

Research paper

Latitudinal patterns of tree β -diversity and relevant ecological processes vary across spatial extents in forests of southeastern China



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ARTICLE INFO

Article history:

Received 22 May 2024

Received in revised form

29 October 2024

Accepted 8 November 2024

Available online 13 November 2024

Keywords:

Environmental filtering

Latitudinal pattern

Forest beta diversity

Spatial extent

Species spatial aggregation

Regional community

ABSTRACT

Latitudinal patterns of tree β -diversity reveal important insights into the biogeographical processes that influence forest ecosystems. Although previous studies have extensively documented β -diversity within relatively small spatial extents, the potential drivers of β -diversity along latitudinal gradients are still not well understood at larger spatial extents. In this study, we determined whether tree β -diversity is correlated with latitude in forests of southeastern China, and if so, what ecological processes contribute to these patterns of tree β -diversity. We specifically aimed to disentangle the relative contributions from interspecific aggregation and environmental filtering across various spatial extents. We delineated regional communities comprising multiple nearby national forest inventory (NFI) plots around random focal plots. The number of NFI plots in a regional community served as a surrogate for spatial extent. We also used a null model to simulate randomly assembled communities and quantify the deviation (β -deviation) between observed and expected β -diversity. We found that β -diversity decreased along a latitudinal gradient and that this pattern was clearer at larger spatial extents. In addition, latitudinal patterns of β -deviation were explained by the degree of species spatial aggregation. We also identified environmental factors that drive β -deviation in these forests, including precipitation, seasonality, and temperature variation. At larger spatial extents, these environmental variables explained up to 84% of the β -deviation. Our results reinforce that ecological processes are scale-dependent and collectively contribute to the β -gradient in subtropical forests. We recommend that conservation efforts maintain diverse forests and heterogeneous environments at multiple spatial extents to mitigate the adverse effects of climate change.

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1. Introduction

β -diversity measures compositional changes in species assemblages across space. This essential indicator of biological diversity plays a significant role in ecological conservation and ecosystem management (Whittaker, 1960; Zhang et al., 2020a). The latitudinal patterns of β -diversity have garnered considerable attention in

recent years, stemming from its profound implications for unraveling biodiversity patterns and elucidating ecological processes across diverse spatial extents (Kraft et al., 2011; De Cáceres et al., 2012; Legendre and De Cáceres, 2013; Myers and LaManna, 2016; Xing and He, 2019). However, the relationship between latitude and β -diversity remains controversial. β -diversity in different taxa has been shown to be positively and negatively correlated with latitude. Furthermore, β -diversity metrics and sampling units have produced inconsistent results (Condit et al., 2002; Koleff et al., 2003; Kraft et al., 2011; Zhang et al., 2020b). Regardless, recent studies generally agree that ecological processes may contribute to differences in latitudinal patterns of β -diversity by influencing the composition of the regional species pool (Myers et al., 2013; Siefert

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Peer review under the responsibility of Editorial Office of Plant Diversity.

et al., 2013). To better understand the latitudinal patterns of β -diversity, it is essential to employ robust analytical methods and comprehensive datasets to disentangle the relative contributions of different ecological processes.

The latitudinal patterns of β -diversity may result from niche-based and dispersal-based processes (Zhang et al., 2020b). Environmental filtering, as a niche-based process, has been implicated in elucidating the latitudinal gradient of β -diversity through its association with environmental heterogeneity. Pianka (1966) hypothesized there is a negative relationship between latitude and environmental heterogeneity, suggesting environmental conditions tend to be more heterogeneous in regions closer to the equator and become more homogeneous towards the poles (Rodríguez and T. Arita, 2004). Several studies have supported this hypothesis, demonstrating correlations between specific environmental factors and β -diversity patterns across different regions (Qian et al., 2013; Schnitzer et al., 2020; Padilla Perez et al., 2022). For instance, topsoil sand fraction and precipitation seasonality have been found to be linked to forest β -diversity in North America (Xing and He, 2019). In addition, elevation and slope have been shown to impact β -diversity gradients (Gallardo-Cruz et al., 2009). These findings underscore the significance of environmental filtering effects, which encompass soil composition, topographical features, and climatic conditions, in shaping the latitudinal patterns of β -diversity (Tang et al., 2012; Xing and He, 2019).

An additional process that directly impacts regional β -diversity is the ability of species to disperse among sites within a region (Xu et al., 2015). Species with high dispersal ability generally reduce both β -diversity and the diversity of regional communities by extending the distribution of the dominant species (Savary et al., 2024). Conversely, dispersal limitation can result in spatial heterogeneity in species distributions, where different sites or habitats support distinct communities and present higher β -diversity communities (Savary et al., 2024). Studies have corroborated the positive relationship between β -diversity and dispersal limitation at relatively small extents on account of aggregated distributions of species in space (Williams, 1997; Qian and Ricklefs, 2007). Although both niche- and dispersal-based processes may produce communities with spatially aggregated species, the relative contributions of these ecological processes have been shown to be distinct across regions (Xing and He, 2019). Moreover, β -diversity can be impacted by stochastic processes, species interactions, or priority effects by altering the abundance of individuals or species within a community (Carrara et al., 2015; Ge et al., 2021).

Importantly, latitudinal patterns of β -diversity, as well as these ecological assembly processes, are scale-dependent (Zhang et al., 2018; Ren et al., 2022). Studies have suggested that species interactions and environmental heterogeneity were generally discovered to exert greater influence at finer spatial extents, while environmental filtering and dispersal limitation tended to be more prevalent at broader spatial extents (Wiens, 1989; Fritsch et al., 2020). However, the spatial extents examined in previous studies are generally less than 500 m in distance, which were deemed insufficient to represent the range of species distributed across the regional communities (Kraft et al., 2011; Zhang et al., 2018). Consequently, those close-range communities might capture species spatial aggregation at relatively small spatial extents but may potentially fail to adequately reveal latitudinal patterns of β -diversity at larger regional spatial extents (Wang and Loreau, 2016; Qiao et al., 2022). Moreover, the extent of the regional species pool significantly affects β -diversity through sampling effects (Zhang et al., 2020a). Larger regional species pools encompass a greater variety of species, increasing the likelihood of encountering distinct species compositions between sites or habitats, thus elevating β -diversity (Zhang et al., 2020b). Therefore, both spatial extent and

sampling effect should be appropriately controlled in such analyses (Burkle et al., 2016).

In this study, we conducted a forest field survey spanning 3876 plots across tropical-subtropical regions, including three southeastern coastal provinces of China, covering a broad latitudinal range. Thus, this extensive dataset provides a robust environmental gradient ideal for probing regional-scale geographical patterns of tree β -diversity. Rigorous controls were implemented over both spatial extents and sampling units, ensuring the reliability of our findings. To facilitate a quantitative study of the mechanisms of tree β -diversity patterns associated with changes in the regional species pool and community processes, we ensured that the number of sites was consistent across latitudes. We aimed to address the following questions relevant to the tropical-subtropical forest region in China: (a) What is the latitudinal pattern of tree β -diversity in the southeastern forest community of China? (b) How do ecological processes contribute to the tree β -diversity pattern? By answering these questions, we aim to provide valuable insights into the ecological dynamics of forest communities in this region and contribute to a deeper understanding of regional-scale biodiversity patterns.

2. Materials and methods

2.1. Study area and forest field survey data

The study area covers a large forested area in southeastern China that includes three coastal provinces: Zhejiang, Fujian, and Guangdong (Fig. 1a and b). This extensive area is characterized by diverse forest ecosystems and a humid subtropical climate. The climate is generally mild, with warm and temperate conditions prevailing for most of the year. According to the Köppen-Geiger climate classification system, the region exhibits variations in its climate patterns: Zhejiang and Fujian are classified as Cfa, and Guangdong is classified as Cwa (Chan et al., 2016). The annual average temperature in the regional area spans from 15 to 23 °C, with a few months that average below 0 °C. Annual precipitation in the region varies between 1100 and 1900 mm, reflecting significant variability in rainfall. Precipitation mostly occurs between April and September, resulting in a pronounced wet season characterized by abundant rainfall. Conversely, the winter months experience considerably less precipitation, leading to a distinct dry season.

We conducted this study using plot data from the Ninth National Forest Inventory (NFI; <https://www.forestdata.cn>) of China. A total of 3876 square forest plots were included (Fig. 1 and Table S1). The forest plots in Guangdong and Fujian each covered an area of 0.067 ha, whereas in Zhejiang, the plot size was, at 0.08 ha, slightly larger. In the subtropical forests, it has been reported that forest plots with an area greater than 500 m² is adequate for forest diversity studies (Fang et al., 2012; Zhang et al., 2020a). In addition, differences in plot area across regions can be ignored. For each forest plot, we recorded geographical coordinates (latitude, longitude) and topographic variables (altitude, aspect, and slope) (Zhang et al., 2020a). All individual trees with a diameter at breast height (DBH, 1.3 m) greater than 5 cm were identified and mapped for each plot.

2.2. Regional communities across different spatial extents

To standardize the assessment of β -diversity metrics across various spatial extents, we adhered to an established framework named the nearest n neighborhood method (Xing and He, 2019; Lin et al., 2023). This approach mitigates biased comparisons of tree β -diversity across space and arbitrary definitions of regional communities in forests (Xing and He, 2019; Zhang et al., 2020a). The

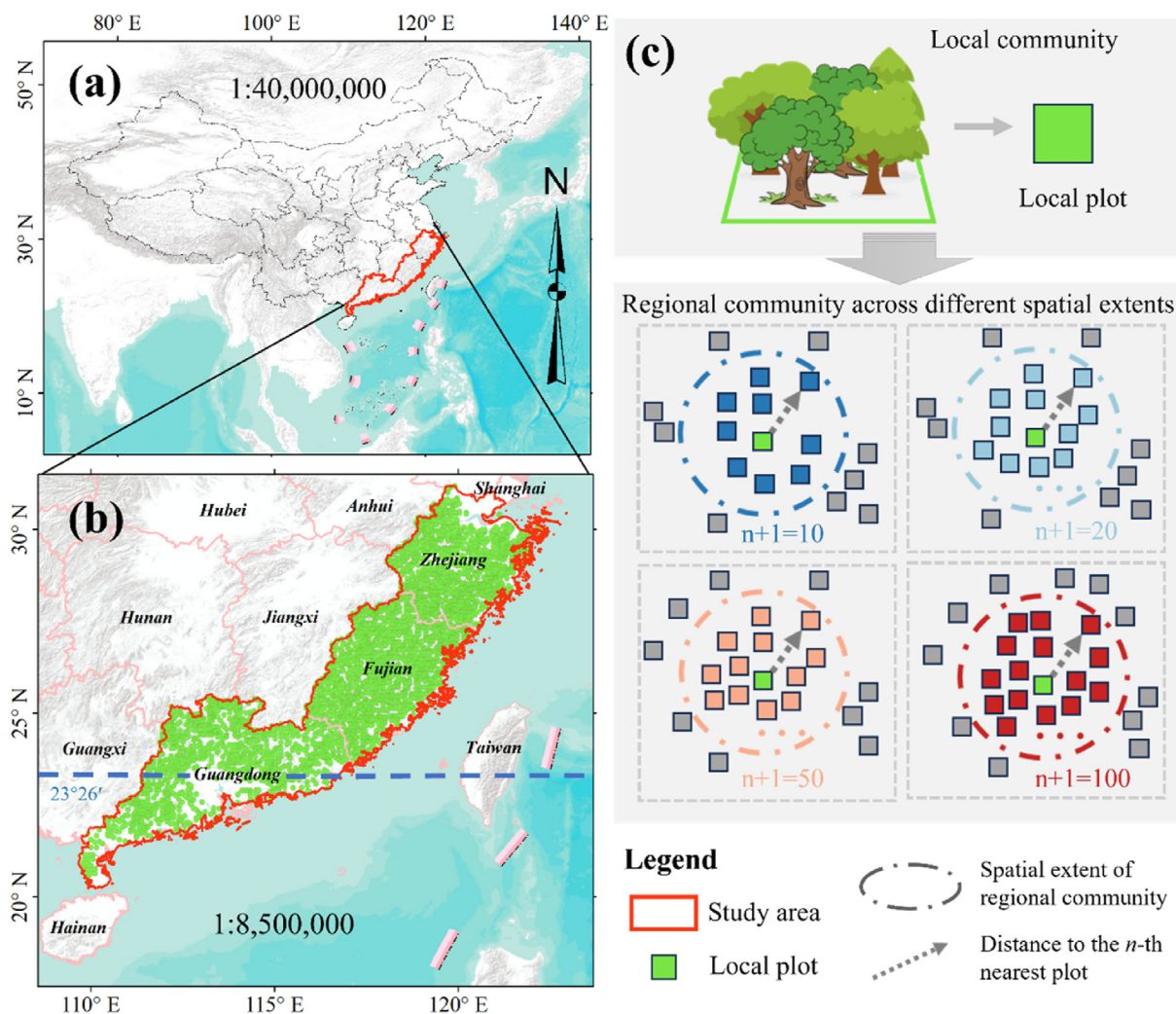


Fig. 1. Spatial distribution of the local plots and the regional communities at different spatial extents. (a) Location of the study area in China; (b) A total of 3876 local forest plots from the National Forest Inventory (NFI) were included from southeastern China; (c) Example showing how regional communities were formed by aggregating the nearest local plots at different spatial extents.

study area was divided into 100 km × 100 km grid cells. We randomly selected one local plot in each of the cells as the focal plot. We then defined a regional forest community as the selected focal forest plot along with its nearest n neighboring plots, as shown in Fig. 1c. Each regional forest community, thus, comprised $n + 1$ forest plots, forming the basis for calculating a regional species pool. This species pool was the basis for subsequent assessment of regional β -diversity and its corresponding ecological processes. By adjusting the value of n , we were able to add regional communities with different spatial extents and systematically evaluate how variations in the extent of regional species pools influence β -diversity. In this study, we set n as 9, 19, 49, and 99; thus, the regional forest communities consisted of 10, 20, 50, and 100 forest plots. The spatial extent of a regional community ranged from 20 km ($n = 9$) to 80 km ($n = 99$) (Fig. S1).

To explore the association between community similarity and geographical distance across various spatial extents among the studied plots, we further analyzed the spatial correlation of community composition using the Mantel correlogram (Legendre and Legendre, 2012; Legendre et al., 2015). This analysis first computes pairwise dissimilarities between the community compositions of all pairs of sites, while calculating pairwise geographical distances between the same sites. The Mantel test is then applied to

these dissimilarity and distance matrices to assess whether a significant correlation exists between community dissimilarity and geographical distance (Legendre and Legendre, 2012). This calculation was conducted using the “mantel.correlog” function within the *vegan* R package (Dixon, 2003). The findings, outlined in the supporting information, revealed that neighboring plots often shared similar community compositions, whereas plots separated by distances exceeding 207 km exhibited greater dissimilarity in forest communities (Fig. S2). The maximum spatial extent among regional communities (80 km) in this study was lower than the extent that lost positive spatial autocorrelation (207 km), indicating the four spatial extents examined were appropriate for defining regional communities (Figs. S1 and S2).

2.3. β -Diversity and β -deviation

After defining the regional communities as collections comprising 10, 20, 50, and 100 local plots, we constructed an abundance matrix (Xing and He, 2019; Zhang et al., 2020a). In this matrix, species were represented in columns while local plots were represented in rows. For instance, one of the regional community matrices, denoted as $S = [s_{ij}]$, encapsulated abundance values for m species (represented as x_1, x_2, \dots, x_m) observed across n plots

(represented as y_1, y_2, \dots, y_n). We then used the consensus biodiversity metrics, Hill numbers, to partition gamma diversity into alpha and β -diversity. Hill numbers represent a comprehensive set of diversity measures that combine both species richness and species relative abundance (Chao and Chiu, 2016; Chao et al., 2021, 2024; Chen et al., 2024). These measures are characterized by a diversity order parameter, denoted as q ($q \geq 0$). Hill numbers of local communities with orders $q = 0, 1$, and 2 transform into three fundamental indices of alpha-biodiversity: Species richness ($q = 0$, representing the effective number of rare species), Shannon entropy ($q = 1$, representing the effective number of common species), and Simpson index ($q = 2$, representing the effective number of dominant species), respectively (Chen et al., 2024). In the main text, we solely present results for $q = 0$; results for $q = 1, 2$ can be found in Fig. S3. Equations of Hill numbers are as follows:

$${}^qD_\alpha = \begin{cases} \frac{1}{N} \left(\sum_{i=1}^S \sum_{k=1}^N (P_{ik})^q \right)^{1/(1-q)}, & q \geq 0, q \neq 1, \\ \exp \left(- \sum_{i=1}^S \sum_{k=1}^N (P_{ik}) \log(P_{ik}) - \log N \right), & q = 1 \end{cases} \quad (1)$$

$${}^qD_\gamma = \begin{cases} \left(\sum_{i=1}^S (P_i)^q \right)^{1/(1-q)}, & q \geq 0, q \neq 1, \\ \exp \left(- \sum_{i=1}^S (P_i) \log(P_i) \right), & q = 1 \end{cases} \quad (2)$$

$${}^qD_\beta = {}^qD_\gamma / {}^qD_\alpha \quad (3)$$

where P_{ik} represents the proportion of the i -th species abundance in the k -th local community and P_i denotes the proportion of the i -th species abundance in the regional community; S and N are the numbers of species and local communities, respectively, in the regional community.

As raw scores of β -diversity were constrained by the underlying regional distribution of species abundances, the observed β -diversity inevitably deviated from expected β -diversity value based on random spatial distribution simulations. To quantify these deviations, we used the null model to simulate a collection of random species assemblages. Specifically, for each simulated regional community, all individual trees were randomly redistributed among the component local plots while retaining both the abundance of each species in the regional community and the total number of individuals across all species in each local plot to generate the ideal random spatial patterns of β -diversity (Kraft et al., 2011; Ulrich et al., 2017). Then, we ran 1000 simulations of this null model to calculate a mean, random β -diversity. β -deviation was calculated as $(\beta_{\text{observed}} - \bar{\beta}_{\text{Expected}}) / SD_{\beta_{\text{Expected}}}$. We conducted additional analysis to explore the latitudinal patterns of β -deviation and its potential drivers through the following statistical analysis.

2.4. Variation partition

Recognizing the potential influence of local community assembly mechanisms on the latitudinal patterns of β -diversity, we utilized interspecific aggregation and environmental filtering variables to test these ecological processes. Partitioned β -deviation was analyzed for interspecific aggregation and environmental

filtering (Legendre and De Cáceres, 2013). The partitioned β -deviations were analyzed as follows.

- (A) Interspecific aggregation: species spatial aggregation, influenced by dispersal limitation, environmental filtering, or both, leads to clustering of individuals in specific areas. This clustering reduces available dispersal space and the accessibility of rare nutrients, thereby altering latitudinal patterns of β -diversity. In our initial variation partitioning analysis, we highlighted species spatial aggregation as a pivotal factor in dissecting the β -deviation. To precisely quantify this aggregation, we employed the Morisita index within the framework of our null model (Crist et al., 2003; Xing and He, 2019). This index allowed us to gauge the degree of clustering or dispersion of individuals across species within the regional communities. Specifically, we computed the average Morisita index across common species that exhibited a higher abundance of individuals compared to the number of constituent local communities. This method enabled us to discern the extent to which species tended to aggregate within the study area, offering valuable insights into their spatial distribution patterns and their potential impact on β -diversity.
- (B) Environmental filtering: The second variation partitioning was to quantify the contribution of environmental filtering to the β -deviation. We prepared a total of 20 environmental variables and grouped these variables into three types, including climate, topography, and soil, to serve as drivers of the niche-based ecological process. As for climate variables, we extracted 10 variables (BIO1–BIO10) from the WorldClim database v.1 (Hijmans et al., 2005). The remaining 10 variables comprised 4 topographic factors (elevation, slope, slope aspect, and geomorphology), recorded by the National Forest Inventory (NFI), and 6 soil features extracted from SoilGrids (Poggio et al., 2021): (1) bulk density of the fine earth fraction, (2) cation exchange capacity of the soil, (3) proportion of clay particles (< 0.002 mm) in the fine earth fraction, (4) total nitrogen (N), (5) soil pH, and (6) soil organic carbon content in the fine earth fraction. The standard deviations of these environmental filtering variables were calculated for each of the regional communities across above mentioned different spatial extents.

Species spatial aggregation and latitude were directly used to partition the β -deviation into four explanatory components: [a] explained by species spatial aggregation alone, [b] explained by latitude alone, [c] explained by species spatial aggregation and latitude jointly, and [d] unexplained portion. Regarding the environmental filtering variables, we initially assessed the explanatory power of individual variables using the values of R^2 . We conducted bidirectional selection on these environmental variables through the “ordistep” function in the *vegan* R package, retaining only the selected variables for further analysis in the variation partitioning (Dixon, 2003). To evaluate the association between β -deviations and various explanatory variables, we employed a series of partial regressions, utilizing R^2 values to represent the strength of these relationships (Xing and He, 2019). These partitioning analyses were performed by the “varpart” function available in the *vegan* R package. Note that collinear variables in the explanatory tables do not require removal before the partitioning process. For variation partitioning, the significance of each unique fraction was tested using 999 permutations, whereas joint fractions were not tested (Zhang et al., 2020a).

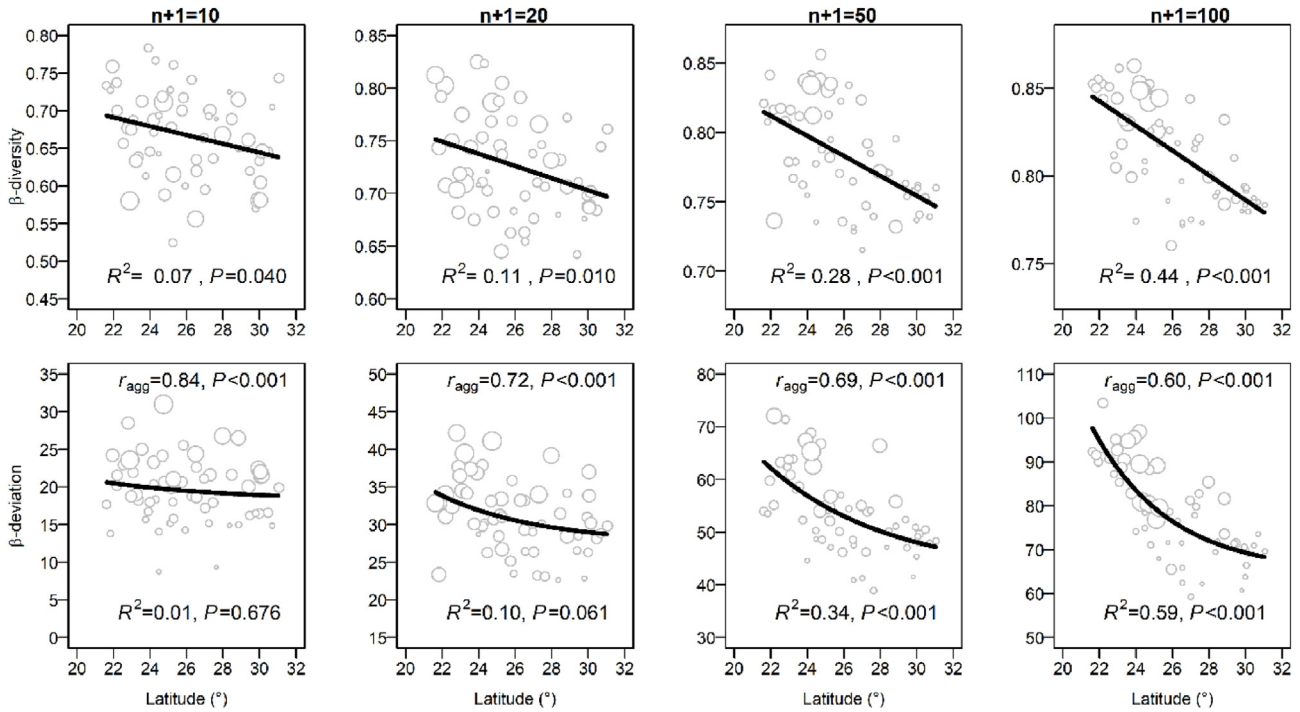


Fig. 2. Forest β -diversity (a) and β -deviation (b) along latitudinal gradients for regional communities constituting 10, 20, 50, and 100 local plots, respectively. The size of the bubbles indicates the degree of species spatial aggregation of the regional community, with larger bubbles representing higher aggregation. The best-fit regressions were linear and exponential decay lines for β -diversity and β -deviation, respectively. R^2 values are shown at the bottom of the panel (a) and (b). Pearson correlation coefficients (r_{agg}) between β -deviation and the species spatial aggregation matrices are shown at the top of the panel (b). Results for other measures can be found in Fig. S3.

3. Results

3.1. Latitudinal patterns of forest β -diversity and β -deviation

β -diversity and latitude were negatively correlated (Fig. 2). This correlation between β -diversity and latitude was stronger at larger spatial extents (e.g., for 100 plots, $R^2 = 0.44$; $P < 0.001$) than at smaller spatial extents (e.g., for 10 plots, $R^2 = 0.07$; $P = 0.040$). After we controlled for the sampling effect of the regional community, β -deviation exhibited non-linear patterns with latitude across spatial extents (Fig. 2b). Specifically, at larger spatial extents (50 and 100 plots), the highest β -deviation occurred at low latitudes and decreased to the lowest point around $\sim 30^\circ\text{N}$. The β -deviations demonstrated a strong positive correlation with the regional-community level species spatial aggregation across all spatial extents, with correlation coefficients ranging from 0.60 to 0.84 ($P < 0.001$).

3.2. β -Deviation partitioned by latitude and species spatial aggregation

Latitude and species spatial aggregation together explained approximately 50–70% of the variation in the β -deviations across different spatial extents (Fig. 3). Notably, when regional communities were relatively small, β -deviation was largely explained by species spatial aggregation. However, as the spatial extent of the regional community expanded, the proportion of variation explained solely by species spatial aggregation decreased. Instead, at larger spatial extents, the proportion explained by the joint effects of latitude and species spatial aggregation increased, reaching its peak when the regional communities consisted of 100 local plots. The proportion of β -deviation explained solely by latitude

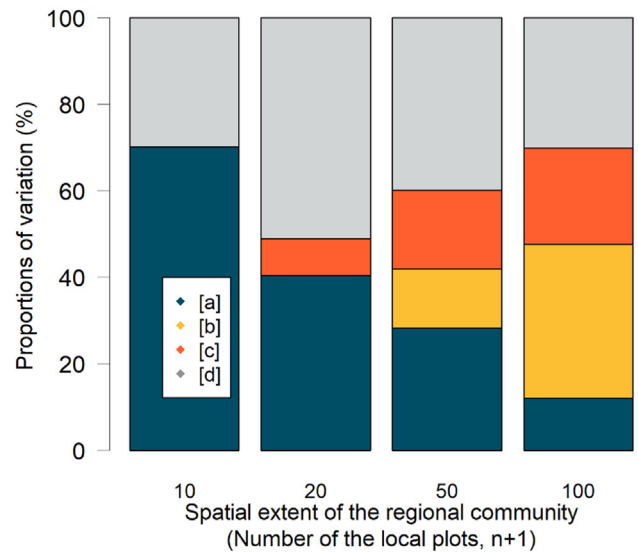


Fig. 3. Proportions of variation for β -deviation explained by latitude and the species spatial aggregation across regional communities constituting 10, 20, 50, and 100 local plots. [a] explained by species spatial aggregation alone, [b] explained by species spatial aggregation and latitude jointly, [c] explained by latitude alone, [d] unexplained portion.

increased from under 1% for regional communities comprising only 10 local plots to 22% for those with 100 local plots.

3.3. β -Deviation partitioned by latitude and environmental variables

Climatic and soil variables were correlated with latitude in patterns consistent with the relationship between latitude and β -

deviation (Fig. 4 and Table S2). Topographic variables, in contrast, were not significantly correlated with latitude. Climate variables with the strongest correlations to latitude included precipitation of the warmest quarter (BIO10) and annual precipitation (BIO05) ($R^2 \geq 0.5$), indicating that these variables strongly affect β -deviation, especially over a large spatial extent (i.e., 100 local plots). These climate variables, which serve as proxies for precipitation seasonality, particularly precipitation of the warmest quarter (BIO10) and precipitation of the wettest month (BIO06), were consistently correlated with β -deviation across different spatial extents. In addition to precipitation, temperature-related climate variables including isothermality (BIO02), temperature seasonality (BIO03), and temperature annual range (BIO04) exhibited significant effects, especially at spatial extents exceeding 50 local plots. Soil variables, including bulk density (SOIL01) and soil organic carbon content (SOIL06), presented as key influence factors to β -deviation.

Variation partitioning analysis revealed that the total proportion in β -deviation explained by the environmental filtering variables increased as the size of regional communities expanded from 10 to 100 local plots with the unexplained fraction decreasing from 0.69 to 0.16 (Fig. 5). The bidirectional selection process identified climate variables as significant contributors, i.e., isothermality (BIO02), precipitation of the driest quarter (BIO09), and precipitation of the

warmest quarter (BIO10). These climate variables accounted for the largest proportion of the explained variation in the β -deviation. Some soil variables tested also significantly explained the β -deviation. Conversely, the topographic variables only showed significant but little effects (0.04) until the regional communities constituted 100 local plots. Furthermore, the shared fraction between climate and soil variables increased with the spatial extent of regional communities, rising from 0.01 for those comprising 20 local plots to 0.25 for those comprising 100 local plots. When incorporating species spatial aggregation and environmental variables into the integrated variation partitioning model, the result showed that a large portion of the contribution from species spatial aggregation was mostly due to environmental heterogeneity (Fig. S5).

4. Discussion

Previous studies on the drivers of latitudinal patterns in β -diversity have focused on nearby communities with spatial extents limited to a few hundred meters (Kraft et al., 2011; De Cáceres et al., 2012; Qian et al., 2012), until recent studies turned to larger areas (Myers et al., 2013; Qian et al., 2013; Myers and LaManna, 2016; Xing and He, 2019; Zhang et al., 2020a). This paradigm shift gradually enriched our understanding of the mechanisms that shape

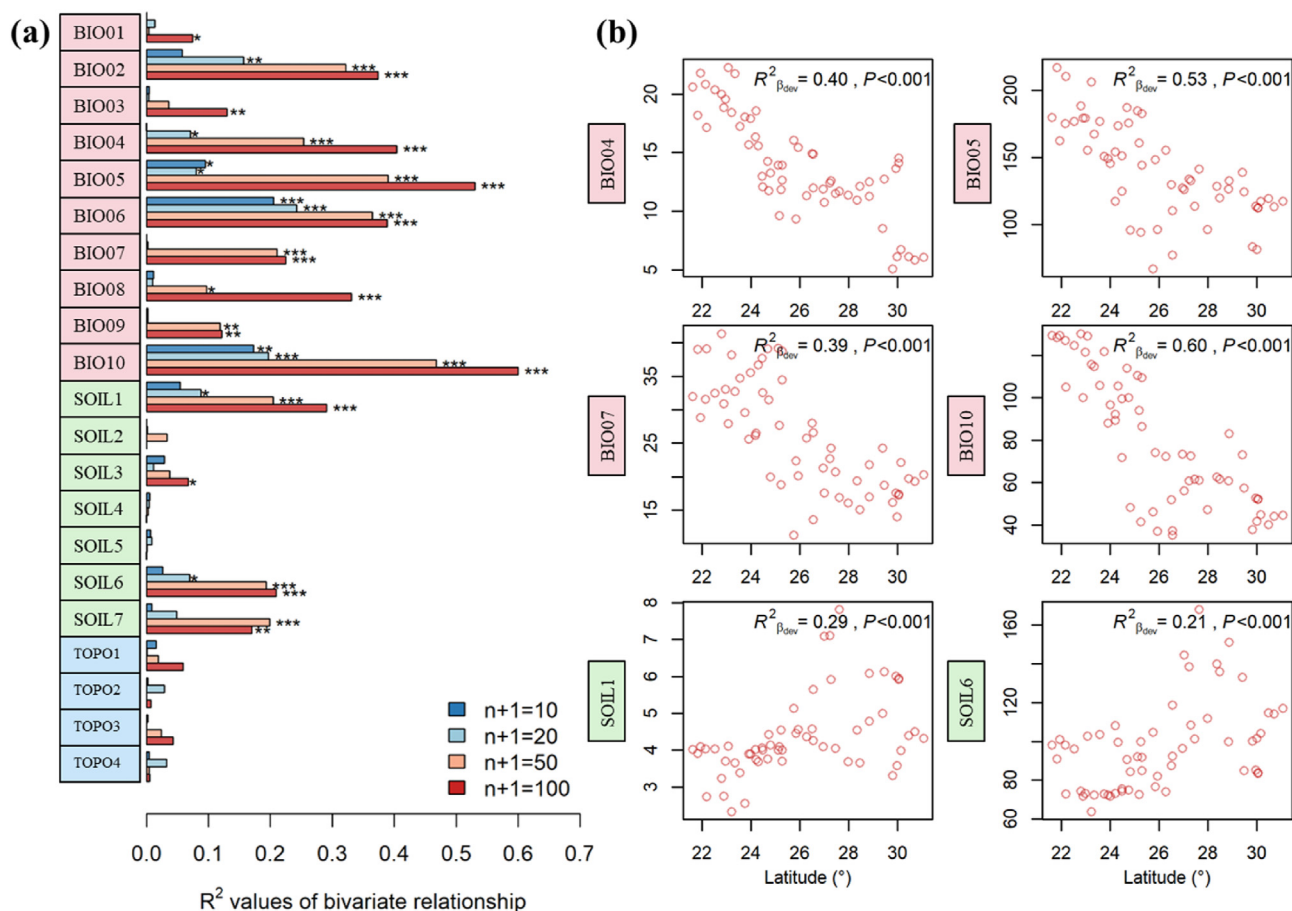


Fig. 4. (a) Bivariate correlations between the β -deviation and the standard deviation of environmental filtering variables for regional communities consisting of 10, 20, 50, and 100 local plots. * $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$; (b) Latitudinal patterns of top environmental filtering variables in 100 local plots are presented in the right panels. Abbreviations: BIO01: annual mean temperature, BIO02: isothermality, BIO03: temperature seasonality, BIO04: temperature annual range, BIO05: annual precipitation, BIO06: precipitation of wettest month, BIO07: precipitation of driest month, BIO08: precipitation seasonality, BIO09: precipitation of driest quarter, BIO10: precipitation of warmest quarter; SOIL01: bulk density of the fine earth fraction, SOIL02: cation exchange capacity of the soil, SOIL03: proportion of clay particles (< 0.002 mm) in the fine earth fraction, SOIL04: total nitrogen, SOIL05: soil pH, SOIL06: soil organic carbon content in the fine earth fraction, SOIL07: soil type; TOPO1: elevation, TOPO2: slope, TOPO3: slope position, TOPO4: aspect.

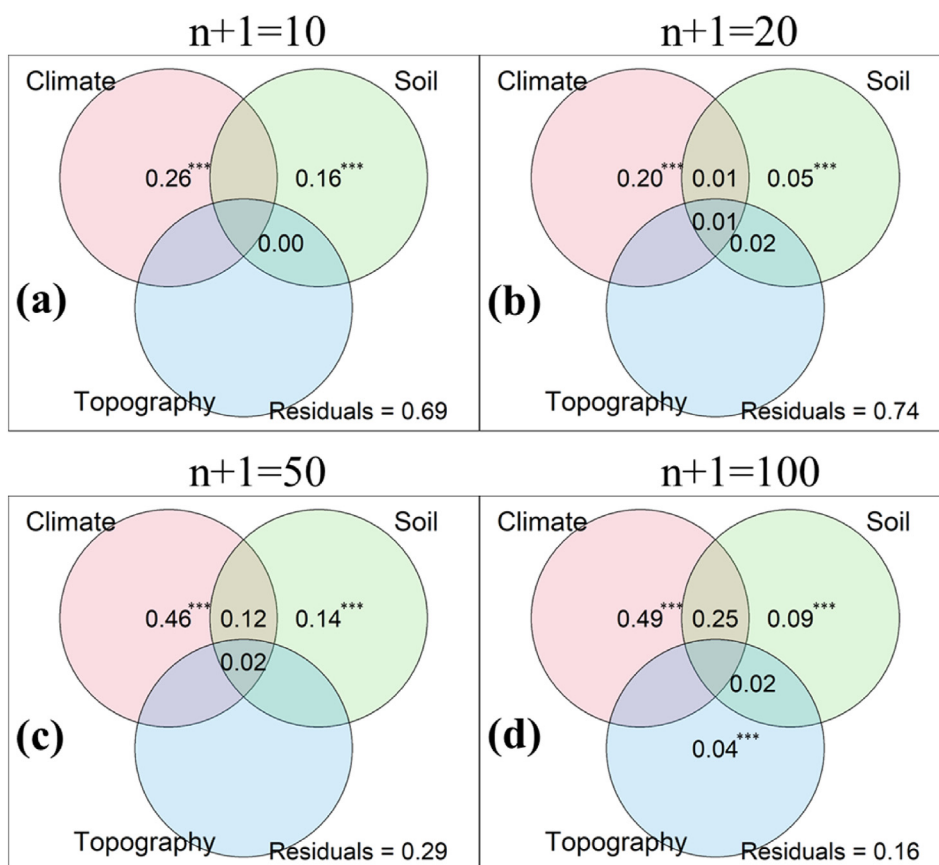


Fig. 5. The proportion of variation for β -deviation is explained by environmental filtering variables categorized into climate, soil, and topography across various spatial extents (a–d). The numbers within the Venn diagrams represent R^2 values, which indicate the proportions of variation accounted for by individual variables and their combinations. The components less than 0 are not displayed in the Venn diagrams. The right bottom value is the residual, representing the unexplained fraction. The results partitioned with latitude and species spatial aggregation can be found in Figs. S4 and S5.

regional β -diversity (Qian et al., 2013; Xing and He, 2021; Chao et al., 2024). Our study leveraged the large spatial extent of National Forest Inventory (NFI) data in southeastern China and introduced a pragmatic approach to constructing regional forest communities and revealed scale-dependent latitudinal patterns of β -diversity. Specifically, forest data from southeastern China confirmed that tree β -diversity is negatively correlated with latitude (Fig. 2a), which is consistent with previous studies in the eastern U.S. (Xing and He, 2019) and northeastern temperate China (Zhang et al., 2020a). We also discovered that the relationships between β -diversity and latitude can be well-fitted by the exponential decay function and exhibited a non-linear decreased pattern. Furthermore, this pattern became more significant with the larger spatial extents, which aligns with the scale-dependent pattern in northeastern China (Zhang et al., 2020a).

In our study, the β -deviations presented non-linear patterns with latitude, presenting higher values at lower latitudes. Meanwhile, this study area coincided with the conversion from the tropical to the subtropical region across the area of the Tropic of Cancer (Fig. 1b). This phenomenon may suggest the presence of an ecological transition zone, where biogeographical regions typically exhibit greater environmental variation, leading to higher rates of species turnover (Speziale et al., 2010; Ferro and Morrone, 2014; Morrone, 2024). As latitude increased within the subtropical region, the β -deviation exhibited a rapid decline due to decreasing environmental heterogeneity, which correlated with smaller standard deviations of climatic variables in Fig. 4b. These findings corroborate the theoretical model concluded by Xing and He (2019)

and Williams (1997), which posited that β -diversity generally decreases with increasing latitude. Furthermore, the non-linear relationship observed between β -deviation and latitude underscores the influence of environmental conditions.

Our study showed that latitudinal variations in the degree of species spatial aggregation, regardless of the measures employed, were responsible for latitudinal patterns of β -deviation (Fig. 2b). While previous studies highlighted the role of species abundance distribution in explaining latitudinal patterns of β -diversity (Myers et al., 2013; Xu et al., 2015; Myers and LaManna, 2016), our findings revealed that all regional communities exhibited significantly positive deviations of observed β -diversity from expected values. These observed variations in β -diversity compared to the expected values generally reflected the outcomes of spatial aggregation (Myers et al., 2013; Myers and LaManna, 2016). Our results indicated that intraspecific aggregation mainly attributed to environmental variables played an important role in shaping the latitudinal patterns of β -diversity (Fig. S5). Similarly, temperate forest communities also indicated that the environmental filtering hypothesis was tightly associated with community disparity (Zhang et al., 2020a). A collection of recent studies aligned with this view and supported environmental filtering as a pivotal driver in determining community assembly processes (Myers et al., 2013; Xing and He, 2019; Zhang et al., 2020a).

As environmental filtering explained a major proportion of the β -deviation in this study, we further explored the bivariate relationships between specific environmental variables and β -deviation across different spatial extents (Fig. 4). Firstly, we observed

that climatic variables, especially those related to precipitation seasonality and temperature variation, were largely responsible for shaping the β -deviation of tree diversity in southeastern China and that the interpretability of climatic variables increased with spatial extent (Xing and He, 2019). The precipitation of the warmest quarter (BIO10) accounted for the largest proportion in explaining β -deviation due to it providing essential moisture to forest communities during the hottest months when moisture was most critical in our study area. Thus, this climatic variable played a crucial role in determining the spatial distribution of forest diversity and was also commonly utilized as a predictor in modeling plant distribution (Liang et al., 2016; Xing and He, 2019). Remarkably, temperature isothermality (BIO02), describing the uniformity of temperature across the diurnal cycle and throughout the year in a given area, emerged as the most influential variable among those associated with temperature and previous studies have also corroborated its dominant role in determining the global distribution of tree diversity (Duivenvoorden et al., 2002).

Many studies have also found that soil features drive the spatial distribution of tree species. For instance, researchers in a Bornean rainforest reported strong correlations between soil texture and the spatial distribution of two sympatric dipterocarp species (Itoh et al., 2003). Our results showed that the bulk density of the fine earth fraction, as well as one indicator of soil texture, was a significant variable in determining the distributions of forests in southeastern China (Fig. 4). While soil organic carbon (SOILO6) and total nitrogen (SOILO4) were commonly used indicators of soil fertility in previous studies (Augusto and Boča, 2022; Chen et al., 2023; Cui et al., 2024), our findings revealed that only soil organic carbon exhibited a significant relationship with β -deviation in our studied subtropical area. This relationship may be attributed to the role of soil organic carbon through improving soil moisture retention and nutrient availability to enhance resilience against occasional environmental stressors (Trumbore, 1997; Beillouin et al., 2023), such as flash droughts and temperature fluctuations, thereby influencing tree distributions in southeastern China.

According to our findings, a pivotal question regarding the scale dependence of latitudinal patterns of β -deviation and its potential drivers may further unfold. While the regional communities comprising only 10 and 20 local plots did not show a significant latitudinal pattern in β -deviation, the corresponding extent was approximately 30 km and 40 km, respectively. However, a significant relationship was observed in regional communities consisting of 50 local plots. This suggested that there existed a threshold of the spatial extent of the regional community below which there was no latitudinal gradient for β -deviation. We tested the detailed gradient with regional communities consisting of 15–30 local plots and explored this threshold was 41 km for forest tree assemblages in southeastern China (Fig. S6). The latitudinal patterns of β -deviation would not be observed when the spatial extent of regional communities is smaller than 41 km in this study area. This threshold was previously suggested to be smaller than 7 km in the eastern U.S. (Xing and He, 2019), indicating substantial habitat heterogeneity at relatively small spatial extents. The differences between various findings commonly underscore the importance of assessing the influence of fine-scale habitat heterogeneity on diversity patterns, highlighting the necessity for intensified conservation efforts across larger spatial extents (Xing and He, 2019; Zhang et al., 2020a).

5. Conclusions

Our study utilized a multiscale framework to explore the latitudinal patterns of β -diversity across various spatial extents in southeastern China. We found that β -diversity was negatively

correlated with latitude and that the strength of this correlation increased over larger spatial extents. These findings highlight the need to carefully define the spatial extent of regional communities when interpreting drivers of β -diversity. Our investigation reinforces the pivotal role of environmental filtering in driving latitudinal patterns of β -deviation in subtropical forests. We found that precipitation seasonality and temperature variation play dominant roles in environmental filtering. Our findings also underscore the importance of environmental heterogeneity in shaping latitudinal patterns of β -diversity in subtropical forest regions in southeastern China and establish a foundation for modeling future ecosystem dynamics under severe climate change.

CRedit authorship contribution statement

Maochou Liu: Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Wenxiang Wu:** Writing – review & editing, Visualization, Validation, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization. **Ke Wang:** Writing – review & editing, Investigation, Data curation. **Xinshuai Ren:** Writing – review & editing, Investigation, Data curation. **Xueqin Zhang:** Writing – review & editing, Investigation, Data curation. **Lei Wang:** Writing – review & editing, Investigation, Data curation. **Jing Geng:** Writing – review & editing, Investigation, Data curation. **Bo Yang:** Writing – review & editing, Investigation, Data curation.

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.

Acknowledgments

This research was jointly supported by the National Natural Science Foundation of China (42271317) and the Innovation Research Team Project of the Natural Science Foundation of Hainan Province (422CXTD515). The authors extend their sincerest gratitude to the reviewers, whose comments and suggestions have greatly improved this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.pld.2024.11.003>.

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