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Original Research Article

Patterns of diversity change for forest vegetation across different climatic regions - A compound habitat gradient analysis approach



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ABSTRACT

Biotic diversity of ecological communities can be driven by a mixture of climatic, soil and biotic factors from local to regional scales. Patterns of diversity change were often examined along latitudinal or elevational gradients, which were mainly driven by climatic factors. However, few studies have assessed biodiversity patterns along both abiotic and biotic gradients simultaneously. Here, we established 309 forest dynamics plots of typical forest vegetation types (tropical rainforest, subtropical evergreen deciduous broad-leaf mixed forest, warm temperate conifer broad-leaf mixed forest, and temperate conifer forest) in seven biogeographic regions across four climatic regions (tropical, subtropical, warm temperate, and temperate regions) in China. A total of 46,280 tree individuals of 801 species in these plots were tagged, investigated and mapped, and six functional traits and seven soil factors were sampled and measured, in addition, data on three climatic factors were extracted from Worldclim. Principal component analysis (PCA) was used to build the compound habitat gradient (CHG) combining the biotic and abiotic factors. Patterns of changes in species and functional diversity along the CHG were analyzed. Results showed that species richness, Shannon-Wiener index and functional richness (FRic) increased but functional divergence (FDiv) decreased along the first axis of the CHG. The models using the first four PCA axes of the CHG and models with the individual variables had more power to explain species diversity than functional diversity. PC1 was the most important predictor in explaining patterns of diversity variation. The null models of FRic and FDiv were significantly negatively correlated with PC1 in the compound habitat gradient, and not with other axes. Our study demonstrates that the compound habitat gradient analysis is an effective approach of exploring patterns of biodiversity change and understanding both the abiotic and biotic factors driving community assembly across different climatic regions.

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1. Introduction

Understanding the factors that determine patterns of biodiversity along environmental gradients remains a challenge for ecology, has been a hot topic for ecologists, a great deal of research has been done on different types of forests and grasslands (Gaston, 2000; Cadotte et al., 2011; Araujo and Costa-Pereira, 2013; Arnan et al., 2015; Chu et al., 2019). Previous biodiversity studies are often based on the assumption of ecological equivalence for all species (Hubbell, 2005). However, simple species diversity is difficult to fully reflect the important role of biodiversity in ecosystem processes and functions. Many studies have shown that functional diversity is more closely related to ecosystem functions and processes than other biodiversity factors (Díaz and Cabido, 2001), determine the intensity of the relationship between species diversity and ecosystem function and the specific forms of action. Functional diversity can reflect the degree of complementarity of resource utilization among species. A system with high functional diversity has higher resource efficiency (Lepš et al., 2006; Elmqvist et al., 2003; Díaz and Cabido, 2001). Therefore, analyzing the variation of species diversity and functional diversity along environmental gradient can show the mechanism of forest community construction and maintenance.

Species diversity and functional diversity were generally based on a single environment gradient in previous studies. For example, Zhang et al. studied on the functional diversity on the elevation gradient of Baihua Mountain show that the functional divergence shows a single peak change law with the increase of altitude. In general, species composition varies greatly with latitude, and species diversity decreases with increasing latitude (Araujo and Costa-Pereira, 2013). However, in large-scale studies, the effects of single latitude do not provide us with the effects of various habitat factors (such as climate, soil and biotic factors) within different communities on community diversity. Studies have found that, species diversity along an environmental gradient is not only determined by abiotic factors but also by various biotic interactions at local scales, such as competition (Gaston, 2000; Roslin et al., 2017). Biotic environmental conditions affect species composition, resulting in differences in community diversity (Waide et al., 1999), as well as drive species richness and traits within plant communities (Schluter, 2016; Pausas and Verdu, 2010). Meanwhile, the biotic variables related to community structure affect the functional composition and niche space available for species coexistence (Fortunel et al., 2018). The distribution patterns of biodiversity at large scales is one of the most interesting fields in ecology. So, biotic and abiotic factors might be combined into a compound habitat gradient that affects species and functional diversity. However, few studies have simultaneously considered the influence of both the biotic and abiotic factors on biodiversity (Forister et al., 2010; Jeffers et al., 2015).

China is one of the most biodiverse countries in the world. The enormous plant diversity results from broad environmental gradients, distinct geological conditions, as well as evolutionary history (Fang et al., 2013). Although there are several recent studies of national-scale species diversity and functional traits in China (He et al., 2018; Han et al., 2011; Wang et al., 2015), we still know less about the relative effects of biotic and abiotic drivers of species and functional diversity (Li et al., 2015). The studies that integrate species diversity and functional diversity address differences in the response of the two diversity facets to environment and in relation to the different scales considered (Arnan et al., 2015; Gonçalves-Souza et al., 2015; Purschke et al., 2013), which can help us understand rules of community construction at biogeographic scales.

The formation and maintenance of species diversity in community construction mainly involve two biotic mechanisms, one is the deterministic process associated with niche theory, the other is the stochastic process associated with neutral theory (Carroll et al., 2012). Habitat filtering improves species similarity, makes functional traits present convergent (convergence) characteristics, and reduces the range of functional traits. Interspecific interactions make functional traits exhibit differentiated (divergence) characteristics, reduce overlap of resource niches, and more uniform distribution of species on the resource axis, thus improving resource utilization (Weither et al., 2011). Compared with the deterministic processes of habitat filtration and interspecific interactions, neutral theory pays more attention to stochastic (stochastic) processes such as species extinction, migration and diffusion on regional scales (Carroll et al., 2012). Therefore, we try to test the difference between the range of traits and distribution characteristics of forest communities in different climatic regions of China generated by random processes in neutral theory and actual communities by null test (Azeria et al., 2009), making it clear whether random or deterministic processes dominate community construction. Here, We constructed a compound habitat gradient containing biotic and abiotic factors of forest communities in different climatic regions (tropical, subtropical, warm temperate, and cold temperate) of China. Based on data from 46,280 trees of 801 species in 309 forest dynamics plots, we constructed a compound habitat gradient with biotic and abiotic factors, calculated species diversity, functional diversity and null model for functional diversity of forest communities. We would like to explore the following questions: (1) What are the differences in species diversity and functional diversity of forest communities in different climatic regions and how do they change along the compound habitat gradient? (2) We expect to identify the main factors controlling the change of biodiversity of forest vegetation in different climate regions through CHG methods. which biotic and abiotic variables determine the diversity change mechanism of the compound habitat gradient? (3) What is the community construction mechanism for the variation of community functional diversity on the compound habitat gradient? Is the community construction mechanism dominated by deterministic processes or stochastic processes in different climatic regions of China? Through the multi-angle analysis of the functional diversity of forest communities in different climatic regions, we can further reveal the rules of forest construction in different climatic regions, which has important theoretical and practical value for the

formulation of forest management and monitoring measures in different climatic regions, and can provide scientific basis for the protection and sustainable utilization of forest resources across climatic regions.

2. Materials and methods

2.1. Study area

We selected seven sites with well-protected forests across four climate regions in China, including tropical (three sites), subtropical (two sites), warm temperate (one site), and temperate regions (one site) (Table 1). The three tropical sites (Jianfengling and Bawangling in Hainan Province and Xishuangbanna in Yunnan Province) are covered by tropical rain forest with a monsoon climate, with the wet season from May to October and the dry season from November to April. The two sites in the subtropical region (Xingdoushan and Mulinzi, Hubei Province) were tropical evergreen-deciduous broad-leaf mixed forest. In the warm temperate site (Xiaolongshan, Gansu Province) was in temperate coniferous broad-leaf mixed forest. The cold temperate site (Kanasi, Xinjiang Uygur Autonomous area) was in boreal coniferous forest. These are relatively old forests that have not been artificially disturbed or preserved for more than 100 years. Sample distribution, species information, soil climate and biotic information are shown in Table 1.

Table 1

The general information of the 309 0.04-ha forest dynamics plots across different climatic regions of China.

sits		Jianfenglin	Bawanglin	Xishuangbanna	Mulinzi	Xingdoushan	Xiaolongshan	Kanasi	
Climatic zone		Tropical			Subtropical		Warm temperate	Temperate	
Number of plots		50	50	40	44	25	50	50	
number of species		247	236	208	130	94	111	7	
elevation		896.34 ± 124.98	958.93 ± 63.98	790.51 ± 85.15	1534.31 ± 133.43	1660.01 ± 84.34	1864.2 ± 28.65	1710.54 ± 129.41	
Latitude		18.71–18.80	19.02–19.16	21.58–21.63	29.89–30.10	30.00–30.07	34.29–34.43	48.69–48.70	
Longitude		108.84–108.92	109.07–109.17	101.56–101.60	109.22–110.12	100.21–110.22	106.08	86.94–86.95	
soil	pH	Soil pH	4.81 ± 0.29	4.37 ± 0.35	4.91 ± 0.56	4.41 ± 0.25	4.49 ± 0.31	5.7 ± 0.53	5.54 ± 0.2
	SOM	Soil organic matter (g/kg)	15.62 ± 5.62	6.39 ± 1.83	3.19 ± 0.76	8.4 ± 2.05	9.21 ± 2.2	9.69 ± 2.92	3.38 ± 1.03
	TN	Soil total N content (g/kg)	1.32 ± 0.43	2.11 ± 0.81	1.34 ± 0.44	5.9 ± 1.72	6.54 ± 1.51	3.58 ± 1.17	1.06 ± 0.34
	TP	Soil total P content (g/kg)	0.14 ± 0.08	0.33 ± 0.19	0.31 ± 0.07	0.5 ± 0.16	0.68 ± 0.33	0.38 ± 0.11	0.64 ± 0.13
	AN	Soil available N(mg/kg)	183.22 ± 54.1	193 ± 46.7	156.69 ± 27.93	299.38 ± 73.7	355.99 ± 102.12	266.03 ± 82.37	64.29 ± 19.53
	AP	Soil available P(mg/kg)	192.14 ± 136.72	179.9 ± 123.2	84.49 ± 28.69	34.59 ± 11.99	23.25 ± 12.47	60.37 ± 27.78	37.5 ± 16.61
	AK	Soil available K(mg/kg)	125.54 ± 53.66	150.18 ± 43.78	130.6 ± 58.25	142.84 ± 34.04	134 ± 33.78	186.19 ± 53.12	227.84 ± 58.83
climate	CVPS	Precipitation seasonality (coefficient of variation) (%)	79.8 ± 0.45	80.44 ± 0.5	72.93 ± 0.47	71.91 ± 23.45	63.44 ± 18.53	78.62 ± 0.49	56.28 ± 0.81
	MAP	Mean annual precipitation (mm)	1633 ± 49.81	1579.08 ± 145.02	1584.43 ± 27.03	1213.91 ± 363.31	1385.24 ± 301.54	671.6 ± 5.16	316.34 ± 4.77
	MAT	Annual mean temperature (°C)	205.18 ± 5.42	211.52 ± 15.59	217.4 ± 3.88	96.52 ± 54.39	95.2 ± 34.91	81.18 ± 2.79	−9.9 ± 2.83
biotic	DBH	Individual mean diameter at breast height (DBH, cm)	6.34 ± 1.38	5.62 ± 0.84	6.98 ± 2.94	11.06 ± 3.79	10.68 ± 1.21	7.03 ± 1.91	15.39 ± 2.87
	CH	Canopy height (m)	18.43 ± 4.65	25.9 ± 5.34	37.25 ± 14.14	20 ± 3.19	18.46 ± 3.14	15.72 ± 1.58	23.76 ± 1.8
	BA	Basal area (≥ 1 cm DBH) (m ² ha ^{−1})	34.93 ± 11.94	45.77 ± 14.9	51.75 ± 20.03	35.14 ± 10.09	28.88 ± 9.53	33.86 ± 6.6	46.84 ± 10.66
	CVDBH	The coefficient of variation of DBH (%)	125.55 ± 24.39	158.26 ± 23.22	164.4 ± 51.23	87.15 ± 28.56	54.74 ± 12.23	110.48 ± 20.22	88.43 ± 15.24
	CVH	The coefficient of variation of tree height (%)	59.91 ± 12.14	79.96 ± 8.36	95.37 ± 28.94	50.65 ± 15.42	32.69 ± 9.33	62.7 ± 11.1	67.1 ± 9.03

Table 2
Ecological significance of functional traits and sampling information.

Functional trait	Unit	Ecological meaning	Number of species collected	Number of individuals collected	Collection criteria
Specific leaf area(SLA)	mm ² ·mg ⁻¹	Positively related to photosynthetic rate and negatively to leaf longevity.	721	19971	In each permanent forest dynamics plot, branches and leaves were collected from all individuals with DBH ≥ 10 cm. For individuals whose DBH was less than 10 cm, the five largest individuals of each species were sampled. If there were fewer than five individuals of a species in a sample plot, then all individuals of the species in the sample plot were sampled.
leaf dry matter content (LDMC)	mm ² ·mg ⁻²	Positively related to photosynthetic rate and negatively to leaf longevity.	721	19971	
Leaf nitrogen concentration (LNC)	mg·g ⁻¹	Related to the proteins in photosynthetic machinery and maximum photosynthetic rate.	619	11462	
Leaf phosphorus concentration (LPC)	mg·g ⁻¹	Related to maximum photosynthetic rate and high nutritional quality in food webs.	619	11462	
Nitrogen-phosphorus ratio (N:P)	%	served as an indicator of which nutrient element is restricting plant community productivity.	619	11462	
Wood density (WD)	g·cm ⁻²	co-varied with other hydraulic traits and is thought to reflect variation in water acquisition and drought tolerance strategies.	739	10793	

2.2. Data collection: Forest dynamics plots and traits

Across the seven sites, a total of 309 forest dynamic plots (20 m × 20 m) were established. We tagged the DBH (diameter at breast height) and height of a total of 46280 individuals which DBH ≥ 1 cm. Six functional traits were measured: specific leaf area (SLA, mm²/mg), leaf dry matter content (LDMC, mm²/mg²), leaf nitrogen content (LNC, mg/g), leaf phosphorus content (LPC, mg/g), wood density (WD, g/cm²), and nitrogen-phosphorus ratio (N:P) (%). Measurements of plant functional traits were conducted according to Pérez-Harguindeguy et al. (2013). The leaf area was first measured with a LI-3000A leaf area meter (LI-COR Inc., Lincoln, NE). After weighing the mass of the fresh leaves, samples were then dried for 72 h in a 60 °C oven. We calculated SLA as the ratio of leaf area to leaf dry mass (cm²/g). We further quantified leaf nutrients (LNC and LPC) in the lab at Hainan University. To avoid negative effects on tree growth from the sampling process, we did not take tree trunk cores in forest stands. Instead, WD was calculated from measurements of 1–2 cm diameter branches. Bark was removed from the branches before measuring branch volume using an electronic balance. We dried branches in a 105 °C oven for 72 h and then recorded the dry weight. Nitrogen/phosphorus ratio was the ratio of leaf nitrogen content to leaf phosphorus content. The ecological significance and sampling information of each trait are shown in Table 2.

2.3. Data collection: Biotic and abiotic factors

The biotic factors were components of stand structure (Table 2), we selected five biotic factors (Baraloto et al., 2011). The abiotic factors included climatic and soil data (Table 2). We used 19 bioclimatic variables from WorldClim Version 2 (Fick and Hijmans, 2017) that are commonly used in ENM (ecological niche model) studies (Bradie and Leung, 2017; Fourcade et al., 2017). These variables are average values derived from temperature and precipitation values recorded from weather stations across the globe between 1960 and 1990 (Fick and Hijmans, 2017). Given the difference in range size among our study species, we used 30" resolution rasters for the range-restricted *D. compactus* and *L. woosnami* and 2.5' resolution rasters for the widespread *I. graduacauda* and *C. leucophrys*. Removing highly correlated predictor variables from ENMs can increase model performance (Cooper et al., 2016); therefore, we calculated pairwise Pearson correlation coefficients for each of the variables within the defined study extent. We removed those variables with correlation above 0.8, and three climate variables were selected (Table 1). In each plot, we collected five randomly-located soil samples (0–20 cm depth) and thoroughly mixed the samples to create one bulked sample per plot for analysis. The samples were analyzed for pH, soil organic matter, total nitrogen, total phosphorus, available nitrogen, available phosphorus, and available potassium. These soil factors include nutrients, inorganic matter, most related to species spatial distribution and ecosystem productivity.

2.4. Data analysis

To construct the compound habitat gradient of 15 biotic and abiotic factors using principal component analysis (PCA), we chose to evaluate environmental filtering in principal component (PC) space using PCs for all variables and for the subset of bioclimatic variables that did not show high correlations. To investigate a potential solution to this issue, The first four PCs

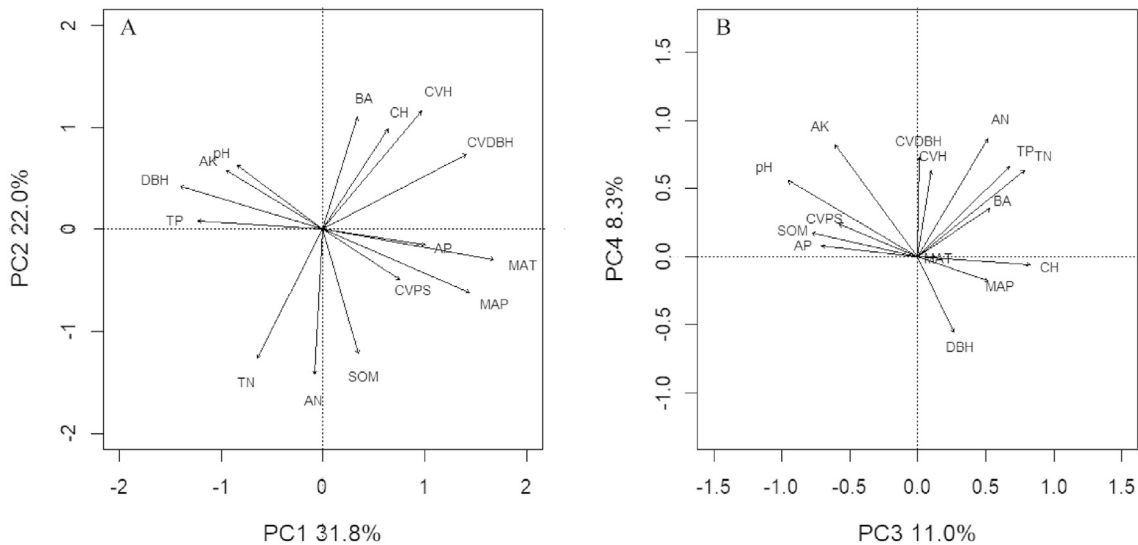


Fig. 1. The four principal component analysis (PCA) axes of biotic factors and abiotic factors of forests across different climatic zones in China. The full name of variables abbreviation are listed in Appendix Table 1.

consistently contained over 70% of the variation, so we constructed filters using the first two, three, and four PCs. We ran a principal component analysis (PCA) using the ‘factoextra’ package in the software R. The first four axes of the PCA explained 73.1% of the total variation of all 15 variables. The first axis (PC1) accounted for 31.8% of variation. Two climatic variables (MAP and MAT) and CVDBH were positively correlated with PC1 and DBH was negatively correlated with this axis (Fig. 1A). The second axis (PC2) explained 22.0% of variation. Stand structural variables (CVH, BA and CH) were positively correlated and TN and AN were negatively correlated with PC2 (Fig. 1A). The third and fourth axes of the PCA contributed less to total variation but were mainly related to community structure and soil variables (Fig. 1B).

Following Villéger et al. (2012), we standardized all traits to make them dimensionally homogeneous and put equal weight on each trait in the calculations of functional diversity. We used species richness and Shannon-Wiener index as indicators of species diversity and functional richness (FRic) and functional divergence (FDiv) as indicators of functional diversity (Carroll et al., 2012) (The ecological significance of each index and its formula are shown in Table 3). Species richness values were log₁₀-transformed to give normally-distributed residuals and equal variances. The species diversity calculated with the ‘vegan’ package (Oksanen et al., 2013) and functional diversity calculated with the ‘FD’ package (“citation”) in R 3.2.5 (R Development Core Team, 2016).

2.5. Construction of null model

Using the null model to construct random communities, the ecological processes that play a major role in community construction are judged by comparing the spatial value differences of characters between real and random communities (Gotelli, 2001). Previous studies have shown that the range of species distribution within the functional space (which can be expressed by the functional richness index) and the divergence of species distribution on the functional axis (which can be expressed by the functional divergence index) have a strong test ability for habitat filtration and inter-species interaction (Pakeman, 2011). All species present in the sample plot are used as the regional species bank in the calculation, assuming that the probability of each species appearing in any sample plot is the same. For each sample plot at a spatial scale, the species in the species bank are randomly selected under the actual species richness of the sample plot, the corresponding random community is constructed, and the spatial values of the traits of the sample plot are calculated. Each sampled sample square was repeatedly extracted 999 times, and the average value of the simulated values of all samples under this scale was calculated to obtain the null model simulation value of character space under this scale. This study calculated the standardized effect value (SES) of the functional diversity index, which can effectively determine the difference between the actual value of functional diversity and random value. The formula is as follows:

$$\text{SES.FRic} = \frac{\text{FRic}_{\text{obs}} - \text{FRic}_{\text{null}}}{\text{SD}(\text{FRic}_{\text{null}})} \quad (1)$$

Table 3
The formula of functional diversity and species diversity indices.

Index	Formula	Variables	References
Richness	$R = S$	S is the number of species in the sample	Species richness is the most direct and effective means to reflect community conditions, reflecting the number and complexity of community species.
Shannon-Wiener	$H = -\sum_i^n p_i \ln p_i$	p_i is the comprehensive dominance ratio of species i , n is the total species number in the sample square.	Shannon diversity index is a measure of the degree of diversity and heterogeneity at the species level.
Functional richness	The functional richness index (FRic) is calculated using the minimum convex hull, i.e., the presence of a minimum convex polygon within the trait space so that the points of all species are within its range or on sides. First, the endpoint is determined based on the species with trait extremum; then it is connected to generate a minimum convex polygon; and finally its area or volume is calculated.		The functional richness corresponds to the volume of the functional space occupied by the species, indicating the functional niche occupied by the species in the community (Mouchet et al., 2010).
Functional divergence	$FDiv = \frac{\sum_{i=1}^S w_j \left(a - \frac{1}{S} \sum_{i=1}^S a \right) + \frac{1}{S} \sum_{i=1}^S a}{\sum_{i=1}^S w_j \left(a - \frac{1}{S} \sum_{i=1}^S a \right) + \frac{1}{S} \sum_{i=1}^S a}$	The $a = \sqrt{\frac{\sum_{k=1}^T \left(X_{jk} - \frac{1}{v} \sum_{i=1}^v X_{jk} \right)^2}{T}}$, T is the functional trait, the X_{jk} is the position of the species i on the trait axis, the v is the volume of the functional space occupied by the species i , the w_j is the relative abundance of the species j , and S is the number of species.	FDiv shows the complementary degree of species in niche, and quantitatively describes the heterogeneity of neutral values of the community.

$$SES.FDiv = \frac{FDiv_{obs} - FDiv_{null}}{SD(FDiv_{null})} \quad (2)$$

In [Formula \(1\) and \(2\)](#), $FRic_{obs}$ and $FDiv_{obs}$ are the functional diversity index calculated by the actual community, $FRic_{null}$ and $FDiv_{null}$ are the average values of the functional diversity index calculated by 999 random communities, $SD(FRic_{null})$ and $SD(FDiv_{null})$ are the standard deviation of the functional diversity index calculated by 999 random communities (Mendez et al., 2012). The hypothesis of null model in this study is: if $SES.FRic$ is significantly less than zero, indicating that the range of real community functional space is lower than that of random communities, proving the existence of habitat filtration and inter-species interactions as a deterministic process. on the contrary, it shows that the actual community is dominated by random processes. if $SES.FDiv$ is significantly more than zero, indicating that the mechanism of community construction is random (Cornwell et al., 2006).

2.6. Statistical testing and data analysis

We used lowess regression to fit the null model of functional diversity with the compound habitat gradient to a predictive trend consistent with the overall rule, and use a confidence interval level of 0.95. The null model of functional diversity as response variables, and compound habitat gradients as explanatory variables. Linear mixed effects (lme) models were used to calculate the effects of abiotic, biotic factors and the compound habitat gradient (random factors) on response variables of species diversity and function diversity (fixed factors). At community scale, random effects included plots nested within elevational belts. For all linear mixed models (LMMs), we first specified a full model for each response variable to test predictor variables and their potential interaction effects. To interpret the direction and magnitude of parameter estimates during model selection, we scaled and standardised all predictor variables to a mean of zero and a standard deviation of one. We implemented the linear mixed model to account for random effects. Linear mixed models were using the lmer function which conducted in "nlme" package. All statistical analyses were performed in R 3.2.5 (R Development Core Team, 2016).

3. Results

3.1. Patterns of variation and the drivers in plant diversity along the CHG

The fitting effect of compound habitat gradient on species diversity was better than that on functional diversity. And also, the fitting effect of the compound habitat gradient was close to that of the biotic and abiotic factors, which could replace the

biotic and abiotic factors to a certain extent and simplify the number of factors. PC1 was the most important factor affecting species diversity and functional diversity in the compound habitat gradient (Fig. 2). Among the biotic and abiotic factors, climate had the most significant effect on the biodiversity of forest communities in different climatic regions of China, among which precipitation and temperature were the main factors (Fig. 3). Species richness and Shannon-Wiener index were significantly positively correlated with PC1 and PC4 axes and negatively correlated with PC2, PC3. The FRic was only positively correlated with PC1, was not significantly correlated with other axes of the compound habitat gradient. FDiv was significantly negatively correlated with PC1 and PC3, positively correlated with PC2 (Fig. 2).

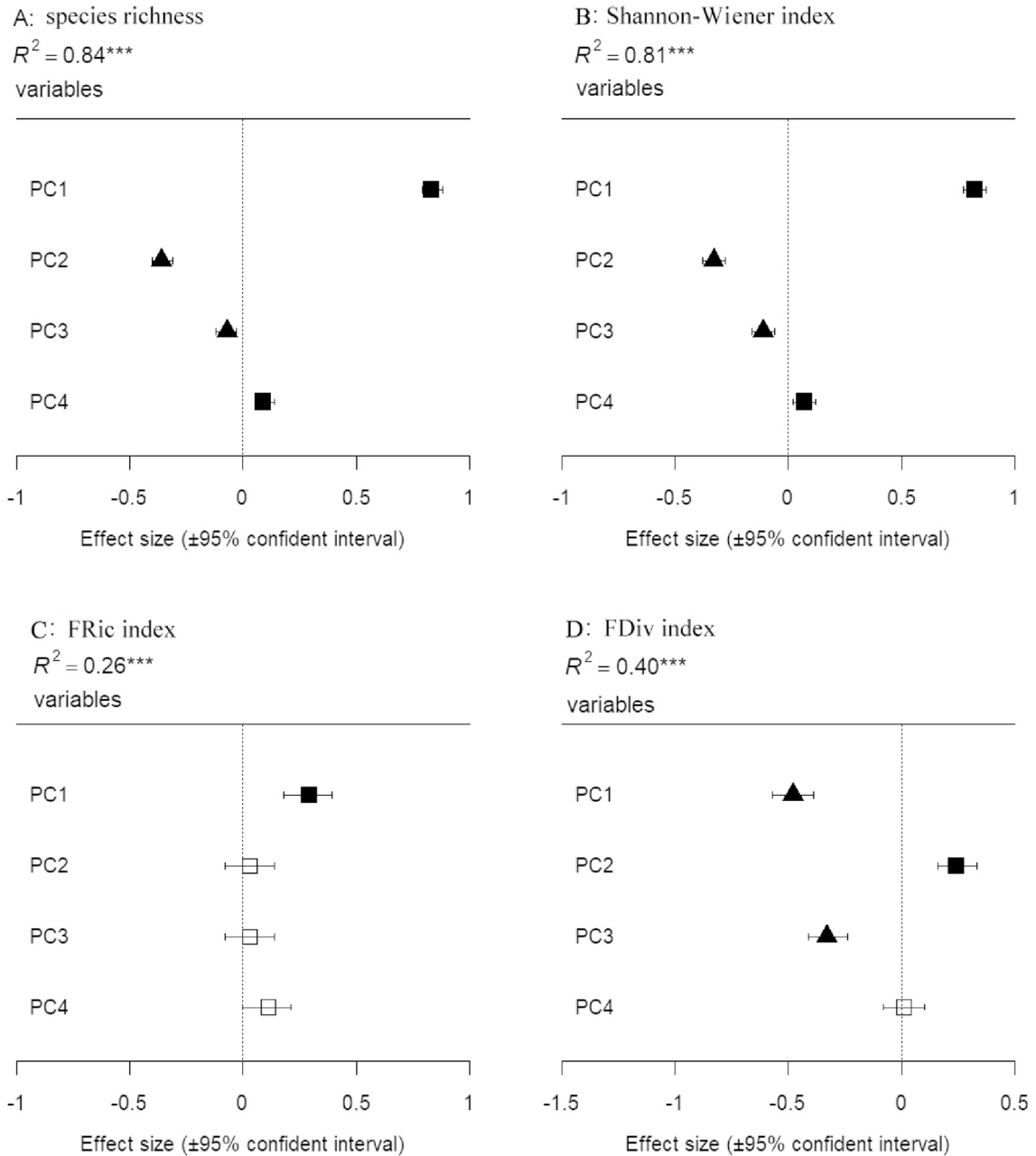


Fig. 2. Effects of the four compound habitat PCA axes on species richness (A), Shannon-Wiener (B), FRic (C) and FDiv (D) index of forests in China. Effect sizes are standardized coefficients from linear mixed models estimated separately for each predictor variable. The lines indicate 95% confidence intervals, solid black squares indicate significant positive effects and solid black triangles indicate significant negative effects. The open symbols indicate a non-significant effect.

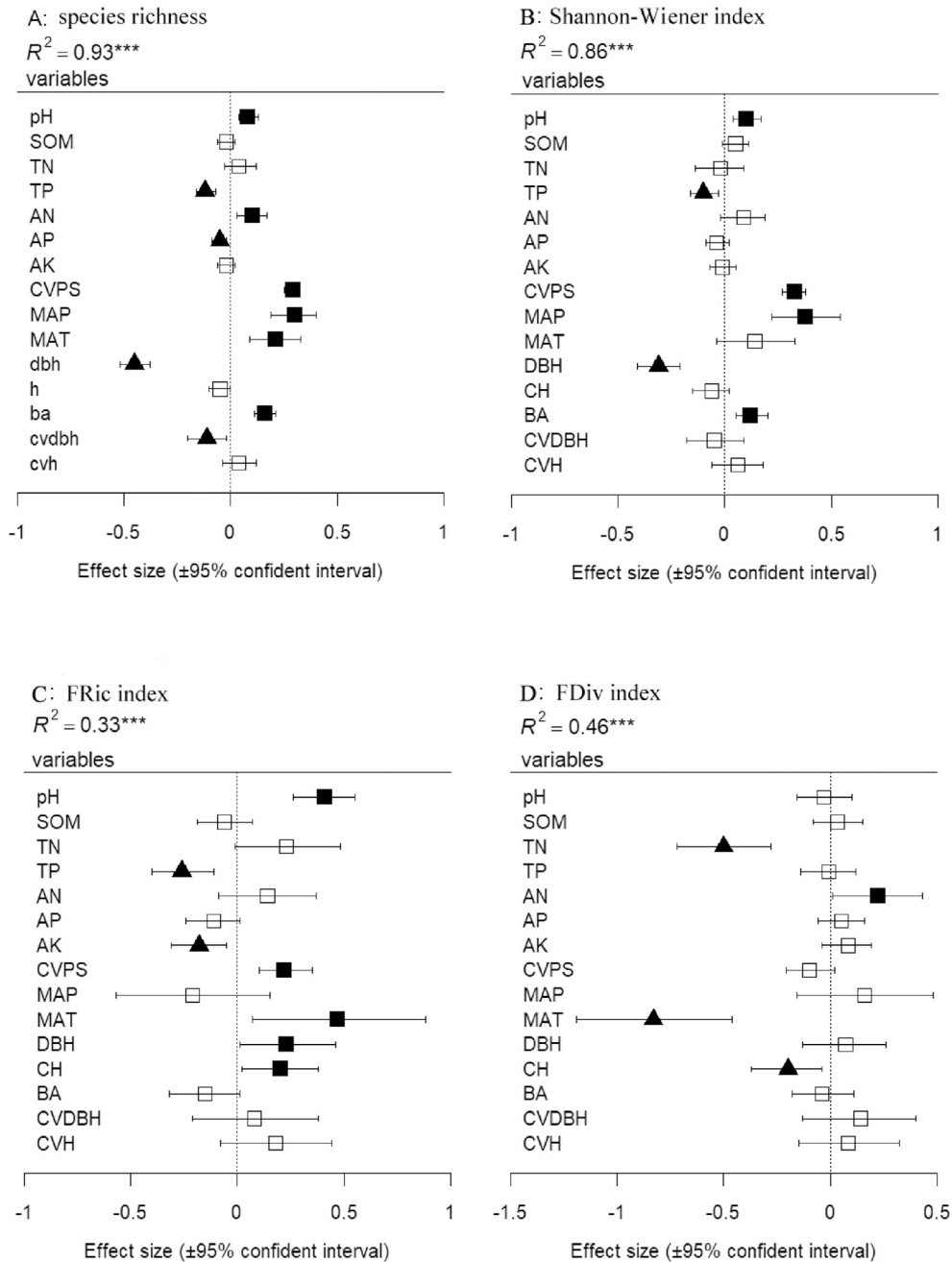


Fig. 3. Effects of each biotic and abiotic factors on species richness (A), Shannon-Wiener (B), FRic (C) and FDiv (D) index of forests in China.

3.2. The drivers of diversity change along the CHG

The null models of FRic and FDiv were significantly negatively correlated with PC1 in the compound habitat gradient, and not with other axes (Fig. 4). We found that the SES.FRic and SES.FDiv value decreases with PC1 increasing. In temperate forest communities, the null model values of functional diversity were all greater than zero, but in tropical forest communities, the null model values of functional diversity were all less than zero (Fig. 4).

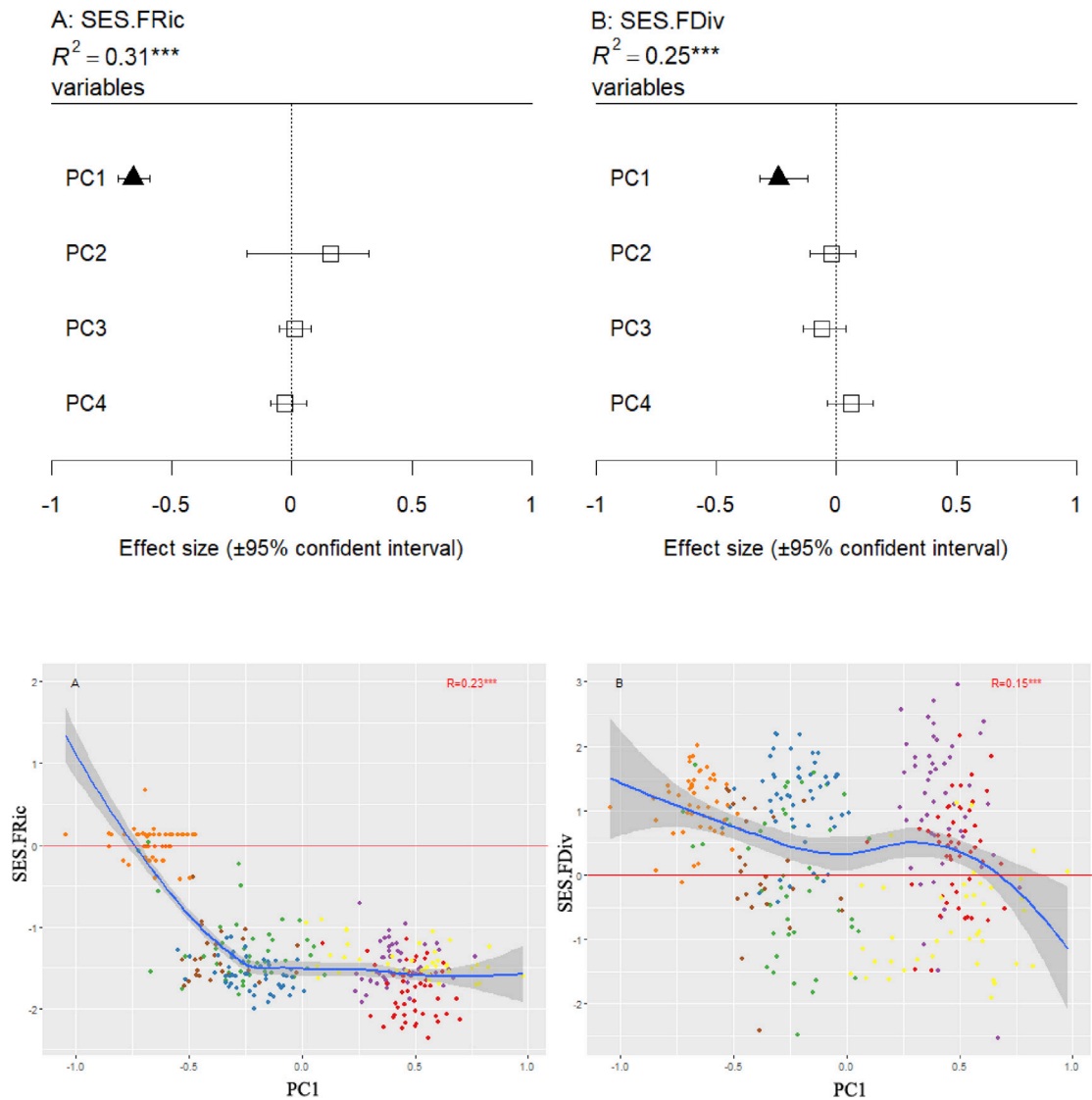


Fig. 4. Effects of the four compound habitat PCA axes on null model of functional diversity (top), and variation in null model of functional diversity along the first PCA axes (low) of the CHG in China. Different colors represent different study sites: Jianfengling (red), Bawangling (blue), Xishuangbanna (green), Xingdoushan (purple), Mulinzi (orange), Xiaolongshan (yellow), Kanasi (brown). Different colors represent different study sites: Jianfengling (red), Bawangling (blue), Xishuangbanna (green), Xingdoushan (purple), Mulinzi (orange), Xiaolongshan (yellow), Kanasi (brown).

4. Discussion

4.1. Trends of species diversity and functional diversity with compound habitat gradient

Species diversity can reflect functional diversity to some extent, and functional diversity affects ecosystem function through ecological complementary mechanisms. Therefore, studying the response of species diversity and functional diversity to environmental change or disturbance and its relationship with ecosystem function is the key to reveal the mechanism of species diversity maintenance and to formulate forest community management strategies (Díaz and Cabido, 2001). We found that the species diversity of forests in different climate regions of China increases as the PC1 axis increases, which is consistent with the variation of species diversity along the latitude gradient (Hillebrand, 2004; Rodríguez and Arita, 2004). The latitudinal gradient of diversity is the result of resource limitation and saturation, which enables more species to coexist and leads to higher species richness in the tropics than temperate areas (Qian and Ricklefs, 2010). Additionally, the tropics have had more time and resource accumulation than seasonal temperate regions (assuming the same age and area, Iwasa et al., 1995; Ricklefs, 2006). Only a small number of tropical plants can settle in temperate regions (Gaston, 2000), which means that this process will inevitably lead to lower species diversity in temperate than tropical areas.

We found that the functional richness of forest communities in different climatic regions of China increased with the increasing gradient of compound habitats. That's probably because FRic increase in species richness (Díaz and Cabido, 2001; Lohbeck et al., 2012; Petchey and Gaston, 2002). We can understand that in temperate forest communities, low FRic due to low species, and the addition of each new species increases the potential functional space as the compound habitat gradient increases. Because of the functional inequality of different species in the community (Mouchet et al., 2010), the increase of species diversity causes a significant increase in functional diversity, but did not show a non-linear relationship. In tropical forest communities, species richness is relatively highest, and species niche complementation is stronger, which leads to higher FRic, which further verifies the conclusion that the FRic obtained in this paper is closely related to species richness.

The degree of functional divergence reflects the degree of complementation of ecological sites between species in the community. As the gradient of the compound habitat increases, the functional divergence decreases. Probably because the low functional divergence in the ecosystem is closely related to the strong niche overlap and competition intensity between species (Zhang and Fan, 2011). In the temperate climate region of China, there are few species, only evergreen coniferous and deciduous species, which were the two sides of the trait distribution trait axis, the overlap effect of species niche and the competition of resources are weak, which forms a high degree of functional divergence. However, with the increase of compound habitat gradient, species increase gradually, the competition of resources intensifies, and the functional divergence of the community decreases significantly. Tropical forest communities, which may be conducive to the fuller use of resources, have significantly enhanced ecosystem functions (Ding et al., 2012), while temperate regions are affected by a variety of impacts and species have significant geographical limitations. The trend of functional divergence is also influenced by the functional traits of the species with higher abundance. If the functional traits of the species with higher abundance are close to the center of the trait space, the functional divergence is less, indicating that among tropical communities, species will adopt similar adaptation strategies to cope with community environmental changes, resulting in similar functional traits (Cornwell et al., 2006). In ecosystems with high functional diversity, the ecosystem can operate more effectively because of the large differences in species functional traits to achieve complementary utilization of resources (Carlos et al., 2016). The loss of plant functional traits, the change of functional traits, or the decrease of spatial dimension of traits will lead to the change of functional diversity, which will affect the function of communities or ecosystems (Saito et al., 2015). Therefore, it is suggested that the information of community species richness should be taken into account when comparing the functional diversity among communities, and the function diversity index should be standardized to eliminate the influence of species richness difference between communities.

4.2. Biotic and abiotic factors affect species diversity and functional diversity together

Studies have shown that community species composition is generally the result of coupling environmental filtering and biotic interactions on a spatial scale (Cornwell et al., 2006). Climate variables played the dominant role in driving species diversity from the tropical to the temperate regions of China. However, our study also found some elements of community structure and soil nutrient availability affected species diversity in multi-regression models as individual variables or as the compound habitat gradient (first four axes of PCA). The high amount of variation explained (Figs. 2 and 3) further indicated the importance of simultaneously integrating biotic and abiotic factors in exploring species diversity patterns (Fortunel et al., 2018). Species diversity was mainly affected by the climate variables of temperature and precipitation at large spatial scales (Chu et al., 2019). However, the sensitivity of biotic diversity to biotic factors is relatively weak at these large scales (Daniel and Scott, 2007). The results of Gómez-Aparicio et al. showed that within a small area, the effect of competition intensity on tree growth is greater than that of climate. The variation in species diversity at the local scale was still determined by community structure and soil nutrients (Clark et al., 1999). Extremely high competition for light is one of the important mechanisms for explaining high species diversity in tropical rain forests (Kobe, 1999) and compound community structure creates vertical light gradients from the forest canopy to the understory. Relatively poor nutrient availability further increases the intensity of aboveground competition for light (Coomes and Grubb, 2000). Our results found that PC2 had a negative effect on species diversity, suggesting that a compound community structure with poor soil nutrient availability might result in high species richness.

In previous studies, functional diversity was sensitive to changes in the environment (Pakeman, 2011), this study also confirms this conclusion. Climate factors are the main factors affecting the functional diversity of forest communities in large regions. Wiczyński et al. (2018) the first study to examine how climate affects the functional traits of forest communities globally—evidence of significant changes in these characteristics that may affect forest productivity and composition, and even forest distribution globally. our study complements the evidence that forest communities in China are affected by climate. However, in tropical forest communities, the interaction between species intensifies (Ding et al., 2012), the functional evenness of the community is improved, and the habitat filtering is continuously weakened, ultimately increasing overall functional diversity. Intense resource competition drives tree species to differentiate different functional traits through long-term evolution and phenotypic plasticity (Cornwell et al., 2006), increased the diversity of functional traits in tropical forest communities. Moreover, variation between and within traits in different habitats (Violle et al., 2012) further increasing the variability of functional diversity, while in species-rich communities, variability may be higher with higher functional diversity.

4.3. The rule of community construction in different climate regions

Mouchet et al. (2010) noted in his study, in the process of exploring community construction, the key problem is to determine the relative strength of different construction mechanisms. We found that forest communities in different climatic regions in China were mainly affected by habitat filtering and interspecific interaction in niche theory, but less by stochastic processes associated with neutral theory, mainly because stochastic processes may play a role on larger regional scales (Carroll et al., 2012). Studies have shown that when interspecific interactions dominate, higher functional divergence is produced than that of communities dominated by random processes, which also confirms the high functional divergence of tropical forest communities. When habitat filtering is dominant, there is a smaller functional richness and functional divergence than the random processes (Mouchet et al., 2010). A large number of studies conducted in tropical forest communities have found that habitat filtering often dominates the process of community construction. Andersen et al. (2012) found that undergrowth palm in tropical forests tended to have similar functional traits under low concentrations of soil nutrients, and species with similar traits tended to exhibit higher symbiosis than expected. The role of environmental factors in some tropical forest communities was also found to lead to convergence of community lineages (Andersen et al., 2012). Pakeman (2011) through the study of plant communities in the west coast of Scotland, it was found that in the environment with high productivity and high disturbance, the functional richness was lower than that dominated by random processes, indicating that habitat filtering played a greater role. Bernard-Verdier et al. (2012) found that the plant traits tend to disperse in the shallow environment of the layer, with the increase of soil layer thickness, the plant traits tend to aggregate, but the whole is affected by strong habitat filtering. Therefore, in communities where environmental constraints exist, habitat filtering often dominates the community construction process. Since deterministic processes determine species coexistence by filtering for species functional traits, we infer that there is interaction with localized habitat filtering and biotic competition in tropical forest communities in China (Bernard-Verdier et al., 2012). It is generally believed that niche theory and neutral theory are not contradictory, and there is often more than one mechanism that affects the structure and function of the community, which can be carried out simultaneously to explain the coexistence mechanism and functional diversity pattern of species in different scales, different aspects and angles complementary.

4.4. Application of the compound habitat gradient (CHG)

Many studies show that variation in species and the functional features cannot be attributed to a single driver, but rather to a combination of environmental factors (Simpson et al., 2016; Le Bagousse-Pinguet et al., 2017). In particular, large-scale studies have generally focused on climatic drivers but ignored local drivers (Borgy et al., 2017), such as soil nutrient availability (Le Bagousse-Pinguet et al., 2017) and species interactions within their communities (Roslin et al., 2017), even though topography, soil nutrients, neighborhood competition, and community structure have all been demonstrated to drive species diversity and functional diversity at local scales (Clark et al., 1999; Estrada-Villegas et al., 2019; Fortunel et al., 2018). It is therefore particularly important to integrate the biotic and abiotic variables collected at local scales in large-scale ecological studies based on plot data. In order to comprehensively and systematically analyze mechanisms of community assembly, we collected information on many influencing factors, and through PCA dimension reduction, redundant data could be eliminated and the analyses could be simplified (Lee and Jun 2011) to find the main factors affecting community construction. We selected the two or three principal component axes that explained the most variation in our analysis. This process can better reflect the differences between communities rather than attempting to select the specific factors (Lee and Jun 2011). The PCA axes reflect the variables that best explain variation, so the change and trend of influencing factors can be more accurately understood from the compound habitat gradient, because it contains both biotic and abiotic factors. The compound habitat gradient can also reflect environmental variation within the same latitude (that is, local environmental variation) (Luskin and Potts, 2011), which is more intuitive than that across latitudes (Fig. 1) and can show the habitat heterogeneity of different climatic zones (Chen, 2016). Species interactions and local soil properties play significant roles in determining community assembly at large scales, both alone and in interaction with climate (Simpson et al., 2016). The compound habitat gradient had a better explanation on species and functional diversity, which may be due to the synergistic or antagonistic interactions between the influencing factors, which the compound habitat gradient eliminates or weakens to a certain extent (Lee and Jun 2011). The compound habitat gradient provides insight into how biotic and abiotic factors drive variation in forest communities at large scales.

5. Conclusion

By combining biotic and abiotic variables in a PCA, we constructed a compound habitat gradient for forests across four climatic regions in China. The first axis of the CHG reflected variation in climate and community structure, from sites with many small- and few very large-sized trees in warm and wet conditions to sites with larger and more even-sized trees in cold and dry conditions. Species richness, the Shannon-Wiener index, and functional richness increased while functional divergence decrease along this first axis of the CHG. Compared with the approaches of analyzing individual biotic and abiotic factors driving patterns of biodiversity change, the approach of examining diversity patterns of vegetation along the CHG could reveal a more general pattern, indicating the joint driving effects by climatic or community structural features at large scales. Our study demonstrates that the compound habitat gradient analysis is an effective approach of exploring patterns of

biodiversity change and understanding mechanisms of community assembly for forest vegetation across different climatic regions. The multi-angle analysis of the functional diversity of forest communities can further reveal the rules of forest construction in different climatic regions, which has important theoretical and practical value for the formulation of forest management and monitoring measures, and can provide scientific basis for the protection and sustainable utilization of forest resources.

6. Application of the compound habitat gradient (CHG)

Many studies show that variation in species and the functional features cannot be attributed to a single driver, but rather to a combination of environmental factors (Simpson et al., 2016; Le Bagousse-Pinguet et al., 2017). In particular, large-scale studies have generally focused on climatic drivers but ignored local drivers (Borgy et al., 2017), such as soil nutrient availability (Le Bagousse-Pinguet et al., 2017) and species interactions within their communities (Roslin et al., 2017), even though topography, soil nutrients, neighborhood competition, and community structure have all been demonstrated to drive species diversity and functional diversity at local scales (Estrada-Villegas et al., 2019; Fortunel et al., 2018). It is therefore particularly important to integrate the biotic and abiotic variables collected at local scales in large-scale ecological studies based on plot data. In order to comprehensively and systematically analyze mechanisms of community assembly, we collected information on many influencing factors, and through PCA dimension reduction, redundant data could be eliminated and the analyses could be simplified (Lee and Jun 2011) to find the main factors affecting community construction. We selected the two or three principal component axes that explained the most variation in our analysis. This process can better reflect the differences between communities rather than attempting to select the specific factors (Lee and Jun 2011). The PCA axes reflect the variables that best explain variation, so the change and trend of influencing factors can be more accurately understood from the compound habitat gradient, because it contains both biotic and abiotic factors. The compound habitat gradient can also reflect environmental variation within the same latitude (that is, local environmental variation) (Luskin and Potts, 2011; Wang et al., 2015), which is more intuitive than that across latitudes (Fig. 1) and can show the habitat heterogeneity of different climatic regions (Chen, 2016). Species interactions and local soil properties play significant roles in determining community assembly at large scales, both alone and in interaction with climate (Simpson et al., 2016). The compound habitat gradient had a better explanation on species and functional diversity, which may be due to the synergistic or antagonistic interactions between the influencing factors, which the compound habitat gradient eliminates or weakens to a certain extent (Lee and Jun 2011). The compound habitat gradient provides insight into how biotic and abiotic factors drive variation in forest communities at large scales.

Declaration of competing interest

This is the first submission of this manuscript and no parts of this manuscript are being considered for publication elsewhere. All authors have read and approved the content of the manuscript. No financial, contractual and other interest conflicts exist for the study.

CRediT authorship contribution statement

Liangjing Yao: Data curation, Writing - original draft, Writing - review & editing. **Yi Ding:** Conceptualization, Methodology. **Han Xu:** Data curation. **Fuying Deng:** Data curation. **Lan Yao:** Data curation. **Xunru Ai:** Data curation.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.gecco.2020.e01106>.

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