stages. Climate modulated these patterns, with the negative association between EM dominance and woody species diversity strongest in cold regions, while the diversity peak in mixed AM–EM forests was most pronounced in median climates and diminished towards warm and cold climates. In addition, woody species evenness was more consistently highest in forests with mixed mycorrhizal strategies across stand development stages compared to woody species richness, suggesting that mycorrhizal coexistence promotes more equal species abundances. These findings highlight that associations between mycorrhizal strategies and woody species diversity depend on forest developmental stage, underpinning new understanding of subtropical and tropical forest recovery under global change.

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Introduction

Subtropical and tropical forests support a large part of Earth's biodiversity, but they are threatened by human-driven environmental change (Taubert et al. 2018, Esquivel-Muelbert et al. 2019, Winkler et al. 2021). The impacts of deforestation, tree logging, and recurrent natural disturbances such as typhons, storms, and droughts are driving the conversion of intact subtropical and tropical forest landscapes into mosaics of early development stands and remnant late-development patches (Chazdon et al. 2009). Research focused on understanding biodiversity changes across stages of forest stand development can be useful for informing conservation and restoration strategies under accelerating global change (Poorter et al. 2021).

During forest stand development, antagonistic species interactions contribute to shape tree species coexistence. Conspecific negative density dependence (CNDD) is a well-documented mechanism that tends to limit tree species dominance and promote tree species diversity. For example, tropical tree species display lower performance at high conspecific densities (Comita et al. 2010) mostly because both generalist and specialist natural enemies drive strong CNDD (Terborgh 2012). In a different way, positive species interactions, shared habitat preferences, or niche partitioning may also allow the spatial co-occurrence of multiple species and hence favour species coexistence (Calatayud et al. 2019).

Previous works suggest that the symbiotic mutualism between woody plants and mycorrhizal fungi can modulate species interactions and, consequently, determine forest community diversity (Zahra et al. 2021). Most woody plant species associate with either arbuscular mycorrhizal (AM) or ectomycorrhizal (EM) fungi (Brundrett and Tedersoo 2018), which differ in their functional roles. For example, EM fungi can mobilize organic-bound nutrients and typically offer stronger pathogen protection, which may reduce CNDD effects in EM-associated trees relative to AM-associated trees (Laliberté et al. 2015). In contrast, AM fungi depend on the activity of saprotrophic fungi to access mineral nutrients. Consequently, AM-dominated communities tend to occur in soils with abundant communities of both saprotrophic and facultative pathogenic fungi which can increase CNDD (Eagar et al. 2025). Based on these functional differences, it is hypothesised that EM-dominated forests support lower tree species diversity compared to AM-dominated forests (Tedersoo et al. 2020). This prediction is consistent with observational and experimental evidence showing that EM trees often exhibit conspecific facilitation, while AM trees exhibit strong conspecific inhibition (Bennett et al. 2017). Another hypothesis suggests that niche partitioning of nutrient acquisition between mycorrhizal strategies can favour the coexistence of both mycorrhizal types and promote plant

coexistence (Liu et al. 2018). In accordance with this prediction, tree species diversity across broad environmental gradients is highest in forest communities where AM and EM strategies coexist (Carteron et al. 2022). However, recent evidence supports an additional hypothesis that predicts the co-occurrence of both patterns, with tree species diversity being highest in mixed AM–EM forests and lowest under EM dominance (Jiang et al. 2025; H1 in Fig. 1). Moreover, climate and soil conditions likely modulate the association between mycorrhizal dominance and tree diversity patterns. While the reduction in tree species diversity under EM dominance is stronger in tropical forests, likely due to more intense CNDD in AM-dominated communities, mixed AM–EM forests support the highest diversity in temperate and boreal regions, likely reflecting greater niche partitioning between mycorrhizal strategies (Jiang et al. 2025).

Despite these patterns, how the relationships between mycorrhizal strategies and woody species (trees and shrubs) diversity vary with forest stand development has been rarely explored. The mycorrhizal composition of dominant canopy trees largely determines soil fungal communities and soil abiotic conditions, thereby influencing the environment experienced by other woody plants and, consequently, the outcomes of competitive and facilitative dynamics across stand development stages (Eagar et al. 2025). CNDD tends to be strongest in early tree life stages (Zhu et al. 2015) and, therefore, it can be expected that the influence of mycorrhizal dominance on density-dependence processes is higher during early forest development. However, positive interactions may also drive patterns in community dynamics during early-stage development. Complementarity among tree species can be stronger in early development forests and weaken as forests develop to later stages (Gao et al. 2025). In addition, complementarity effects may depend on the spatial co-occurrence of different mycorrhizal strategies (Luo et al. 2023). We therefore hypothesize that in early development stands AM-dominated forests may exhibit higher woody species diversity than EM-dominated forests due to stronger CNDD, while mixed AM–EM stands may support the highest diversity because of increased niche partitioning combined with moderate CNDD (H2 in Fig. 1).

In contrast, the structure of late development forests can result from long-term biotic interactions and environmental filtering. In subtropical and tropical forests of southeast Asia, EM-dominated canopies often develop over a diverse AM-rich understory of trees and shrubs, likely reflecting recruitment dynamics mediated by functional differences in nutrient acquisition and pathogen protection between mycorrhizal strategies (Johnson et al. 2023). Other highly diverse communities are dominated by AM-associated trees, reflecting distinct ecological contexts (Steidinger et al. 2019) and stronger plant–soil feedbacks mediated by natural

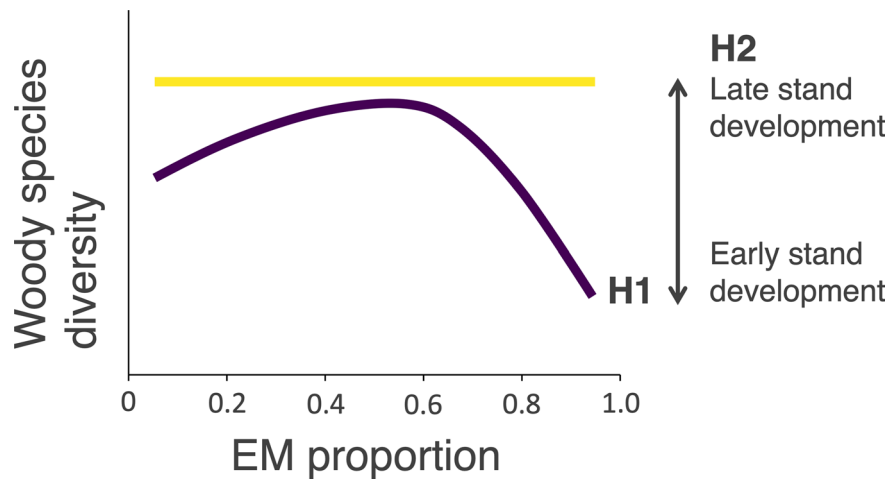


Figure 1. Conceptual representation of two hypotheses regarding the association between mycorrhizal dominance and woody species diversity. Ectomycorrhizal (EM) dominance is taken as reference, and it refers to the proportion of EM-associated species across canopy-dominant trees in a forest community (see main text for details). Hypothesis 1 (H1): Woody species diversity peaks in mixed AM–EM forests through niche partitioning and complementarity but remains higher in AM-dominated forests due to stronger conspecific negative density dependence compared to EM-dominated forests. Hypothesis 2 (H2): Early development forests show H1-like patterns, whereas in late development forests woody species diversity is constant across the EM dominance levels due to stabilising processes within AM and EM-dominated stands and saturation of the benefits of mixed mycorrhizal stands.

enemies and generalist fungal partners associated with AM strategies (Delavaux et al. 2023). Across late-development forests, therefore, we predict that woody species diversity may remain high regardless of mycorrhizal dominance because the mycorrhizal influence of dominant-canopy trees may promote recruitment dynamics that favour the accumulation of less abundant woody species (Eagar et al. 2025), while complementary effects among co-occurring mycorrhizal strategies may become progressively saturated over time (H2 in Fig. 1).

In this study, we examine how mycorrhizal dominance relates to local woody species diversity across gradients of forest stand development and climate in subtropical and tropical forests. By comparing early- and late-development stands varying in AM and EM dominance, we contrast observed patterns with two hypotheses (H1–H2 in Fig. 1) that propose distinct roles of mycorrhizal strategies in shaping distributional patterns of woody species diversity.

Material and methods

Study system and dataset

The study system covers tropical and subtropical forests distributed in Taiwan, a mountainous island that straddles the Tropic of Cancer. Across the island, temperature variability is mostly driven by a wide elevational gradient that ranges from sea level to more than 3900 m a.s.l., while precipitation patterns are strongly influenced by monsoonal exposure. Forest types are distributed along this elevational gradient, with broadleaved and evergreen forests in lowlands, and mixed and coniferous forests at mid- and high elevations, respectively (Li et al. 2013). Deforestation and logging were extensive from low to mid elevations and more localised at high

elevation up to the 1980s, while natural disturbances (including landslides) are common due to the complex topography and the occurrence of typhoons and earthquakes (Lu et al. 2001, Chen et al. 2004, Yang et al. 2022). As a result, regenerating early development forests and late development stands are distributed across the entire elevational gradient.

We used data from the 4th Taiwan National Forest Inventory (NFI; www.forest.gov.tw/0000052), a systematic, plot-based survey conducted across the forested mountainous regions of Taiwan between the 9 August 2008 and 23 January 2013. The NFI includes data over 1548 plots, spaced on average 2871 m apart, and encompasses > 80 000 trees and shrubs across 444 species. Each standard plot is approximately 0.05 ha (from 0.013 to 0.110 ha), with one plot side fixed at 17.6 m perpendicular to the slope and the other side with variable size and parallel to the slope to maintain the projected plot area and ensure a standard plot size in remote sensing imagery. All trees and shrubs with diameter at breast height (dbh) greater than 5 cm were identified to species level and measured within each plot. A detailed description of the NFI dataset can be found in O'Sullivan et al. (2021). Species names were standardised according to the 'World Checklist of Vascular Plants' (Govaerts et al. 2021).

Temperature and cold tolerance limits have been shown to be a strong driver of global distribution of mycorrhizal types (Barceló et al. 2019). Therefore, we used the mean winter temperature (coldest quarter of the year) for the period 1981–2010 from CHELSA ver. 2.1 climatic dataset (Karger et al. 2017) to characterise the climatic variability along the elevation range covered by the NFI plots (from 0 to 3769 m a.s.l.), encompassing tropical, subtropical, temperate and alpine climate zones (Li et al. 2013). Although precipitation varies across the island due to the influence of

monsoons and topography, it negatively correlates with mean winter temperature (Supporting information). Therefore, we used mean winter temperature as single variable to represent the climatic variability along the elevational gradient, and to maintain parsimony in our modelling approach. We additionally obtained soil pH and soil (N) nitrogen data from SoilGrids ver. 2.0 (Poggio et al. 2021) to explore the potential contribution of soil conditions to woody species diversity. Soil pH and soil N were calculated as average values weighted across the six soil depth levels.

For the assignments of mycorrhizal types, we used the FungalRoot ver. 2.0 database, as it is currently the largest global database of mycorrhizal trait information for plants (Soudzilovskaia et al. 2022). We successfully assigned mycorrhizal type to 98% of the tree and shrub species in the data, using recommended genus-level classifications where species-level data was not available. Across species, 358 were classified as AM-associated, 45 as EM-associated, 3 as dual AM/EM-associated and 38 as ericoid mycorrhizal, non-mycorrhizal, non-mycorrhizal/dual AM/EM, or uncertain. All species were maintained in the dataset because they contribute to species diversity of the plots. The most abundant species across plots included *Machilus japonicus*, *Actinodaphne acuminata*, *Machilus thunbergii*, *Quercus longinix*, *Tsuga chinensis* and *Lithocarpus kawakamii* representing both AM- and EM-associated species. A complete list of species and assigned mycorrhizal type is provided in Supporting information.

From the tree diameter measurements, we identified the largest 100 trees per hectare in each plot and calculated two metrics derived from this subset of trees. On the one hand, we used the mean dbh of these dominant trees as indicator of plot-level stand development. Lower values indicate early development stands, while higher values correspond to late development stands. This metric has been shown to correlate well with established indicators of forest stand development, such as stand age (Ducey and Kershaw 2023). On the other hand, we calculated the proportion of total basal area, estimated from the largest 100 trees per hectare, assigned to AM and EM strategies. We focused on the largest trees because they not only spatially dominate the stand but also are typically the oldest individuals and, therefore, have the greatest influence on soil properties and fungal communities (Wardle et al. 2004, Eagar et al. 2025). These effects make these trees a proper indicator of spatial and temporal mycorrhizal dominance. The basal area of dual AM/EM tree species was assigned as half AM and half EM in the calculation of mycorrhizal dominance (Carteron et al. 2022). We used the proportion of EM trees as an indicator of mycorrhizal type dominance in the analyses because most plots are dominated by either EM or AM trees (90% of plots with EM + AM proportions ≥ 0.9) and, therefore, their proportions are largely inverse (Carteron et al. 2022).

Finally, we calculated two metrics of woody species diversity: woody species richness, that is, the number of observed woody species in each plot, and woody species evenness estimated using the inverse of Simpson's index, using species basal area as indicator of species relative abundance.

Across plots, woody species richness averaged 11.3 species (range = 1–46), while woody species evenness averaged 3.9 (range = 1.0–14.8). Diversity metrics were calculated using the 'vegan' R package (Oksanen et al. 2001).

Analyses

We quantified the effect of EM dominance, climate, and stand development on woody species diversity by fitting generalized additive models (GAMs) (Wood 2000, Pedersen et al. 2019), implemented with the 'mgcv' R package (Wood 2000). Woody species richness and evenness were modelled following a negative binomial and gamma distribution, respectively. Each model included a tensor product smooth of EM proportion, stand development, and mean winter temperature of each plot, with cubic regression splines as the basis for smooths terms. The models also incorporated a bivariate smooth of plot longitude and latitude to account for spatial dependence and reduce residual spatial autocorrelation in woody species diversity. We also included the natural logarithm of both total woody plant density and plot area as fixed effects. Woody plant density was included to account for the fact that plots with higher density support more individuals and thus a greater probability of having higher species diversity. Plot area was included to adjust for differences in sampling effort among plots. Because soil pH and soil N strongly covaried with mean winter temperature (correlation coefficients: soil N = -0.83 ; soil pH = 0.67) they were not included in the main analyses. However, we evaluated the potential effect of soil variables by including them as fixed effects in alternative models, but model performance did not significantly improve.

Model diagnostics were conducted by inspecting residual plots using the 'mgcv', 'gratia', and 'DHARMA' R packages (Wood 2000, Hartig 2016, Simpson 2019). We assessed the relationships between the response variables and key predictors using the 'visreg' R package (Breheny 2012), visualized smooth terms using 'gratia' R package (Simpson 2019), and evaluated model performance using the performance R package (Lüdtke et al. 2019), including predictive accuracy against observed values (see <https://doi.org/10.5281/zenodo.20516321> for further details and to reproduce results of the models).

To contrast observed patterns with main hypotheses on the association of EM dominance with woody species diversity (Fig. 1), we used average predictive comparisons (Gelman and Pardoe 2007). Specifically, we predicted woody species diversity setting EM dominance under three levels: 1) EM-dominated forests (EM proportion = 0.99, i.e. the 95th percentile based on its observed distribution), 2) AM-dominated forests (EM proportion = 0, i.e. the 5th percentile based on its observed distribution), and 3) mixed AM–EM forests (EM proportion = 0.5). Each of these three predictions were repeated with stand development set to three different levels based on the distribution of mean dbh of the largest 100 trees per hectare: 1) the 5th percentile (i.e. early stand development), 2) the 95th percentile (i.e. late stand development), and 3) the 50th percentile (i.e. median

stand development). For each level of stand development, we calculated the predicted differences in woody species diversity among the three EM dominance levels: EM versus AM, EM versus mixed AM–EM, and mixed AM–EM versus AM. These comparisons allowed us to evaluate how woody species diversity associates not only with dominance by a particular mycorrhizal type but also with coexistence between EM and AM tree species. Changes in woody species diversity were summarized as the median difference in predicted values. Positive values indicate higher woody species diversity in the first term of each comparison (e.g. EM > AM), while negative values indicate lower woody species diversity. Additionally, we computed the median predicted woody species richness and evenness for each combination of EM dominance and stand development levels to visualize the expected association between EM dominance and woody species diversity across stand development stages.

To evaluate how the associations of EM dominance and stand development with woody species diversity change with climatic conditions, we repeated the average predictive comparisons including mean winter temperature as a factor. We selected three representative climate scenarios by setting mean winter temperature to the median of three climatic regions along the temperature gradient across our dataset, i.e. the 12.5th percentile (cold climate), 50th percentile (median climate), and 87.5th percentile (warm climate). Because both the mean dbh of the largest 100 trees per hectare and the proportion of EM-associated woody plants decrease with increasing temperature (Supporting information), we conditioned the values of stand development and EM dominance on their observed distributions within each climatic region. Specifically, for each temperature scenario, we fixed 1) stand development to the 5th, 50th, and 95th percentiles, based on its observed distribution within each temperature region,

and 2) EM proportion to the 95th percentile, based on its observed distribution within each temperature region, and to 0 (AM-dominated forests) and 0.5 (mixed AM–EM forests). This approach ensured that predictions reflected realistic combinations of forest stand development and EM dominance under the different climatic conditions. It is important to note that the realized range of EM dominance varied across climates and stand development stages. In cold regions, plots spanned the full EM dominance gradient (0–1), whereas in median and warm climates the gradient was truncated, with high EM dominance (≥ 0.8) mainly observed in early development stands. Consequently, EM-dominated, late-development stands as those observed in cold climates were absent in median and warm climates, and predictions for these combinations should be interpreted accounting for the fact that late development stands in median and warm climates correspond to structurally younger forests relative to late development stands in cold regions. We then compared predicted woody species diversity across EM dominance levels within each level of stand development, summarizing outcomes as median differences in predicted woody species richness and evenness, and visualising the median of predictions in woody species richness and evenness for each combination of EM proportion and stand development levels.

Results

We found that patterns in woody species richness were linked to variation in EM dominance and forest stand development (Fig. 2A, Supporting information). Specifically, EM dominance was related to lower woody species richness across early stand development, whereas in late stand development, EM dominance showed little association with woody species

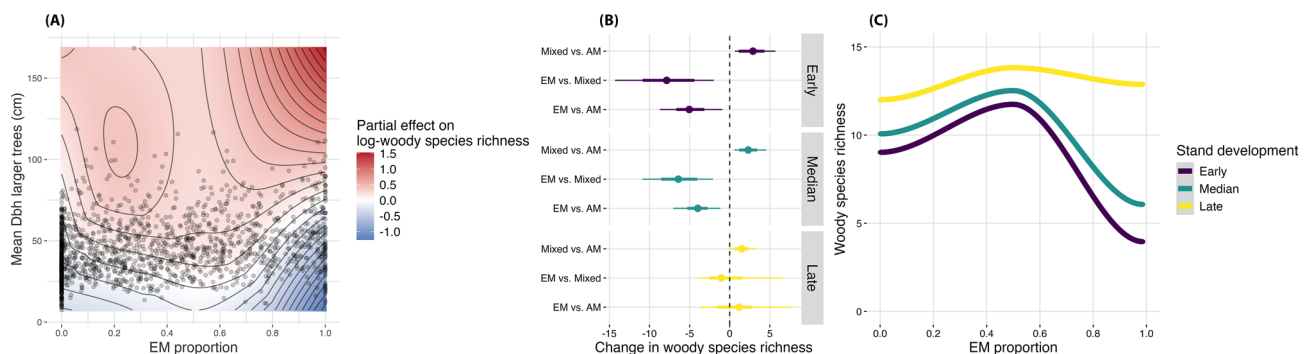


Figure 2. Associations among ectomycorrhizal (EM) dominance, stand development and woody species richness. (A) Partial effects of EM proportion and stand development (mean dbh of the largest 100 trees ha^{-1} , in cm) on changes in woody species richness (log-scale), based on generalized additive model (GAM) predictions. Observed data points are overlaid for reference. (B) Average predictive comparisons of woody species richness across three EM dominance levels: EM versus AM, EM versus mixed AM–EM, and mixed AM–EM versus AM, and at three scenarios of stand development defined by the 5th percentile (early stand development), 50th percentile (median stand development), and 95th percentile (late stand development) of mean dbh of the largest 100 trees ha^{-1} . Points represent median predicted differences in woody species richness; bars indicate 66 and 95% equitailed CI. Positive values indicate higher woody species richness in the first term of each comparison, while negative values indicate lower woody species richness. (C) Median predicted woody species richness across the full range of EM dominance and stand development levels, illustrating their joint effects. Predictions on woody species richness along EM dominance are shown as a continuous line for clarity but are based on three representative EM dominance levels (Material and methods) and should be interpreted as expected trends rather than direct data coverage.

richness (Fig. 2A). Additionally, woody species richness increased towards warmer climates regardless of EM dominance and was generally higher in late stand development, although it should be noted that late development forests as those observed in cold climates were absent from median to warm climates (Supporting information).

We found that woody species richness was 26% lower on average in EM-dominated forests when compared to AM-dominated forests, and 40% lower on average when compared to mixed AM–EM forests, while it declined by 18% on average in AM-dominated forests when compared to mixed AM–EM forests (Fig. 2B–C). However, these patterns were evident in early- and median-development stands. In contrast, in late-development stands, woody species richness remained similar between EM-dominated, AM-dominated, and mixed AM–EM forests (Fig. 2B–C).

Across the three climatic scenarios, we found that woody species richness decreased more under EM dominance in cold climates consistently across all stages of stand development and in median climates in early development stages (Fig. 3, Supporting information). In cold regions, EM-dominated forests exhibited 38 and 42% lower woody species richness on average compared to AM- and mixed mycorrhizal forests, respectively (Fig. 3). Differences between AM-dominated and mixed AM–EM forests were minimal under cold conditions

(Fig. 3, Supporting information). In median climates, woody species richness was 12% lower in EM-dominated forests compared to AM-dominated ones only in early stand development, while mixed AM–EM forests consistently supported 22 and 23% higher woody species richness on average than EM- and AM-dominated forests, respectively (Fig. 3). However, in late-development stages under median climates, woody species richness was comparable between EM-dominated, AM-dominated, and mixed AM–EM forests (Fig. 3, Supporting information). In warm climates, mixed AM–EM forests had 30 and 8% higher woody species richness on average than AM- and EM-dominated forests at early stand development, respectively. However, at median and late-development stages, woody species richness was similar or even increased in EM-dominated forests relative to mixed AM–EM forests (Fig. 3, Supporting information).

Patterns in woody species evenness were partially consistent with those observed for species richness. Evenness was consistently highest in mixed AM–EM forests across stand development stages, averaging 59% higher than in EM-dominated forests and 31% higher than in AM-dominated forests (Fig. 4), and this pattern held across all climatic regions (Fig. 5). EM-dominated forests exhibited 40% lower evenness on average compared to AM-dominated forests (Fig. 4). These effects were most pronounced in median and cold climates,

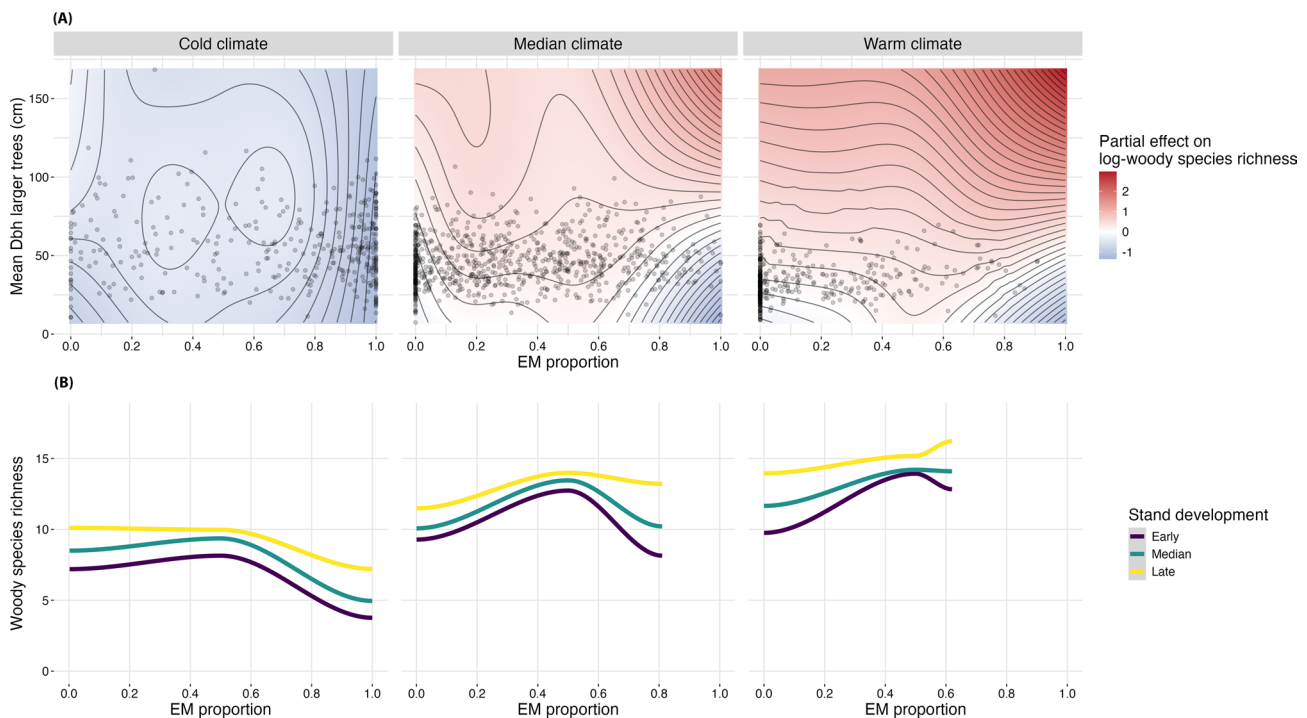


Figure 3. Associations among ectomycorrhizal (EM) dominance, stand development and woody species richness. (A) Partial effects of EM proportion and stand development (mean dbh of the largest 100 trees ha^{-1} , in cm) on changes in woody species richness (log-scale) based on generalized additive model (GAM) predictions, across three climatic regions. Observed data points are overlaid for reference. (B) Median predicted woody species richness along the range of EM dominance across stand development and climatic levels, illustrating their joint effects. Predictions on woody species richness along EM dominance are shown as a continuous line for clarity but are based on three representative EM dominance levels (Material and methods) and should be interpreted as expected trends rather than direct data coverage. See Supporting information for corresponding results in average predictive comparisons.

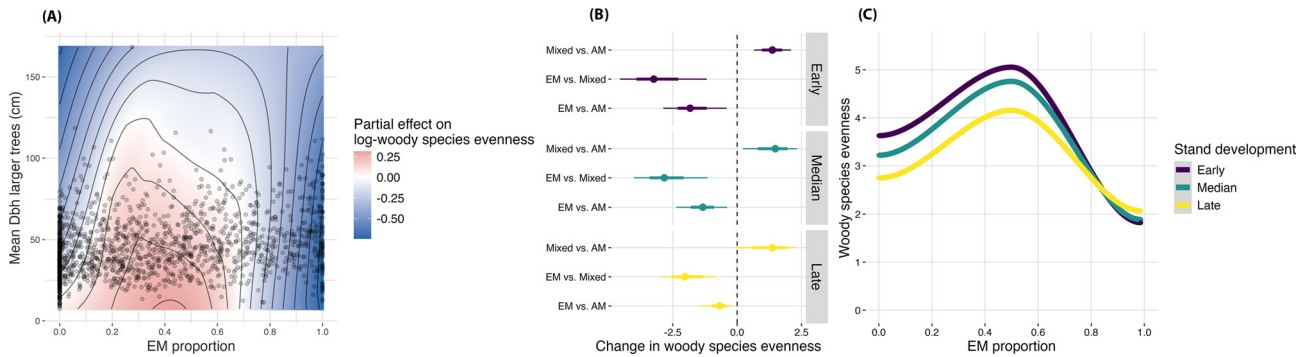


Figure 4. Associations among ectomycorrhizal (EM) dominance, stand development and woody species evenness. (A) Partial effects of EM proportion and stand development (mean dbh of the largest 100 trees ha^{-1} , in cm) on changes in woody species evenness (log-scale), based on generalized additive model (GAM) predictions. Observed data points are overlaid for reference. (B) Average predictive comparisons of woody species evenness across three EM dominance levels: EM versus AM, EM versus mixed AM–EM, and mixed AM–EM versus AM, and at three scenarios of stand development defined by the 5th percentile (early stand development), 50th percentile (median stand development), and 95th percentile (late stand development) of mean dbh of the largest 100 trees ha^{-1} . Points represent median predicted differences in woody species evenness; bars indicate 66 and 95% equitailed CI. Positive values indicate higher woody species evenness in the first term of each comparison, while negative values indicate lower woody species evenness. (C) Median predicted woody species evenness across the full range of EM dominance and stand development levels, illustrating their joint effects. Predictions on woody species evenness along EM dominance are shown as a continuous line for clarity but are based on three representative EM dominance levels (Material and methods) and should be interpreted as expected trends rather than direct data coverage.

while differences among forest types were less marked in warm regions (Fig. 5, Supporting information). Although the influence of EM dominance on woody species evenness diminished in late-development stages – EM-dominated

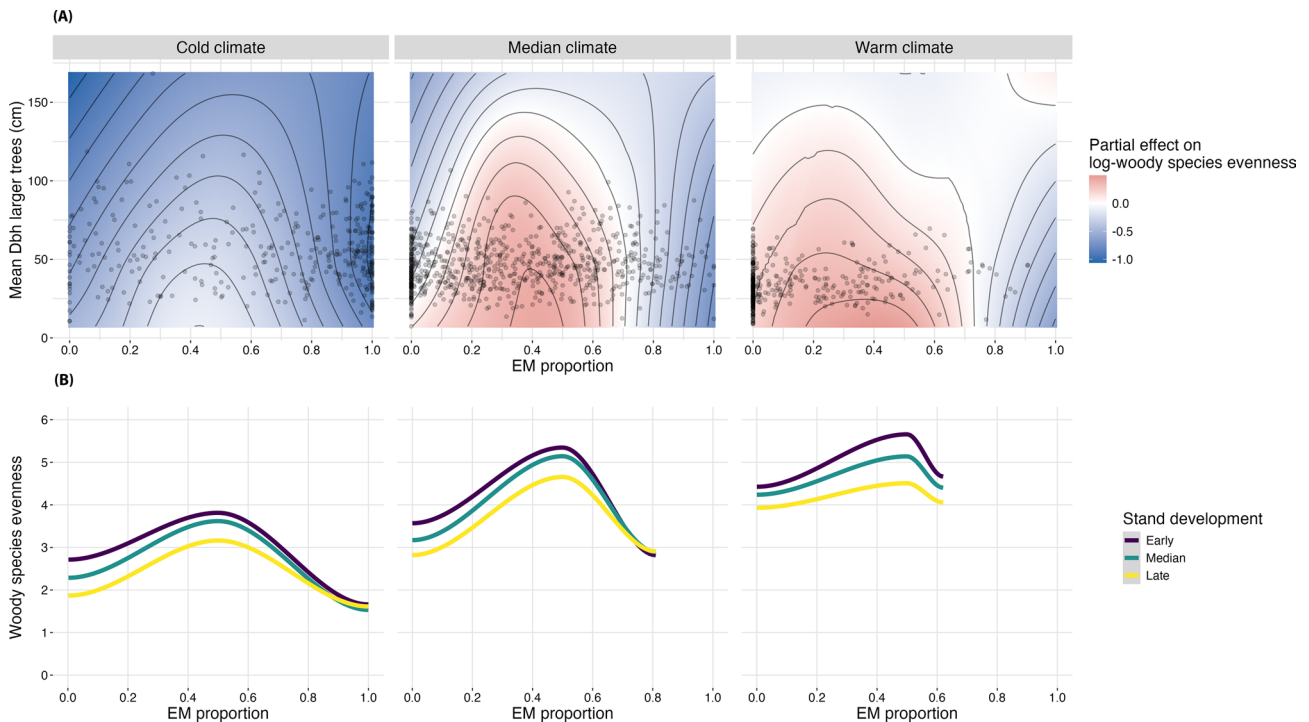


Figure 5. Associations among ectomycorrhizal (EM) dominance, stand development and woody species evenness. (A) Partial effects of EM proportion and stand development (mean dbh of the largest 100 trees ha^{-1} , in cm) on changes in woody species evenness (log-scale) based on generalized additive model (GAM) predictions, across three climatic regions. Observed data points are overlaid for reference. (B) Median predicted woody species evenness along the range of EM dominance across stand development and climatic levels, illustrating their joint effects. Predictions on woody species evenness along EM dominance are shown as a continuous line for clarity but are based on three representative EM dominance levels (Material and methods) and should be interpreted as expected trends rather than direct data coverage. See Supporting information for corresponding the results from average predictive comparisons.

forests in warm climates exhibited 14% lower evenness on average compared to mixed AM–EM forests and similar evenness on average relative to AM-dominated forests – overall patterns remained consistent across stages of stand development (Fig. 5, Supporting information).

Discussion

Woody species diversity in subtropical and tropical montane forests is related to mycorrhizal dominance, but this association varies with stand development and climate. Our results corroborate H1 (Fig. 1), confirming that woody species richness is lower in EM-dominated stands and highest in mixed AM–EM forests. However, as predicted by H2 (Fig. 1), these patterns clearly emerge in early development stages and dissipate in late development stages. In addition, the reduction in richness associated with EM dominance was strongest in cold regions, diversity peaks in mixed AM–EM forests were most evident in median climate and early development stands, and the convergence in woody species richness across levels of mycorrhizal dominance was clearest in late-development forests under median and warm climatic conditions. Woody species evenness showed a simpler pattern, in accordance with H1. Mixed AM–EM stands maintained the most even communities, while EM-dominated forests were generally less even, although these differences weakened toward warmer climates. Together, these findings reveal that the influence of mycorrhizal dominance on woody species diversity emerges through interactions with forest development and climate, providing new understanding of community dynamics in subtropical and tropical forests.

Observed patterns across forest stand development support H2, which predicts stronger mycorrhizal-dominance effects in early- than in late development stands (Fig. 1). In early development stands, woody species richness and evenness were lower in EM-dominated forests, suggesting that EM canopy-dominant trees can alleviate conspecific negative density-dependence (CNDD) and limit heterospecific recruitment. This pattern is consistent with experiments showing that EM trees foster more positive plant–soil feedbacks relative to AM trees in temperate (Kadowaki et al. 2018) and tropical forests (Segnitz et al. 2020). This EM advantage could be due to greater allocation of host photosynthates, the ability to exploit organic nutrient pools, and stronger pathogen resistance compared to AM trees (Eagar et al. 2025). By contrast, mixed AM–EM stands showed both higher woody species richness and evenness in early development forests, likely reflecting species complementarity resulting from the combined effects of partitioning in nutrient acquisition and reduced pressure of natural enemies. These processes can be particularly strong among early tree life stages (Pu et al. 2020).

In late development forests, woody species richness did not vary with mycorrhizal dominance. This result is consistent with the structure of tropical and subtropical forests in many locations in Asia, where EM trees achieve canopy

dominance through efficient phosphorus acquisition and pathogen resistance while maintaining diverse AM-rich understories (Johnson et al. 2023, Mao et al. 2024). In addition, tropical EM fungi, likely less host-specific than previously assumed, may also promote the coexistence among different EM woody species (Corrales et al. 2018). Elsewhere, AM-dominated stands may sustain high diversity by strong CNDD or facilitation through their generalist fungal symbionts (Delavaux et al. 2023). Differences between early- and late development stands may also reflect shifts in nutrient acquisition strategies. Whereas early development forests rely on extensive fine-root proliferation for rapid nutrient uptake, increasing competition, late development stands depend more on root exudation and enzymatic mineralization (Rondina et al. 2019, Wang et al. 2024). These differences could promote a diversification of nutrient-mobilisation strategies that facilitates coexistence in late development forests. Other key ecological processes operating throughout tropical forest development, such as seed movement through the landscape (Dent and Estrada-Villegas 2021), may also contribute to differences among developmental stages and the convergence in woody species richness across mycorrhizal dominance levels at late development stages.

Climate influenced the associations between woody species diversity and mycorrhizal dominance. In cold regions, EM-dominated forests showed lower woody species richness and evenness, which is consistent with weak CNDD that allows EM-associated plant species to perform well under altitudinal stressors such as cold temperatures and nutrient scarcity (Wagg et al. 2011, Burg et al. 2024), likely contributing to upslope shifts of high elevation woody species in Taiwan (O’Sullivan et al. 2021). In median and warm climates, woody species richness peaked in mixed AM–EM forests in early stand development, while the negative association between woody species richness and EM dominance weakened or even reversed in late-development stands. It is worth to note that “late development stands” in median and warm climatic conditions correspond to younger forests as compared to late development stands in cold regions (Fig. 3, Supporting information), likely reflecting the more intense past deforestation and logging from mid- to low elevations (Yang et al. 2022). Thus, estimates of woody species richness in late development stands across median and warm climates may not reflect the diversity of a fully developed stand as those found in cold climates. Given that many early development forests in median and warm climates are dominated by EM woody species (e.g. EM proportion ≥ 0.7 ; Fig. 3), it is possible that the observed convergence in species richness across the mycorrhizal dominance levels in these climatic regions could be potentially stronger if EM-dominated, fully late development stands were present. These patterns align with the fact that nutrient-limited forests in southeast Asia often develop EM-dominated canopies, once trees invest in EM symbioses to access recalcitrant forms of phosphorus (Johnson et al. 2023). Therefore, variation in soil nutrients likely contributes to the observed patterns in woody species diversity. However, soil pH and soil nitrogen strongly covaried with mean winter temperature in

our dataset, with warm forests generally associated with more basic and N-poor soils and cold forests with more acidic and N-rich soils. This collinearity limits our ability to disentangle the effects of climate from soil conditions. The observed elevational patterns also differ from Jiang et al. (2025), who reported stronger negative associations between tree species diversity and EM dominance in warm low-latitude forests and mixed AM–EM forest peaks in cold regions, underscoring that elevational and latitudinal climatic gradients are not necessarily analogous and that stand development can interact with climate to determine forest community patterns.

Across climates, mixed AM–EM forest communities supported the highest woody species diversity. This pattern is strongly in line with H1, which posits that mycorrhizal coexistence favours forest community diversity (Fig. 1). Interestingly, some distinct patterns emerged between diversity metrics across stand development stages. While woody species richness converged in late development stands, mixed mycorrhizal forests maintained more even woody species abundances across stand development stages. This result suggests that co-occurring mycorrhizal strategies could promote more equal species abundances than high species richness through processes that maximise the performance across plant species present in a community. For example, mixed mycorrhizal stands can foster heterogeneity in the soil and through the canopy, diversifying resource acquisition strategies (Liu et al. 2018) and thus favouring community productivity (Luo et al. 2023). Moreover, plant populations occurring in more diverse plant communities can experience lower impact of species-specific natural enemies (Xi et al. 2025). Therefore, the stabilisation of species coexistence could emerge from complex recruitment dynamics mediated by feedback effects between co-occurring mycorrhizal strategies (Eagar et al. 2025).

Previous studies have shown that tree species diversity tends to peak in mixed mycorrhizal communities (Carteron et al. 2022) and decline under EM dominance, with these relationships influenced by climate (Jiang et al. 2025). However, the role of forest stand development has remained less explored in this context. Our findings indicate that the influence of mycorrhizal strategies on woody species coexistence shifts across forest developmental stages, offering new insights into emergent distributional patterns of woody species diversity. While resolving the diversity and drivers of mycorrhizal fungi in southeast Asia remains a priority (Corrales et al. 2022), our study suggests that understanding shifts in their communities and ecological roles across forest development will be pivotal for predicting subtropical and tropical ecosystem recovery under global change.

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Author contributions

Albert Vilà-Cabrera: Conceptualization (lead); Data curation (equal); Formal analysis (lead); Funding acquisition (supporting); Methodology (equal); Validation (equal); Visualization (equal); Writing – original draft (lead); Writing – review and editing (lead). **Julen Astigarraga:** Conceptualization (supporting); Data curation (supporting); Formal analysis (supporting); Methodology (equal); Validation (equal); Visualization (equal); Writing – review and editing (supporting). **Kirsten S. W. O'Sullivan:** Data curation (equal); Writing – review and editing (supporting). **Karina E. Clemmensen:** Writing – review and editing (supporting). **Henna Tyyskä:** Data curation (supporting); Writing – review and editing (supporting). **Sarah Greenwood:** Writing – review and editing (supporting). **Josep Padullés Cubino:** Data curation (supporting); Writing – review and editing (supporting). **Jan-Chang Chen:** Funding acquisition (lead); Investigation (lead); Resources (lead); Supervision (lead); Writing – review and editing (supporting). **Alistair S. Jump:** Conceptualization (supporting); Funding acquisition (supporting); Methodology (supporting); Writing – review and editing (supporting).

Transparent peer review

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Data availability statement

We used data from the 4th Taiwan National Forest Inventory (www.forest.gov.tw/0000052). The dataset and R code used in this study are openly available in Zenodo at: <https://doi.org/10.5281/zenodo.20516321> (Vilà-Cabrera et al. 2026).

Supporting information

The Supporting information associated with this article is available with the online version.

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