Canopy height and stand density mask nature's inherent synergy between forest structural complexity and diversity

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Abstract

Tree species diversity is widely assumed to correlate positively with structural complexity in forests, as differences in crown architecture among species enhance structural complexity through physical complementarity. While this complex-diversity relationship has been confirmed experimentally, it frequently weakens or reverses in natural forests. The mechanisms underlying this inconsistency remain unclear. We used the field measurements and drone-derived LiDAR data from the Tiantong 20-ha forest community in eastern China to calculate tree species diversity and forest structural complexity. To assess the mechanism driving the complex-diversity relationship, we calculated stand density and canopy height. We try to answer the following questions: (a) What is the relationship between structural complexity and species diversity in the forest plot? (b) How stand density or canopy height mediates the interplay between structural complexity and species diversity? (c) When controlling for stand density and canopy height effects, would a positive complexity-diversity relationship be revealed? We revealed that canopy height and stand density jointly mediate the observed negative complexity-diversity relationship: tall canopies reduced understory species diversity via shading, disproportionately excluding shade-intolerant species; while high stand density suppressed structural complexity, possibly by limiting vertical branching. When these mediating variables were statistically controlled for, a positive complexity-diversity relationship emerged. Our findings, therefore, resolve the apparent inconsistency by demonstrating that structural complexity and diversity inherently facilitate mutual reinforcement in natural forests, but confounding factors like canopy height and stand density may mask this relationship.

Keywords: forest structural complexity, tree diversity, canopy height, stand density, LiDAR, disturbance, light competition

树冠高度和林分密度掩盖了森林结构复杂度和多样性之间的内在关系

摘要：一般认为树木的物种多样性与森林结构复杂度呈正相关关系，因为不同物种可以通过树冠结构的互补作用促进森林结构复杂度。虽然复杂度与多样性的正关系已在控制实验中得到证实，但在自然森林中却常常会减弱或逆转。这种不一致的机制尚不清楚。本研究利用中国东部的天童20公顷森林群落的实地测量数据和无人机获取的激光雷达数据分别计算树木的物种多样性和森林结构复杂度。为了评估复杂度与多样性关系的机制，本研究计算了林分密度和树冠高度，试图回答以下问题：(1)在森林样地中，森林结构复杂度与物种多样性之间存在怎样的关系？(2)林分密度或树冠高度如何调节森林结构复杂度和物种多样性之间的关系？(3)在控制了林分密度和树冠高度的影响后，森林结构复杂度与物种多样性的关系是否为正？结果发现，观测到的复杂度与多样性之间的负相关关系是由树冠高度和林分密度共同影响的：高大的树冠通过遮荫作用减少了林下物种的多样性，而且主要是不耐阴的物种；密集的树木个体则可能通过限制垂直分枝来抑制森林结构复杂度的增加。当这些变量在统计上得到控制后，森林结构复杂度和物种多样性之间为正相关关系。综上，本研究证明了在自然森林中，森林结构复杂度和多样性本身会促进相互强化，而树冠高度和林木密度等干扰因素可能会掩盖两者之间的正关系。

关键词：森林结构复杂度，树木多样性，树冠高度，林分密度，激光雷达，干扰，光照竞争

INTRODUCTION

Forest structural complexity describes the heterogeneity of vegetation within a forest canopy, characterized by variations in tree sizes, crown architectures, and three-dimensional spatial arrangements (Ehbrecht *et al.* 2021). This complexity creates diverse abiotic conditions (e.g. light availability) that directly promote tree species diversity (Gámez and Harris 2022). Meanwhile, experimental studies reveal that diverse tree communities amplify structural complexity through varied growth forms (e.g. crown morphology), which in turn boost productivity (Williams *et al.* 2017; Ray *et al.* 2023). This reciprocal positive relationship has profound practical significance: protecting structurally complex forests safeguards biodiversity (Deere *et al.* 2020) while managing diversity enhances productivity via structural complexity (Jiang *et al.* 2024; Liu *et al.* 2024). However, in natural forest ecosystems, this relationship frequently weakens or even reverses (Supplementary Table S1), with the mechanisms underlying these discrepancies remaining unclear. Such inconsistencies hinder the translation of experimental insights into actionable management strategies (Coverdale and Davies 2023; LaRue *et al.* 2023).

A key factor potentially confounding the positive relationship between forest structural complexity and species diversity is stand density, which is the number of trees per unit area. While elevated stand density may increase the likelihood of observing diverse species due to sampling effects (Marquard *et al.* 2009; Storch*et al.* 2018; Chu *et al.* 2019), it may simultaneously suppress structural complexity by restricting the development of varied tree sizes, crown morphologies, and vertical stratification (Jack and Long 1991; Ehbrecht *et al.* 2017). If these opposing effects of stand density dominate in natural forests, the mutually reinforcing relationship between structural complexity and diversity could weaken or even reverse. Notably, natural forests often exhibit pronounced heterogeneity in stand density, with high-density stands frequently occurring on slopes prone to recurrent disturbances such as droughts, frost events, and storms (Álvarez-Yépiz *et al.* 2018; Ibanez *et al.* 2024). In contrast, experimental studies typically enforce strict controls over stand density by planting trees at equal densities and removing unwanted recruits (Perles-Garcia *et al.* 2021; Ray *et al.* 2023). Despite this divergence, whether stand density is a primary driver of discrepancies in the complexity-diversity relationship between experimental and natural ecosystems remains untested.

Another potential factor complicating the relationship between forest structural complexity and species diversity is canopy height, defined as the three-dimensional boundary encompassing both vegetation and airspace within the forest's upper layers (Gough *et al.* 2020; LaRue *et al.* 2023). Although taller canopies are often associated with greater structural complexity owing to the development of distinct vertical vegetation layers (Gough *et al.* 2020), they may simultaneously reduce understory light availability due to denser canopy cover (Matsuo *et al.* 2021; Binkley *et al.* 2010). This limited light resource could intensify competitive exclusion among understory species, thereby suppressing species diversity (Eskelinen *et al.* 2022). Consequently, canopy height may exert opposing influences on the relationship, enhancing structural complexity while indirectly diminishing species diversity. These counteracting effects may be more pronounced in natural forests than in short-term experimental settings, as natural systems often support taller, denser canopies with more intense understory light competition (Perles-Garcia *et al.* 2021). However, empirical studies have yet to confirm if canopy height drives the differing complexity-diversity patterns observed in experimental versus natural ecosystems.

To investigate how stand density and canopy height shape the complexity-diversity relationship in natural forests, we analyzed a 20-ha subtropical mature forest plot dominated by evergreen broad-leaved tree species in a monsoon-driven coastal region (Yang *et al.* 2011). This ecosystem experiences frequent typhoons, creating pronounced spatial variability in stand density and canopy height (Lu *et al.* 2021; Wang *et al.* 2014). We assessed the spatial patterns of stand density and canopy height across the plot and evaluated their individual and combined contributions to structural complexity and tree species diversity. Specifically, we asked the following questions: (a) What is the relationship between structural complexity and species diversity in the forest plot? (b) How does stand density or canopy height mediate the interplay between structural complexity and species diversity? (c) When controlling for stand density and canopy height effects, would a positive complexity-diversity relationship be revealed?

MATERIALS AND METHODS

Forest plot, quadrats, and tree species diversity

Our study was conducted in a 20-ha subtropical evergreen broadleaf forest plot on Tiantong Mountain in eastern China (29.80° N, 121.78° E, hereafter referred to as the Tiantong plot). The Tiantong plot receives an annual mean precipitation of 1,480 mm and an annual mean temperature of 16.4 ℃. The dominant soil type is yellow soil (Yang *et al.* 2011). The plot spans an elevation range of 304.26 to 602.89 m, with a mean elevation of 447.25 m. The plot was first inventoried in 2010 (Yang *et al.* 2011). Since then, it has been re-censused every five years using the same protocol (Davies *et al.* 2021). All woody plants (excluding lianas) with a diameter at breast height (DBH) of ≥ 1 cm have been tagged, measured, located, and identified to the species level. In 2020, the plot contained 106,551 free-standing trees representing 148 species. The dominant evergreen tree species of this plot include *Litsea elongata, Lithocarpus henryi*, and *Cyclobalanopsis nubium,* while dominant deciduous trees include *Choerospondias axillaris*, *Carpinus viminea*, and *Alniphyllum fortunei.*

To examine the relationship between forest structural complexity and species diversity within the Tiantong plot, we divided the entire plot into non-overlapping 20 m × 20 m quadrats. Within each quadrat, we estimated tree species diversity and forest structural complexity (details in the following section "Quantifying forest structural complexity"). The tree species diversity was estimated by species richness, Shannon entropy, and inverse Simpson concentration (referred to as Simpson diversity) using 2020 census data from the 20-ha Tiantong plot. For simplicity, we presented results based on species richness in the main text, as the results for the other two diversity indices were similar and were provided in Supplementary Table S2. To test the robustness of our findings, we repeated the above and following analyses at 10 m × 10 m and 50 m × 50 m quadrat scales. Given the consistent negative relationships across all three quadrat scales, we will focus our subsequent analysis on the 20 m quadrat scale.

Quantifying forest structural complexity

To gain a more detailed understanding of the forest structural complexity of the Tiantong plot, high-density point cloud data of the forest structure were acquired in March 2022 using a drone (D200; Feima Robotics, Shenzhen, China) equipped with a RIEGL miniVUX-1 laser scanner. To prevent point cloud density inconsistencies caused by variable aircraft height, we implemented a terrain-following flight strategy. This approach dynamically adjusts absolute flight elevation with terrain topography while preserving a fixed 71 m sensor-to-ground distance, thereby mitigating potential bias in forest structural complexity estimates arising from differential point densities. To get enough point density, the course spacing and side overlap rate were set as 14 m and 93%, respectively. The average point density of point cloud data was 446.50 ± 85.31 (mean ± SD) points·m^{-2}.

To ensure the accuracy of the point cloud data, several preprocessing steps were implemented following standard procedures. These steps aimed to remove noise and unwanted points (e.g. ground points) while preparing the data for further analysis. (1) Outlier removal: This process addressed points potentially influenced by wind, birds flying through the scan area, or multiple laser pulses hitting the same target. Points were identified as outliers if their distance to neighboring points exceeded the local average distance plus 5 standard deviations (mean + 5 × SD), calculated over their 30 nearest neighbors. This approach was combined with visual inspection for additional confirmation. (2) Ground filtering: This step categorized LiDAR points as either ground (terrain) or non-ground (vegetation). A progressive triangulated irregular network densification filtering (Zhao *et al.* 2016) was employed for this purpose. The UAV manager software (Version 1.6.7; Feima Robotics, Shenzhen, China) facilitated the implementation of both outlier removal and ground filtering. (3) Normalization: To minimize the influence of terrain variation on the point cloud, a normalization step was performed. This involved subtracting the elevation of each point from the corresponding ground elevation obtained from a digital elevation model (DEM) generated using the Kriging method in the "*gstat*" R package (Gräler *et al.* 2016). Additionally, points below 2 m were removed as our field survey only included trees with a DBH ≥ 1 cm. Trees with such small diameters (DBH ≤ 1 cm) typically have heights less than 2 m. The average point density of the final prepared point cloud data was 436.78 ± 81.65 (mean ± SD) points·m^{-2}. This point cloud density, nearly 5 times greater than typical values in recent studies (Liu *et al.* 2024), allows for a significantly more comprehensive representation of forest structural complexity.

Based on the final point cloud data of forest structure, canopy entropy was selected to quantify forest structural complexity for each quadrat since it fully considers the three-dimensional arrangements and space occupations of all canopy elements (e.g. leaves, branches, and stems) (Liu *et al.* 2022). Forests with varied DBH, height, and vertical canopy layers often exhibit greater structural complexity and canopy entropy. The canopy entropy, CE, was defined by the following formula (Eq. 1),

$$CE = \sqrt{{CE_{XY}}^2 + {CE_{XZ}}^2 + {CE_{YZ}}^2} \quad (1)$$

where CE_{XY}, CE_{XZ}, and CE_{YZ} present canopy entropy estimates for the XY-plane (horizontal dimension), XZ- and YZ-planes (vertical dimension), respectively. These estimates are calculated from the probability density function derived using kernel density estimation of the point cloud projected onto each plane (see Fig. 3 in Liu *et al.* 2022). For example, given the point density projected on the XY-plane, CE_{XY} was estimated by the probability density $p(x, y)$ at a location $l = [x, y]$ as the following equation (Eq. 2),

$$p(x, y) = p(l) = \frac{1}{n}\sum_{i=1}^{n} K_H(l - l_i) \quad (2)$$

where l_i is the location vector of the i^{th} point on the XY-plane, *n* is the total number of points on the plane, and K_H is the kernel function. Here, we selected the commonly used 2D Gaussian kernel, which can be expressed as follows,

$$K_H(l - l_i) = \frac{1}{2\pi\sqrt{|H|}} e^{-\frac{1}{2}(l-l_i)^T H^{-1}(l-l_i)} \quad (3)$$

$$H = \begin{vmatrix} h & 0 \\ 0 & h \end{vmatrix} \quad (4)$$

where *H* is a covariance matrix composed of bandwidth *h*. Bandwidth *h* determines the smoothness of the estimated probability density (Scott 2015). In addition to *CE*, the individual entropy values for each plane provide distinct insights into forest structural complexity. Specifically, the entropy of the XY-plane, CE_{XY}, primarily reflects variations in stand density, while the entropies of the vertical planes, CE_{XZ} and CE_{YZ}, are more indicative of variations in the number of vertical canopy layers (Liu *et al.* 2022).

Except for the canopy entropy, three additional structural complexity indices, foliage height diversity (FHD), coefficient of variation of height (CV_{ht}), and rumple, were calculated based on the final point cloud data. FHD quantifies the richness and evenness of vertical vegetation stratification by assessing the distribution of vegetation heights at 2 m, 5 m, 10 m, and 15 m. CV_{ht} measures internal canopy height heterogeneity as the coefficient of variation of vegetation heights across the entire point cloud. Rumple, a measure of the roughness of the outer canopy's surface (Kane *et al.* 2010), was calculated as the ratio of the outer surface area of the height of the canopy within a 1-m square grid to the ground area. All these indices were computed in the "*lidR*" package version 4.0.3 (Roussel *et al.* 2020).

Linking structural complexity and species diversity

Considering the various indices of forest structural complexity (i.e. foliage height diversity, CV of height, and rumple), we calculated Pearson's correlation coefficients between these indices. Many of these indices exhibited high correlations (Supplementary Table S2). Similar patterns were observed for various tree species diversity indices (i.e. species richness, Shannon diversity, and Simpson diversity) (Supplementary Table S2). To simplify our analysis, we focused on the relationship between canopy entropy and tree species richness, as similar relationships emerged for other structural complexity and diversity indices (Supplementary Fig. S1).

We employed simple linear regressions to evaluate the relationship between forest structural complexity and species diversity, utilizing “*gls*” function from the "*nlme*" package version 3.1.157 (Pinheiro *et al.* 2025). Given strong spatial autocorrelations in the residuals from these linear regressions (Moran’s test; Supplementary Table S3), we further examined the complexity-diversity relationship using three different spatial simultaneous autoregressive (SAR) models (spatial error model, lagged model, and mixed model) (Kissling and Carl 2008). The final SAR mixed model was selected based on achieving the lowest AIC values among candidate models (Supplementary Table S3). This approach accounts for spatial autocorrelation by considering its influence on both response and explanatory variables, encompassing both “inherent spatial autocorrelation” and “induced spatial dependence” (Bivand *et al.* 2021). The SAR mixed model can be mathematically expressed as follows,

$$Y = \rho WY + X\beta + WX\gamma + e \qquad (5)$$

Where Y denotes the response variable (forest structural complexity); X is the predictor matrix of tree species richness; β is a vector of slopes, and e represents the spatially independent errors; W is the spatial weights matrix (an $n \times n$ matrix with elements W_{ij} presenting a measure of the connection between locations i and j); ρW is included for the spatial autocorrelation in the response variable Y, and γ describes the autoregression coefficient of the spatially lagged explanatory variables (WX). The parameters of these spatial simultaneous autoregressive models were estimated using the "*spdep*" package version 1.3.3 (Bivand 2022).

Quantifying stand density and its impacts

Stand density was calculated as the ratio of the total number of recorded trees to the quadrat area (stems·m^{-2}). To simplify the initial analysis, we used simple linear regression models to evaluate the impact of stand density on tree species diversity and forest structural complexity. Subsequently, given the pronounced spatial autocorrelation observed in structural complexity (Supplementary Table S3), stand density, and tree species diversity (Supplementary Table S4), the Moran's I test revealed that the residuals from these linear regression models between stand density and either tree species diversity or forest structural complexity have statistically significant positive spatial autocorrelation (Supplementary Tables S4 and S5). We quantified the impacts of stand density either on tree species diversity or forest structural complexity using the method described in section "Jointly modeling the effects of stand density and canopy height" (model comparisons were presented in Supplementary Tables S4 and S5).

Quantifying canopy height and its impacts

We calculated the maximum canopy height for each 1-m² grid across the quadrat using the canopy height model. Subsequently, we computed the mean of these maximum canopy heights for each quadrat to obtain a measure of canopy height. We employed the simple linear models to explore the relationship between canopy height and either tree species diversity or forest structural complexity, and then evaluated the spatial autocorrelation of the regression residuals utilizing Moran's test (Supplementary Tables S6 and S7). Due to the significant spatial autocorrelation of the regression residuals, we quantified the impacts of canopy height either on tree species diversity or forest structural complexity using the method described in section 2.3 (model comparisons were presented in Supplementary Tables S6 and S7).

If high canopy height can influence species diversity by filtering out some species through reducing understory light conditions, species diversity of the understory would decline with canopy height at the quadrat scale. To test this, we categorized each tree based on its height into either the understory layer (height < 10m) or the canopy layer (height ≥ 10 m) and recorded the number of species in each layer for each quadrat. The height of every tree in the plot was estimated using a mixed effect model from the R package "*lme4*" (Bates *et al.* 2015): $\ln(Height) = \alpha + (\beta + \nu)\ln(DBH) + \upsilon + \varepsilon$, where α and β are the global intercept and the population mean slope, respectively; ν is the deviation of individual slopes from the population mean slope; υ is the deviation of mean individual trait values from the population mean; ε is the residual error—assuming a normal distribution with mean 0 and variance V_R. The random terms ν and υ are multivariate normally distributed with variances of V_ν and V_υ, respectively, and a covariance of $V_{\nu,\upsilon}$. We found statistical support for random slope model that allowed the effects of DBH to vary among species (AIC of random intercept *vs.* slope: 4473.3 *vs.* 1682.6), demonstrating that the shape of heigh-DBH relationship was different across species ($\chi^2 = 2794.7$, $P < 0.001$). Parameters of the model were determined using measured DBH and the heights of 100,878 trees in the Tiantong plot. Height measurements for trees ≤ 7 m were obtained directly using a height ruler during the 2015 census. For the tallest trees whose canopy can be observed from a drone, heights were extracted from a LiDAR-derived canopy height model based on their observed locations in the plot. The 2015 census also recorded DBH for all trees with DBH ≥ 1 cm in the plot. Subsequently, the height of each tree in the Tiantong plot in 2020 was predicted using the fitted model based on their 2020 DBH measurements. Finally, we used simple linear regression models to investigate the relationship between canopy height and species richness in both the canopy and understory layers.

Furthermore, if high canopy height reduces understory light availability and consequently species richness, we expect a more pronounced decline in the richness of shade-intolerant species compared to shade-tolerant species. To investigate this, we categorized each tree species in the Tiantong plot into shade-tolerant and shade-intolerant groups based on a previous study (Song 2013). We then calculated the species richness of each group within the understory and canopy layers for each quadrat. Finally, we used simple linear regression to analyze the relationship between canopy height and the species richness of shade-tolerant and shade-intolerant groups in each layer. To account for canopy height heterogeneity across the Tiantong plot, we repeated the above analyses by a relative height threshold approach for canopy stratification. For each tree in the 2015 census, individuals were classified as either canopy or understory based on their position relative to local canopy maxima, and the recruitment in the 2020 census was classified as understory.

Jointly modeling the effects of stand density and canopy height

Considering that stand density and canopy height may simultaneously impact tree species diversity and/or forest structural complexity, we performed structural equation modeling (SEM) to jointly model the effect of stand density and canopy height on tree species diversity and forest structural complexity. Additionally, tree mortality due to the dynamics of natural forests (e.g. natural disturbance, forest succession, competition) was an important cause for the spatial heterogeneity of stand density and canopy height within forest communities. Therefore, the fitted SEM also included tree mortality as a factor causing the variation in stand density and canopy height. We calculated tree mortality rates by the standard method (Condit *et al.* 1999) from 2015 to 2020 for each quadrat: $m = \left(\ln(n_{2015}) - \ln(S_{2020})\right)/5$, where m is given as the percentage of trees dead in five years. n_{2015} is the population size in 2015. S_{2020} is the number of survivors at the time of 2020.

Based on the prior knowledge, we built an initial SEM that included four main paths: 1) a direct effect of species diversity on forest structural complexity, 2) a direct effect of mortality on tree species diversity and forest structural complexity, 3) an indirect effect of mortality on species diversity and forest structural complexity via its effect on stand density and canopy height, and 4) an interaction between stand density and canopy height. All variables, except the tree mortality, have been estimated for each quadrat.

The goodness of fit of our SEM was assessed using Fisher's *C* statistic (Shipley 2000), and potentially missing paths were evaluated with the *d*-separation test (Lefcheck 2016). We ensured there was no collinearity (variance inflation factor: $\text{VIF} < 5$) among the predictors used in the SEM (Supplementary Tables S8). Poisson error structure was used for tree species diversity and stand density response variables. The SEM was simplified by removing nonsignificant paths step by step and refined by comparing both Shipley's full model Akaike information criterion (AIC, $\Delta\text{AIC} > 2$) values and Fisher's C statistic ($P > 0.05$) (Shipley and Douma 2020).

All statistical analyses in this study were performed in R 4.4.3 (R Core Team 2025) using packages "*dplyr*" (Wickham *et al.* 2023), "*piecewiseSEM*" (Lefcheck 2016), and "*ggplot2*" (Wickham 2016).

RESULTS

Observed negative complexity-diversity relationship

We observed a negative relationship between forest structural complexity and tree species diversity at the 20 m quadrat scale ($P < 0.001$; Fig. 1a). Specifically, high species diversity was associated with low forest structural complexity in the northwest portion of the Tiantong plot, while low species diversity coincided with high forest structural complexity in the southeast portion (Fig. 1b and c). Similar negative relationships were observed using different metrics (i.e. foliage height diversity, CV of height, and rumple) at other quadrat scales (Supplementary Table S2). This negative relationship remained significant even after accounting for spatial autocorrelation in forest structural complexity (Moran's I from residuals = –0.02, $P = 0.74$; Supplementary Table S3).

Individual effects of stand density and canopy height

Stand density and canopy height mediate the observed negative complexity-diversity relationship through divergent effects on structural complexity and species diversity together. Specifically, stand density exhibited a strong negative correlation with forest structural complexity ($P < 0.001$; Fig. 2a) but a positive association with tree species diversity ($P < 0.001$; Fig. 2b). Canopy height exhibited a significantly positive correlation with forest structural complexity ($P < 0.001$; Fig. 3a) but showed a negative correlation with tree species diversity ($P < 0.001$; Fig. 3b). These opposing relationships remained robust even after controlling for spatial autocorrelation in both structural complexity (Supplementary Tables S4 and S6) and species diversity (Supplementary Tables S5 and

S7).

The negative relationship between canopy height and species diversity is likely driven by the disproportionate loss of understory tree species in taller-canopy communities. This is supported by a strong negative correlation between understory tree species diversity and canopy height ($R^2 = 0.28$, $P < 0.001$; Fig. 3c, blue line). While tree species diversity in the up-canopy layer increased with canopy height ($R^2 = 0.16$, $P < 0.001$; Fig. 3c, yellow line), this trend was outweighed by the steeper decline in understory diversity. Further analyses suggest that light competition might be the primary driver underlying understory species loss, since as canopy height increased, shade-intolerant species diversity markedly declined ($R^2 = 0.20$, $P < 0.001$; Supplementary Fig. S2b).

Hidden positive complexity-diversity relationship

When incorporating the joint effects of stand density and canopy height in the SEM, the key relationships identified in Figures 2 and 3 remained significant (Fig. 4a). Stand density exerted a direct positive effect on tree species diversity but a negative effect on forest structural complexity. Conversely, canopy height showed a direct negative association with tree species diversity and a positive association with forest structural complexity (Fig. 4a). Notably, after controlling for stand density and canopy height, the relationship between forest structural complexity and tree species diversity became significantly positive (Fig. 4b).

DISCUSSION

Our findings reveal an observed negative correlation between forest structural complexity and tree species diversity in natural forest communities. Within the Tiantong plot, this inverse relationship arises from the spatial heterogeneity of stand density and canopy height, as these factors exert divergent effects on structural complexity and diversity while themselves being negatively correlated across the landscape (Fig. 4b). However, when the confounding influences of stand density and canopy height are statistically accounted for, the relationship shifts to a positive association. This aligns with experimental studies in controlled tree communities where stand density and canopy height were standardized (Ray *et al.* 2023; Perles-Garcia *et al.* 2021).

The alignment between experimental findings and adjusted natural patterns indicates that the positive relationship between structural complexity and tree species diversity remains universal. Structural complexity fosters diverse microhabitats and ecological niches (MacArthur and MacArthur 1961), which support higher species richness, while diverse tree communities enhance complexity through distinct growth forms and canopy layering (Ray *et al.* 2023). However, this mutual reinforcement does not necessarily produce a positive complexity-diversity relationship in natural forests, as factors like stand density and canopy height simultaneously influence both variables. These confounders could also contribute to the negative complexity-diversity relationships in other forests in Supplementary Table S1. For the same reason, the negative complexity-diversity correlations observed in natural forests cannot invalidate experimental findings (Pretzsch 2014; Williams *et al.* 2017), as controlled experiments largely isolate the confounding effects of stand density and canopy height.

Our study contributes to the field by elucidating that stand density can serve as a critical confounder in mediating the complexity-diversity relationship in natural forests. High stand density is often associated with elevated species diversity (Denslow 1995), likely due to sampling effects that enhance the inclusion of rare species (Colwell and Coddington 1994). This positive correlation is evident in our Tiantong plot data (Fig. 2b). However, high stand density simultaneously intensifies competition for light, prompting trees to optimize vertical crown arrangement through reduced tillering or branching (Postma *et al.* 2021). Aligning with this assumption, we found that vertical complexity decreased with stand density from median density levels (Supplementary Fig. S5e and f). A parallel negative relationship between stand density and structural complexity has been documented by Li *et al.* (2022). This trade-off reduces structural complexity, resulting in homogenized canopy layers.

While a previous study (Liu *et al.* 2022) suggests that initial increases in stand density (from very low levels) may temporarily enhance structural complexity, our findings demonstrate that a high degree of stand crowdedness due to excessive stand density exacerbates the negative effects of light competition, ultimately constraining the development of complex forest structures. Our analysis reveals a nuanced relationship by disaggregating structural complexity into horizontal (XY-plane variation) and vertical (XZ- or YZ-plane variation) components. Specifically, horizontal complexity increases with stand density at lower levels but plateaus at intermediate densities (Supplementary Fig. S5d). In contrast, vertical complexity exhibits an overall negative correlation with stand density (Supplementary Fig. S5b and c). These results partially validate earlier assumptions about the positive role of stand density in fostering structural complexity, but only for horizontal dimensions. Crucially, prior perspectives have overlooked the fact that high stand density intensifies light competition (Postma *et al.* 2021), which restricts branching development and thereby suppresses vertical structural complexity. This dual role of stand density highlights the need for density thresholds to balance diversity benefits against structural trade-offs.

Similarly, our study showed that canopy height is another crucial factor shaping the negative relationship between structural complexity and species diversity, as it plays a dual role in influencing both forest structural complexity and tree species diversity in natural forests. Although taller canopies may enhance structural complexity by creating additional niche spaces (Seidel *et al.* 2019; Cazzolla Gatti *et al.* 2017), they also intensify light competition below the canopy due to the more light interception at taller heights, which can suppress species diversity (Matsuo *et al.* 2021; McDowell *et al.* 2018). For instance, taller trees often form densely packed canopies with minimal gaps in the 32-year-old forest, most likely because the amount of foliage within the crown is closely related to tree height and because foliage is more concentrated at taller heights (Matsuo *et al.* 2021). This significantly reduces understory light availability to levels insufficient for shade-intolerant species, leading to their local exclusion (Ray *et al* 2024). Consistent with this, we observed a negative correlation between canopy height and the richness of shade-intolerant species in Tiantong (Supplementary Fig. S2b), a pattern corroborated by LaRue *et al.* (2023; 2024). While canopy height positively correlates with the diversity of up-canopy layer species (Fig. 3c), this effect is outweighed by the rapid decline in understory diversity (Fig. 3c), resulting in an overall reduction in species diversity. Thus, although taller canopies may foster structural heterogeneity, their dominance often undermines species diversity through competitive exclusion.

We recognize that stand density and canopy height are not real drivers, but intermediate patterns shaped by underlying ecological processes (Hardiman *et al.* 2018). Among potential drivers, we propose that disturbances, particularly typhoons, play a pivotal role, at least in our Tiantong plot. First, typhoons recurrently impact the Tiantong forest, with intensity peaking at higher elevations (Wang *et al.* 2014). This aligns spatially with the northwest section of the plot, where elevation is greatest, stand density reaches its maximum, and canopy height is minimized. Such patterns suggest that typhoon-driven physical damage disproportionately affects high-elevation zones, suppressing canopy development while promoting dense, low-statured regeneration. Second, using tree mortality as a proxy for disturbance intensity, we identified a negative correlation between mortality and canopy height (Supplementary Fig. S6), supporting the hypothesis that disturbances modulate canopy height. However, the link between disturbances and stand density is less straightforward than canopy height in the Tiantong plot (Supplementary Fig. S6). This complexity likely arises because disturbances can either reduce or increase stand density, depending on their intensity and the forest's recovery stage (Sapkota *et al.* 2009). Taken together, typhoon-driven disturbances likely generate spatial heterogeneity in stand density and canopy height across the Tiantong plot. When combined with light competition, a process that suppresses shade-intolerant species under dense canopies, these disturbances may explain the observed negative complexity-diversity relationship in the Tiantong plot.

Although both our conceptual framework and structural equation modeling examine how stand density and canopy height mediate the relationship between tree diversity and forest structural complexity, the underlying ecological dynamics are inherently more intricate. For example, diversity may itself influence stand density and canopy structure, thereby altering the diversity-complexity relationship (Ma *et al.* 2024; Tatsumi and Loreau 2023). Similarly, forest structural complexity may reciprocally affect stand density and canopy development (Ehbrecht *et al.* 2021). Thus, our findings should not be interpreted as suggesting reality conforms to the simplified pathways in our model. Rather, constrained by data limitations, this study explores one plausible configuration within these complex interactions. A rigorous investigation of causal relationships among stand density, canopy structure, tree diversity, and forest structural complexity would require longitudinal data incorporating additional covariates.

In summary, our study reveals an initial negative correlation between forest structural complexity and tree species diversity, driven by opposing effects of stand density and canopy height. Statistically controlling for these variables reveals a positive relationship, consistent with BEF experimental findings. This divergence highlights that the actual relationship between diversity and complexity in natural forests is mediated by ecological characteristics such as density and canopy dynamics. This linkage challenges the assumption that protecting structurally complex forests inherently safeguards biodiversity. Effective management must therefore account for these mediating factors to align conservation strategies with ecological reality.

Authors' contributions

Jin Chao: writing – original draft, reviewing and editing, methodology, data curation. Yang Jing: visualization, data curation. Wu Siyu: investigation. Yu Qiuwu: investigation. Wang Xihua: resources, supervision. Shen Guochun: writing – review and editing, conceptualization, funding acquisition.

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Conflict of interest statement. The authors declare that they have no conflict of interest.

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Figure legends

Figure 1: Observed relationship between forest structural complexity and tree species diversity (a), spatial structures of tree species diversity (b), and forest structural complexity (c) at 20 m quadrat scale in the Tiantong plot. Tree species diversity was simply measured by species richness. Structural complexity was quantified as canopy entropy from drone-derived LiDAR point cloud data. Panel (a) shows the single linear regression line ($P < 0.001$) with a 95% confidence interval (grey area) and the results from the simultaneous autoregressive model (SAR). See Supplementary Table S2 for the results using other diversity and structural complexity indices.

Figure 2: Effect of stand density on forest structural complexity (a) and tree species diversity (b) at 20 m quadrat scale in the Tiantong plot. Tree species diversity was represented by tree species richness. Structural complexity was quantified as canopy entropy from drone-derived LiDAR point cloud data. Simple linear regression lines ($P < 0.001$) were shown with 95% confidence intervals (grey area) and the results from the simultaneous autoregressive models (SARs).

Figure 3: Effect of canopy height on forest structural complexity (a), tree species diversity (b), and the relationship between canopy height and tree species diversity in the understory (< 10 m, blue) and up-canopy (≥10 m, yellow) layers (c) at 20 m quadrat scale in the Tiantong plot. Tree species diversity was represented by species richness. Structural complexity was quantified as canopy entropy from drone-derived LiDAR point cloud data. Panels (a) and (b) display the simple linear regression lines ($P < 0.001$) with 95% confidence intervals (grey area) alongside the results from the simultaneous autoregressive models (SARs). Panel (c) presents the r-squares (R^2), and P-values derived from simple linear regression.

Figure 4: Piecewise structural equation modeling (SEM) of the relationships between forest structural complexity and tree species diversity (a), and the partial effect of diversity on complexity controlled by variation of stand density and canopy height (b) at 20 m quadrat scale in the Tiantong plot. Tree species diversity was represented by species richness. Structural complexity was quantified as canopy entropy from drone-derived LiDAR point cloud data. Significant positive (black) and negative (red) paths are indicated by arrows, with width proportional to standardized path coefficients and asterisks denoting significance (*P < 0.05, **P < 0.01, ***P < 0.001). The standardized path coefficients indicated statistical control for the relationship between variates. *R*-square (R^2) values in panel (a) showed the proportion of variance in tree species diversity and structural complexity explained by the SEM. See Figure S6 for the full SEM. Panel (b) shows the single linear regression line with a 95% confidence interval (grey area), r-square (R^2), and *P*-value. Units of adjusted tree species diversity and forest structural complexity are standardized residual deviations from predicted partial scores.

Supplementary Material

Supplementary material is available at *Journal of Plant Ecology* online.

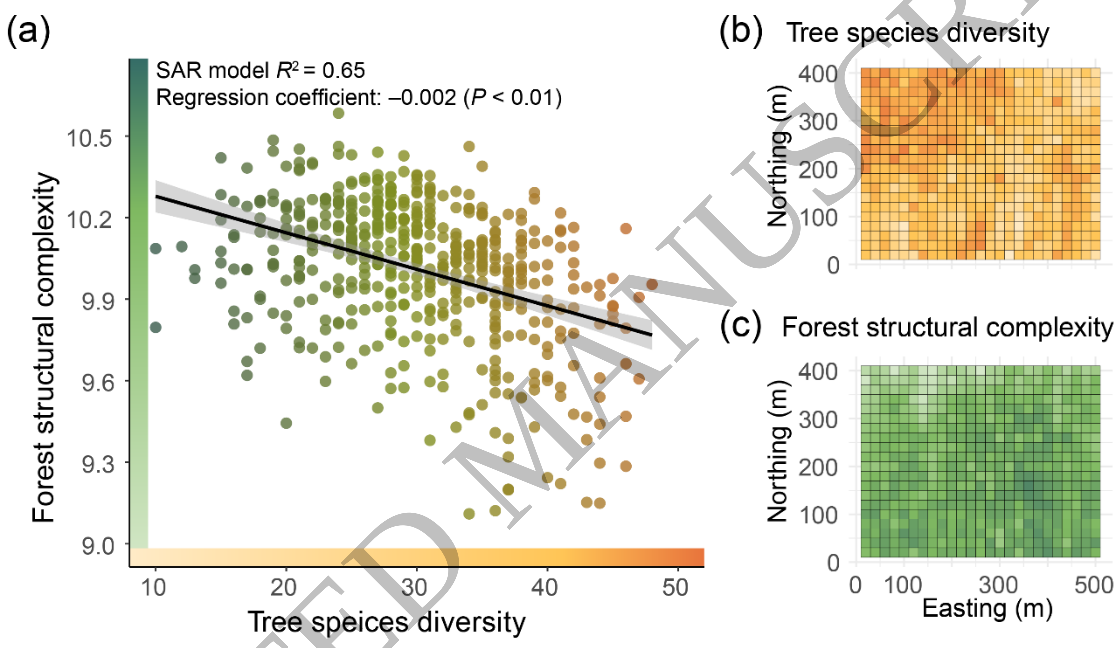

Figure 1

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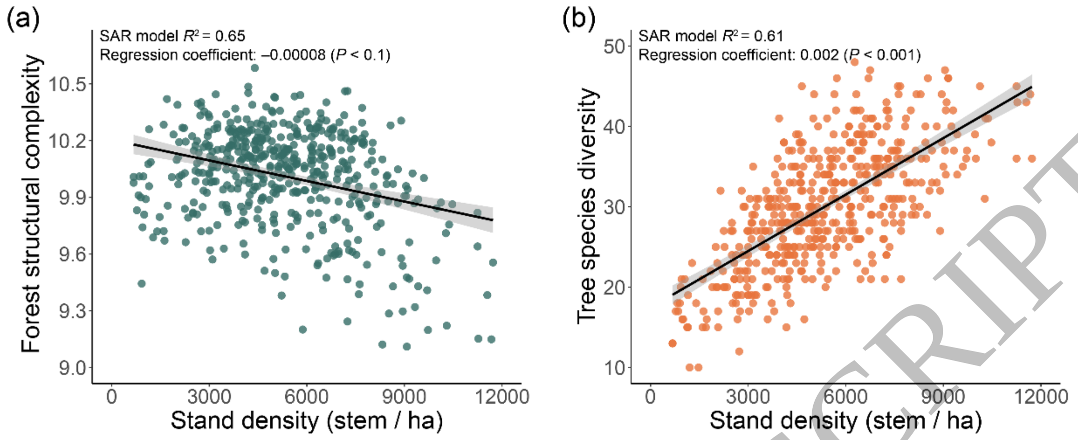

Figure 2

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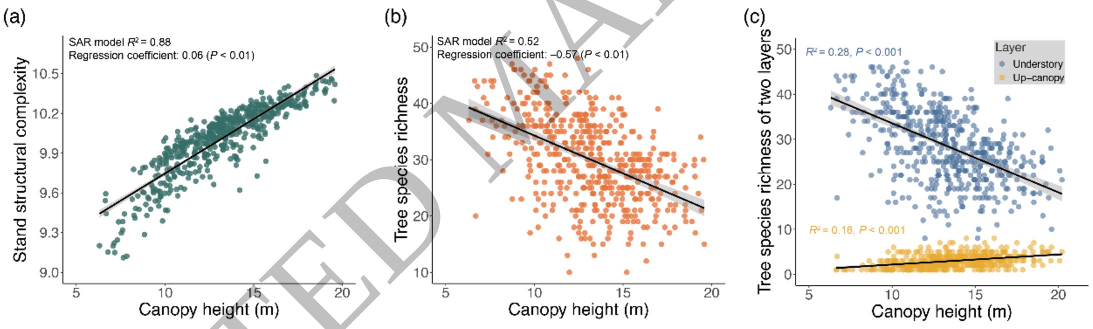

Figure 3

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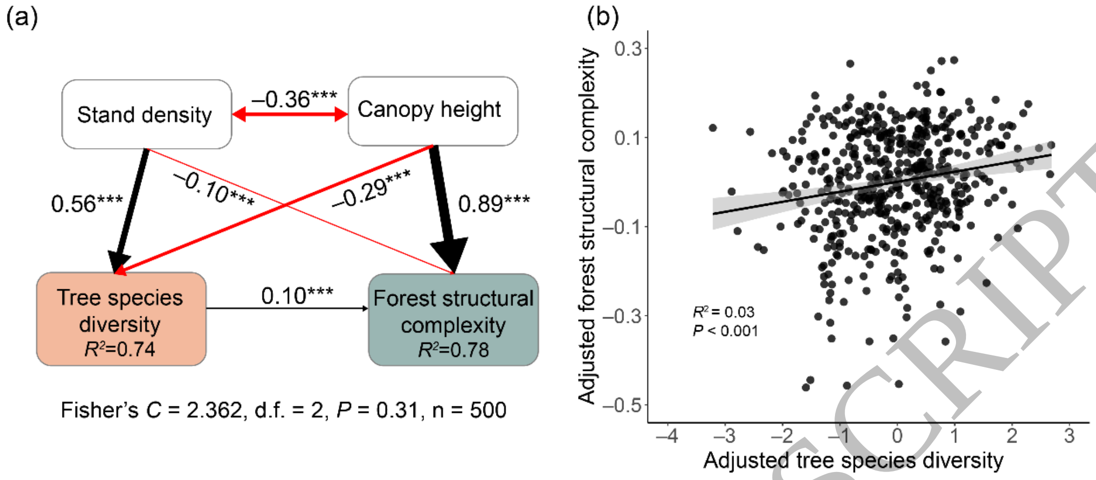

Figure 4

147x64 mm (DPI)