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## RESEARCH ARTICLE



# Multiple processes jointly determine ecological uniqueness across forest plant life-forms in Northeast China

Yue Chen<sup>1,2,3</sup> | Jonathan A. Myers<sup>4</sup> | Alejandro Ordonez<sup>5,6,7</sup> | Jinghua Yu<sup>1</sup> | Ji Ye<sup>1,3</sup> | Fei Lin<sup>1,3</sup> | Shuai Fang<sup>1,3</sup> | Zikun Mao<sup>1,3</sup> | Xugao Wang<sup>1,3</sup>

<sup>1</sup>CAS Key Laboratory of Forest Ecology and Management, Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang, China

<sup>2</sup>University of Chinese Academy of Sciences, Beijing, China

<sup>3</sup>Key Laboratory of Terrestrial Ecosystem Carbon Neutrality, Shenyang, China

<sup>4</sup>Department of Biology, Washington University in St. Louis, St. Louis, Missouri, USA

<sup>5</sup>Section for Ecoinformatics and Biodiversity, Department of Biology, Aarhus University, Aarhus C, Denmark

<sup>6</sup>Department of Biology, Center for Biodiversity Dynamics in Changing World (BIOCHANGE), Aarhus University, Aarhus C, Denmark

<sup>7</sup>Department of Biology, Center for Sustainable Landscapes under Global Change (SustainScapes), Aarhus University, Aarhus C, Denmark

### Correspondence

Xugao Wang, CAS Key Laboratory of Forest Ecology and Management, Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang 110016, China. Email: wangxg@iae.ac.cn

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## Abstract

**Aim:** Ecological uniqueness is an essential component of biodiversity. However, the mechanisms underlying patterns of ecological uniqueness remain unresolved. This study aims to assess the relative importance as well as interactive roles of four hypothesized processes (regional climate filtering, local environmental filtering, biotic heterogeneity and disturbance intensity [DI]) in shaping ecological uniqueness across three forest plant life-forms (trees, shrubs and herbs) in a large temperate forest region. **Location:** Northeast China.

**Methods:** We quantified ecological uniqueness as abundance and incidence-based local relative contributions to beta diversity (i.e. LCBD indices) in the study region. Multiple beta regression analyses and piecewise structural equation models were used to determine the relative direct and interactive effects of four processes in shaping ecological uniqueness across forest plant life-forms.

**Results:** The southern area of the region exhibited consistently greater LCBD values across plant life-forms, highlighting its importance for conservation. All four processes jointly affected ecological uniqueness but their relative importance varied across plant life-forms. Generally, regional climate had the dominant effect on tree LCBD while biotic heterogeneity was the most important process driving shrub and herb LCBDs. Local environmental filtering was less important in driving LCBD of all life-forms. The significant direct effect of DI was only found in the herb group. Despite its weak direct effect, DI could indirectly shape tree and shrub LCBDs via biotic heterogeneity.

**Main Conclusions:** Our study suggests that current patterns of ecological uniqueness (i.e. LCBD) across forest plant life-forms result from multiple processes, with regional climate filtering and biotic heterogeneity having the strongest effects on uniqueness patterns across all life-forms. Meanwhile, DI is more critical for shaping ecological uniqueness of herbs than trees or shrubs. We highlight the interactive roles of biotic and abiotic filtering in shaping biologically distinct communities important for biodiversity conservation.

## KEYWORDS

beta-diversity, biodiversity conservation, biotic heterogeneity, disturbance intensity, ecological uniqueness, forest plant life-forms, local environmental filtering, regional climate filtering

## 1 | INTRODUCTION

A central issue in ecological research is to understand the mechanisms underlying spatial patterns of biodiversity at local and regional scales (Chesson, 2000; Ricklefs, 1990) and their applications to biodiversity conservation strategies (Socolar et al., 2016). Traditional biodiversity conservation mainly focuses on the number of species in particular locations (Kier et al., 2009; Li et al., 2015; Zhao et al., 2016). However, the ecological uniqueness of local communities-quantified as their local contributions to beta diversity (LCBD) in a region-has received increasing attention as a key indicator of biodiversity (Legendre & De Cáceres, 2013; Tonkin et al., 2016). Understanding spatial patterns of ecological uniqueness is essential for achieving conservation goals because sites with high uniqueness may often harbour functionally unique and/or valuable endemic species that contribute to regional biodiversity (Harper et al., 2022; Hill et al., 2021; Vilmi et al., 2017). Yet the mechanisms that determine spatial patterns of ecological uniqueness remain unclear and controversial, especially in forest ecosystems (Legendre & De Cáceres, 2013; Yao et al., 2020).

Four mechanistic processes have been hypothesized to explain spatial patterns of ecological uniqueness. First, the local environmental filtering hypothesis posits that ecological uniqueness is associated with local environmental conditions (e.g., topography, soil nutrients) that determine fine-scale variation in forest structure and composition (Costa et al., 2005; Yao et al., 2020). Previous studies have found that patterns of ecological uniqueness are influenced by distinct hydrological and temperature conditions along elevational gradients that determine the presence of rare species or variation in species richness (Punchi-Manage et al., 2014; Qiao et al., 2015; Yao et al., 2020). In addition, soil properties may influence the competitive advantages or niche creation, thus determining uniqueness through altering the abundance of rare species in the communities (Paoli et al., 2006; Suding et al., 2005).

Second, the regional climate filtering hypothesis posits that regional climate conditions over time influence ecological uniqueness by shaping species range sizes, richness patterns or species pool size (Guo et al., 2022; Jiménez-Alfaro et al., 2018; Tang et al., 2012). Accumulating evidence suggests that current climate conditions (e.g., temperature and precipitation seasonality [PS]) emerge as a strong driver of changes in vegetation diversity across large regions, which are likely to shape ecological uniqueness by increasing compositional variations among communities (Xing & He, 2019; Zhang et al., 2020). In addition, historical climate fluctuations (i.e., palaeoclimate) could impose long-lasting effects on species pool via their effects on habitat refugia, migration, range shifting or extinction events (Svenning & Skov, 2007). For instance, areas of high climatic instability may select for species with high dispersal abilities that enable them to track rapid spatial displacement of climatic conditions, resulting in species with broader distributions (Jansson & Dynesius, 2002; Qian et al., 2020). Importantly, increased stability of long-term climate conditions should generate more

distinct species assemblage (i.e., higher ecological uniqueness) (Zuloaga et al., 2019). However, the role of regional climate over time frames in determining patterns of ecological uniqueness remains largely unexplored.

Third, the biotic heterogeneity hypothesis posits that biotic attributes of local communities (e.g., richness, stand size complexity and vegetation quantity) are capable of determining forest ecological uniqueness. It is supposed that species interactions and competition for limited resources (e.g., light, water) can influence local species composition, relative abundance and richness (Hakkenberg et al., 2016; Yao et al., 2020). For instance, stem density (SD) or stand basal area could determine species richness due to competition, and probably impact ecological uniqueness by altering the ratio of common species in the communities or shared species with other communities (Yao et al., 2020). Additionally, stand size complexity provokes variations in light acquisitions at the forest floor and on soil conditions; it may regulate ecological uniqueness by creating ecological niches or gaps for rare or exotic taxa (Terborgh, 1985; Yuan et al., 2021). Specifically, the relationships between ecological uniqueness and species richness (i.e., negative, positive and nonsignificant) are vital for biodiversity conservation (Legendre & De Cáceres, 2013), as a negative relationship suggests that it may be insufficient to preserve sites with high species richness because those low-richness sites are more likely to contain high proportions of rare or endemic species which should be equally emphasized in the conservations (Harper et al., 2022). Hence, biotic heterogeneity might also play a key role in determining patterns of ecological uniqueness (Yao et al., 2020).

Finally, the disturbance intensity (DI) hypothesis suggests that the intensity of anthropogenic disturbance (e.g., fire or logging) influences ecological uniqueness by altering the composition, diversity or structure of communities (Crandall & Platt, 2012; Myers et al., 2015). For instance, if forest trees are selectively logged, changes in stand size complexity following stem removal would provide diverse biological properties or microclimatic conditions for some understorey species (Yuan et al., 2021), increasing spatial aggregations of species and ecological uniqueness within local communities. In addition, increasing DI may also influence ecological uniqueness by developing species richness, because substantial amounts of previously limited resources (e.g., light, moisture and nutrients) become available (Danneyrolles et al., 2019; Thom & Seidl, 2016). However, little is known about how changes in DI affect ecological uniqueness.

Moreover, while aforementioned processes emphasize the roles of different ecological drivers in shaping ecological uniqueness, they are not mutually exclusive (Heino & Gronroos, 2017; Kong et al., 2017). Indeed, it has been shown that biotic heterogeneity and local environmental filtering could jointly determine ecological uniqueness (Yao et al., 2020). Furthermore, DI and local environmental filtering could strongly affect community attributes associated with species distributions and spatial turnover (Myers et al., 2015; Wang et al., 2021). Therefore, these processes are capable of shaping ecological uniqueness both directly and indirectly, requiring simultaneous consideration of multiple drivers of ecological uniqueness (Yao et al., 2020). Although studies have attempted to combine several of these processes to explain variations in ecological uniqueness, the comprehensive integration of all four hypothesized processes has yet to be undertaken. Therefore, the relative importance of each process remains unresolved.

Plant diversity in forests consists of contributions from various life-forms (e.g., canopy trees, shrubs and the herbaceous ground layer), which could be assembled according to different ecological processes (Murphy et al., 2016). Previous studies suggest differences in the processes that shape species diversity across different forest plant life-forms (Wang et al., 2021). However, the role of these processes in determining patterns of ecological uniqueness across plant life-forms is still not well understood. The importance of these hypothesized processes is expected to differ in determining patterns of ecological uniqueness across life-forms. For instance, the effect of regional climate filtering may be more pronounced for tree and shrub groups given strong effects of climate change on woody plant species compositions and range size (Wang et al., 2012). In addition, the distributions of herbaceous species have been shown to correlate strongly with overstorey characteristics (e.g., tree size structure; SD) and local habitat conditions; thus, it is likely that biotic heterogeneity and local environmental filtering would have relatively greater roles in shaping ecological uniqueness of herb group than other processes (Machado & de Almeida, 2019; Murphy et al., 2016). Hence, a comprehensive understanding of these underlying processes on forest ecological uniqueness requires the considerations of different plant life-forms.

In this study, we use an extensive dataset of permanent forest plots distributed over a large region in northeast China to better understand how multiple processes (i.e. regional climate filtering, local environmental filtering, biotic heterogeneity and DI) regulate spatial patterns of ecological uniqueness, and examine the relative role of the four processes across plant life-forms. We use local contribution to beta diversity (i.e. LCBD indices) to quantify the ecological uniqueness of local communities and integrate the above-hypothesized processes into a single conceptual model (Legendre & De Cáceres, 2013). We hypothesize that all these processes would directly regulate ecological uniqueness across plant life-forms, while the regional climate, local environmental filtering and DI would shape ecological uniqueness indirectly via biotic heterogeneity (Figure 1). The conceptual model leads to the following predictions: (I) The regional climate filtering has a larger influence on the ecological uniqueness of tree and shrub groups than herbs since regional climate plays a major role in affecting woody species compositions and distributions (Qian et al., 2020; Ulrich et al., 2014). (II) The effect of DI and biotic heterogeneity on ecological uniqueness would be more pronounced for understorey shrub and herb groups since both of them have substantial impacts on overstorey forest structure or resource availability which influence the performance and distributions of understorey species (Chu et al., 2019; Wang et al., 2021).

## 2 | MATERIALS AND METHODS

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## 2.1 | Study area

Our study area is located in northeast China (39-48° N, 122-133° E; 400,000 km<sup>2</sup>), covering Heilongjiang, Jilin and Liaoning provinces (Figure 2). This region has a temperate continental climate, and annual precipitation is 600-1000 mm while mean annual temperature (MAT) is about 7°C. The main forest type in this region is the broadleaved-Korean pine (*Pinus koraiensis*) mixed forest.

## 2.2 | Plant data collection

We used a dataset of vascular plants across life-forms (i.e. trees, understorey shrubs and herbs) compiled from a total of 801 standardized forest plots of  $900 \text{ m}^2$  each  $(30 \text{ m} \times 30 \text{ m})$  (Wang et al., 2021; Figure 2). These forest plots were established and surveyed from 2008 to 2012. Within each plot, trees with diameter at breast height (DBH)  $\geq$  1 cm in each plot were identified to species, tagged and measured for DBH. Each forest plot was divided into 36 5 m×5 m subplots and 10 of them were randomly selected to record shrub species and their abundance. In each selected subplot, 10 1 m×1 m quadrats were set up to record herbaceous species. Totally, 1134 vascular plant species were recorded, including 108 tree species, 119 shrub species and 907 herb species (including ferns), bryophytes were not included in our study (see Appendix S1 for details).

# 2.3 | Quantifications of regional climate filtering, local environmental filtering, biotic heterogeneity and DI

We tested the four hypothesized processes using a combination of abiotic, biotic and disturbance variables (Table S1). To quantify the regional climate filtering process, we selected six predictors including both paleoclimate and current climate conditions. Paleoclimate data were obtained based on the Last Glacial Maximum (LGM) temperature and precipitation climate surfaces from the WorldClim database (https://www.worldclim.org/). Two paleoclimate variables, that is, temperature anomaly (TA) and precipitation anomaly (PA), were calculated as contemporary annual means of temperature and precipitation minus their respective LGM annual means (Loarie et al., 2009). For current climate data, we used mean annual precipitation (MAP), MAT, PS and temperature seasonality (TS), which were extracted from the WorldClim database with 30 arc seconds spatial resolution (Hijmans et al., 2005).

Soil and topographic variables were chosen to quantify the local environmental filtering. Soil variables including pH and total nitrogen (TN) were obtained from the National Earth System Science Data Center, National Science & Technology Infrastructure of China (http://www.geodata.cn) with a spatial resolution of 30m. The topographic variables (i.e., altitude, slope and aspect) of each plot were



FIGURE 1 Conceptual model of expected relationships between ecological uniqueness (i.e. local contributions to beta diversity indices) across plant life-forms and regional climate filtering (i.e., current and paleoclimate climate), local environmental filtering (i.e., topography and soil), biotic heterogeneity (i.e., forest structure consists of stem density, tree size variation, total basal area and species richness across plant life-forms) and disturbance intensity.

measured during the plot survey. The aspect data were transformed into a sine value (i.e., Sin(aspect)) to represent the eastness of each plot (Hirzel et al., 2002).

As for biotic heterogeneity, the total basal area (TBA), stand tree size variation (SV), SD and species richness across plant life-forms were included in the study. TBA was calculated as the sum of stem basal area of all trees and SV was defined as the coefficient of variation of tree DBH within each plot (Yuan et al., 2021). Meanwhile, tree species richness (TSR), shrub species richness (SSR) and herb species richness (HSR) were calculated as the number of species within each plot across life-forms (Table S1).

The DI was evaluated based on records of the strength of anthropogenic activities (Wang et al., 2021). Collectively, we measured DI index using three categorical levels: (I) low intensity (code 1), which refers to primary forests with no or slight human activity; (II) medium intensity (code 2), which mainly consists of secondary forests with obvious traces of anthropogenic disturbance; (III) high intensity (code 3), which represents continuous and strong disturbance in the secondary forests (see classification details in Table S2).

## 2.4 | Beta diversity and ecological uniqueness

We followed the method proposed by Legendre and De Cáceres (2013) to calculate total beta diversity ( $BD_{total}$ ) within the research area (Figure 2).  $BD_{total}$  was computed as the total variance of **Y** defined as a site by species matrix:

$$\mathsf{BD}_{\mathsf{total}} = \mathsf{Var}(\mathbf{Y}) = \mathsf{SS}(\mathbf{Y}) / (n-1),$$

where  $\mathbf{Y}[\mathbf{y}_{ij}]$  is a Hellinger-transformed site-by-species data matrix, each element in the matrix represents the relative abundance or presence/absence of species *j* in site *i* (i.e. abundance-based and incidence-based data format). **SS**(**Y**), the total sum of squares, is estimated as the sum of all species and sites of the squared deviations

## Study region and sampling details



**FIGURE 2** Location of the study region (a) and sampling plots (b) in northeast China. The location of the study region is indicated in dark red and tree sampling plots  $(30 \text{ m} \times 30 \text{ m})$  are indicated in black dots. Within each tree plot, 10 squares are randomly selected as shrub plots  $(5 \text{ m} \times 5 \text{ m})$ , each of which includes a nested herb plot  $(1 \text{ m} \times 1 \text{ m})$ .

from the species means (Yao et al., 2020), and n is the number of sites.

The degree of ecological uniqueness across plant life-forms was measured as LCBD (i.e., LCBD indices), representing each site's relative contributions to the total variation in species composition (i.e., beta diversity) among 801 plots in our study area. It should be noted that species contributions to beta diversity (i.e. SCBD) derived from BD<sub>total</sub> and some unique functional traits could also represent ecological uniqueness to some extent (Legendre & De Cáceres, 2013; Li et al., 2023), thus to avoid confusion, the ecological uniqueness only refers to the LCBD (i.e. LCBD indices) in the present study. The LCBD indices are comparative indicators of ecological uniqueness of species assemblages in sampling sites, where greater values indicate a relatively larger contribution of a local assemblage to variation in species composition (Legendre & De Cáceres, 2013). It can be decomposed by the total beta diversity described above and is calculated as:

$$\mathsf{LCBD}_i = \sum_{j=1}^p s_{ij} / \mathsf{SS}(\mathbf{Y})$$

where  $s_{ij}$  refers to the square of the difference between the element value  $y_{ij}$  in the matrix and the mean value of *j*th column; the LCBD indices measure how unique a site is compared with the centroid of all sites, that is, the average conditions of species composition of the entire area. The sum of all LCBD values is 1. Although we calculated both abundance and incidence-based (i.e. presence-absence) LCBD indices of each sampling plot separately for tree, shrub and herb groups, we mainly focused on the abundance-based LCBD in the present study since species abundance information is essential for understanding patterns and determinants of plant diversity as previously reported (Chisholm et al., 2013; Currie et al., 2004).

## 2.5 | Statistical analysis

Using multiple beta regression analysis with sets of logit link function (Cribari-Neto & Zeileis, 2010), we tested the relative effects of four hypotheses on abundance and incidence-based ecological uniqueness (i.e. LCBD indices) across plant life-forms. Before modelling, variable collinearity was checked using variance inflation 6 \_\_\_\_\_\_ WILEY \_\_\_\_\_ Journal of Biogeogra

factor (VIF) statistics (Table S3), and predictors with VIF >10 were removed. Hence, 14 variables were retained in our analysis for predicting ecological uniqueness across all groups, including: (I) five regional climate variables (TA, PA, MAT, PS and TS); (II) four local environmental variables (pH, altitude, slope and Sin(aspect)); (III) four biotic community attributes (TBA, SV, SD and SR); (IV) and one DI variable. All continuous predictors were standardized by subtracting the average value and dividing by the standard deviation. We also performed all subsets regression analysis and selected the optimal model that had the lowest AIC, (i.e., Akaike information criterion). We used  $\Delta AIC_c = 2$  as the cut-off point and obtained the standardized regression coefficient ( $\beta$ ) of each uniqueness predictor using a model averaging approach based on those model subsets with  $\Delta AIC_c < 2$  (Burnham & Anderson, 2004). The relative importance of predictors in the multiple beta regression analysis was estimated as the ratio of the standardized regression coefficient to the sum of all absolute coefficients in the above-averaged model (Yuan et al., 2021). The obtained relative importance of predictors was then grouped into four identifiable variance fractions based on the hypothesized processes above (i.e., regional climate filtering, local environmental filtering, biotic heterogeneity and DI).

Finally, we constructed piecewise structural equation modelling (pSEM) to investigate direct and indirect effects of these hypothesized processes on both abundance and incidence-based ecological uniqueness across life-forms (Lefcheck, 2016). In the pSEM analysis, we used explanatory variables retained in the model selection processes described above. Among those model subsets with  $\Delta AICc < 2$ , we selected the model with the highest weight (see Tables S4 and S5 for details) as the optimal model. In addition, we kept DI in the combinations of variables although it was not retained in optimal models for abundance-based tree and shrub LCBDs as well as incidence-based LCBDs across all life-forms (Tables S4 and S5), because our previous study has found the significant role of DI on biotic heterogeneity (Wang et al., 2021), which greatly indirectly shaped ecological uniqueness. These variables were then combined to represent the four processes from the full multiple beta regressions. We assumed that biotic heterogeneity directly affected ecological uniqueness, while regional climate, local environmental filtering and DI imposed both direct and indirect effects via biotic heterogeneity on ecological uniqueness (Figure 1). The model fit of pSEM was assessed using the Fisher's C statistic, it was considered to have an adequate model fit when the model had a Fisher's C statistic with p-value > 0.05 (Shipley, 2009). Meanwhile, indirect effects of multiple processes were calculated as the product of the corresponding path coefficients, and total effects were the sum of direct and indirect effects derived from pSEM models (Yuan et al., 2021). It is difficult to use beta regression under the current version of pSEM analysis (Lefcheck, 2016), we thus alternatively used generalized linear models (GLMs) with the distribution of beta family, in order to treat LCBD values as conforming to a beta distribution in the analysis. However,  $R^2$  of the beta family-based GLMs is also hard

to calculate in the current pSEM systems (Lefcheck, 2016); therefore, we calculated pseudo- $R^2$  based on fitting identical combinations of variables in the beta regression analysis to represent the variations of ecological uniqueness explained by these processes (Cribari-Neto & Zeileis, 2010).

All statistical analyses were performed in R 4.1.0 (R Core Team, 2021). We used the 'beta.div' function available from the 'adespatial' package (Dray et al., 2018) to calculate total beta diversity and ecological uniqueness (i.e., LCBD indices). Beta regressions were conducted using 'betareg' function in the 'betareg' package (Cribari-Neto & Zeileis, 2010), and model subset procedures were performed using 'dredge' function in the 'MuMIn' package (Bartoń, 2020). pSEM analyses were conducted using the 'piecewiseSEM' package (Lefcheck, 2016). The link function of beta family used in the GLMs was available in the 'glmmTMB' package (Brooks et al., 2017).

#### 3 RESULTS

Overall, results from the incidence-based analyses were similar to those from the abundance-based analyses (Figures 3-5; Figures S3-S5). So, we mainly showed the abundance-based results since species abundances provide important quantitative insights into the determinants of ecological uniqueness. The incidence-based results were provided in the Supporting Information (see Figures S2-S5; Tables S7, S11-S13). In addition, differences between incidencebased and abundance-based results were highlighted in the last section (i.e., 3.4).

#### Beta diversity and spatial patterns of LCBD 3.1 across forest plant life-forms

Total beta diversity  $\left(\!\mathsf{BD}_{\mathsf{total}}\!\right)$  of tree, shrub and herb groups in the area are 0.73, 0.75 and 0.86, respectively. Spatial patterns in LCBD (i.e. LCBD) differed across plant life-forms (Figure S1). Among all 801 plots, a total of 107, 90 and 106 plots showed significantly higher abundance-based LCBD values relative to mean species composition for tree, shrub and herb groups, respectively (Figure S1).

#### Drivers of LCBD across forest plant life-forms 3.2

The four hypothesized processes jointly influenced LCBD, but their relative effects varied across life-forms (Figure 3). The multiple beta regression models explained 21.0%, 33.0% and 37.0% of variations in tree, shrub and herb LCBD respectively (i.e.  $R^2 = 0.21, 0.33, 0.37$ respectively; Figure 3). For tree group, regional climate filtering had the dominant effect, accounting for 60.0% of the explained variations of abundance-based LCBD, followed by biotic heterogeneity (34.2%) and local environmental filtering (5.6%), DI had weak effect size (<1.0%). Specifically, TA, MAT and PS had significantly positive effect while TS had negative effect (Figure 3a; Table S6). Tree LCBD



FIGURE 3 Explanatory power of predictor variables for (a) tree, (b) shrub and (c) herb abundance-based ecological uniqueness (i.e. local contributions to beta diversity indices) from multiple beta regression models. Each continuous predictor is standardized by subtracting the average value by dividing the standard deviation. Filled circles indicate significant effects (p < 0.05), and hollow circles indicate non-significant effects. The relative importance of each factor (expressed as the percentage of variance explained) is shown where the contribution of regional climate filtering is drawn in lilac, local environmental filtering in brown, biotic heterogeneity in green and DI in red. PA and TA indicate the magnitude of change in mean annual precipitation or MAT, respectively, between the Last Glacial Maximum (LGM) and present-day; DI, disturbance intensity; HSR, herb species richness; MAT, mean annual temperature; pH, soil pH; PS, precipitation seasonality; SD, stem density; SSR, shrub species richness; SV, tree size variation; TBA, total basal area; TS, temperature seasonality; TSR, tree species richness.

showed significantly negative associations with TSR, tree SV and SD. No significant effect was detected for local environmental variables, and tree LCBD was also not significantly correlated with DI (Figure 3a; Table S6).

For shrubs, regional climate and biotic heterogeneity had similar effects, accounting for 38.6% and 38.1% of explained variations in LCBD respectively, followed by local environmental filtering (23.2%), with little effect for DI (<1.0%). Shrub LCBD was positively associated with TA, PS and altitude, while negatively associated with

TS, pH and SSR. DI also had no significant effect on shrub LCBD (Figure 3b; Table S6).

For herbs, biotic heterogeneity explained the largest fractions of variations in LCBD (55.2%), followed by regional climate (15.6%), local environmental conditions (14.7%) and DI (14.6%). Herb LCBD significantly decreased with increasing TS, SV, SD, HSR and DI. Meanwhile altitude had significant positive effect. Moreover, the effects of TA and PA were not significant (Figure 3c; Table S6).



**FIGURE 4** Piecewise structural equation models linking *abundance-based* ecological uniqueness (i.e. local contributions to beta diversity indices) to regional climate filtering, local environmental filtering, biotic heterogeneity and disturbance intensity across (a) tree, (b) shrub and (c) herb group. Solid black lines represent significant (p < 0.05) positive relationships and solid blue lines represent significant negative relationships, while paths with non-significant relationships are shown in dashed grey lines. Model fit statistics (i.e. Fisher's C statistics and *p*-value) are given in each panel. All abbreviations follow the legend to Table S1, and annotations of legend indicating each process follow Figure 3. The <sup>\*</sup> indicates p < 0.05, while <sup>\*\*\*</sup> indicate p < 0.01 and p < 0.001 respectively.

## 3.3 | Interactive drivers of LCBD

The final pSEMs revealed that variations of LCBD across life-forms were jointly explained by these four hypothesized processes (Figure 4). The tree pSEM explained 21.0% of the total variation in abundancebased LCBD ( $R^2$ =0.21; Figure 4a). TA, MAT and PS had significant positive direct effect while TS, SD and TSR showed significant negative direct effect. For indirect effects, TA, MAT, PS and TS had negative indirect effects while DI imposed positive indirect role via biotic heterogeneity (Figures 4a and 5a; Table S8). The relative contributions of total effects derived from the tree pSEM showed regional climate filtering occupied the largest relative importance (54.0%) in affecting tree abundance-based LCBD, followed by biotic heterogeneity (36.9%), while local environmental filtering and disturbance showed little effect (4.0% and 5.1%, respectively) (Figure 5d).

The shrub pSEM explained 32.0% of the total variation in the abundance-based LCBD ( $R^2$ =0.32; Figure 4b). TS, pH and SSR had significantly negatively direct correlations with LCBD, whereas TA, PS and altitude had positive direct effect in the pSEM. Negative indirect effect was found for TA and positive indirect effect was found for pH, altitude and DI (Figures 4b and 5b; Table S9). Collectively, biotic heterogeneity had dominant relative contributions (39.1%), followed by regional climate (29.7%), local environmental filtering (22.5%) and DI (8.7%) (Figure 5d).



**FIGURE 5** Direct and indirect effects of multiple hypothesized processes on *abundance-based* ecological uniqueness (i.e. local contributions to beta diversity indices) across (a) tree, (b) shrub and (c) herb group and (d) their relative contributions. The solid colour-filled bar represents a direct effect whereas pattern colour filled bar represents an indirect effect. Note that only those variables with indirect associations to ecological uniqueness show indirect effects. All abbreviations follow the legend to Table S1, and annotations of legend indicating each process follow Figure 3.

The herb pSEM showed that 36.0% of the variance was explained by multiple processes ( $R^2 = 0.36$ ; Figure 4c). TS, SV, HSR and DI had significant negative direct effects, whereas altitude had positive direct effect in the model. For indirect effects, altitude and DI yielded negative indirect effects while MAT showed positive indirect effect (Figures 4c and 5c; Table S10). In summary, biotic heterogeneity had largest contributions (47.0%) on herb LCBD, while DI showed larger relative importance (22.5%) than regional climate (20.5%) and local environmental filtering (10.0%) (Figure 5d).

## 3.4 | Differences between drivers of abundance and incidence-based LCBD across plant life-forms

Some incidence-based LCBD results were found to be differed from the abundance-based results. For instance, we found multiple processes explained much larger proportions of variations in incidence-based tree LCBD than abundance-based LCBD in the beta regression model and pSEM (49.0% vs. 21.0%; Figures 3a and 4a; Figures S3a and S4a). For herb group, the relative effect of DI in the abundance-based beta regression model was much larger than that in the incidence-based model (14.7% vs. <1.0%; Figure 3c; Figure S3c). DI had significant negative direct effect on abundancebased herb LCBD but non-significant effect on incidence-based herb LCBD (Figure 3c; Figure S3c). Moreover, results from pSEM showed that regional climate had much lower relative contribution to the incidence-based tree LCBD than to the abundance-based tree LCBD (25.1% vs. 54.0%) (Figure 5d; Figure S5d).

## 4 | DISCUSSION

## 4.1 | Relative roles of four hypothesized processes

Our study provides the first and critical insight into the distinct roles of four hypothesized processes (i.e., regional climate, local environmental filtering, biotic heterogeneity and DI) in shaping spatial patterns of ecological uniqueness (i.e. LCBD) across lifeforms. However, the relative effects of these processes vary in direction and magnitude depending on plant life-forms. We found regional climate had major effect on tree ecological uniqueness among the four hypothesized processes, which is consistent with our expectation (Figure 3a). However, weak effects of climate on ecological uniqueness have also been reported in northern Europe -WILEY- Journal of Biogeography

(e.g., Niskanen et al., 2017). Such discrepancy in climate-uniqueness relationships may result from the differences in climatic variables and spatial extent among studies. For example, Niskanen et al. (2017) examined the effects of accumulated temperature and water balance, while our study considered the effects of climate conditions over time frames. In addition, our study region spanned a much wider spatial extent, where variations in climate conditions were supposed to capture larger explanation power on ecological uniqueness of species assemblages. Paleoclimate (i.e., TA) had a significant effect on tree and shrub ecological uniqueness while no significant effect was found for herb LCBD, which indicates the major role of long-time scale climate fluctuations in shaping woody species compositions (Xu et al., 2021). The generation time of herbaceous species is generally shorter than that of woody plants which may lead to a higher evolutionary rate (Qi et al., 2014; Smith & Donoghue, 2008) and in turn allow herbaceous plants to have a faster micro-evolutionary adaptation (Liu et al., 2019). Due to the short life history, herbaceous species are capable of adapting to new environments and therefore are more likely to respond rapidly to changes in the current climate (Albuquerque et al., 2011; Liu et al., 2019).

Although previous studies had detected the effects of local environmental conditions on ecological uniqueness in forest communities (Yao et al., 2020), how these factors varied across plant life-forms remained unclear. In this study, we provided evidence that the effect of local environmental filtering was more pronounced for understorey groups (i.e., shrub and herb) than for trees (Figure 3; Figure S3), which was consistent with Murphy et al. (2016) that local environmental conditions explained a larger proportion of the variation in species composition for herb than for tree species. These indicate that the ecological uniqueness of understorey species assemblage would suffer from stronger effects of local abiotic conditions (Su et al., 2022). The relatively weak effect of local abiotic factors on tree ecological uniqueness could partly be due to tree species having wider niche breadths, which were not captured by those local variables. Furthermore, other important local environmental factors that may affect tree ecological uniqueness were not explicitly included in this study, such as soil nutrients (e.g., organic carbon, phosphorous) (Feng et al., 2021; Ulrich et al., 2014), hydrological characteristics (e.g., topographic wetness index and altitude above channels) (Song & Cao, 2017). In summary, together with regional climate filtering, these results highlight the importance of considering the separate roles of regional and local filtering when investigating patterns of biodiversity across different plant life-forms (Wang et al., 2021).

Consistent with previous studies, we showed the important effect of biotic heterogeneity hypotheses on forest ecological uniqueness (Yao et al., 2020). However, our results further revealed that various biotic community attributes (e.g., density and SVs) explained larger fractions of herb ecological uniqueness than tree and shrub, indicating the dominant role of biotic heterogeneity in determining herb assemblages. The abundance-based herb ecological uniqueness was significantly associated with SVs and SD (Figure 3c), suggesting

the contribution of heterogeneity in overstorey structure to herb composition. The SVs and density of tree layers directly determine the effective light intensity under the forest which indirectly shapes the composition and abundance of herbaceous species (Chastain et al., 2006; Wagner et al., 2011). Notably, ecological uniqueness was strongly negatively associated with species richness across all groups (Figure 3; Figure S3). Such negative associations were attributed to the greater chance of sharing species with other sites when a community harbours relatively high proportion of common species (Maloufi et al., 2016). Meanwhile, the directionality of this relationship in forests may be highly dependent on the proportion of rare versus common species in the community, and it tended to be negative when common species predominated but positive when the proportion of rare species increased (Benito et al., 2020; Leão et al., 2020; Yao et al., 2020). However, our analysis has limitations in the quantification of biotic heterogeneity. Other biological interaction processes, such as interactions among different vertical layers (e.g. canopy vs. sub-canopy) or competition among neighbouring individuals (Hakkenberg et al., 2016), have not been reflected in the present research. Future studies need to take more detailed factors into consideration in order to better represent these biotic processes

Our results showed that abundance-based rather than incidence-based herb ecological uniqueness significantly decreased with increasing DI, meanwhile, a non-significant effect was found for tree and shrub groups (Figure 3; Figure S3). This suggests the uniqueness of herb species assemblages might be more susceptible to anthropogenic activities; meanwhile, the ignorance of essential abundance information might mask the impact of this key process. The unique understorey habitat conditions, such as disturbanceinduced forest gaps, would have key roles in shaping assemblages of herb layer abundance, potentially by altering competitive exclusions or intraspecific aggregations due to resource availability differences (Chastain et al., 2006).

## 4.2 | The interactive drivers of ecological uniqueness

In addition to direct effects, we showed regional climate, local environmental filtering and DI indirectly shaped ecological uniqueness via biotic attributes. First, for tree and shrub groups, paleoclimate (e.g., TA) imposed indirect effects on ecological uniqueness via the influence on species richness. Long-term historical factors have been reported to be well correlated with various aspects of diversity at large geographic scales (Feng et al., 2017; Qian et al., 2020). Consistent with former studies, we provided evidence the present tree ecological uniqueness patterns to be strongly correlated with TA since the LGM (Svenning & Skov, 2007), highlighting the importance of biogeographic history in shaping present-day patterns of forest diversity components. Such a pattern may reflect a strong filtering on tree assemblages by climate change oscillation (Wang et al., 2012), which could leave a legacy effect on biodiversity via speciation, extinction or dispersal events (Sandel et al., 2011). Moreover, areas that are climatically distinct from their regional surroundings are supposed to select for species adapted to these conditions, which in turn promote small range sizes in those localities (i.e., climate distinctiveness hypotheses; Ohlemüller et al., 2008). The existence of glacial refugia with relatively moist and warm conditions in our study area (e.g., the Changbai Mountain) may benefit the survival of some small-range sized, long-lived tree genera, potentially contributing to a higher degree of ecological uniqueness (McGlone et al., 2016).

The seasonality of current temperature (i.e., TS) was found to negatively shape ecological uniqueness across life-forms, suggesting the essential role of current climate variability in shaping distributions of species endemism. It is suggested that greater seasonal variability in temperature might select for species that could tolerate a wider range of temperature, exhibiting larger geographical range sizes (Sunday et al., 2011; Zuloaga et al., 2019). Hence, communities experiencing higher TS tend to show lower ecological uniqueness, owing to the larger proportions of species with broad distributions which lead to the reduction in community dissimilarity or species turnover. It is noteworthy that the relative contribution of regional climate filtering to abundance-based tree ecological uniqueness was much lower than that to incidence-based ecological uniqueness (Figure 5d; Figure S5d). This might suggest that the consideration of abundance information in the analysis is vital for understanding determinants of the observed diversity patterns. Tree species abundance is usually a key indicator of dominance in forests; meanwhile, the species-energy hypothesis posits that climate strongly influences the energy available for individuals, thereby indirectly affecting tree diversity via its key impact on the number of individuals that can be supported (Chu et al., 2019). Therefore, including only incidence-based information may, to some extent, misunderstand the relative importance of these hypothesized processes on ecological uniqueness.

Local environmental conditions were also found to have an indirect impact across life-forms. The redistribution of light, temperature, water or nutrients induced by local variables (e.g. topography) might cater to the requirements or preferences of species for multiple resource conditions, thus leading to the observed distinct species composition (Andersen et al., 2014; Jucker et al., 2018). Our pSEMs revealed that altitude was an important local factor determining shrub and herb ecological uniqueness (Figure 4b,c). Altitude regulates the richness and assemblages of understorey groups by affecting litter coverage, forest canopy density or soil properties (Feng et al., 2021). It is reported that litter coverage has a particularly significant impact on herbaceous layer assemblages (Mestre et al., 2017), while the difference in light transmittance under different canopy densities along altitude gradients might be a key factor for understorey assemblages (Zhang et al., 2021). Additionally, altitude can significantly alter soil nutrients (e.g., N:P; total N, total K), which were tightly associated with the proportions of rare species in understorey assemblages (Paoli et al., 2006; Suding et al., 2005).

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Although little evidence was found for direct impact, DI indirectly shaped ecological uniqueness across plant life-forms. Our results showed that communities with higher DI had lower species richness across tree and shrub groups, thus increasing their ecological uniqueness (Figure 4a,b). A possible reason for this is that higher DI could induce significant changes in the microenvironment (e.g., light, moisture), filtering disturbance-intolerant species in particular habitats due to narrow habitat breadths across environment gradients (Myers et al., 2015). Thus, those distinct conditions should contain species assemblages of a lower shared proportion with other communities owing to the presence of more spatially aggregated species (Crandall & Platt, 2012). Moreover, the impact of DI was more pronounced for herb than tree and shrub. This may be attributed to the fact that disturbance-induced changes in forest structure and environment heterogeneity were more important for the distribution and occurrence of herb layer species (Wang et al., 2021).

Finally, our study may also, to some extent, have non-negligible implications for biodiversity conservation. For instance, the observed abundance and incidence-based ecological uniqueness were consistently higher in the southern area of this study region irrespective of life-forms (Figures S1 and S2). It is likely that more conservation efforts focusing on plant species are required to encompass this area, in order to preserve communities with relatively different species identities (Wang et al., 2021). As we demonstrated that variation in ecological uniqueness across plant life-forms was highly associated with biotic heterogeneity, it might be feasible for conservation biologists to pay more attention to maintain appropriate vegetation quantity or size structure in the practical strategies. Moreover, our results suggest that communities with higher ecological uniqueness tend to harbour lower richness. Under such circumstances, it depends on the priorities we set in the practices since it is difficult to protect all the areas in the whole region owing to the limited resources (da Silva et al., 2018; Sor et al., 2018). From the viewpoint of stressing distinctiveness, these communities with higher uniqueness should be more valuable in the conservation (Yao et al., 2020).

## 5 | CONCLUSIONS

Our study demonstrates the roles of four hypothesized processes (i.e., regional climate, local environmental filtering, biotic heterogeneity and DI) in shaping spatial patterns of ecological uniqueness (i.e. LCBD) across plant life-forms. However, the relative effects of these processes vary in direction and magnitude depending on lifeforms. The dominant role of regional climate filtering on the ecological uniqueness of tree group is observed, while uniqueness of herb group is mainly attributed to the influence of biotic heterogeneity, despite direct or total interactive effects are considered. For shrubs, regional climate and biotic heterogeneity have a similar direct effect, but biotic heterogeneity imposes the largest impact when both direct and indirect effects are taken into account. Local environmental filtering as well as DI have relatively small effect size among all WILEY- Journal of Biogeograp

hypothesized processes, local environmental filtering shows larger effect on the ecological uniqueness of shrub than others, while the impact of DI is more pronounced in herb. We thus suggest more detailed studies of these hypothesized processes could improve understanding of the ecological processes underlying patterns of species composition or endemism, and guide conservation practices that prioritize biologically distinct communities.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in https://doi.org/10.5061/dryad.547d7wmdh. We have also included the data in the Supporting Information.

## ORCID

Yue Chen D https://orcid.org/0000-0002-0190-5253

## REFERENCES

- Albuquerque, F. S., Olalla-Tárraga, M. Á., Montoya, D., & Rodríguez, M. Á. (2011). Environmental determinants of woody and herb plant species richness patterns in Great Britain. *Écoscience*, 18(4), 394–401. https://doi.org/10.2980/18-4-3426
- Andersen, K. M., Turner, B. L., & Dalling, J. W. (2014). Seedling performance trade-offs influencing habitat filtering along a soil nutrient gradient in a tropical forest. *Ecology*, 95(12), 3399–3413. https:// doi.org/10.1890/13-1688.1
- Bartoń, K. (2020). MuMIn: Multi-model inference. R package Version 1.43.17. https://CRAN.R-project.org/package=MuMIn
- Benito, X., Vilmi, A., Luethje, M., Carrevedo, M. L., Lindholm, M., & Fritz, S. C. (2020). Spatial and temporal ecological uniqueness of Andean diatom communities are correlated with climate, geodiversity and long-term limnological change. *Frontiers in Ecology and Evolution*, 8, 260. https://doi.org/10.3389/fevo.2020.00260
- Brooks, M. E., Kristensen, K., Benthem, K. J. V., Magnusson, A., Berg, C.
  W., Nielsen, A., Skaug, H. J., Machler, M., & Bolker, B. M. (2017).
  glmmTMB balances speed and flexibility among packages for zeroinflated generalized linear mixed modeling. *The R Journal*, 9(2), 378– 400. https://doi.org/10.32614/rj-2017-066
- Burnham, K. P., & Anderson, D. R. (2004). Multimodel inference: Understanding AIC and BIC in model selection. *Sociological Methods* & *Research*, 33(2), 261–304. https://doi.org/10.1177/0049124104 268644

- Chastain, R. A., Currie, W. S., & Townsend, P. A. (2006). Carbon sequestration and nutrient cycling implications of the evergreen understory layer in Appalachian forests. *Forest Ecology and Management*, 231(1-3), 63-77. https://doi.org/10.1016/j.foreco.2006.04.040
- Chesson, P. (2000). Mechanisms of maintenance of species diversity. Annual Review of Ecology and Systematics, 31(1), 343–366. https:// doi.org/10.1146/annurev.ecolsys.31.1.343
- Chisholm, R. A., Muller-Landau, H. C., Abdul Rahman, K., Bebber, D. P., Bin, Y., Bohlman, S. A., ... Coomes, D. (2013). Scale-dependent relationships between tree species richness and ecosystem function in forests. *Journal of Ecology*, 101(5), 1214–1224. https://doi.org/10. 1111/1365-2745.12132
- Chu, C., Lutz, J. A., Král, K., Vrška, T., Yin, X., Myers, J. A., Abiem, I., Alonso, A., Bourg, N., Burslem, D. F. R. P., Cao, M., Chapman, H., Condit, R., Fang, S., Fischer, G. A., Gao, L., Hao, Z., Hau, B. C. H., He, Q., ... He, F. (2019). Direct and indirect effects of climate on richness drive the latitudinal diversity gradient in forest trees. *Ecology Letters*, 22(2), 245–255. https://doi.org/10.1111/ele.13175
- Costa, F. R. C., Magnusson, W. E., & Luizao, R. C. (2005). Mesoscale distribution patterns of Amazonian understorey herbs in relation to topography, soil and watersheds. *Journal of Ecology*, 93(5), 863– 878. https://doi.org/10.1111/j.1365-2745.2005.01020.x
- Crandall, R. M., & Platt, W. J. (2012). Habitat and fire heterogeneity explain the co-occurrence of congeneric resprouter and reseeder Hypericum spp. along a Florida pine savanna ecocline. *Plant Ecology*, 213(10), 1643–1654. https://doi.org/10.1007/s11258-012-0119-0
- Cribari-Neto, F., & Zeileis, A. (2010). Beta regression in R. Journal of Statistical Software, 34, 1-24.
- Currie, D. J., Mittelbach, G. G., Cornell, H. V., Field, R., Guegan, J.-F., Hawkins, B. A., Kaufman, D. M., Kerr, J. T., Oberdorff, T., O'Brien, E., & Turner, J. R. G. (2004). Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecology Letters*, 7(12), 1121–1134. https://doi.org/10.1111/j.1461-0248. 2004.00671.x
- da Silva, P. G., Hernández, M. I. M., Heino, J., & Andersen, A. (2018). Disentangling the correlates of species and site contributions to beta diversity in dung beetle assemblages. *Diversity and Distributions*, 24(11), 1674–1686. https://doi.org/10.1111/ddi.12785
- Danneyrolles, V., Dupuis, S., Fortin, G., Leroyer, M., de Römer, A., Terrail, R., Vellend, M., Boucher, Y., Laflamme, J., Bergeron, Y., & Arseneault, D. (2019). Stronger influence of anthropogenic disturbance than climate change on century-scale compositional changes in northern forests. *Nature Communications*, 10(1), 1265. https:// doi.org/10.1038/s41467-019-09265-z
- Dray, S., Bauman, D., Blanchet, G., Borcard, D., Clappe, S., Guenard, G., Jombart, T., Larocque, G., Legendre, P., Madi, N., & Wagner, H. H. (2018). adespatial: Multivariate multiscale spatial analysis. R package Version 0.3-14. https://CRAN.R-project.org/package= adespatial
- Feng, G., Huang, J., Xu, Y., Li, J., & Zang, R. (2021). Disentangling environmental effects on the tree species abundance distribution and richness in a subtropical forest. Frontiers in Plant Science, 12, 622043. https://doi.org/10.3389/fpls.2021.622043
- Feng, G., Ma, Z., Benito, B. M., Normand, S., Ordonez, A., Jin, Y., Mao, L., & Svenning, J.-C. (2017). Phylogenetic age differences in tree assemblages across the northern hemisphere increase with long-term climate stability in unstable regions. *Global Ecology and Biogeography*, 26(9), 1035–1042. https://doi.org/10.1111/geb.12613
- Guo, Q., Qian, H., & Zhang, J. (2022). On the relationship between species diversity and range size. *Journal of Biogeography*, 49(11), 1911– 1919. https://doi.org/10.1111/jbi.14477
- Hakkenberg, C. R., Song, C., Peet, R. K., White, P. S., & Rocchini, D. (2016). Forest structure as a predictor of tree species diversity in the North Carolina Piedmont. *Journal of Vegetation Science*, 27(6), 1151–1163. https://doi.org/10.1111/jvs.12451

- Harper, L. M., Lefcheck, J. S., Whippo, R., Jones, M. S., Foltz, Z., & Duffy, J. E. (2022). Blinded by the bright: How species-poor habitats contribute to regional biodiversity across a tropical seascape. *Diversity* and Distributions, 28(11), 2272–2285. https://doi.org/10.1111/ddi. 13632
- Heino, J., & Gronroos, M. (2017). Exploring species and site contributions to beta diversity in stream insect assemblages. *Oecologia*, 183(1), 151–160. https://doi.org/10.1007/s00442-016-3754-7
- Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, 25(15), 1965–1978. https://doi.org/10.1002/joc.1276
- Hill, M. J., White, J. C., Biggs, J., Briers, R. A., Gledhill, D., Ledger, M. E., Thornhill, I., Wood, P. J., & Hassall, C. (2021). Local contributions to beta diversity in urban pond networks: Implications for biodiversity conservation and management. *Diversity and Distributions*, 27(5), 887–900. https://doi.org/10.1111/ddi.13239
- Hirzel, A. H., Hausser, J., Chessel, D., & Perrin, N. (2002). Ecological-niche factor analysis: How to compute habitat-suitability maps without absence data? *Ecology*, 83(7), 2027–2036. https://doi.org/10.1890/ 0012-9658(2002)083[2027:Enfaht]2.0.Co;2
- Jansson, R., & Dynesius, M. (2002). The fate of clades in a world of recurrent climatic change: Milankovitch oscillations and evolution. Annual Review of Ecology and Systematics, 33(1), 741–777. https:// doi.org/10.1146/annurev.ecolsys.33.010802.150520
- Jiménez-Alfaro, B., Girardello, M., Chytrý, M., Svenning, J. C., Willner, W., Gégout, J. C., Agrillo, E., Campos, J. A., Jandt, U., Kącki, Z., Šilc, U., Slezák, M., Tichý, L., Tsiripidis, I., Turtureanu, P. D., Ujházyová, M., & Wohlgemuth, T. (2018). History and environment shape species pools and community diversity in European beech forests. *Nature Ecology & Evolution*, 2(3), 483–490. https://doi.org/10.1038/s4155 9-017-0462-6
- Jucker, T., Bongalov, B., Burslem, D., Nilus, R., Dalponte, M., Lewis, S. L., Phillips, O. L., Qie, L., & Coomes, D. A. (2018). Topography shapes the structure, composition and function of tropical forest landscapes. *Ecology Letters*, 21(7), 989–1000. https://doi.org/10.1111/ ele.12964
- Kier, G., Kreft, H., Lee, T. M., Jetz, W., Ibisch, P. L., Nowicki, C., Mutke, J., & Barthlott, W. (2009). A global assessment of endemism and species richness across Island and mainland regions. Proceedings of the National Academy of Sciences of the United States of America, 106(23), 9322–9327. https://doi.org/10.1073/pnas.0810306106
- Kong, H., Chevalier, M., Laffaille, P., & Lek, S. (2017). Spatio-temporal variation of fish taxonomic composition in a South-East Asian flood-pulse system. *PLoS One*, 12(3), e0174582. https://doi.org/10. 1371/journal.pone.0174582
- Leão, H., Siqueira, T., Torres, N. R., & Montag, L. F. A. (2020). Ecological uniqueness of fish communities from streams in modified landscapes of Eastern Amazonia. *Ecological Indicators*, 111, 106039. https://doi.org/10.1016/j.ecolind.2019.106039
- Lefcheck, J. S. (2016). piecewiseSEM: Piecewise structural equation modelling in r for ecology, evolution, and systematics. *Methods in Ecology and Evolution*, 7(5), 573–579. https://doi.org/10.1111/2041-210x.12512
- Legendre, P., & De Cáceres, M. (2013). Beta diversity as the variance of community data: Dissimilarity coefficients and partitioning. *Ecology Letters*, 16(8), 951–963. https://doi.org/10.1111/ele.12141
- Li, R., Kraft, N. J. B., Yu, H., & Li, H. (2015). Seed plant phylogenetic diversity and species richness in conservation planning within a global biodiversity hotspot in eastern Asia. *Conservation Biology*, 29(6), 1552–1562. https://doi.org/10.1111/cobi.12586
- Li, Z., Heino, J., Zhang, J., Ge, Y., Liu, Z., & Xie, Z. (2023). Unravelling the factors affecting multiple facets of macroinvertebrate beta diversity in the World's Third Pole. *Journal of Biogeography*, *50*, 792–804. https://doi.org/10.1111/jbi.14574

Liu, Y., Su, X., Shrestha, N., Xu, X., Wang, S., Li, Y., Wang, Q., Sandanov, D., & Wang, Z. (2019). Effects of contemporary environment and quaternary climate change on drylands plant diversity differ between growth forms. *Ecography*, 42(2), 334–345. https://doi.org/10.1111/ ecog.03698

urnal of ogeography

- Loarie, S. R., Duffy, P. B., Hamilton, H., Asner, G. P., Field, C. B., & Ackerly,
   D. D. (2009). The velocity of climate change. *Nature*, 462(7276), 1052–1055. https://doi.org/10.1038/nature08649
- Machado, M. A., & de Almeida, E. B. (2019). Spatial structure, diversity, and edaphic factors of an area of Amazonian coast vegetation in Brazil1. The Journal of the Torrey Botanical Society, 146(1), 58–68. https://doi.org/10.3159/torrey-d-18-00025.1
- Maloufi, S., Catherine, A., Mouillot, D., Louvard, C., Couté, A., Bernard, C., & Troussellier, M. (2016). Environmental heterogeneity among lakes promotes hyper β-diversity across phytoplankton communities. Freshwater Biology, 61(5), 633–645. https://doi.org/10.1111/ fwb.12731
- McGlone, M. S., Buitenwerf, R., & Richardson, S. J. (2016). The formation of the oceanic temperate forests of New Zealand. New Zealand Journal of Botany, 54(2), 128–155. https://doi.org/10.1080/00288 25x.2016.1158196
- Mestre, L., Toro-Manríquez, M., Soler, R., Huertas-Herrera, A., Martínez-Pastur, G., & Lencinas, M. V. (2017). The influence of canopy-layer composition on understory plant diversity in southern temperate forests. *Forest Ecosystems*, 4(1), 6. https://doi.org/10.1186/s4066 3-017-0093-z
- Murphy, S. J., Salpeter, K., & Comita, L. S. (2016). Higher beta-diversity observed for herbs over woody plants is driven by stronger habitat filtering in a tropical understory. *Ecology*, 97(8), 2074–2084. https:// doi.org/10.1890/15-1801.1
- Myers, J. A., Chase, J. M., Crandall, R. M., Jiménez, I., & Austin, A. (2015). Disturbance alters beta-diversity but not the relative importance of community assembly mechanisms. *Journal of Ecology*, 103(5), 1291–1299. https://doi.org/10.1111/1365-2745.12436
- Niskanen, A. K. J., Heikkinen, R. K., Väre, H., & Luoto, M. (2017). Drivers of high-latitude plant diversity hotspots and their congruence. *Biological Conservation*, 212, 288–299. https://doi.org/10.1016/j. biocon.2017.06.019
- Ohlemüller, R., Anderson, B. J., Araujo, M. B., Butchart, S. H., Kudrna, O., Ridgely, R. S., & Thomas, C. D. (2008). The coincidence of climatic and species rarity: High risk to small-range species from climate change. *Biology Letters*, 4(5), 568–572. https://doi.org/10.1098/ rsbl.2008.0097
- Paoli, G. D., Curran, L. M., & Zak, D. R. (2006). Soil nutrients and beta diversity in the Bornean Dipterocarpaceae: Evidence for niche partitioning by tropical rain forest trees. *Journal of Ecology*, 94(1), 157–170. https://doi.org/10.1111/j.1365-2745.2005.01077.x
- Punchi-Manage, R., Wiegand, T., Wiegand, K., Getzin, S., Gunatilleke, C. V., & Gunatilleke, I. A. (2014). Effect of spatial processes and topography on structuring species assemblages in a Sri Lankan dipterocarp forest. *Ecology*, 95(2), 376–386. https://doi.org/10.1890/ 12-2102.1
- Qi, W., Bu, H., Liu, K., Li, W., Knops, J. M. H., Wang, J., Li, W., & Du, G. (2014). Biological traits are correlated with elevational distribution range of eastern Tibetan herbaceous species. *Plant Ecology*, 215(10), 1187–1198. https://doi.org/10.1007/s11258-014-0377-0
- Qian, H., Jin, Y., Leprieur, F., Wang, X., & Deng, T. (2020). Geographic patterns and environmental correlates of taxonomic and phylogenetic beta diversity for large-scale angiosperm assemblages in China. *Ecography*, 43(11), 1706–1716. https://doi.org/10.1111/ecog.05190
- Qiao, X., Li, Q., Jiang, Q., Lu, J., Franklin, S., Tang, Z., Wang, Q., Zhang, J., Lu, Z., Bao, D., Guo, Y., Liu, H., Xu, Y., & Jiang, M. (2015). Beta diversity determinants in Badagongshan, a subtropical forest in central China. *Scientific Reports*, *5*, 17043. https://doi.org/10.1038/ srep17043

- R Core Team. (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing.
- Ricklefs, R. E. (1990). Seabird life histories and the marine environment: Some speculations. *Colonial Waterbirds*, 13(1), 1. https://doi.org/10. 2307/1521414
- Sandel, B., Arge, L., Dalsgaard, B., Davies, R. G., Gaston, K. J., Sutherland, W. J., & Svenning, J. C. (2011). The influence of late quaternary climate-change velocity on species endemism. *Science*, 334(6056), 660–664. https://doi.org/10.1126/science.1210173
- Shipley, B. (2009). Confirmatory path analysis in a generalized multilevel context. *Ecology*, 90(2), 363–368. https://doi.org/10.1890/ 08-1034.1
- Smith, S. A., & Donoghue, M. J. (2008). Rates of molecular evolution are linked to life history in flowering plants. *Science*, 322(5898), 86–89. https://doi.org/10.1126/science.1163197
- Socolar, J. B., Gilroy, J. J., Kunin, W. E., & Edwards, D. P. (2016). How should beta-diversity inform biodiversity conservation? *Trends in Ecology & Evolution*, 31(1), 67–80. https://doi.org/10.1016/j.tree.2015.11.005
- Song, C., & Cao, M. (2017). Relationships between plant species richness and terrain in middle sub-tropical Eastern China. *Forests*, 8(9), 344. https://doi.org/10.3390/f8090344
- Sor, R., Legendre, P., & Lek, S. (2018). Uniqueness of sampling site contributions to the total variance of macroinvertebrate communities in the Lower Mekong Basin. *Ecological Indicators*, 84, 425–432. https://doi.org/10.1016/j.ecolind.2017.08.038
- Su, X., Zheng, G., & Chen, H. Y. H. (2022). Understory diversity are driven by resource availability rather than resource heterogeneity in subtropical forests. *Forest Ecology and Management*, 503, 119781. https://doi.org/10.1016/j.foreco.2021.119781
- Suding, K. N., Collins, S. L., Gough, L., Clark, C., Cleland, E. E., Gross, K. L., Milchunas, D. G., & Pennings, S. (2005). Functional- and abundance-based mechanisms explain diversity loss due to N fertilization. Proceedings of the National Academy of Sciences of the United States of America, 102(12), 4387–4392. https://doi.org/10.1073/ pnas.0408648102
- Sunday, J. M., Bates, A. E., & Dulvy, N. K. (2011). Global analysis of thermal tolerance and latitude in ectotherms. *Proceedings of the Royal Society B: Biological Sciences*, 278(1713), 1823–1830. https://doi. org/10.1098/rspb.2010.1295
- Svenning, J.-C., & Skov, F. (2007). Ice age legacies in the geographical distribution of tree species richness in Europe. *Global Ecology and Biogeography*, 16(2), 234–245. https://doi.org/10.1111/j.1466-8238.2006.00280.x
- Tang, Z., Fang, J., Chi, X., Feng, J., Liu, Y., Shen, Z., Wang, X., Wang, Z., Wu, X., Zheng, C., & Gaston, K. J. (2012). Patterns of plant betadiversity along elevational and latitudinal gradients in mountain forests of China. *Ecography*, 35(12), 1083–1091. https://doi.org/10. 1111/j.1600-0587.2012.06882.x
- Terborgh, J. (1985). The vertical component of plant species diversity in temperate and tropical forests. *The American Naturalist*, 126(6), 760–776. https://doi.org/10.1086/284452
- Thom, D., & Seidl, R. (2016). Natural disturbance impacts on ecosystem services and biodiversity in temperate and boreal forests. *Biological Reviews of the Cambridge Philosophical Society*, 91(3), 760–781. https://doi.org/10.1111/brv.12193
- Tonkin, J. D., Heino, J., Sundermann, A., Haase, P., & Jähnig, S. C. (2016). Context dependency in biodiversity patterns of central German stream metacommunities. *Freshwater Biology*, 61(5), 607–620. https://doi.org/10.1111/fwb.12728
- Ulrich, W., Soliveres, S., Maestre, F. T., Gotelli, N. J., Quero, J. L., Delgado-Baquerizo, M., Bowker, M. A., Eldridge, D. J., Ochoa, V., Gozalo, B., Valencia, E., Berdugo, M., Escolar, C., García-Gómez, M., Escudero, A., Prina, A., Alfonso, G., Arredondo, T., Bran, D., ... Zaady, E. (2014). Climate and soil attributes determine plant species turnover in global drylands. *Journal of Biogeography*, 41(12), 2307–2319. https://doi.org/10.1111/jbi.12377

- Vilmi, A., Karjalainen, S. M., Heino, J., & MacIsaac, H. (2017). Ecological uniqueness of stream and lake diatom communities shows different macroecological patterns. *Diversity and Distributions*, 23(9), 1042– 1053. https://doi.org/10.1111/ddi.12594
- Wagner, S., Fischer, H., & Huth, F. (2011). Canopy effects on vegetation caused by harvesting and regeneration treatments. *European Journal of Forest Research*, 130(1), 17–40. https://doi.org/10.1007/ s10342-010-0378-z
- Wang, S., Jiménez-Alfaro, B., Pan, S., Yu, J., Sanaei, A., Sayer, E. J., Ye, J., Hao, Z., Fang, S., Lin, F., Yuan, Z., & Wang, X. (2021). Differential responses of forest strata species richness to paleoclimate and forest structure. *Forest Ecology and Management*, 499, 119605. https://doi. org/10.1016/j.foreco.2021.119605
- Wang, Z., Fang, J., Tang, Z., & Shi, L. (2012). Geographical patterns in the beta diversity of China's woody plants: The influence of space, environment and range size. *Ecography*, 35(12), 1092–1102. https:// doi.org/10.1111/j.1600-0587.2012.06988.x
- Xing, D., & He, F. (2019). Environmental filtering explains a U-shape latitudinal pattern in regional beta-deviation for eastern North American trees. *Ecology Letters*, 22(2), 284–291. https://doi.org/10. 1111/ele.13188
- Xu, Y., Shen, Z., Zhang, J., Zang, R., & Jiang, Y. (2021). The effects of multiscale climate variability on biodiversity patterns of Chinese evergreen broad-leaved woody plants: Growth form matters. *Frontiers in Ecology* and Evolution, 8, 540948. https://doi.org/10.3389/fevo.2020.540948
- Yao, J., Huang, J., Ding, Y., Xu, Y., Xu, H., Zang, R., & Barnes, A. (2020). Ecological uniqueness of species assemblages and their determinants in forest communities. *Diversity and Distributions*, 27(3), 454– 462. https://doi.org/10.1111/ddi.13205
- Yuan, Z., Ali, A., Loreau, M., Ding, F., Liu, S., Sanaei, A., Zhou, W., Ye, J., Lin, F., Fang, S., Hao, Z., Wang, X., & Le Bagousse-Pinguet, Y. (2021). Divergent above- and below-ground biodiversity pathways mediate disturbance impacts on temperate forest multifunctionality. *Global Change Biology*, 27(12), 2883–2894. https://doi.org/10. 1111/gcb.15606
- Zhang, C., He, F., Zhang, Z., Zhao, X., Gadow, K., & Field, R. (2020). Latitudinal gradients and ecological drivers of β-diversity vary across spatial scales in a temperate forest region. *Global Ecology and Biogeography*, 29(7), 1257–1264. https://doi.org/10.1111/geb.13101
- Zhang, Y., Liu, T., Guo, J., Tan, Z., Dong, W., & Wang, H. (2021). Changes in the understory diversity of secondary *Pinus tabulaeformis* forests are the result of stand density and soil properties. *Global Ecology and Conservation*, 28, e01628. https://doi.org/10.1016/j.gecco.2021.e01628
- Zhao, L., Li, J., Liu, H., & Qin, H. (2016). Distribution, congruence and hotspots of higher plants in China. *Scientific Reports*, 6(1), 19080. https://doi.org/10.1038/srep19080
- Zuloaga, J., Currie, D. J., Kerr, J. T., & Pither, J. (2019). The origins and maintenance of global species endemism. *Global Ecology and Biogeography*, 28(2), 170–183. https://doi.org/10.1111/geb.12834

## BIOSKETCH

Yue Chen, Jinhua Yu, Ji Ye, Fei Lin, Shuai Fang, Zikun Mao and Xugao Wang are mainly interested in understanding the biogeographical and ecological processes underlying plant diversity and ecosystem functions. An essential part of these authors' research is to assess the effects of multiple biotic and abiotic processes on forest diversity across large scales and to develop sustainable forest management strategies. Jonathan A. Myers and Alejandro Ordonez are mainly interested in studying the processes that determine the assembly, diversity, and dynamics of ecological communities from local to global scales. **Author Contributions**: X.W. and Y.C. conceived the study. J.Y., J.Y., F.L. AND X.W. helped in the collection of forest censuses data. Y.C. and X.W conducted statistical analyses. Y.C. and X.W. wrote the first draft supported by J.A.M., A.O., S.F. and Z.M. All authors contributed to the revisions of the manuscript.

## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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