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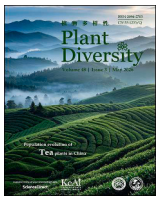

Research paper

Stand structural attributes exert stronger and scale-dependent control on forest biomass than tree diversity across typical forest ecosystems in China

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ABSTRACT

Understanding how biodiversity-ecosystem functioning (BEF) relationships scale spatially and temporally remains critical under global change. Here, using continuous monitoring databases across temperate, subtropical and tropical natural forests in China from 2004 to 2020, we quantified multiscale tree diversity-biomass dynamics. Linear mixed-effect and structural equation models were used to further disentangle the direct and indirect pathways through which tree diversity influences forest biomass at different scales. The results revealed significant positive linear relationships between tree species richness and stand biomass at 1200 and 400 m^2 scales ($P < 0.05$), whereas no significant association was detected at 100 m^2 scale ($P > 0.05$). Notably, these demonstrated relationships exhibited consistent temporal stability across all spatial scales throughout the study period. Importantly, the direct effect of tree diversity on biomass intensified with increasing spatial scale, while indirect effects mediated through stand structural attributes (CV_DBH and tree density) became proportionally stronger at finer scales. Further analyses showed that stand structural attributes emerged as the strongest predictor of biomass variation across all scales, surpassing both diversity and climate effects. Furthermore, spatial variation of climate factors (mean annual temperature and mean annual precipitation) mainly affected stand biomass through the indirect effects on tree species diversity and stand structural attributes. Overall, multiscale analyses revealed stand structural attributes dominates biomass prediction, with climate acting indirectly. Scaling biodiversity-structure strategies can enhance forest resilience under global change. Future work should integrate cross-scale mechanisms into climate-smart afforestation for sustainable carbon sequestration.

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1. Introduction

Understanding the biodiversity-ecosystem function (BEF) relationship has been a central goal in ecology and biological conservation (Grime, 1973; Naeem et al., 2012). However, the importance of plant diversity in maintaining forest ecosystem functions in response to long-term climate change is poorly resolved, especially for natural forest ecosystems (Gao et al., 2024). While numerous studies have reported that biodiversity in global and regional

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ecosystems has positively influenced ecosystem functions over recent decades (Gillman and Wright, 2006; Liang et al., 2016; Mensah et al., 2020), the shape and direction of the relationships remain contentious. Other substantial empirical reported the relationships could be humped-back (Fraser et al., 2015), negative (Zhang et al., 2023), and neutral or inconsistent (Adler et al., 2011). These controversial findings on the BEF relationships may be modulated by community succession (Lasky et al., 2014; Gao et al., 2024), spatial scale (Gonzalez et al., 2020; Mao et al., 2023), community composition (Albrecht et al., 2021), and environmental variables (Poorter et al., 2017; Chen et al., 2023). Especially, several studies have indicated that the BEF relationships changed with different community dynamics and their driving mechanisms were also different (Lasky et al., 2014). Furthermore, it was well-established that BEF relationships were scale-dependent (Chisholm et al., 2013; Mao et al., 2023), with the strength and even the direction of these relationships changing predictably with spatial grain and extent. While both temporal dynamics and spatial scale were established drivers of the BEF relationship variation, their interactive effects over time remain underexplored. This gap persists because studies typically investigate either temporal changes or spatial scaling in isolation, rarely integrating both dimensions (Hagan et al., 2021). Therefore, an integrated framework synthesizing temporal trajectories with scale-dependent feedbacks is critical to elucidate how the BEF relationships evolve over time at different spatial scales, which is crucial for the restoration of ecosystem functions in habitat fragmentation landscapes.

The BEF relationships displayed temporal dynamics during plant community development stages, with rapid taxonomic turnover and structural reorganization (e.g., shifts in canopy layering) driving transient functional states through niche-driven assembly processes (Cardinale et al., 2007; Satdichanh et al., 2019; Gao et al., 2024). For example, based on two long-term grassland control experiments ($\geq$ 13 years), Reich et al. (2012) revealed that the impact of plant diversity on biomass production tends to be saturated at early stages, but that its positive effect is stronger as the experimental time increases. Similarly, using 11 years of growth records from a large diversity experiment, Urgoiti et al. (2023) demonstrated that the impact of diversity on forest productivity intensifies over time. Species obtained more opportunities to alter their utilization of the limited resources in the environment over time, which led to the increasing importance of the impact of diversity. In contrast, using experiments in tropical forests at different development stages, Lasky et al. (2014) have reported that the BEF relationships were positive during early succession stages, but the relationships were weakly correlated in late-successional systems. This pattern was attributed to constrained niche complementarity as expanding species richness saturated multidimensional resource space (Tilman et al., 2014). Therefore, it remains a critical challenge to understand how BEF relationships and their maintenance mechanisms change over time, especially on a large regional area.

The organisms and ecosystem processes in many terrestrial ecosystems were generally nonrandom spatial distributions (e.g., aggregations or regular) (Klausmeier, 1999). Accordingly, spatial scale may play an important role in regulating the BEF relationships, and the intensity of BEF relationships would change with the increase of spatial scale. For example, based on 25 large forest plots around the world, Chisholm et al. (2013) found that tree species richness in the plots was generally positively correlated with productivity and biomass at finer spatial scale (400 m^2), while the both relationships were inconsistent at larger spatial scales (2500 and 10,000 m^2), with negative correlations becoming more common. By contrast, Craven et al. (2020) used data from forests in the United States and found that the relationship between diversity and productivity was not significant at a finer spatial scale (672 m^2), but showed a significant positive correlation at a larger spatial scale (35,677 km^2). Moreover, Zhang et al. (2024) based on a 30 ha permanent forest plot and also demonstrated that the correlation between diversity and biomass weakened progressively from small (400 m^2) to intermediate scales (67,600 m^2), and then increased again from intermediate to large scales (230,400 m^2). The magnitude of spatial scale reflected the resources availability. Specifically, biotic interactions (e.g., competition) played a dominant role at finer spatial scales, while environmental heterogeneity increased with spatial scale, making abiotic filtering more pronounced (Chisholm et al., 2013). Importantly, spatial scale can also greatly affect the BEF relationship. Therefore, it is necessary to consider spatial scales to understand how changes in the BEF relationships in natural ecosystems.

Two main ecological mechanisms, selection effect and complementarity effect, were proposed by previous studies to expound the positive impact of biodiversity on ecosystem functions (Loreau and Hector, 2001; Barry et al., 2019). The selection effect emphasized that one or several species had a higher contribution to ecosystem function in diverse communities (Lisner et al., 2023). In contrast, the complementarity effect attributed functional enhancement to niche differentiation among species, where diversified resource use in heterogeneous communities elevates overall biomass production (Noulèkoun et al., 2024). To disentangle these mechanisms, current studies increasingly integrate structural attributes metrics (e.g., vertical stratification quantified by tree height/diameter variation) with traditional taxonomic diversity indices (e.g., species richness). In this context, structural dominance often reflects the outcome of the selection effect, while high species diversity is a prerequisite for strong complementarity effects. This dual approach captures both the identity-driven selection processes and the niche-based complementarity dynamics (Zhang and Chen, 2015; Chen et al., 2023). For instance, Noulèkoun et al. (2024) demonstrated that stand structural attributes (quantified by tree size variation in diameter and height) served as a key predictor of aboveground biomass in African natural forests. They proposed that this relationship was driven by the optimization of resource use and the packing of three-dimensional space within the forest, a mechanism that can arise from both the selection of highly efficient structures and interspecific complementarity. Furthermore, plant diversity indirectly enhanced biomass through structural mediation: diverse communities developed multi-layered architectures that optimized light-use efficiency and resource partitioning, a pattern corroborated by cross-continental studies in Asian, African, and American forests (Mensah et al., 2020; Kohyama et al., 2023). Moreover, climatic drivers further modulate these biological processes through direct and indirect pathways: direct effects of temperature and precipitation are well-established, whereas climate also indirectly influences biomass production by mediating both species diversity and structural attributes across biogeographic gradients (Stein et al., 2014; Ali et al., 2019). Resolving these multifaceted interactions, particularly how biome-specific attributes mediate climate-ecosystem functions linkages, remains pivotal for advancing mechanistic understanding of the BEF.

China's forests are characterized by rich biodiversity and abundant resources, and make them integral to global ecological processes and the conservation of biodiversity, which provide ideal habitats for research on species diversity and ecosystem functions (i.e. biomass and productivity) (Sun et al., 2022; Zhang et al., 2025). Elucidating the temporal dynamics of relationships between biomass and stand structural attributes in China would provide valuable insights for global forest ecosystem management in the

context of global change. In this study, we used survey data related to plant communities from 12 permanent plots of typical forest ecosystems in China during 2004–2020 to explore the long–term relationship between tree species diversity and stand biomass at different spatial scales, and further investigated the effects of stand structural attributes and climate on stand biomass. This study addresses a central question: how do tree species diversity, stand structural attributes, and climate jointly regulate forest biomass across spatial and temporal scales? Specifically, we explore whether and how the relative importance of diversity and stand structural attributes shifts with spatial scale, how their interactions sustain the temporal stability of tree species diversity–biomass relationships, and to what extent stand structure mediates the indirect climatic and diversity effects on biomass variation.

2. Materials and methods

2.1. Study sites and forest sample plot surveys

Our study utilized a dataset comprising 12 permanent forest plots collected from nine typical forest ecosystems between 2004 and 2020, spanning tropical, subtropical, and temperate zones, with each plot representative of the dominant forest types within its respective region to ensure coverage of key environmental gradients (e.g., precipitation and temperature) (Fig. S1 and Table 1) (Li et al., 2025). To minimize selection bias, sample plots were established according to standardized protocols (e.g., fixed-area plots with random subsampling), and their spatial distributions were validated with previous survey data (Zhou et al., 2014; Guo et al., 2021). Specifically, sites in this study located in Xishuangbanna (BN), Dinghushan (DH), Ailaoshan (AL), Huitong (HT), Shennongjia (SN), Gonggashan (GG), Maoxian (MX), Beijing (BJ), and Changbaishan (CB) (Fig. S1), covered a wide range of climate gradients, with mean annual temperatures (MAT) ranging from 3.11 to 23.10 °C and mean annual precipitation (MAP) ranging from 293 to 2182 mm. In this study, we selected twelve permanent forest plots (labeled as BN1, BN2, DH1, DH2, AL1, AL2, HT, GG, SN, MX, BJ, and CB, respectively) from nine typical forest ecosystems in China (Table 1). Each permanent forest plot has an area of 1200 m^2 and consists of 12 subplots with an area of 10 m × 10 m. These forest plots are regularly surveyed every five years in subplots (10 m × 10 m) according to a standardized census protocol formulated by the Chinese Ecosystem Research Network (CERN) (https://www.cnern.org.cn/data/initDRsearch). In each of the subplots (10 m × 10 m), field workers measured species name, height (H) and diameter at breast height (DBH, breast height = 1.3 m) of all individual trees with DBH ≥ 2 cm. For a more detailed description of the investigation methods, see Zhou et al. (2014). New individuals that meet the above criteria are also identified and tagged in the next survey. In addition, individuals that die are also recorded during the monitoring process.

2.2. Stand biomass estimation

Biomass production, as an important component of ecosystem functions, is a key mechanism for linking biodiversity and ecosystem function (Loreau and Hector, 2001; Ma et al., 2010). To accurately assess forest carbon stock in China, previous researchers reconstructed allometric equations according to 900 sets of allometric equations from published literature on forest ecosystems in China (Chen et al., 2023). These allometric equations operationalize metabolic scaling theory to translate tree architectural traits (DBH and height) into ecosystem-level biomass predictions and were widely applied to evaluate forest biomass (See Tables S1–S4 for details) (Tang et al., 2018). The biomass of each living individual tree with DBH ≥ 2 cm was estimated using specific allometric equations. Specifically, using the diameter versus biomass allometric growth equation (Tables S1–S4), we first calculated the above- and below-ground biomass of all living individuals in each subplot (10 m × 10 m) in this study. We then summed the above- and below-ground biomass within each subsample plot to obtain forest stand biomass. The above- and below-ground biomass within each subplot was summed to obtain stand biomass. The sum of stand biomass in 12 subplots was used as the biomass in the permanent forest plot (1200 m^2).

2.3. Species diversity and other explanatory variables

We integrated tree species diversity and stand structural attributes as core predictors to disentangle the mechanisms driving forest biomass dynamics. This dual-focus approach is consistent with empirical evidence demonstrating that both biodiversity and stand

Table 1
Description for 12 permanent forest plots (BN1, BN2, DH1, DH2, AL1, AL2, HT, GG, SN, MX, BJ, CB) selected from nine field ecological stations (BN, Xishuangbanna; DH, Dinghushan; AL, Ailaoshan; HT, Huitong; SN, Shennongjia; GG, Gonggashan; MX, Maoxian; BJ, Beijing; CB, Changbaishan). For each plot, the table shows plot code, the location (latitude and longitude), mean annual temperature (MAT), mean annual precipitation (MAP), forest age, years of censuses used in this study. These results are from Chinese Ecosystem Research Network (https://www.cnern.org.cn/).

Ecological station	Plot code	Ecological zone	Longitude (°)	Latitude (°)	MAT (°C)	MAP (mm)	Forest age (year)	Years of censuses used in analyses
BN	BN1	Seasonal rain forest	101.2	22.0	22.0	1354.3	> 200	2005, 2010, 2015, 2020
	BN2	Seasonal rain forest	101.3	21.9	22.0	1354.3	> 100	2005, 2010, 2015, 2020
AL	AL1	Evergreen broad-leaved forest	101.0	24.5	11.7	1373.7	> 200	2005, 2010, 2015, 2020
	AL2	Evergreen broad-leaved forest	101.0	24.5	11.7	1373.7	> 200	2005, 2010, 2015, 2020
DH	DH1	Monsoon evergreen broad-leaved forest	112.5	23.2	22.2	1950.6	> 400	2004, 2010, 2015, 2020
	DH2	Monsoon evergreen broad-leaved forest	112.6	23.2	22.2	1950.6	> 100	2004, 2010, 2015, 2020
HT	HT	Secondary broad-leaved evergreen forest	112.5	23.2	16.5	1297.2	> 50	2005, 2010, 2015, 2020
GG	GG	Dark coniferous forest	102.0	29.6	4.2	1610.2	> 65	2005, 2010, 2015, 2020
SN	SN	Evergreen broad-leaved mixed forest	110.5	31.3	10.6	1150.7	> 80	2005, 2010, 2015, 2020
MX	MX	Deciduous-coniferous mixed forest	103.0	31.0	9.5	716.9	> 30	2005, 2010, 2015, 2020
BJ	BJ	Deciduous broad-leaved forest	115.4	40.0	5.2	427.9	> 50	2004, 2010, 2015, 2020
CB	CB	Deciduous broad-leaved forest	128.1	42.4	3.6	712.3	> 200	2005, 2010, 2015, 2020

Note: The dominant species for each permanent plot are as follows: BN1, *Pometia pinnata*, *Barringtonia fusicarpa*, *Ardisia thyrsiflora*, and *Orophea laui*; BN2, *Pittosporopsis kerrii*, *Aidia pycnantha*, *Baccaurea ramiflora*, and *Imbralyx leptobotrya*; AL1, *Camellia tsaii* and *Ilex gintungensis*; AL2, *Rhododendron leptothrium*, *Camellia tsaii*, and *Castanopsis wattii*; HT, *Cunninghamia lanceolata*; GG, *Sorbus multijuga* and *Abies fabri*; SN, *Quercus multinervis*, *Rhododendron hypoglaucum*, *Fagus engleriana*, and *Cornus kousa*; MX, *Pinus armandii*; BJ, *Betula platyphylla*; CB, *Pinus koraiensis*.

structural attributes are pivotal yet complementary drivers of biomass production (Chen et al., 2023; Kohyama et al., 2023). We quantified species diversity using species richness (SR), defined as the total count of tree species within each plot. While other diversity indices (e.g., Shannon–Wiener or Simpson index) can provide additional insights, we prioritized SR due to its unambiguous interpretability in cross-scale analyses and its established linkage to ecosystem productivity in forests (Gotelli and Colwell, 2001; Chisholm et al., 2013).

Stand structural attributes metrics were selected based on their demonstrated capacity to mediate light interception, moisture retention, and nutrient allocation in forest ecosystems (Zhang and Chen, 2015; Kohyama et al., 2023; Zeng et al., 2024). For example, canopy stratification may enhance light-use efficiency, thereby amplifying complementarity effects among species (Pretzsch, 2014). Specifically, forest stand structural attributes are calculated as the coefficient of variation (CV) of tree diameters at breast height (DBH) and tree height (i.e. CV_DBH and CV_ height), following Schnabel et al. (2019). Meanwhile, we also calculated the tree density, which is the number of trees within each plot. These parameters reflect key structural dimensions influencing resource partitioning and biomass accumulation, as validated in forest structural studies (Pretzsch, 2014; Fotis et al., 2018; Kholdaenko et al., 2022). Moreover, we gathered meteorological data for the same period (from 2004 to 2020) from the CERN for each ecological station, including mean annual temperature (MAT) and mean annual precipitation (MAP).

2.4. Statistical analyses

To examine the scale-dependence of the relationship between tree species diversity and stand biomass in typical forest ecosystems in China, we first divided each permanent forest sample plot into three non-overlapping sample plots in this study (including 1200 m^2, 400 m^2 and 100 m^2 sampling spatial scales). To improve normality and linear relationship, this study performed logarithmic transformation for all variables before analysis.

To explore the relationship between tree species diversity and forest stand biomass and its temporal dynamics at three spatial scales (1200, 400, and 100 m^2), this study used the "*lm*" function in R (R Core Team, 2023) to develop linear regression models between residuals of tree species richness and residuals of stand biomass at different spatial scales during 2005–2020. The three spatial scales were chosen to represent a gradient of ecological organization, from local neighborhoods to forest patches and broader communities. This nested design allowed us to test how the BEF relationships were contingent upon the spatial scale of observation. Firstly, we separately regressed stand biomass and tree species richness against the climate variables (MAT, MAP) and stand structural attributes (CV_DBH, CV_height, tree density) at three spatial scales, and extracted the residuals from each regression. Then, we regressed the residuals of stand biomass against the residuals of tree species richness to estimate the unbiased slope of their relationship after controlling for the effects of covariates at three spatial scales. Meanwhile, the linear-relationship slopes between residuals of tree species diversity and residuals of forest stand biomass were analyzed and compared by standardized major axis (SMA) regression analysis by using "*SMATR*" package in R to assess whether their relationship changes over time (Warton et al., 2006). Then, we used simple linear regression to explore bivariate relationship between tree species richness, forest structure attributes (including CV_DBH, tree density, and CV_height) and climate factors (MAT and MAP) and forest biomass at three spatial scales. Subsequently, simple linear regression was used to explore bivariate relationship between tree species richness, forest structure attributes and climate factors and forest biomass at three spatial scales. Meanwhile, the multiple linear regression models were used to further analyze the impact of each factor including species diversity, stand structural attributes, and climatic factors on forest biomass at different spatial scales. There may be collinearity among variables since the strong correlation between variables (Fig. S2). To mitigate multicollinearity, predictors were retained in models only if variance inflation factors (VIF) was less than five (Uriarte et al., 2012). Therefore, final model included a diversity variable (SR), two stand structure attribute variables (CV_DBH and Density), and two climate variables (MAP and MAT). This analysis was completed using the "*car*" package in R language. To estimate the relative contributions of species diversity and other factors (including forest structure attributes and climate factors) to the biomass of typical forest ecosystems in China, this study used the "*rdacca.hp*" package in R to perform variance decomposition at three spatial scales.

The structural equation model (SEM) was used to disentangle direct and indirect pathways through which tree diversity, stand structural attributes, and climatic drivers influence forest biomass. In the SEM, we constructed composite variables to represent latent impact. For example, stand structure attributes were formed as a linear combination of CV_DBH and tree density. The CV_DBH and tree density were first standardized (mean = 0, standard deviation = 1) to remove unit differences, and then averaged to create the composite variable scores. Similarly, climate was created by standardizing their respective indicators (MAT and MAP) and computing mean scores. This approach allowed us to represent the combined effects of multiple related variables as a single variable in the model. Based on previous research and ecological hypotheses (Table S5), we formulated a structural equations conceptual model (Fig. 1). First, the SEM comprised direct pathways from species diversity, stand structural attributes, and climatic factors to stand biomass, which represent potential mechanisms driving the biomass. Second, effects from the indirect pathway of climatic factors were incorporated because climatic factors can influence stand biomass through species and stand structural attributes. The SEMs in this study were implemented using the "*piecewiseSEM*" package in R, with model fit assessed via the *Fisher's C*, *P* values, Comparative Fit Index (CFI) and Goodness of Fit Index (GFI).

All statistical analyses and visualizations were conducted in R v.3.5.1, with statistical significance evaluated at $P < 0.05$.

3. Results

3.1. The relationships between tree species diversity and stand biomass at different spatial scales and their temporal dynamics

The relationship between forest biomass and tree species diversity varied significantly across different spatial scales. From

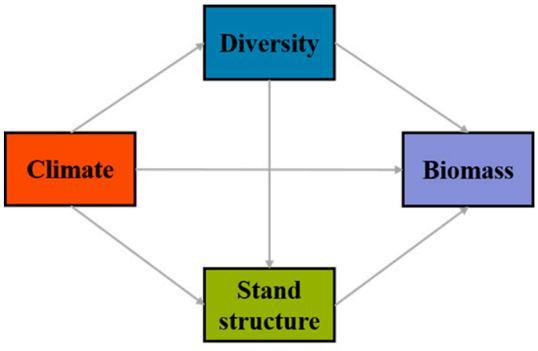

Fig. 1. The structural equation conceptual model. A hypothetical conceptual diagram for studying the relationship between stand biomass and diversity (tree species richness), stand structural attributes (CV_DBH and tree density), and climatic factors (MAT and MAP) of typical forest ecosystem in China.

2005 to 2020, residuals of tree species richness were positively correlated with stand biomass at the 1200 and 400 m^2 scales ($P < 0.05$; Fig. 2a–h), while no significant correlation was observed at the 100 m^2 scale during the same period ($P > 0.05$; Fig. 2i–l). Furthermore, the SMA regression analysis indicated that the relationships between residuals of tree species richness and residuals of stand biomass remained consistent over time at each spatial scale (Table 2).

3.2. The effect of tree species diversity and other factors on biomass at different spatial scales

Bivariate analyses showed that forest stand biomass was positively correlated with tree species richness at the 1200 and 400 m^2 (Figs. S3–S5). Among the stand structural attributes, both CV_DBH and CV_height were significantly positively related to stand biomass at three spatial scales. Except for the 1200 m^2, there was a significantly negative correlation between tree density and forest biomass. Similarly, stand biomass was significantly positively related to MAP at three scales, while it was significantly positively related to MAT at 1200 and 400 m^2.

The multiple linear regression models showed that regardless of the spatial scale, the direction of the effect of each factor on the variation of stand biomass was basically consistent (Fig. 3a–c, and e). Specifically, tree species richness showed positive effects on

Table 2
The change in the slope in the relationships between residuals of tree species diversity and residuals of stand biomass at three spatial scales (1200, 400, and 100 m^2) over time based on the standardized major axis (SMA) regression analysis. $P < 0.05$ indicates significant differences between different years at the same spatial scale.

Spatial scale	*Slope*				*P* value
	2005	2010	2015	2020	
1200 m^2	0.72	0.78	0.64	0.67	0.96
400 m^2	0.96	1.12	1.01	0.97	0.82
100 m^2	1.62	1.94	−1.88	1.75	0.46

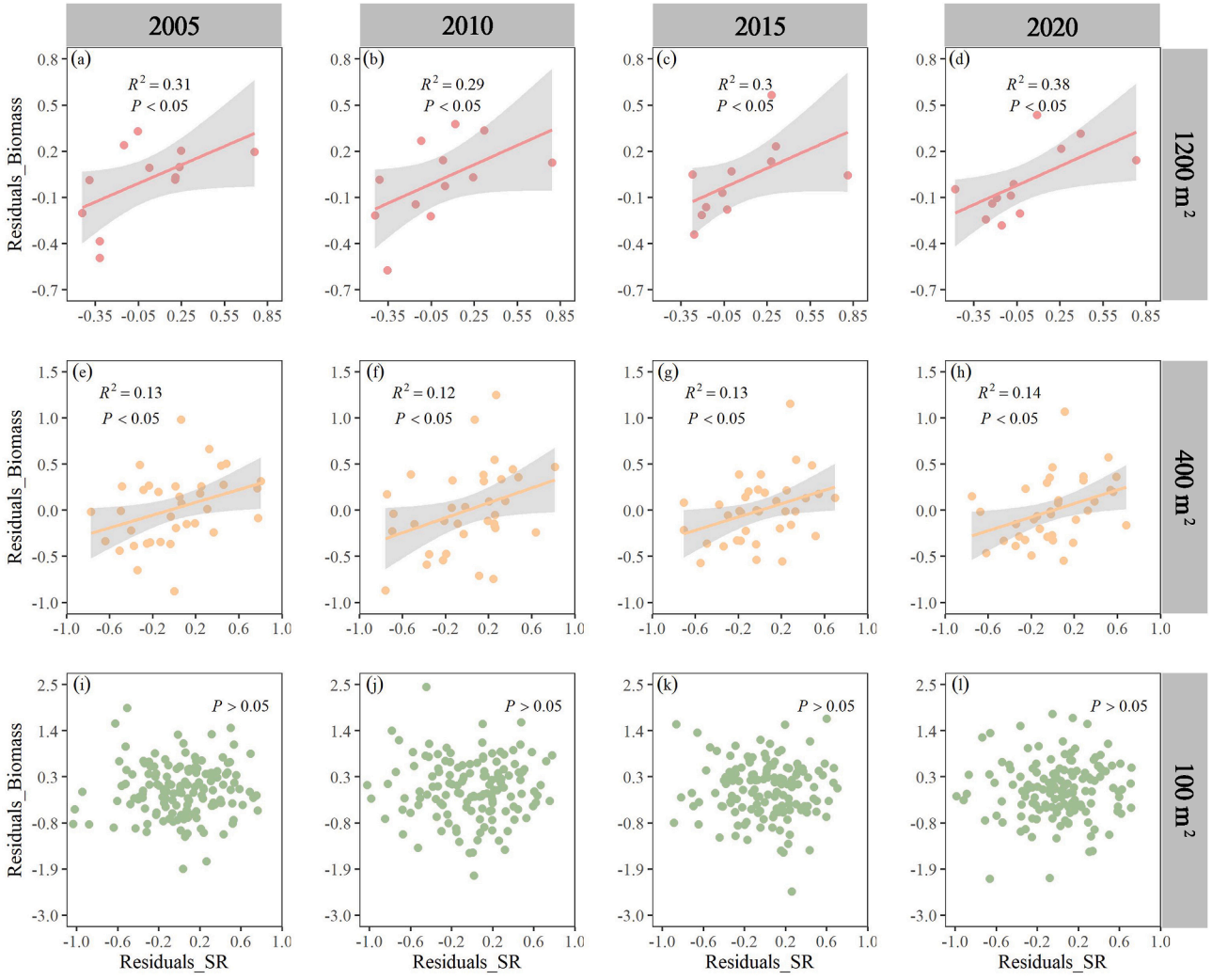

Fig. 2. The relationships between residuals of tree species richness and residuals of stand biomass of typical forest ecosystems in China at three spatial scales and their temporal dynamics. (a), (b), (c) and (d) represent the relationship between residuals of tree species richness and residuals of biomass at a spatial scale of 1200 m^2 in 2005, 2010, 2015 and 2020, respectively. (e), (f), (g) and (h) represent the relationship between residuals of tree species richness and residuals of biomass at a spatial scale of 400 m^2 in 2005, 2010, 2015 and 2020, respectively. (i), (j), (k) and (l) represent the relationship between residuals of tree species richness and residuals of biomass at a spatial scale of 100 m^2 in 2005, 2010, 2015 and 2020, respectively. The shaded area shows the 95% confidence interval. The level of significance is $P < 0.05$. Note: Residuals_SR and Residuals_biomass and represents the residuals after regression of tree species richness and stand biomass against climatic variables (MAT, MAP) and stand structural attributes (CV_DBH, CV_height, tree density), respectively.

stand biomass at the 1200 and 400 m^2, but no significant effect at the 100 m^2. CV_DBH positively influenced stand biomass across all three scales, while tree density and MAT exhibited negative effects. Moreover, MAP showed no significant effect on stand biomass at the 1200 m^2, but demonstrated significant positive effects at the 400 and 100 m^2. The variance partitioning analysis revealed that the relative importance of factors influencing stand biomass varied across spatial scales. At the 1200 m^2 scale, stand structural attributes were the most influential (70.98%), followed by tree species diversity (21.33%) and climatic factors (7.69%) (Fig. 3b). At the 400 m^2 scale, the influence of stand structural attributes increased to 82.81%, while tree species diversity and climatic factors contributed 11.71% and 5.48%, respectively (Fig. 3d). At the smallest scale of 100 m^2, stand structural attributes overwhelmingly dominated (94.24%), with tree species diversity and climatic factors contributing only 2.11% and 3.65%, respectively (Fig. 3f). These findings highlighted diminished roles of tree diversity and climatic drivers at finer spatial scales.

We performed the SEM to determine mechanisms how climate, species diversity and stand structure drove the variation in forest biomass at the different scales. Our models provided solid evidence that stand structure and species diversity consistently had larger positive effects on forest biomass than climate across all spatial scale. Specifically, tree species diversity and stand structural attributes were positively correlated with forest biomass. Tree species diversity and stand structural attributes significantly positive effects on forest biomass. Additionally, tree species diversity exerts an indirect effect on stand biomass through its influence on structural attributes. Among the various structural attributes, the CV_DBH emerged as the most reliable predictor of variations in forest biomass (Fig. 4a–c), demonstrating a positive correlation. Conversely, stand density had a relatively weak negative effect on forest biomass. Although climate factors did not have direct impacts on stand biomass, they mainly have indirect positive effects through their effects on tree species diversity and stand structure attributes. Increased precipitation is frequently associated with enhanced forest biomass. At the same time, with the decrease of sampling spatial scale, the overall interpretation rate of climate, stand structure and biodiversity on forest biomass decreased. The direct effects of tree species diversity on stand biomass diminished with decreasing spatial scales, transitioning to indirect mediation pathways via stand structural attributes (Fig. 4d–f).

4. Discussion

Our findings provided insights for assessing changes in the BEF relationships in different ecological contexts and underlying biotic and abiotic mechanisms driving stand biomass in typical forest ecosystems in China, which have been underrepresented in previous related works. There were the strong scale dependent relationships between tree species diversity and forest stand biomass, but the relationships remained stable at each spatial scale over time. Overall, stand structural attributes had the strongest influence on variations in stand biomass at all three spatial scales (Figs. 3 and 4). Stand biomass emerged as the dominant driver of biomass variation at finer scales, whereas tree species diversity and climatic factors had a weaker influence on biomass (Fig. 4). Interestingly, the contribution of tree species diversity and climatic factors to stand biomass increased with increasing spatial scale, which likely driven by amplified resource heterogeneity and niche complementarity across broader habitat range (Gonzalez et al., 2020; Gonçalves-Souza et al., 2025).

4.1. Temporal dynamics and scale dependence of the relationship between tree species diversity and biomass

Regardless of the spatial scale, we observed that the relationships between tree species richness and stand biomass remained stable over time in this study, which contrasted with some previous findings that suggested the relationships strengthen or shift during ecological succession (Lasky et al., 2014; Bongers et al., 2021; Wagg et al., 2022). This stability in the relationship may be attributed to several factors. Firstly, the forest ecosystems in this study were predominantly mature and natural communities, with minimal anthropogenic disturbances. In such stable ecosystems, species composition and diversity may change more slowly compared to younger or disturbed ecosystems (Lasky et al., 2014; Xi et al., 2024), leading to less pronounced changes in the relationships over shorter time scales. Secondly, compared to grasslands, the stand structural attributes and structural stability of forest ecosystems may buffer against rapid changes in the relationship dynamics (Liu et al., 2024). Forests typically exhibit slower successional processes and stronger resilience (Schnabel et al., 2021; Cadotte, 2023), which could result in more consistent relationships between biodiversity and ecosystem functions over time. Additionally, the duration of this study may have been

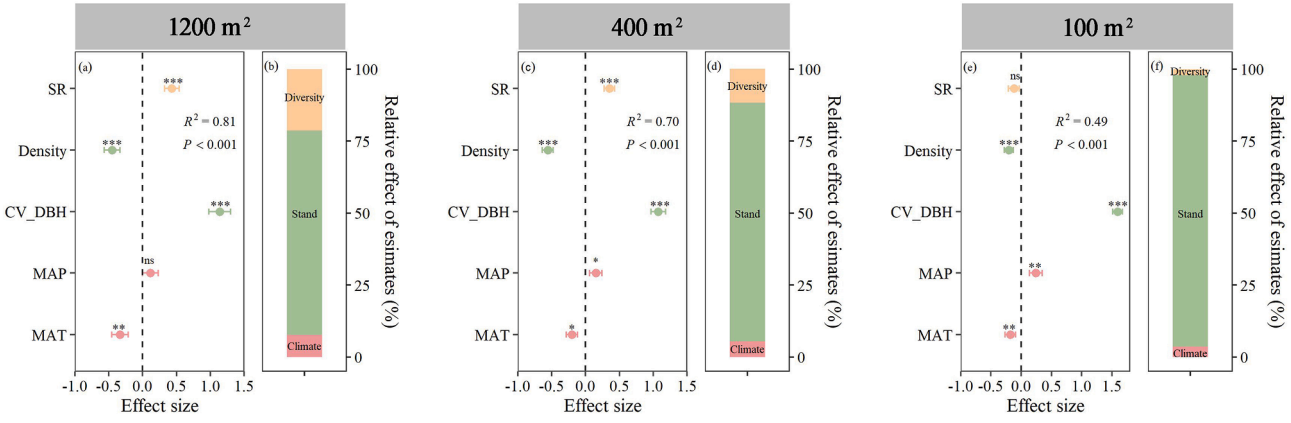

Fig. 3. The effects of predictor variables on biomass of typical forest in China at spatial scale of 1200, 400, and 100 m^2. (a), (c), (e) represent the effects of tree species richness, tree density, CV_DBH, MAP, and MAT on stand biomass in the multivariate linear-regression model at 1200, 400, and 100 m^2, respectively. (b), (d), and (f) represent the relative contribution of the effects of tree species diversity, stand structural attributes, and climatic factors on forest biomass using Variance partitioning analysis at 1200, 400, and 100 m^2, respectively. Note: The results are shown as mean ± SE. *, ***, and ns indicate $P < 0.05$, $P < 0.001$, and $P > 0.05$, respectively.

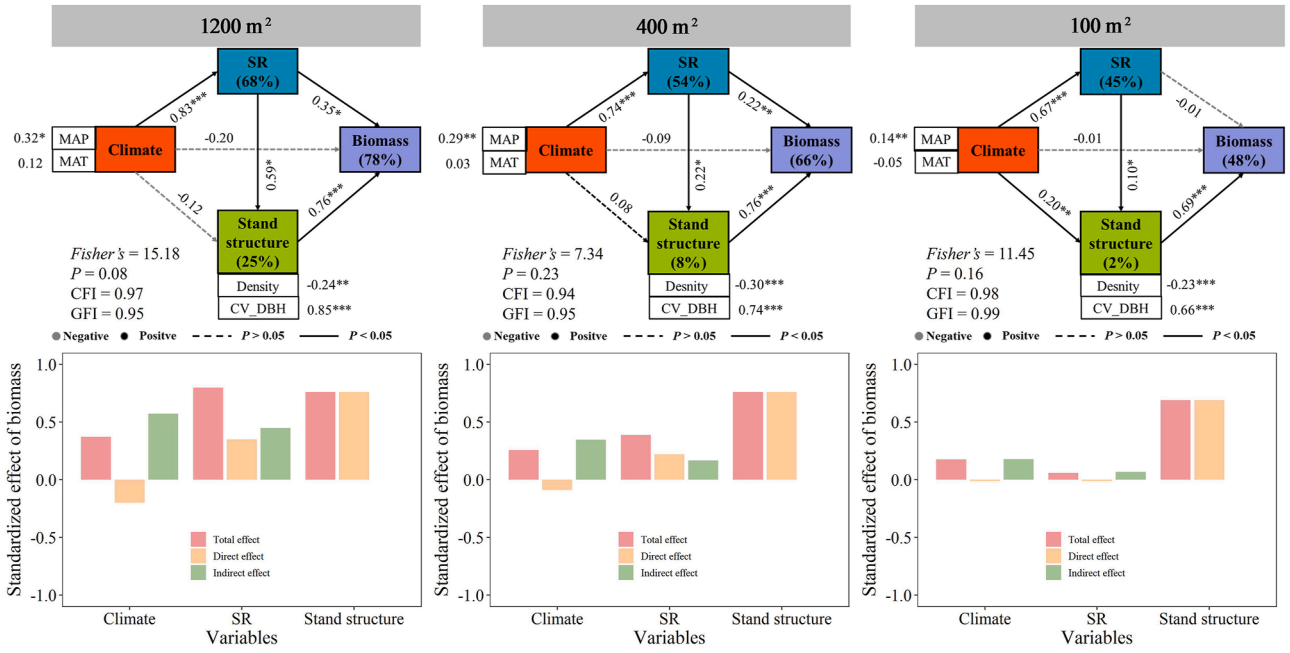

Fig. 4. The structural equation models (SEMs) of biomass of typical forest ecosystems in China between tree species richness, stand structural attributes, and climatic factors at three spatial scales. (a), (b) and (c) represent the SEMs at 1200, 400, and 100 m^2 spatial scales, respectively, and (d), (e) and (f) represent the total, direct, and indirect effects on biomass of each explanatory variable at 1200, 400, and 100 m^2 spatial scales, respectively. Note: the coefficients in Figure (a), (b), and (c) are standardized predictive coefficients for each causal path. solid black lines in the SEMs results indicate significant positive effects, solid gray lines indicate significant negative effects. Continuous solid lines in the SEMs results represent significant paths and dashed lines indicate non-significant. *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

insufficient to capture significant successional changes, as most of the forests were already mature and had reached a relatively stable state (Staude et al., 2023; Gao et al., 2024).

The relationships between tree species richness and biomass in this study remained stable over 20-year time, while we revealed that the relationships significantly changed with sampling scale. Based on data from a long-term survey of typical forest ecosystems in China, our study found that the relationship between tree species diversity and stand biomass varied at different spatial scales. Specifically, there was no significant relationship between tree species richness and stand biomass at finer spatial scales (100 m^2), while there was a significant positive linear relationship between tree species richness and the biomass at larger spatial scales (400 and 1200 m^2). These results indicated that the relationship between species diversity and ecosystem functions had a strong dependence on spatial scales, which is also consistent with many previous studies based on grassland and forest ecosystems (Qiu and Cardinale, 2020; Lisner et al., 2021; Mao et al., 2023). As mentioned above, there was always a positive linear relationship between tree species richness and biomass at larger spatial scales (1200 and 400 m^2), which was consistent with the results of other forest studies (Chisholm et al., 2013; Mao et al., 2023). The significant increase in forest biomass with species diversity was consistent with ecological theories such as selection effects and niche complementarity effects. However, compared to larger spatial scales, there was no significant relationship between tree species richness and stand biomass at finer spatial scale (100 m^2), which was consistent with the findings of Craven et al. (2020). According to the species area relationship, plant communities may often consist of one or a few species at finer spatial scale, resulting in lower species richness (Nijs and Roy, 2000; Qian et al., 2007). Therefore, species diversity effects may not affect forest biomass. Our findings on the scale-dependency of BEF relationships have key implications for ecology and management. This study highlights that the observed relationship between diversity and biomass is contingent on the spatial scale of observation, necessitating multi-scale approaches in forest monitoring to avoid biased conclusions. For management, this demands scale-explicit strategies: at broad landscape or regional scales (> 1 km^2), conservation should prioritize protecting diversity hotspots to leverage the strong direct effects of diversity on carbon storage. At fine, stand-level scales (< 0.1 km^2), management should focus on optimizing stand structural attributes (e.g., via density and size regulation) to enhance biomass, given its prevailing role at this grain.

4.2. Direct and indirect effects on stand biomass at different spatial scales

Increasing researches have suggested that stand structural attributes were robust predictors of biomass or productivity in forest ecosystems (Zhang and Chen, 2015; Mensah et al., 2020; Kazempour Larsary et al., 2025). Stand structural attributes (CV_DBH and CV_height) were positively correlated with stand biomass at different spatial scales, and served as the dominant factors for variations in forest biomass in the SEMs analysis (Fig. 4). These results were consistent with most previous studies based on different types of forests (Fotis et al., 2018; Ali et al., 2019; Mensah et al., 2020). Stand structure attributes represent the complexity of plant community in both horizontal and vertical direction, and determine the ability of individuals in forest ecosystems to capture and utilize resources such as light and water (Yachi and Loreau, 2007; Chen et al., 2023). Higher stand structural attributes imply greater canopy stacking densities and promote the ability of trees to access resources, which increase the potential for biomass production. Furthermore, our findings showed that species diversity indirectly improved stand biomass through stand structural attributes at all spatial scales, suggesting that stand structure attributes play mediating roles in the impact of tree species diversity on forest biomass (Kohyama et al., 2023). Richer

communities facilitate more tree species with different life forms and resource acquisition and utilization to coexist (Noulèkoun et al., 2024), which promote intra- and inter-species to occupy more available ecological niches and enhance resources availability, consistent with ecological niche complementarity effect. The direct effect of diversity on biomass increased with spatial scale can be interpreted within the classic BEF mechanistic framework. This pattern is consistent with the heightened importance of niche complementarity at broader scales, where greater environmental heterogeneity may provide more opportunities for species to partition resources and facilitate each other (Gonzalez et al., 2020). Conversely, the fact that stand structural attributes were the strongest and most consistent predictor of biomass across all scales aligns with the concept of selection effects, where certain traits (e.g., those conferring large size and dominance) disproportionately drive ecosystem function (Ali et al., 2019; Zhai et al., 2024). While our observational design prevents us from definitively partitioning the relative contributions of these two mechanisms, our multi-scale analysis provides inferential evidence that their relative importance is scale-contingent. However, tree density exhibited a significant negative association with stand biomass in this study (Fig. 4). This is consistent with findings of Kholdaenko et al. (2022),who found that stand density had negative impact on tree-level productivity (trunk volume and basal area) in southern taiga of Central Siberia. The possible reason is that the forest trees in our study basically belong to mature forests, and their water and nutrient resources are relatively poor, which leads to intensified competition within the tree species and triggers self-thinning effect (Lonsdale, 1990; Bai et al., 2021).

There generally are close connections between climatic factors and forest biomass production, especially at regional or global scales (Poorter et al., 2017; Kohyama et al., 2023). SEMs analysis revealed that climatic factors (MAT and MAP) had no significant direct impact on forest biomass at the three scales in this study, but rather influenced biomass by indirectly mediating tree species diversity and stand structural attributes. Our results further corroborate previous findings (Poorter et al., 2017; Ali et al., 2019; Noulèkoun et al., 2024), suggesting that environmental factors do not influence biomass through direct effects of physiological processes, but rather constrain biomass through resource constraints on biological factors such as diversity and stand structure. As the spatial scale increases, the contribution of climatic factors to variations in stand biomass increased (Fig. 4d–f). Because climate factors exhibit higher levels of non-uniform variation at larger spatial scales and have more pronounced effects on ecosystem functions, while interactions between biological organisms are stronger at finer scales than the effects of climatic heterogeneity (Chisholm et al., 2013; Cao et al., 2024).

4.3. Limits

This study examined changes over a 15-year period, which captures important inter-annual dynamics but is likely insufficient to observe directional community succession. The temporal stability we documented in the BEF relationship therefore reflects the ecosystem's resilience to short-term environmental variation. True successional shifts involving species replacement and major changes in community structure would likely require observations over decades to centuries (Lasky et al., 2014; Staude et al., 2023). Thus, long-term studies are needed to test how the mechanisms uncovered here (e.g., the dominant role of stand structure) persist or change across genuine successional gradients. Furthermore, while our models primarily elucidated the roles of climate and stand structure, we acknowledge that soil factors (e.g., nutrient availability and soil microorganism) likely constitute a critical dimension in scaling BEF relationships. Abiotic and biotic soil properties arguably act through the very pathways we identified as an environmental filter (Gottschall et al., 2022; Ma et al., 2023). For example, soil gradients (e.g., phosphorus limitation from temperate to tropics) directly influence tree species richness, thereby initiating the diversity-mediated pathway. Crucially, climate governs long-term pedogenic processes, implying that the detected indirect climate effects may be partially channeled through soil formation. Thus, soil factors likely act as a key mediator and effect modifier within the climate-biodiversity-structure–function nexus. Their explicit integration in future multi-scale BEF frameworks is essential to fully resolve the mechanisms driving ecosystem functions.

5. Conclusion

Our findings revealed the temporal dynamics and scale-dependent relationships between tree species diversity and stand biomass through multi-scale analysis and inferred the potential mechanisms through which ecological factors influence forest biomass variations. The relationship between tree species diversity and stand biomass demonstrated temporal robustness across spatial scales, but it exhibited a significant positive–linear correlations with increasing spatial scales. This implies that forest management at large spatial scales (e.g., regional or watershed levels) should prioritize tree diversity conservation to maximize its synergistic effects on carbon sequestration potential, while small-scale strategies (e.g., stand or plot levels) ought to emphasize localized habitat optimization. Furthermore, stand structural attributes emerged as the dominant sdriver of stand biomass variations, highlighting the critical role of structural metrics (e.g., canopy structure) in afforestation practices. Notably, the explanatory power of tree diversity and climatic factors on biomass variation increased progressively with spatial scale, suggesting that large-scale forest restoration initiatives must integrate biodiversity conservation with climate-adaptive strategies (e.g., drought- or heat-tolerant species selection) to address the escalating challenges posed by intensifying extreme climate events under global warming.

CRediT authorship contribution statement

Yonghong Zhang: Writing – original draft, Validation, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Honglin He:** Writing – review & editing, Data curation, Resources, Funding acquisition. **Liang Shi:** Writing – review & editing, Validation, Formal analysis. **Josep Peñuelas:** Writing – review & editing, Formal analysis. **Jordi Sardans:** Writing – review & editing, Formal analysis. **Yijing Bai:** Data curation, Resources. **Chenxi Li:** Data curation, Writing – review & editing. **Jiuying Pei:** Writing – review & editing.

Data availability statement

Our tree-level and climate data can be accessed on CERN website (https://www.cnern.org.cn/data/initDRsearch).

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.pld.2026.01.001.

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