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Variation in the Functional Traits of Forest Vegetation along Compound Habitat Gradients in Different Climatic Zones in China

Liangjin Yao [1,2,3], Yue Xu [2,3], Chuping Wu [1], Fuying Deng [4], Lan Yao [5], Xunru Ai [5] and Runguo Zang [2,3,*]

[1] Zhejiang Academy of Forestry, Hangzhou 310023, China; lj890caf@163.com (L.Y.); wcp1117@hotmail.com (C.W.)
[2] Ecology and Nature Conservation, Chinese Academy of Forestry, Key Laboratory of Forest Ecology and Environment of National Forestry and Grassland Administration, Beijing 100091, China; xuyue@caf.ac.cn
[3] Co-Innovation Center for Sustainable Forestry in Southern China, Nanjing Forestry University, Nanjing 210037, China
[4] School of Earth Sciences, Yunnan University, Kunming 650091, China; dengfuy@163.com
[5] School of Forestry and Horticulture, Hubei University for Nationalities, Enshi 445000, China; hbmyyl@163.com (L.Y.); hbmyaxru@163.com (X.A.)
[*] Correspondence: zangrung@caf.ac.cn

Abstract: Investigating functional plant traits is essential for understanding plant responses and adaptations to global climate change and ecosystem functions. Synchronous observations of multiple plant traits across multiple sites are rare. Here, we obtained community, functional trait, and environmental data for different forest vegetation types in China's tropical, subtropical, warm-temperate, and cold-temperate zones. Using principal component (PC) analysis, we constructed a composite–habitat gradient axis of biotic and abiotic factors across different climatic zones, differentiated functional trait compositions along the axis and their driving factors, and reached three main conclusions. (1) At the community level, the community-weighted mean and variance of each trait level differed across the climatic zones. Specific leaf areas and leaf phosphorus contents decreased with increasing PC1 values, whereas community-weighted means and variances of leaf dry-matter contents, leaf nitrogen-to-phosphorus ratios, and wood densities significantly increased with increasing PC1 values. However, the leaf nitrogen content varied along the PC1 axis. Both the community-weighted skewness and kurtosis of functional traits increased significantly with increasing PC1 values for the composite habitat gradient across the climatic zones. (2) The weighted mean, variance, skewness, and kurtosis of each functional trait exhibited different patterns on the composite habitat gradient PC2 axis than on the PC1 axis across the climatic zones, and the correlation was weak. (3) Most functional traits correlated significantly with the community-weighted mean and variance, kurtosis, and skewness. Therefore, the different functional trait compositions of forest communities in different climatic zones reflected trait convergence caused by the environment and trait differences caused by species competition in response to local-scale filtering.

Keywords: China; climatic zone; community composition; composite habitat zone; environment; forest vegetation; functional trait; principal component analysis; synchronous observation; weighting

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1. Introduction

In recent years, the relationship between plant functional traits and the environment has emerged as a new topic in functional biogeography and macroecology [1–3]. Plant traits under different environmental conditions can provide information on their resource acquisition and utilization strategies [1,3,4], as well as their adaptability to environmental changes [5]. The variation in functional traits of plants under different conditions is often associated with habitat selection, as species that adapt to specific environmental conditions often have similar traits [6]. Environmental heterogeneity within a community can increase trait differences or promote trait coordination, leading to the coexistence of species with different ecological strategies. Therefore, determining how the functional compositions of communities change along environmental gradients provides some insight into the influence of climate on species assemblages by plant traits [5,7].

Exploring trait–environment relationships at both local [8] and macro scales [7] is crucial for developing predictive models in community ecology and for gaining insight into the mechanisms that drive plant diversity changes and the formation of geographic gradients. Functional trait compositions reflect the values and variabilities of traits that arise from changes in non-biotic or biotic conditions that underscore changes in species composition and relative abundances; therefore, they can serve as quantitative tools for evaluating the impact of habitat gradients on forest-community changes [9,10]. Currently, ecologists primarily use the community-weighted mean (CWM) [9], community-weighted variance (CWV) [11], community-weighted skewness (CWS), and community-weighted kurtosis (CWK) [7] to investigate regular changes in community function compositions. The CWM represents the dominant trait value in a community, the CWV represents the dispersion of trait values within a community, the CWS represents the lag in the responses of rare dominant species or plant responses to environmental change over time, and the CWK represents competition or other biotic exclusions.

These four community indicators can directly demonstrate dynamic changes in communities and facilitate the prediction of biogeographic patterns of ecosystem functions. The geographical differentiation pattern of functional trait compositions is usually constrained by non-biotic or biotic conditions. If habitat conditions have dominant selective effects, the community traits should converge, indicating that habitat filtering plays a dominant role in community assembly [11]. However, once species in a regional pool are selected for a community, they must adapt to each other with minimal competition (limiting similarity) to stably coexist [12,13]. Generally, the effects of climate on communities are more significant at large scales, and changes in habitat conditions such as temperature and precipitation can select for trait patterns in different communities [11]. Global-scale studies have shown that the functional composition of forests changes significantly with latitude and altitude [7], where the leaf area (LA) and specific leaf area (SLA) decrease as the water availability decreases [1,3,14]. On the local scale, soil or biotic processes (such as competition or facilitation) [15] help maintain the functional composition and diversity of forest communities. Previous findings have shown that soil nutrients drive variations in leaf and wood traits, with species in nutrient-rich habitats exhibiting faster growth rates, typically characterized by a combination of high SLAs, high tissue-nutrient concentrations (especially nitrogen), and low leaf dry-matter contents, in contrast to the opposite trends observed in species located in nutrient-poor habitats [16].

Close relationships exist between the different traits of plants, such as synergistic or antagonistic interactions. Ecologists have conducted in-depth research on the functional traits of plant leaf, stem, and root tissues and have proposed the following three hypotheses to explain the interactions among different plant traits. (1) The functional-similarity hypothesis suggests that traits with similar functional roles are closely associated. For example, significant correlations have been observed between leaf and root traits; however, correlations with stem traits are less clear because leaf traits play a role in absorbing water and inorganic nutrients from roots, and root traits rely on organic compounds created by leaf photosynthesis [17]. (2) The structural similarity hypothesis suggests that traits with the same structure exhibit stronger interactions. For instance, the woody parts and densities of the root and stem tissues of woody plants have similar anatomical structures [18]; therefore, significant correlations have been observed between root and stem tissues. (3) The overall coordination hypothesis suggests that the plant body is an integrated whole and that the functions of the roots, stems, and leaves are interdependent, making the traits of the root, stem, and leaf tissues closely related [19]. However, currently, validation of the correlations and hypotheses regarding functional traits among different plant tissues is incomplete, and the results vary.

Significant progress has been made in studying the trait–environment relationships of forest vegetation across different climatic regions in China. However, the geographic functional composition patterns and the factors driving these patterns are not well understood. To overcome these challenges and better assess the changes and drivers of functional traits in biogeography, we compiled a dataset encompassing the traits of forest vegetation, soil, climate, and biotic factors in different climatic zones of China in this study. Multiple weighted indices were used to explore the relationships between the various traits and environmental drivers. We established 309 forest dynamic monitoring plots (20 × 20 m) across seven biogeographical regions in China, spanning four climatic zones (tropical, subtropical, warm temperate, and cold temperate).

The plots included tropical rainforests, subtropical evergreen broad-leaved forests, warm-temperate mixed-conifer broad-leaved forests, and cold-temperate coniferous forests. We measured six functional traits for 46,280 individuals (diameter at breast height [DBH] of $\geq$1 cm) belonging to 788 woody plant species. Principal component analysis (PCA) was used to construct a composite-habitat gradient axis that incorporated seven soil, five biotic, and three climate factors to explore the relationship between functional trait compositions and the environment.

In this study, we tested the following three hypotheses: (1) climatic factors play a dominant role in the geographical distribution of functional-composition patterns (mean, variance, skewness, and kurtosis) of forest vegetation in inter-climatic regions in China; (2) soil and community structures are the main factors that affect functional-composition differences within the same climatic zone; and (3) the geographical distribution patterns of forest vegetation functional compositions (mean, variance, skewness, and kurtosis) across climatic regions may exhibit systematic changes, showing coordinated increases or decreases. An increasingly harsh and changing environment has reduced functional diversities, leading to a narrower range of conservative growth strategies [20,21]. Community and biogeographical changes in functional diversities across gradients reflect the directions of ecological strategy shifts. In this study, we created an important catalogue of the relationships between forest traits and various environmental factors, thus providing a more comprehensive and detailed understanding of the complex role of habitat heterogeneity in the functional biogeography of forest communities in different climatic regions of China.

2. Materials and Methods

2.1. Study Area and Sample Setting

This study was based on the standards of the Center for Tropical Forest Science (CTFS) in tropical forest research. In China, a total of 309 20 m × 20 m plots covering the entire forest area were established in four different climate regions, with varying numbers and sizes of plots (0.04 hectares each, Table 1).

These 20 m × 20 m plots have different elevations, terrain traits, nutrient conditions, disturbance histories, successional statuses, community structures, and species diversities, constituting forest communities that vary along gradients of biotic and abiotic factors. These are secondary forest communities that have recovered after disturbance by human activities.

2.2. Vegetation Survey and Determination of Functional Traits

The community establishment time for the forest vegetation types varies across the different climate regions, but all plots were surveyed and sampled during the growing season (June–August) each year. During the vegetation surveys, this study marked all woody plant individuals with a diameter at breast height (DBH) $\geq$ 1 cm at the breast height position (1.3 m above ground) using red paint and assigned them a unique number. The main subsequent work involved identifying species, recording tree species names, measuring DBH and tree height, recording shoot emergence and crown classification, as well as recording the relative coordinates of individual trees within the plot.

Table 1. Basic information on the soil, climate, and forest composition of 309 monitoring plots measuring 20 m × 20 m in different climatic regions of China.

Sites		**Jianfengling (JFL)**	**Bawangling (BWL)**	**Xishuangbanna (XSBN)**	**Mulinzi (MLZ)**	**Xingdoushan (XDS)**	**Xiaolongshan (XLS)**	**Kanasi (KNS)**
Climatic zone		Tropical			Subtropical		Temperate	Cold 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	106.08–106.14	86.94–86.95
Soil pH	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
Soil organic matter (g/kg)	SOM	15.62 ± 5.62	6.9 ± 1.83	3.19 ± 0.76	8.4 ± 2.05	9.21 ± 2.2	9.69 ± 2.92	3.38 ± 1.03
Soil total N content (g/kg)	TN	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
Soil total P content (g/kg)	TP	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
Soil available K (mg/kg)	AK	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
Soil available N (mg/kg)	AN	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
Soil available P (mg/kg)	AP	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
Precipitation seasonality (coefficient of variation) (%)	CVPS	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
Mean annual precipitation (mm)	MAP	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
Annual mean temperature (°C)	MAT	20.51 ± 5.42	21.15 ± 15.59	21.74 ± 3.88	16.52 ± 54.39	15.2 ± 34.91	11.18 ± 2.79	−9.9 ± 2.83
Individual mean diameter at breast height (DBH, cm)	DBH	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
Canopy height (m)	CH	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
Basal area (≥1 cm DBH) (m^2ha^{-1})	BA	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
The coefficient of variation of DBH (%)	CVDBH	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
The coefficient of variation of tree height (%)	CVH	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

According to Perez-Harguinduy et al. [22], this study measured six key functional traits that represent plant strategy axes and their responses to environmental change, including specific leaf area (SLA, mm^2/mg), leaf dry matter content (LDMC, mg^2/mm^2), leaf nitrogen content (LNC, mg/g), leaf phosphorus content (LPC, mg/g), wood density (WD, g/cm^3), and leaf nitrogen-to-phosphorus ratio (N:P, %). The methods used to collect and measure these functional traits at the species level in this study were based on Markesteijn et al. [4]. For each fixed plot, all individuals of species with no more than 10 individuals were sampled, while for species with 10 or more individuals, 10 individuals were sampled in order of decreasing diameter at breast height. For each individual, 5 healthy and mature fully expanded leaves were collected for leaf morphology, chlorophyll content, and leaf nitrogen and phosphorus content analysis. Leaf size was measured using a leaf area meter, and after the weighing fresh leaves, the samples were dried at 60 °C for 72 h. Leaf dry matter content was measured using an electronic balance and an oven, and SLA was calculated as the ratio of leaf area to leaf dry mass (cm^2/g). After collecting and drying the leaves, leaf nutrient (LNC and LPC) content was measured in the laboratory at Hainan University. To avoid negative effects on tree growth from the sampling process, tree cores were not taken in the forest. Instead, WD was calculated based on measurements of branches with diameters of 1–2 cm. Bark was removed from the branches before measuring their volume using an electronic balance. The dried weight of the branches was recorded after drying them in a 105 °C oven for 72 h. Stem density was measured using the sedimentation method with a Sedigraph electronic balance and its density component. The same methods and experimental procedures were used to collect and measure functional traits in forest vegetation in different climatic zones.

2.3. Collection and Analysis of Biotic and Abiotic Factors

(1) Soil sample collection and analysis

Soil samples were collected and analyzed between July 2011 and 2019 (during the fieldwork period of the forestry survey). At each of the 309 forest survey plots across the 8 study sites, this study collected 5 randomly located soil samples (0–20 cm deep) by gently removing the upper layer of litter and using a soil auger. A "quadrant method" was used to create a bulk sample of about 1000 g of homogenized soil from each plot, which was analyzed for soil physical and chemical elements. The processed soil samples were sent to the Quantitative Analysis Laboratory of Hainan University to determine the content of chemical elements in the soil, including soil pH value, soil organic matter (SOM), total nitrogen (TN), total phosphorus (TP), available nitrogen (AN), available phosphorus (AP), and available potassium (AK). These nutrient elements in the soil play a crucial role in plant growth and have been shown to have varying effects on different physiological mechanisms of plants and are known to be related to shaping the species composition of the forest.

(2) Collection of climate data

This study used 19 climate variables from WorldClim2, which are commonly used in ecological niche model (ENM) research [23,24]. These variables represent the average temperature and precipitation values recorded at meteorological stations globally between 1970 and 2000. The derived variables describe the mean and extreme temperature and precipitation at monthly, seasonal, and annual scales and have biotic significance for climate data. Given the differences in range size among the species in this study, a 30′ resolution radar was used to obtain meteorological data for the range-restricted species D. compactus and L. woosnami, while a 2.5′ resolution radar was used for the widely distributed I. graduacauda C. leucophrys [25]. Removing highly correlated predictor variables can improve model performance [26]; therefore, this study calculated the pairwise Pearson correlation coefficients for each variable within the defined study area. For variables that showed correlations greater than 0.8, all variables except the predictor variable were removed, as determined by principal component analysis (PCA) of bioclimatic raster data clipped to the study area [25]. Ultimately, three climate variables were selected: mean annual precipitation (MAP), mean annual temperature (MAT), and coefficient of variation of precipitation seasonality (CVPS). The average annual rainfall is related to the length of the growing season, and the accumulation of biomass increases over time [27]. These climate indicators are important factors influencing plant diversity and critical indicators for testing various ecological hypotheses.

(3) The selection of biotic factors

This study used five biotic factors as components of forest structure: mean diameter at breast height (DBH), mean height, basal area, DBH variability, and height variability of individual plants in each of the 309 forest dynamic plots [28]. Seven forest dynamic plots (20 m × 20 m) were established in different climatic regions of China, and a total of 46,280 individual plants with a DBH $\geq$ 1 cm were marked, identified to species, and measured for DBH and height. The selected biotic factors represent the growth situation of vegetation in the community and are significantly correlated with the overall productivity and canopy closure, reflecting the differences in competitive ability among different species in the community [21,28].

2.4. Data Analysis

(1) Calculation of functional trait composition:

This study calculated the weighted mean, variance, skewness, and kurtosis of each trait using the relative abundance of each species in the community, resulting in CWM, CWV, CWS, and CWK, respectively.

① The formula for calculating the community-weighted mean (CWM) is as follows:

$$\mathrm{CWM} = \frac{\sum_{i=1}^{s} P_i t_i}{\sum_{i=1}^{s} P_i}$$

② The formula for calculating the community-weighted variance (CWV) is as follows:

$$\mathrm{CWV} = \frac{\sum_{i=1}^{s} P_i \,(t_i - \mathrm{CWM})^2}{\sum_{i=1}^{s} P_i}$$

③ The formula for calculating the community-weighted skewness (CWS) is as follows:

$$\mathrm{CWS} = \frac{\sum_{i=1}^{s} P_{i(\frac{t_i - \mathrm{CWM}}{\sqrt{\mathrm{CWM}}})^3}}{\sum_{i=1}^{s} P_i}$$

④ The formula for calculating the community-weighted kurtosis (CWK) is as follows:

$$\mathrm{CWK} = \frac{\sum_{i=1}^{s} P_{i(\frac{t_i - \mathrm{CWM}}{\sqrt{\mathrm{CWM}}})^4}}{\sum_{i=1}^{s} P_i} - 3$$

where s represents the total number of species in the community; p_i represents the relative abundance of species i in the community; and t_i represents the functional trait value of species i. Prior to calculating the functional trait composition, the trait values were standardized. As the original values were not normally distributed, a logarithmic transformation was applied to the CWM and CWV [29]. Prior to data analysis, SLA, LNC, LPC, and other traits were subjected to logarithmic transformation. Normality tests were performed on all trait measurements after data processing.

(2) Principal component analysis

We performed principal component analysis (PCA) on 15 climate, soil, and biotic factors to reduce the redundancy of variables using the “Factoextra” package in R 4.2.1 software.

Based on the contribution of each factor to the PC axis, we determined the primary factors influencing the gradient axis. We used the first four principal components (PC1-PC4) as composite habitat gradients, which explained 74.8% of the variation in the 15 variables (Figure 1). The first axis (PCA1) explained 32.6% of the variation, with climate variables (MAP and MAT) and CVDBH showing a significant positive correlation with PCA1, while DBH showed a significant negative correlation with PCA1. The second axis (PCA2) explained 22.5% of the variation, with biotic variables (CVH, BA, and TH) showing a significant positive correlation with PCA2, while TN and AN showed a significant negative correlation with PCA2. The contributions of the third axis (PCA3) and the fourth axis (PCA4) to the overall variation explained by all variables were relatively low, mainly related to biotic and soil variables (Figure 1).

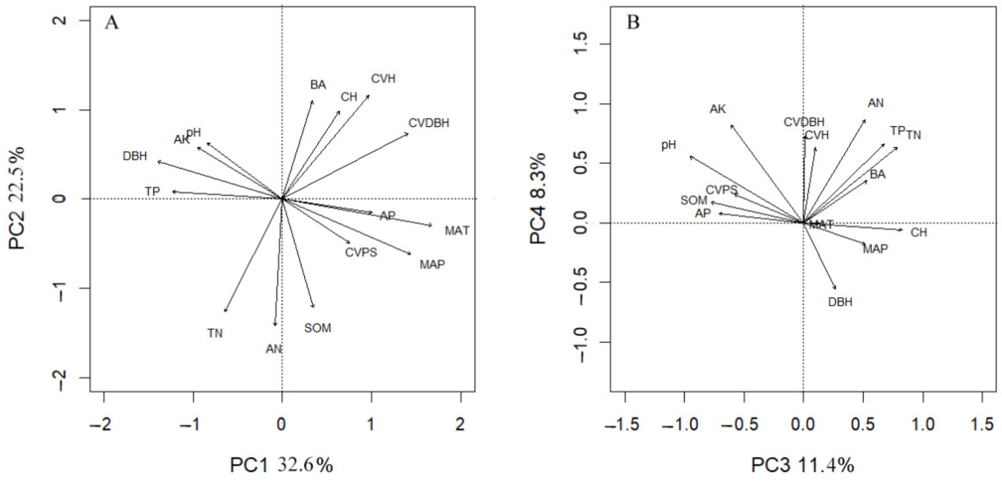

Figure 1. Loadings of biotic and abiotic factors of all forest plots on the first four principal components. The full names of the variable abbreviations are listed in Table 1. Note: (**A**): PC1 and PC2 of the compound habitat gradient axis and (**B**): PC3 and PC4 of the compound habitat gradient axis.

(3) Statistical analysis

This study applies a univariate regression model to test the trend of the functional trait composition index with the change of composite habitat gradient. FD package was used to obtain all CWM and CWV values [30]. Statistical analysis was conducted using Vegan and factoMine packages. This study aims to understand the correlation between functional trait compositions of forest vegetation across climatic zones in China, which was accomplished by correlating the trait matrices of evergreen species with those of deciduous species in each detected trait in R. Therefore, pairwise correlation tests were performed, and the correlation between functional trait compositions was analyzed using methods such as the chi-square test (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$). All analyses were conducted in R 4.2.1 software.

3. Results

3.1. The Pattern of Changes in the Functional Traits of Forest Vegetation along Composite Habitat Gradients across Climatic Zones

Along the composite habitat gradient, the weighted means of functional traits in forest communities from different climatic zones showed a significant decreasing trend in SLA and LPC as the PC1 axis increased, whereas the LDMC, leaf N: P ratio, and WD significantly increased with increases in the PC1 axis ($p < 0.001$). However, the LNC did not show a significant trend with increases in the PC1 axis (Figure 2). The SLA and leaf N: P ratio significantly decreased with increases in the PC2 axis, whereas the LDMC and LPC significantly increased with increases in the PC2 axis. The LNC and WD did not show significant changes along the PC2 axis (Figure 3). The patterns of change in each trait with PC3 and PC4 are presented in Appendix A.

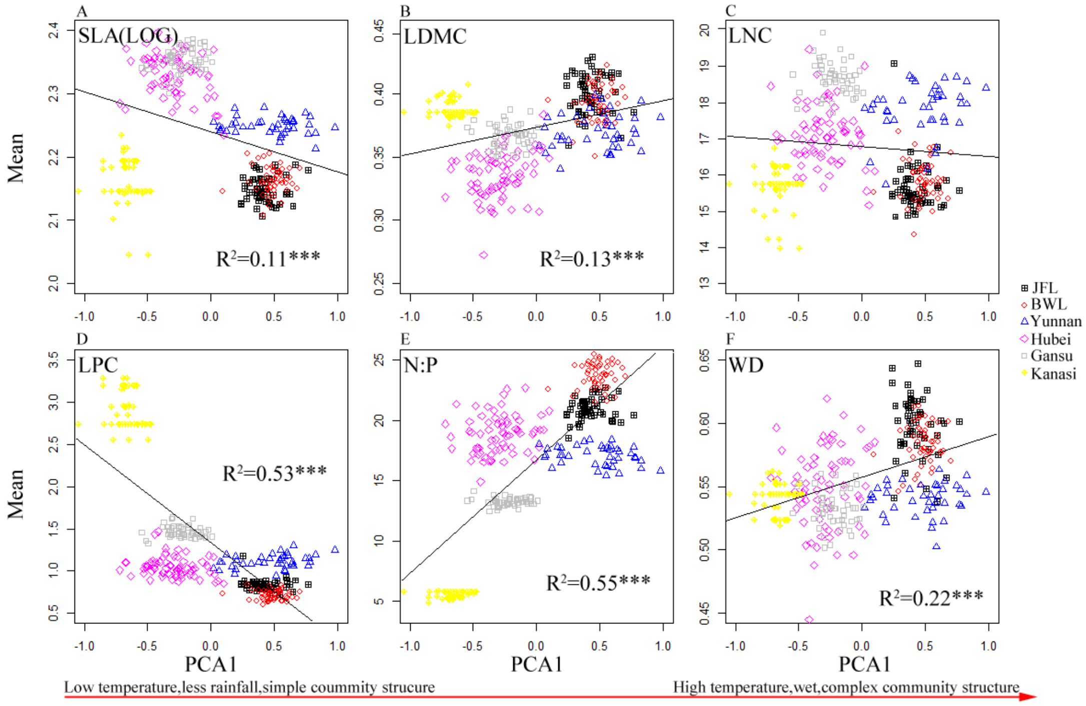

Figure 2. Trends in the weighted mean values of functional traits of typical vegetation communities across climatic zones with the PC1 axes for the compound habitat gradients. Abbreviations: PCA, principal component analysis; SLA, specific leaf area (**A**); LDMC, leaf dry matter content (**B**); LNC, leaf nitrogen content (**C**); LPC, leaf phosphorus content (**D**); N: P, nitrogen to phosphorus (**E**); WD, wood density (**F**). *** $p < 0.001$.

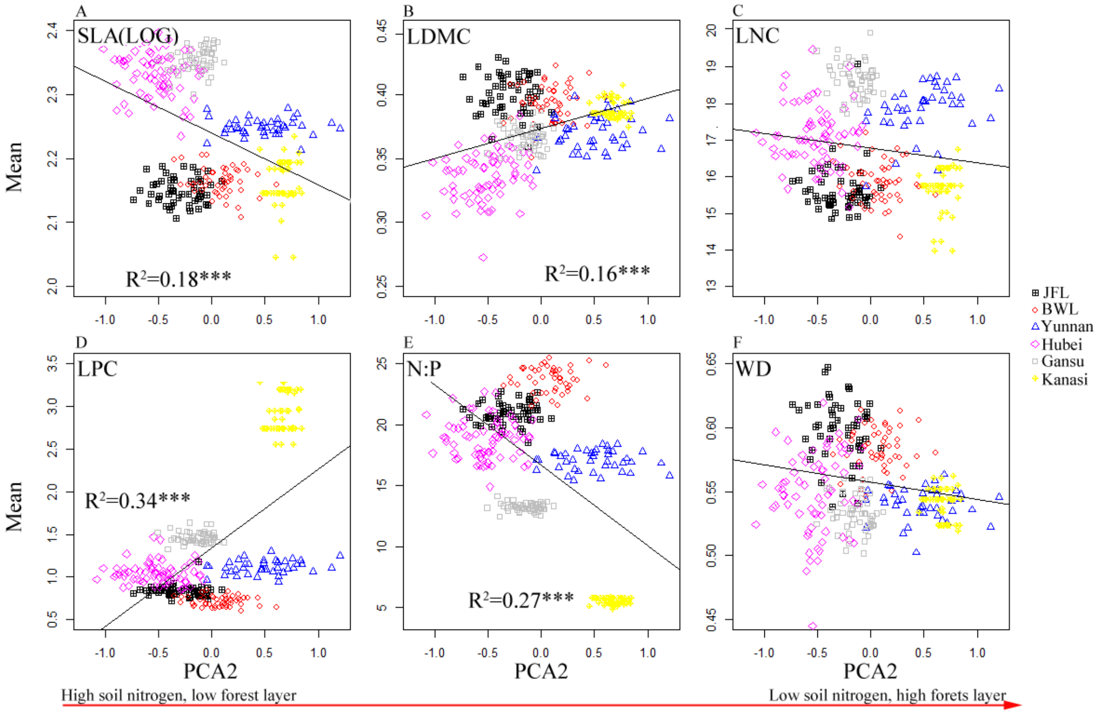

Figure 3. Trends of weighted mean values of functional traits of typical vegetation communities across climatic zones with the PC2 axes for the compound habitat gradients. Abbreviations: PCA, principal component analysis; SLA, specific leaf area (**A**); LDMC, leaf dry matter content (**B**); LNC, leaf nitrogen content (**C**); LPC, leaf phosphorus content (**D**); N: P, nitrogen to phosphorus (**E**); WD, wood density (**F**). *** $p < 0.001$.

The weighted variances of functional traits in different communities exhibited patterns consistent with the weighted trait means along the composite-habitat gradient PC1 axis. The weighted variances of the SLA and LPC significantly decreased with increasing PC1 values, whereas the weighted variance of the LDMC, leaf N: P ratio, and WD significantly increased with increasing PC1 values ($p < 0.001$). However, the LNC did significantly correlate with increasing PC1 values (Figure 4). The CWV of the SLA, LNC, and LPC exhibited significant positive correlations with the PC2 axis, whereas the CWV of the leaf N: P ratio and WD significantly decreased along the PC2 axis. The CWV of the LDMC did not correlate significantly with increasing PC2 values (Figure 5).

The weighted skewness of the functional traits of forest vegetation exhibited the same pattern across the composite environmental gradient PC1 axis, spanning multiple climatic regions. The weighted skewness of all six traits increased significantly with increasing PC1 values and tended towards zero (Figure 6). The weighted skewness of the LNC and N:P ratio decreased significantly along the PC2 axis, whereas the weighted skewness of the other four traits did not show a significant pattern with increasing PC2 values (Figure 7).

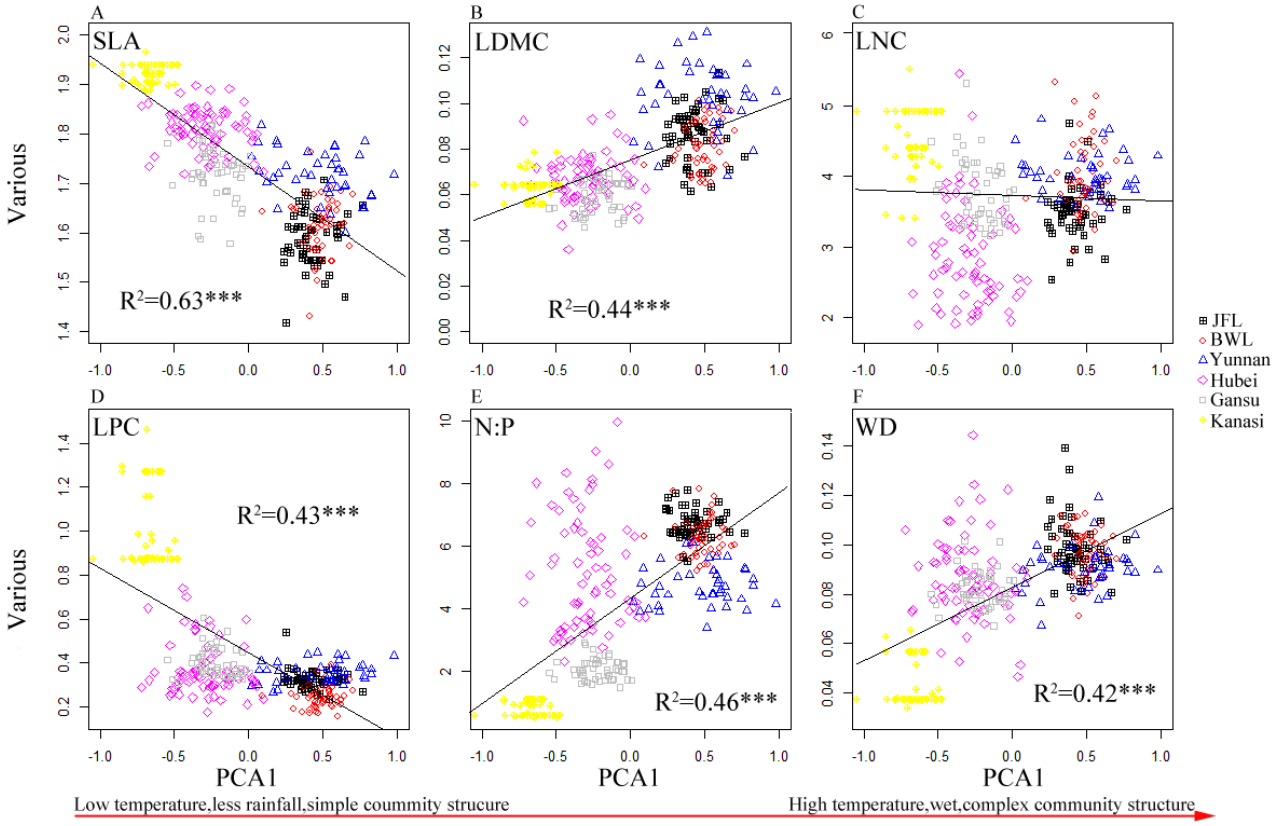

Figure 4. Trends in various weighted values of functional traits for typical vegetation communities across climatic zones with the PC1 axes for the compound habitat gradients. Abbreviations: PCA, principal component analysis; SLA, specific leaf area (**A**); LDMC, leaf dry matter content (**B**); LNC, leaf nitrogen content (**C**); LPC, leaf phosphorus content (**D**); N: P, nitrogen to phosphorus (**E**); WD, wood density (**F**). *** $p < 0.001$.

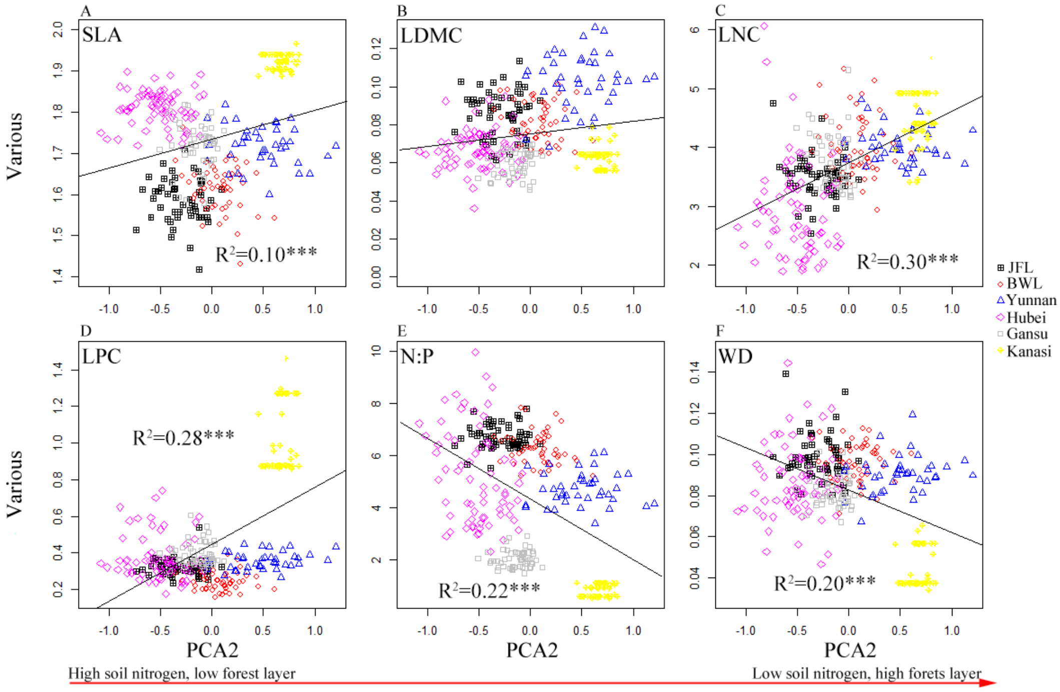

Figure 5. Trends in various weighted values of functional traits for typical vegetation communities across climatic zones with the PC2 axes for the compound habitat gradients. Abbreviations: PCA, principal component analysis; SLA, specific leaf area (**A**); LDMC, leaf dry matter content (**B**); LNC, leaf nitrogen content (**C**); LPC, leaf phosphorus content (**D**); N: P, nitrogen to phosphorus (**E**); WD, wood density (**F**). *** $p < 0.001$.

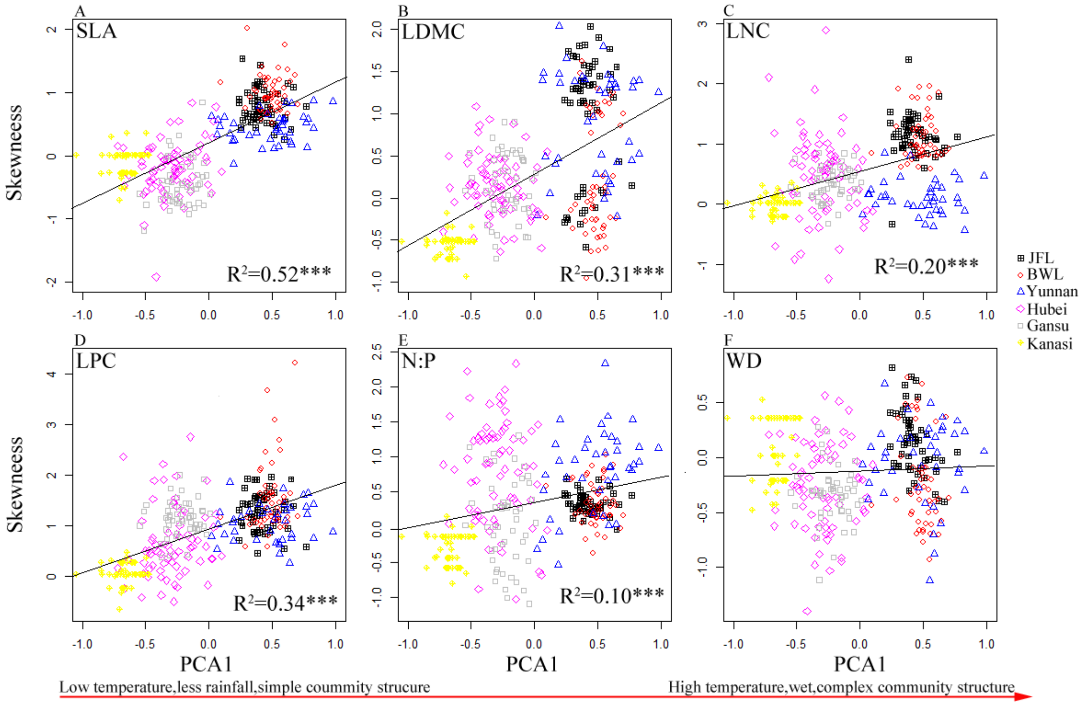

Figure 6. Trends in the weighted skewness values of functional traits of typical vegetation communities across climatic zones with the PC1 axes for the compound habitat gradients. Abbreviations: PCA, principal component analysis; SLA, specific leaf area (**A**); LDMC, leaf dry matter content (**B**); LNC, leaf nitrogen content (**C**); LPC, leaf phosphorus content (**D**); N: P, nitrogen to phosphorus (**E**); WD, wood density (**F**). *** $p < 0.001$.

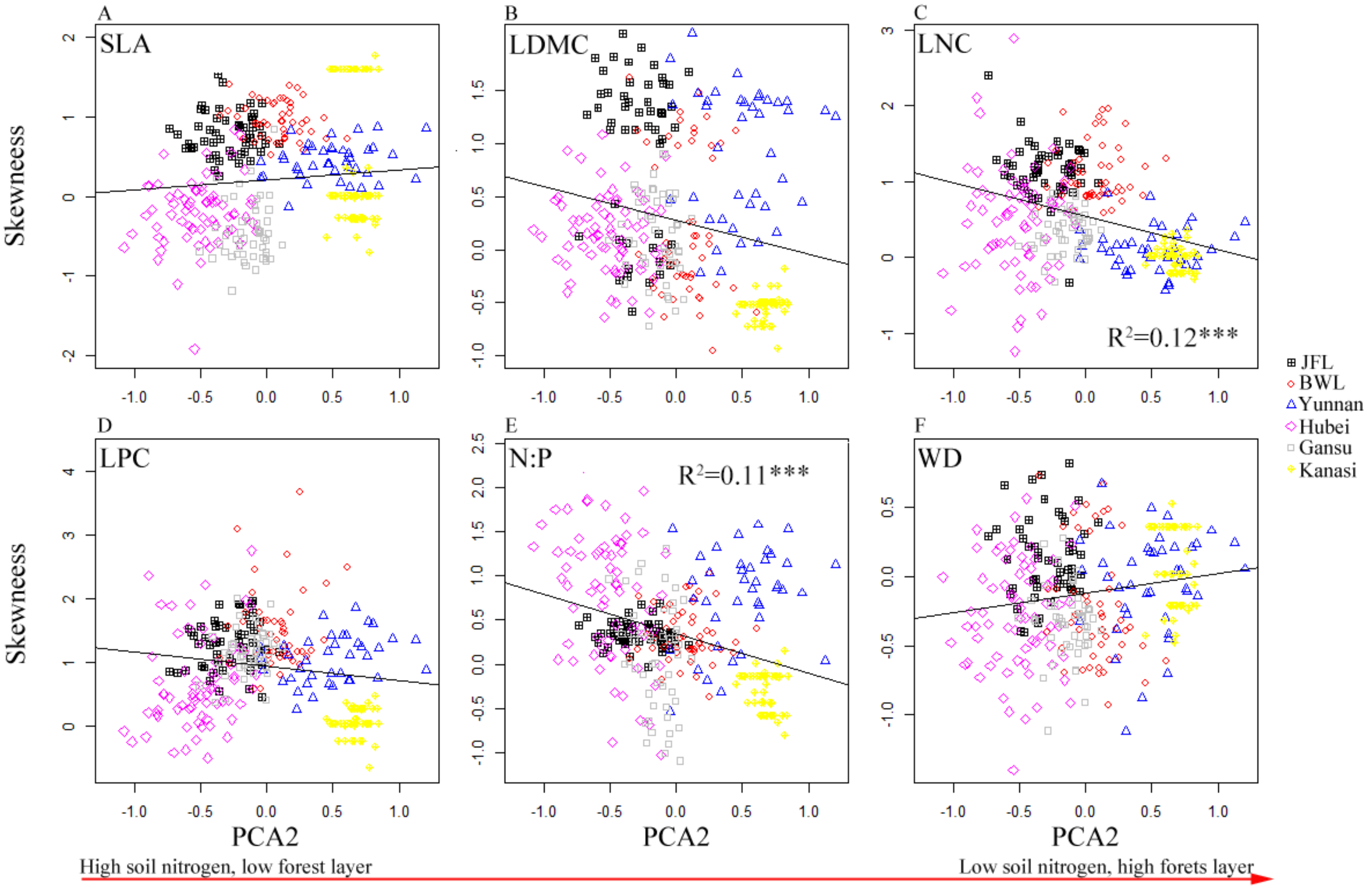

Figure 7. Trends in the weighted skewness values of functional traits of typical vegetation communities across climatic zones with the PC2 axes for the compound habitat gradients. Abbreviations: PCA, principal component analysis; SLA, specific leaf area (**A**); LDMC, leaf dry matter content (**B**); LNC, leaf nitrogen content (**C**); LPC, leaf phosphorus content (**D**); N: P, nitrogen to phosphorus (**E**); WD, wood density (**F**). *** $p < 0.001$.

The weighted kurtosis of the forest vegetation functional traits showed a similar pattern to the weighted skewness along the composite-habitat gradient PC1 axis across different climatic zones. The weighted kurtosis of all six traits increased significantly with increasing PC1 values and deviated from zero (Figure 8). The weighted kurtosis of the SLA, LNC, and WD decreased significantly with increasing PC2 values, whereas the remaining three traits did not correlate significantly with changes along the PC2 axis (Figure 9).

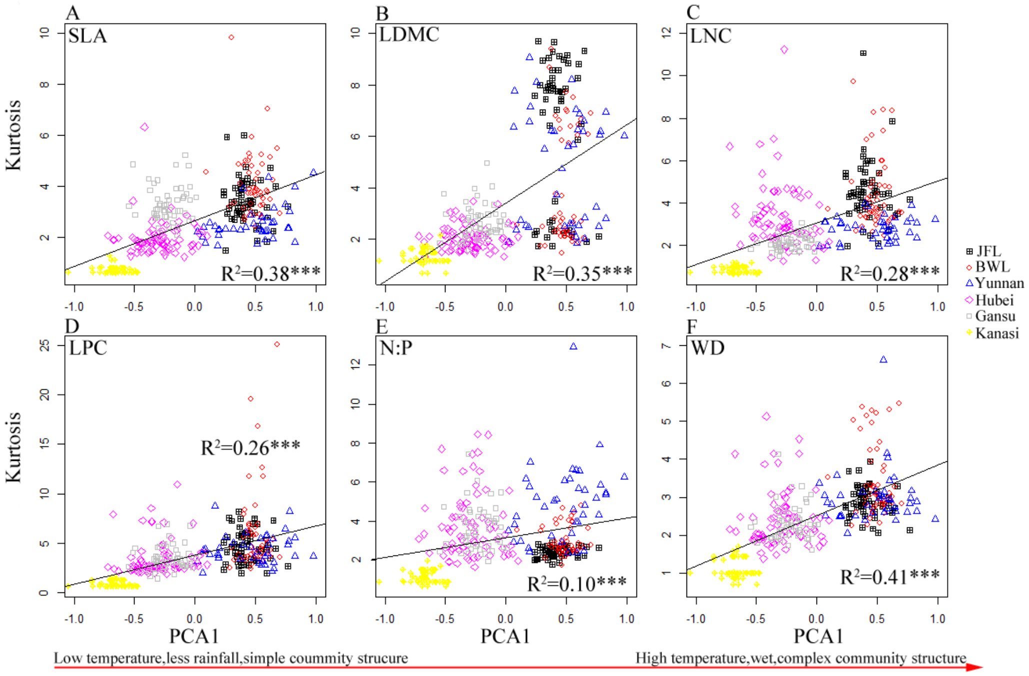

Figure 8. Trends in the weighted kurtosis values of functional traits of typical vegetation communities across climatic zones with the PC1 axes for the compound habitat gradients. Abbreviations: PCA, principal component analysis; SLA, specific leaf area (**A**); LDMC, leaf dry matter content (**B**); LNC, leaf nitrogen content (**C**); LPC, leaf phosphorus content (**D**); N: P, nitrogen to phosphorus (**E**); WD, wood density (**F**). *** $p < 0.001$.

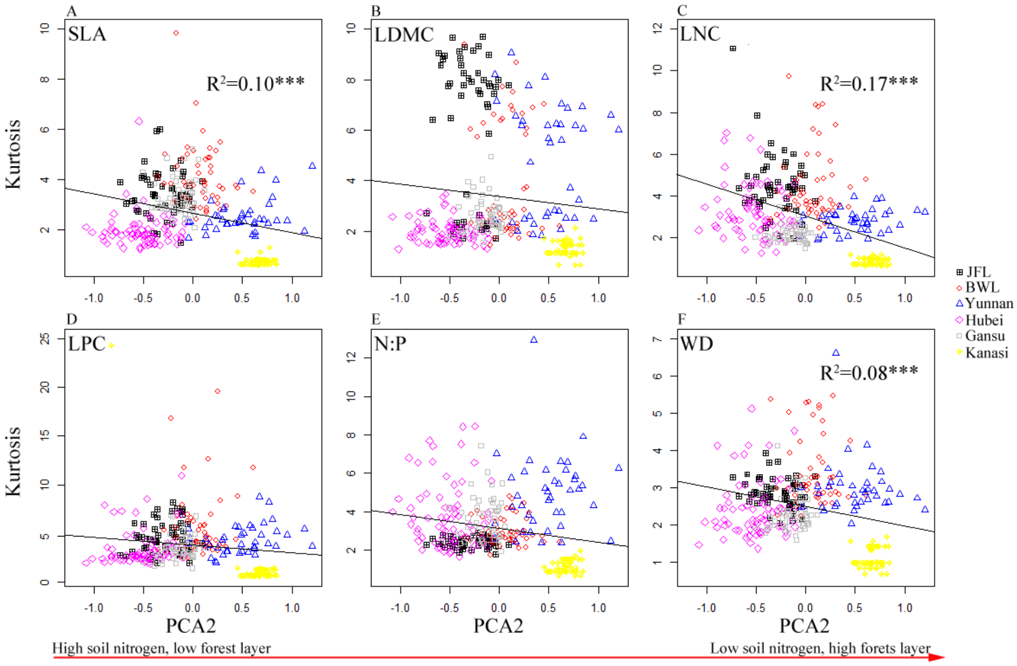

Figure 9. Trends in the weighted kurtosis values of functional traits of typical vegetation communities across climatic zones with the PC2 axes for the compound habitat gradients. Abbreviations: PCA, principal component analysis; SLA, specific leaf area (**A**); LDMC, leaf dry matter content (**B**); LNC, leaf nitrogen content (**C**); LPC, leaf phosphorus content (**D**); N: P, nitrogen to phosphorus (**E**); WD, wood density (**F**). *** $p < 0.001$.

3.2. Interrelationships among Functional Trait Compositions of Forest Vegetation across Climatic Zones

The CWM, CWV, CWK, and CWS values of each functional forest-vegetation trait in China's cross-climatic regions showed significant correlations ($p < 0.001$). Functional-composition analysis revealed strong positive correlations, indicating that the traits promoted each other synergistically (Figure 10). Identifying mutual relationships between traits is crucial for understanding the ecological adaptation and functions of forest vegetation.

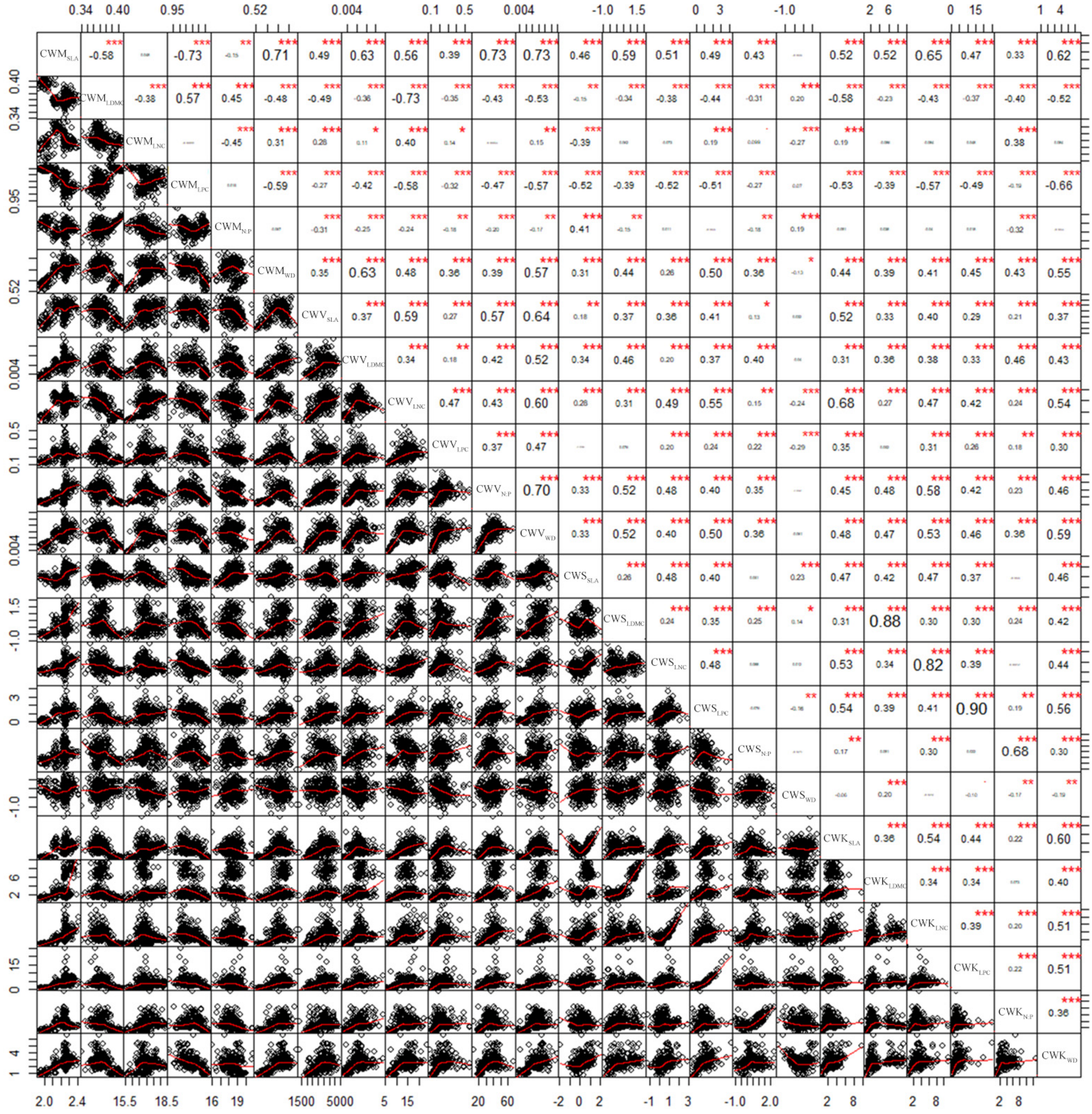

Figure 10. Correlation analysis of functional traits in forest communities across different climatic zones in China. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

4. Discussion

4.1. The Variation Patterns of Forest Vegetation Functional Traits along the Gradients of Composite Habitats in Different Climate Zones

Research based on geographic differentiation patterns of community trait compositions can help in understanding differences and changes occurring in the entire community. Therefore, in this study, we quantified the roles of composite habitat gradients in forming multispecies community traits at the biogeographic scale for forest communities in different climatic regions. The CWM and CWV values of functional traits can serve as quantitative tools to evaluate the impact of habitat gradients on forest community changes, as they indicate the values and variabilities of traits resulting from species-composition changes and relative abundances driven by non-biotic or biotic conditions [9,10]. In this study, we found that the weighted means and variances of various forest-community traits in different climatic regions exhibited different patterns of change with composite habitat gradients. This observation is consistent with the results of global studies conducted by Wieczynski et al. [7] and Buzzard et al. [14], who showed that the functional compositions of forest communities differed significantly at different latitudes and altitudes. Forest communities in high-latitude climate regions with low temperatures, low rainfall, and a simple community structure have high SLA and LPC values and relatively low WD, leaf N: P ratio, and LDMC values. With increasing temperature and rainfall, species diversity in the community increased significantly (e.g., between temperate to tropical regions); the SLA and LPC values decreased; and the WD, leaf N:P ratio, and LDMC values increased significantly. The geographic differentiation patterns of functional trait compositions in forest vegetation observed across different climate zones reflects differences in plant-growth strategies (resource- conservation versus resource acquisition strategies) and the diversity of functional traits in the community. In cold- and warm-temperate climate regions with low temperatures and rainfall levels, deciduous tree species generally occupy the canopy and have relatively high SLAs and low WDs, enabling them to rapidly obtain nutrients and light during the growing season [21]. In environments with superior habitat conditions, evergreen tree species generally acquire a low SLA and a high LDMC to improve the utilization efficiency of resources (such as light), resist pest erosion, and enhance resource acquisition [20,21,31]. The LPC significantly impacts the plant photosynthesis efficiency, and differentiation of the LPCs and N: P ratios in evergreen and deciduous forest communities at different latitudes indicates different resource acquisition and utilization strategies. Therefore, under conditions of poor soil nutrients, deciduous tree species have weaker resource acquisition abilities than evergreen tree species and lack a strong competitive advantage, which is disadvantageous for the competitive dominance of deciduous tree species [32].

In this study, we found that within forests across different climatic zones, the weighted skewness and kurtosis of various functional traits followed the same patterns of changes along the PC1 axes of the composite habitat gradients. Both parameters significantly increased with increasing PC1 axis values and exhibited a trend consistent with (i) the weighted skewness values tending towards zero and (ii) the kurtosis values moving away from zero, as observed in forests worldwide [7]. Geographical differences in CWS and kurtosis values reflect the selection of rare plant phenotypes by the environment. The high degrees of weighted skewness and kurtosis for the functional traits of species in forest communities in China’s low-latitude climate zone do not necessarily imply lower community functional diversity. However, they do indicate that under the influence of habitat filtering and biotic interactions, species adopt similar survival strategies, with most coexisting species having very similar trait values [33,34]. In contrast, forest communities in China’s high-latitude climate zone had lower weighted skewness and kurtosis values in terms of the functional traits, indicating that greater variation occurred in the distributions of community traits, often with a “tail” suffix. These findings may indicate that the average trait differences between coexisting species were elevated [33], reflecting the use of different survival strategies among species.

The relationships between community-level functional traits and environmental conditions vary with different sites and scales [35]. In the present study, we found that the compositions of functional traits in forest communities in different climatic zones of China were significantly influenced by the composite-habitat gradient along the PC1 axis. Forest communities are more significantly influenced by climate on a larger scale, and changes in habitat conditions (such as temperature and precipitation differences) can result in a screening effect on the trait patterns of different communities [11]. The results of this study validate those of previous studies, indicating that the patterns of community traits on a larger scale largely follow a gradient of climate stability [36,37], resulting in geographic differentiation patterns of community functional traits due to climate change. Our findings also support the habitat-filtering hypothesis, suggesting that the similarity of functional traits or close relationships between species in a community are influenced by habitat filtering (such as climate and soil) [37]. For example, species with high SLAs are more likely to settle in forest communities with soil rich in water and mineral nutrients, higher litter quality, and faster decomposition rates (increased leaf N: P ratio) [14,38]. As the temperature and water-use efficiency increased, the leaf N: P ratio, LNC, [39] LDMC, and WD values of the community also significantly increased.

Global-scale research indicates that, as the efficiency of water and/or nutrient use decreases, the LA and SLA decrease [1,3,14]. Therefore, in cold and short growing season ecosystems, selecting species that grow faster in a shorter period of time leads to leaves with lower SLAs, higher LDMCs, and nitrogen deficiencies [14]; buffering of the leaf temperature relative to the air temperature; and promotion of the net photosynthetic rates and plant growth [40,41]. The results of this study are consistent with those of several studies on forest ecosystems conducted in different regions and on different scales [34,42,43]. The trends of differences in the community functional-trait compositions suggest that rare phenotypes at the edge of the trait space are selected for harsher environments and that as the environmental conditions decrease, the habitat filtering becomes more pronounced. Overall, these results suggest that at the biogeographical scale, the climate (i.e., rainfall and temperature levels) may act as primary macro-scale environmental filters that influence variations in community traits [42], where the differences in traits and functional diversities (richness, asymmetry, and evenness) are very pronounced.

Discovering and quantifying the relationships between climate conditions and functional traits is essential for predicting the responses of communities and ecosystems to future environmental changes [21]. The results of this study revealed numerous relationships between functional trait composition and climate conditions, with climate significantly and universally altering the functional trait composition of forests at larger spatial scales, thereby influencing ecosystem productivity and functioning [44]. By using a multivariate weighted index across the entire community potential, this study was able to more comprehensively represent functional composition, which may enhance the accuracy of trait–climate relationships derived from it. The weighted differences of different community trait values along environmental gradients reflected the influence of habitat filtering on community traits and quantified their adaptability [3]. This is crucial for establishing more accurate mechanistic models to predict community structure and ecosystem productivity in relation to climate-driven changes, improving estimates of how past and future climate change will impact ecosystem functioning [1,3].

4.2. Interrelationships among Functional Traits of Forest Vegetation across Climatic Zones

Trade-offs among the traits of different plant tissues can reveal plant responses to different environments, which helps explain species distribution patterns and ecosystem processes [20,21]. In this study, significant positive correlations were observed between the CWM, CWV, CWS, and CWK values of various functional traits of forest vegetation across different climatic regions in China (Figures 5–10). These data are indicative of a certain degree of coordination and mutual promotion between leaf and stem traits [45], supporting the whole plant coordination hypothesis [19], where plants are viewed as holistic entities and stem and leaf function coordination and collaboration with each other are considered indispensable and closely related. However, the degree of coordination among different functional traits of plants (such as wood and leaves) can be multidimensional and influenced by external factors, such as the environment, which leads to different results [21]. In this study, we found that some traits were uncorrelated or were weakly correlated with each other, which may reflect previous observations that different plant organs respond to different selective pressures or the same selective pressures in different ways [46,47]. Correlations were found between traits at some locations within a region, possibly because local processes (such as environmental heterogeneity or biotic interactions) promoted broader ecological strategies. For example, Kembel and Cahil proposed that environmental heterogeneity within communities might promote trait coordination by leading to the coexistence of species with different trait values [46]. Conversely, the lack of a correlation suggests that traits represent different ecological strategies that promote the differentiation of plant organ niches [20,21]. Local biotic processes such as competition and/or facilitation [48] increase trait similarity and promote plant coexistence through niche differentiation [6]. In summary, trade-offs among functional traits reveal major ecological strategies that may provide insights into species distribution and ecosystem processes [44].

5. Conclusions

The results of this study confirmed the geographical differentiation patterns of functional traits in forest vegetation, including the SLA, LDMC, LPC, leaf N: P ratio, and WD, along a complex environmental gradient in different climatic zones in China. The differences in functional trait composition of forest communities across different climate zones are caused by a combination of trait convergence (environmental factors) and trait divergence resulting from species competition at the local scale. These findings support a model whereby the environment selects optimal traits that shape community compositions. By providing a more comprehensive understanding of individual-level trait variations within communities, the insights from this study will help bridge plant economics theories and functional biogeography in future research. Such advances should enable better evaluations and predictions regarding the relationships between the climate, ecosystem structures, and productivity levels. Therefore, the current findings provide insight into broad spatiotemporal ecological patterns and represent an important step toward predicting future changes in ecosystem functions and stabilities.

Author Contributions: Conceptualization, R.Z.; Methodology, X.A.; Resources, L.Y. (Lan Yao); Data curation, C.W.; Writing—original draft, L.Y. (Liangjin Yao); Writing—review & editing, Y.X.; Supervision, F.D. All authors have read and agreed to the published version of the manuscript.

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

Appendix A

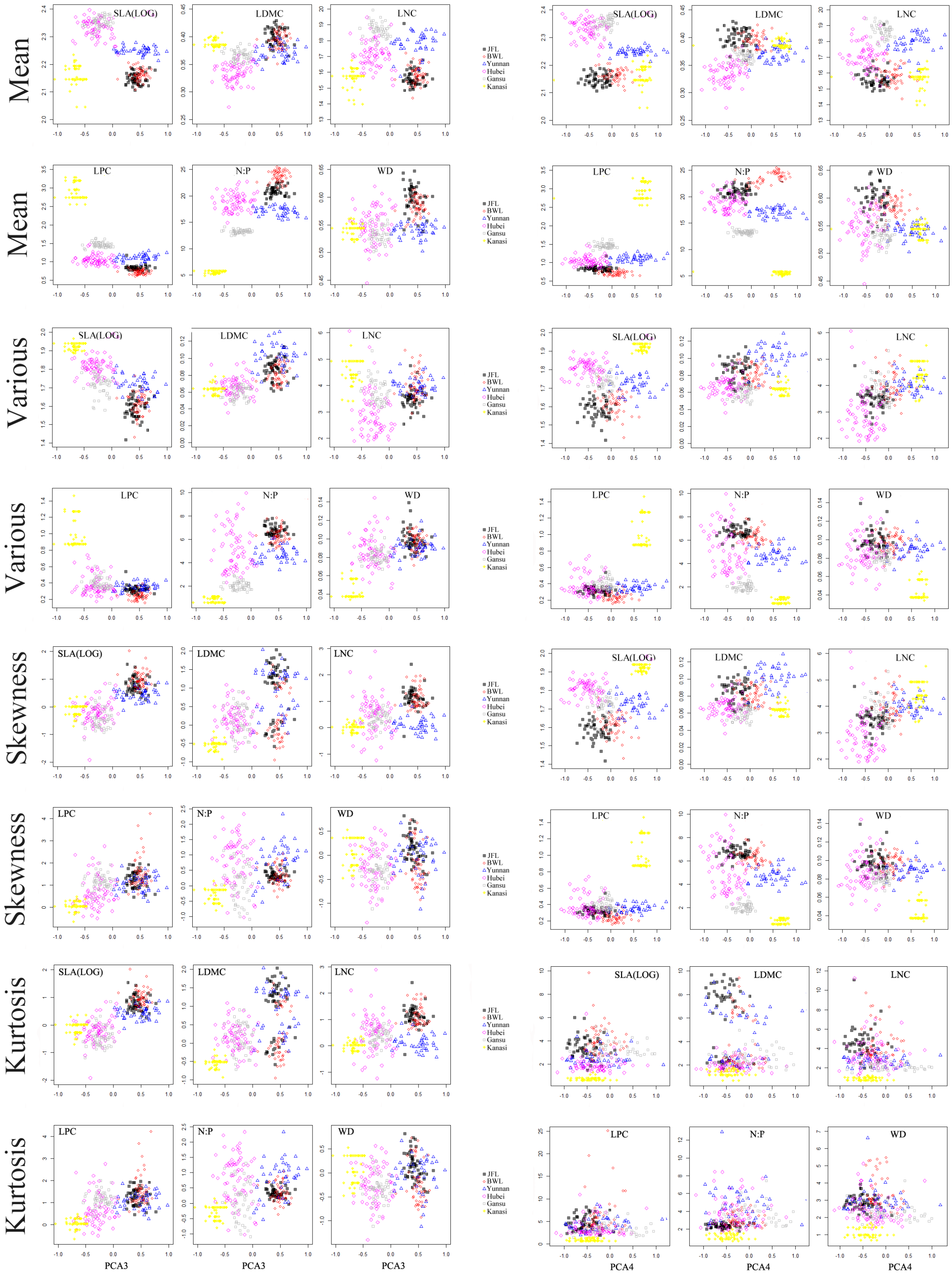

Figure A1. Trends of weighted mean, variance, skewness, and kurtosis values of each functional trait of typical vegetation communities in across-climatic zones with the PC3 and PC4 axis of compound habitats gradient.

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