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Variations in Functional Richness and Assembly Mechanisms of the Subtropical Evergreen Broadleaved Forest Communities along Geographical and Environmental Gradients

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Abstract: Linking functional trait space and environmental conditions can help to understand how species fill the functional trait space when species increase along environmental gradients. Here, we examined the variations in functional richness (FRic) and their correlations with key environmental variables in forest communities along latitudinal, longitudinal, and elevational gradients, by measuring seven functional traits of woody plants in 250 forest plots of 0.04 ha across five locations in the subtropical evergreen broadleaved forests (SEBLF) of China. On this basis, we explored whether environmental filtering constrained the functional volume by using a null model approach. Results showed that FRic decreased with increasing elevation and latitude, while it increased with increasing longitude, mirroring the geographical gradients in species richness. FRic was significantly related to precipitation of driest quarter, soil pH, and total phosphorus. Negative SES.FRic was prevalent (83.2% of the communities) in most SEBLF communities and was negatively related to mean diurnal range. Our study suggested that the geographical variation in the functional space occupied by SEBLF communities was affected mainly by climate and soil conditions. The results of the null model revealed that niche packing was dominant in SEBLF communities, highlighting the importance of environmental filtering in defining functional volume within SEBLF communities.

Keywords: biogeography; subtropical evergreen broadleaved forest; functional richness; environmental variables; community assembly

1. Introduction

Exploring and understanding spatial patterns of biodiversity is central to understanding mechanisms of species coexistence and community assembly processes in natural ecosystems [1,2]. Geographical gradients in species diversity are of widespread concern, and species richness in most plants and animals is generally explained by declining from the tropics to the poles and from low to high elevations [3,4]. Despite the generality of these patterns, it has been recognized that considering species diversity alone (e.g., species richness or taxonomic diversity) is not sufficient to understand the underlying processes that influence communities along geographical gradients [5–7]. Species richness does not explain fully the community structure as the differences among species in their evolutionary history and ecological roles are ignored [6,8]. Thus, recent research argued that the study of biodiversity theories should move beyond species diversity, especially focusing more explicitly on the functional aspects of diversity [5]. Functional diversity can not only mirror species richness along geographical gradients [9] but also complement species richness in explaining species coexistence and ecological processes [10].



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Copyright: © 2022 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https:// creativecommons.org/licenses/by/ 4.0/). Functional trait values of species within communities are a reflection of the ability of species to respond to their environment [11]. Therefore, the location occupied by a species within a multidimensional trait space can also shift across geographical and environmental gradients [12]. Climate is one of the most important drivers shaping the functional structure of forest ecosystems [13]. Specifically, climate harshness and seasonality were proven to be key factors controlling the variation in functional volume in subtropical forests [14]. Researchers predicted that environments that are more abiotically benign will allow the invasion and success of peripheral phenotypes, resulting in a large morphological volume, whereas harsher environments will limit the invasion and success of peripheral phenotypes, resulting in a small morphological volume [15]. For instance, abundant and evenly distributed precipitation and stable temperatures allow communities to contain a large number of species, while species that occur in those regions of drought and temperature instability are strongly limited [14,16]. Soil fertility is another important factor shaping the functional diversity of plant ecosystems [17]. Changes in soil resource availability can directly affect the size of the niche space occupied by species [18].

Studies argued that changes in the functional trait space along an environmental gradient in terms of species richness could be associated with the patterns of functional space occupancy [10]. As species richness increases, communities would change either by tighter packing of species into the niche space (niche packing) or by occupying unexploited portions of the niche space (niche expansion) to accommodate more species in a given environmental condition [19,20]. Niche space characterizes the phenotypic space occupied by a set of species, which can be quantified by assessing the multidimensional trait space [21]. Comparing changes in the occupancy of the multidimensional trait space across communities can allow inferences regarding the association of niche expansion and packing with environments [12]. To test the two patterns of functional trait space, it is necessary to use a functional diversity index that can directly measure the volume and occupancy pattern of the niche space by species and quantify the diversity in trait combinations in the research of biodiversity and community assembly [22]. Functional richness (FRic) is measured as the volume of the minimum convex hull that includes all the species of the community and represents the amount of functional space filled by the community, which has been recognized as the best candidate for this research [23]. It has been widely used in many recent papers to explore the patterns of niche space in different biological groups [12,19,24]. In addition, previous studies also showed that FRic was useful for tracking diversity variations along environmental gradients [25]. Therefore, FRic has reasonable power to detect the changes in the occupancy of the multidimensional trait space under different environmental conditions and reveal how species pack and fill the trait space [5].

Niche packing and expansion are not mutually exclusive and may occur simultaneously [12]. However, the relative importance of the two patterns remains unknown [19]. Quantifying the volume, packing, and expansion of functional trait space and their relative importance enables us to understand the ecological processes structuring functional diversity and ecological strategies [5,26]. In the absence of niche-based processes, the trait composition of a local assemblage is predicted to be a random subset of a shared regional species pool [5,12]. Therefore, comparing the observed value of FRic to a random expectation—that is, computing a standardized effect size (SES.FRic) [15]—allows us to understand whether niche-based processes occur in a given location [12]. Environmental filtering theory predicts that although FRic can also increase with species richness in more stressful environments, FRic will be smaller than the null expectation (negative SES.FRic), revealed by niche packing [5,27]. Conversely, competitive exclusion theory predicts that new species are most likely to fill an expanded variety of niche space; thus, FRic should always be larger than a sampling expectation (positive SES.FRic), revealed by niche expansion [5,28]. Determining which pattern of functional space occupancy is dominant in a given location helps us to understand the relative importance of environmental filtering and biotic competition. Substantial evidence showed that environmental filtering, driven

by a set of environmental variables, is more important than biotic competition in shaping plant diversity [29,30]. Therefore, we expected that the pattern of niche packing would be dominant within the forest communities.

The subtropical evergreen broadleaved forest (SEBLF) is one of the main vegetation types around the world and is widely distributed in China [31,32]. The subtropical region in China hosts unique and rich biodiversity and encompasses different environmental gradients in topography and climate, providing a natural setting for studying patterns of biodiversity change along geographical gradients. While trait–environment relationships have been already explored in some separate sites of subtropical forest ecosystems [33], few studies have been carried out in detecting the patterns of functional trait space (niche packing/expansion) along geographical and environmental gradients. Here, we used a large trait and spatial distributional data set of SEBLF communities to describe the geographical patterns of functional richness, species richness, and their correlations with key environmental factors in the subtropical region of China. Specifically, to test whether niche packing is dominant in the SEBLF of China, we used a null model to test whether the environmental filtering constrained the functional trait space, thereby increasing the packing of species within the SEBLF communities.

2. Materials and Methods

2.1. Study Area

This study was conducted in the 250 permanent forest plots with an area of 0.04 ha $(20 \text{ m} \times 20 \text{ m})$ (latitude: 27.58° - 30.18° N, longitude: 102.95° - 120.00° E; elevation: 200-1948 m) across five locations (Figure S1) in the natural old-growth subtropical evergreen broadleaved forests of China (SEBLF). Locations were selected at random within the study areas and represented an unbiased, representative sample of natural old-growth vegetation. The study areas have a subtropical monsoon climate, with a mean annual temperature of 15.0 °C and mean precipitation of 1391.1 mm. The plots have a rough terrain, with the slope ranging from 4° to 42°. The floristic composition of these plots is characteristic of evergreen broadleaved forests, with Symplocos anomala (Symplocaceae), Camellia fraternal (Theaceae), Loropetalum chinense (Hamamelidaceae), Eurya muricata (Theaceae), Symplocos lucida (Symplocaceae), and Cyclobalanopsis glauca (Fagaceae) being the dominant canopy species. All plots were established and investigated according to the standard of the Center for Tropical Forest Science (CTFS) [34] during the summer of 2018 and 2019. For woody plant species, all individuals with a diameter at breast height ≥ 1 cm were tagged, mapped, and identified to species level with the help of local botanists. The abundances of species were determined by calculating the number of individuals of a certain species in each plot. In total, 292 woody plant species (48,680 individuals) belonging to 59 families and 134 genera were collected.

2.2. Trait Data

We selected seven functional traits that represent the variation in plant form and function. These traits included specific leaf area (SLA, cm² g⁻¹), leaf nitrogen concentration (LNC, g kg⁻¹), leaf phosphorus concentration (LPC, g kg⁻¹), wood density (WD, g cm⁻³), leaf dry matter content (LDMC, g g⁻¹), maximum plant height (Hmax, m), and seed mass (SM, g). Selected traits correlate well with ecological characteristics and are good predictors of resource utilization, tolerance to drought, and mechanical damage [29]. Except for SM, all functional traits were measured according to standardized measurement protocols [35]. SM was compiled from multiple sources and databases, including FOC (http://www.efloras.org/ (accessed on 20 June 2021)), Seeds of Woody Plants in China [36], the TRY Plant Trait Database (https://www.try-db.org/de/ (accessed on 20 June 2021)) from the KEW Seed Information Database [37] and PLANTS Database [38], and the BIEN trait database (accessed using the BIEN package [39] in R). In each 20 m × 20 m plot, ten individuals of every species were sampled. For those species with less than ten individuals, we added additional individuals of the same species from surrounding areas. A detailed

description of the measurement methods for these functional traits can be found in our previous works [40]. The mean functional trait values for each species were applied to all individuals.

2.3. Functional and Species Richness Calculation

Finding a suitable measure of functional space to appropriately quantify the diversity in trait combinations is challenging [22]. Here, we considered functional richness (FRic) as the best candidate measure for our research purposes [23]. FRic measures the extent of the functional volume of an assemblage as the smallest possible multidimensional convex hull volume that contains all species in an assemblage [22,41]. We quantified FRic using the package 'FD' in the program R [42]. To compare the geographical variation between FRic and species diversity and explore the patterns of FRic related to species richness, we also quantified species richness (SR). Species richness in each plot was estimated as the number of species.

There are numerical dependencies between functional and species richness. Functional richness is expected to be positively correlated with species richness. We thus accounted for such variations by computing a null model in which species identities (and therefore trait values) were shuffled 999 times while maintaining species richness and occupancy within each assemblage, and we recalculated the functional richness for each assemblage for each iteration. This generated a null distribution of 999 values for functional richness in each assemblage [15,24]. The observed values and this null distribution were used to calculate a standardized effect size for functional richness (SES.FRic) = [Observed FRicmean expected FRic]/SD expected FRic. The SES.FRic shows how many SDs the observed FRic is above or below the mean expected value from the null models [15,43]. The direction of SES.FRic (higher or lower than the expected null) was correlated with different deterministic processes of community assembly. Negative SES.FRic indicates that the observed functional volume is less than expected by chance, resulting from environmental filtering. Conversely, positive SES.FRic indicates that the observed functional volume is larger than expected given the species richness, resulting from biotic competition [15]. If we predicted that the environmental filtering led to the dominance of niche packing in SEBLF communities, this could be supported by the following two observations. First, the proportions of communities with negative SES.FRic would be higher than those with positive SES.FRic. Second, and more importantly, differences between the observed and simulated FRic, measured as the mean of the associated SES.FRic across all communities, would be significantly lower than the expectation of zero when using a two-tailed Student's t-test [44,45]. Additionally, the magnitude of SES.FRic was interpreted as the strength of the signal of deterministic processes on the assemblages [15]. More negative SES values indicate stronger environmental filtering [46,47].

2.4. Environmental Variables

To estimate the influences of environmental variables on community-level functional richness, we collected 19 climatic and 7 edaphic variables to represent environmental conditions. A detailed description of the data collection and measurement methods for these environmental variables can be found in our previous works [40]. We performed correlations to assess possible multicollinearity and variable redundancy among the environmental variables. Pearson's correlation values (R < 0.8) between explanatory variables were used as a cutoff criterion to retain variables that were more relevant to the FRic (Table 1). Final models were run with precipitation of driest quarter (PDQ), precipitation of wettest quarter (PWQ), mean diurnal range (MDR), mean temperature of driest quarter (TDQ), soil pH (SpH), and soil total phosphorus (STP).

Variables	MDR	TDQ	PDQ	PWQ	STP
TDQ	-0.42 ***				
PDQ	0.22 ***	0.70 ***			
PWQ	0.26 ***	0.25 ***	0.53 ***		
STP	0.16 *	-0.72 ***	-0.70 ***	-0.18 **	
SpH	0.04	0.15 *	0.19 **	0.57 ***	0.11

Table 1. Correlations between environmental variables. Significance levels: *, p < 0.05; **, p < 0.01; ***, p < 0.001.

Abbreviations: mean temperature of driest quarter (TDQ), precipitation of driest quarter (PDQ), precipitation of wettest quarter (PWQ), mean diurnal range (MDR), soil pH (SpH), soil total phosphorus (STP).

2.5. Data Analysis

To assess geographical variation in functional volume and species richness, linear mixed models (LMMs) were used to test shifts in FRic, SES.FRic, and SR along latitude, longitude, and elevation. We also used the LMMs to test the effects of climate and soil on FRic, SES.FRic, and SR. LMMs were conducted using FRic, SES.FRic, and SR as the response variables, and the three geographical variables and the six climatic and edaphic variables as fixed predictors. The site was included as a random effect, given that we could not exclude the potential role of unmeasured, spatially autocorrelated environmental factors in our analysis. Linear mixed models were built using the "lme4" package [48] as implemented in the R statistical software [42]. The proportion of variance explained by the LMMs was assessed using the marginal R^2m (variance explained by the fixed predictors) and the conditional R^2c (variance explained by both the fixed and random effects) [49]. The direction and magnitude of selected predictors were assessed from the sign and values of standardized coefficients. The parameter estimates, t-statistics, and p values were obtained using Satterthwaite's method for denominator degrees of freedom in the "lmerTest" package [50]. The spatial autocorrelations in model residuals were tested using Moran's I, which was conducted using the "spdep" package [51,52].

Finally, we performed hierarchical partitioning (HP) to determine the relative importance and independent contribution of each explanatory factor to FRic SES.FRic, and SR [53], as the multicollinearity between the factors in linear mixed models could not be completely excluded (VIFs of all variables < 10) despite it being controlled in the previous analysis [54]. HP can solve the multicollinearity problems effectively by averaging the contributions of an independent variable in models.

In order to fit assumptions about the uniformity of data and the homoscedasticity of errors, all functional traits (and thus functional richness) and environmental variables, and species richness, were log-transformed prior to analysis.

3. Results

3.1. Geographical Patterns of Functional and Species Richness in the Subtropical Evergreen Broadleaved Forests

We observed significant geographical patterns in FRic and SR (Table 2, Figure 1) along the gradients of latitude, longitude, and elevation. FRic was higher along increasing longitude and lower along increasing latitude and elevation, mirroring the geographical gradients in species richness (Figure 1A–C,G–I). Apparently, the patterns of SR along latitude and elevation were not significant, although they had similar trends to the FRic (Figure 1G,I). SESE.FRic was overall negative, with values of SES.FRic in most communities below null expectations, although they did not shift significantly along geographical gradients (Figure 1D,E).

determination are presented. Values in bold indicate p values < 0.05.							
Model Factors	Latitude	Longitude Elevation		AIC	R ² m	R ² c	
FRic	-2.47	0.070	-0.002	1358.14	0.37	0.41	
SES.FRic	-0.15	-0.004	-0.0002	247.10	0.09	0.58	

-0.0001

-15.45

0.10

0.020

Table 2. Summary of the mixed linear models analyzing the effects of geographic gradients on the functional richness (FRic), standardized effect of the functional richness (SES.FRic), and (log-transformed) species richness [log(SR)]. The marginal (R^2m) and conditional (R^2c) coefficients of



-0.05

SR

Figure 1. (**A–I**) Shifts in the functional richness (FRic), standardized effect of the functional richness (SES.FRic), and (log-transformed) species richness [log(SR)] along geographical gradients. (**A–C**) FRic, (**D–F**) SES.FRic, as well as (**G–I**) log(SR) across latitude, elevation, and longitude. The significance was tested by mixed linear models (see Table 2 for details on the models). Red lines represent significant linear regressions.

0.48

3.2. Correlations of Functional and Species Richness with Environmental Variables

Linear mixed effects models showed significant correlations of FRic, SESE.FRic, and SR with environmental factors (Table 3). The total percentage of variance explained by the LMM was higher (R² conditional = 0.50, 0.50, 0.47, respectively), while the variance explained by fixed predictors taken separately was relatively lower (R² marginal = 0.27, 0.50, 0.12, respectively). This indicated an important contribution of the random factor (i.e., the variability sources related to specific characteristics of sites) that was not reflected by fixed predictors. Results showed that FRic was significantly and positively correlated with precipitation of driest quarter (PDQ), soil pH (SpH), and soil total phosphorus (STP). Similarly, SES.FRic showed significant and positive associations with PDQ and SpH, but a negative association with mean diurnal range (MDR). SR was significantly and positively related to PDQ and MDR.

Table 3. Summary of the mixed linear models analyzing the effects of environmental variables on the functional richness (FRic), standardized effect of the functional richness (SES.FRic), and (log-transformed) species richness [log(SR)]. Estimate values are the standardized regression coefficients of predictors. The marginal (R^2m) and conditional (R^2c) coefficients of determination are presented. Values in bold indicate *p* values < 0.05.

	PDQ	PWQ	TDQ	MDR	SpH	STP	AIC	R ² m	R ² c	Moran's I
FRic	3.40	-0.97	0.10	-0.98	0.81	0.86	242.94	0.27	0.5	0.19
SES.Fric	0.17	-0.01	0.06	-0.28	0.15	0.06	1352.73	0.50	0.5	0.04
SR	2.48	-0.33	-1.08	1.78	0.01	-0.19	1537.93	0.12	0.47	0.18

Abbreviations: precipitation of driest quarter (PDQ), precipitation of wettest quarter (PWQ), mean temperature of driest quarter (TDQ), mean diurnal range (MDR), soil pH (SpH), soil total phosphorus (STP), variance explained by the fixed effects (R^2m), variance explained by both fixed and random effects (R^2c), Akaike Information Criterion (AIC), and Moran's I of linear mixed effects models (Moran's I).

The analysis of hierarchical variation partitioning showed that PDQ and MDR explained most of the variance in the Fric, SES.Fric, and SR (Figure 2). Results indicated the most important effects of PDQ and MDR on the variation in functional trait space and species richness in subtropical forest communities.

3.3. The Assembly Mechanisms of Forest Communities along Geographical Gradients

FRic was positively related to species richness and the relationship was always stronger with increasing species richness (Figure 3A; p < 0.01). However, the FRic was significantly different from the null random expectation after controlling species richness within each plot, indicating that the SEBLF community assembly was primarily governed by deterministic processes based on the FRic. Specifically, observed FRic in 83.2% of communities was lower than expected given species richness (i.e., negative SES.FRic, Figure 3B). Consistent with the prevalence of lower than expected FRic in each forest community, when FRic was evaluated as the mean of SES.FRic across all communities, we also found a significant and negative SES.FRic (Figure 3C). The result indicated that the average FRic was also lower than expected by chance across the study sites.



Figure 2. (**A**–**C**) Summary of hierarchical partitioning results for functional richness (FRic), the standardized effect of the functional richness (SES.FRic), and (log-transformed) species richness [log(SR)]. Each bar is the percentage of the variance obtained by a separate HP analysis for (**A**) FRic, (**B**) SES.FRic, and (**C**) log(SR) by using consistent environmental variables. Abbreviations: precipitation of driest quarter (PDQ), precipitation of wettest quarter (PWQ), mean diurnal range (MDR), mean temperature of driest quarter (TDQ), soil pH (SpH), soil total phosphorus (STP).



Figure 3. (A) Correlations between functional diversity (FRic) and (log-transformed) species richness [log(SR)]. (B) The relative prevalence of negative SES.FRic versus positive SES.FRic in forest communities, evaluated based on standardized effect size of the FRic. (C) Mean (mean \pm 95% confidence interval) of standardized effect size of the FRic across all communities (n = 250). ***, *p* < 0.001.

4. Discussion

We showed significant and similar geographical patterns of functional space and species richness from lower to higher latitudes, longitudes, and elevations, with FRic decreasing with increasing latitude and elevation and increasing with increasing longitude (Table 2, Figure 1). This was consistent with previous studies in which the geographical gradients in niche breadth mirrored the species richness [55]. In general, geographical gradients (latitude, longitude, and elevation) can affect functional space only indirectly through species richness; thus, a geographical pattern of functional space would be observed only when there is a geographical pattern of species richness and an effect of species

richness on functional space [55]. However, it was notable that the functional volume (FRic) and species richness did not shift consistently and significantly along these geographical gradients. For instance, functional richness did not shift significantly as the species richness increased with increasing longitude. This means that the geographical variation in niche space might not mirror the geographical gradients in plant species richness completely. The results also indicated that there may be some limiting factors that restricted the expansion of niche space when the number of species increased. Therefore, the direct influences of environmental factors on functional volume should be considered in accounting for the geographical variation in functional trait space, given that the geographical gradients were closely related to environmental factors and strongly reflected resource use by plant species in our study areas [56,57].

Results showed that the geographical patterns of FRic were significantly and positively linked to precipitation of the driest quarter (PDQ), soil pH (SpH), and soil total phosphorus (STP). These results were consistent with previous studies wherein areas where functional volume was greater (i.e., lower elevations and latitudes) were significantly characterized by high amounts of rainfall during the driest quarter and higher soil nutrient content [58–60]. This suggested that precipitation and soil resources were closely related to the expansion of the niche space of subtropical forests. Greater availability of water and soil nutrients might create a wider niche space, allowing plant individuals with a larger range of viable functional strategies to coexist [58]. Significantly, PDQ outperformed other environmental variables that were not excessively co-linear with it, in accounting for the geographical variation in functional volume. The result was in line with a previous study conducted on BCI in Central Panama, which was dominated by evergreen tropical forests [61]. The significant effects of soil pH and phosphorus on the niche space occupied by plant species could be a result of the poor and acidic soil in subtropical regions of China [60,62,63].

Importantly, consistent with our expectation, the observed FRic was generally smaller than expected after controlling species richness, as indicated by the negative standardized effect sizes [24]. The results indicated that niche packing appeared to be prevalent and dominant in most forest assemblages across the entire study site. This implied that as species richness increased, new species were not preferentially added in unfilled portions of the trait space to expand the functional volume [5,19]. Instead, species tended to enter into the interior of the existing functional space, causing tighter packing of species (niche packing), since the increase in functional trait space was constrained within the SEBLF communities [19,20,64]. For instance, species richness increased significantly with increasing mean diurnal range (MDR), while FRic decreased (although not significant). The results suggested that the species with convergent trait combinations would increase with the increases in MDR, therefore increasing the overlap of niche space (niche packing) [12]. Presumably, the patterns of this species coexistence in our study were determined primarily by environmental filtering [65].

Similarly, we also found significant patterns of negative SES.FRic (niche packing) along environmental gradients, as indicated by significant associations between SES.FRic and environmental variables. The positive correlation of SES.FRic with PDQ and SpH provided evidence that the niche volume appeared to increase (i.e., niche packing decreased) [5] with increasing rainfall and soil pH. In contrast, a negative relationship between SES.FRic and mean diurnal range (MDR) was found, which indicated that temperature variability was the key factor in the prevalent pattern of niche packing. The result was in line with many previous studies. For instance, Thakur et al. reported that "temperature filtering" can result in a narrow niche [66]. Specifically, SES.FRic generally changed more quickly with the mean diurnal range (MDR) compared to other environmental variables. This result implied that the relative role of environmental filtering changed faster across MDR gradients in the subtropics, with stronger relevance in the assembly of communities with larger temperature fluctuations [40,67,68]. Less change for niche packing along gradients of precipitation and soil suggested that environmental filters are relatively homogeneous across water and soil conditions in subtropical forests, regardless of their importance [69]. Therefore, our results suggested that even if both niche patterns might accompany the increase in species richness, the niche expansion was insufficient to become the dominant pattern at the upper end of the precipitation and soil pH gradients. Instead, the temperature variability might play a stronger role in niche pattering than the actual increase in resources of water and soil nutrients, leading to more frequent niche packing in SEBLF communities [12]. Together, our study results suggested that climate and soil significantly affected the variation in functional volume along geographical gradients. The increase in functional trait space was constrained within the SEBLF communities. Environmental filtering, especially associated with temperature variability, probably defined the functional volume and caused the tighter packing of species into the niche space (niche packing).

A previous conceptual framework proposed that species first pass through an environmental filter at a regional scale, which constrains their functional trait space and thereby increases the packing of species. Next, the species pass through a biotic filter within a limited functional volume, which maximizes the possible functional diversity by competition or facilitation [24]. However, the importance of biotic interactions was not tested in our study. Many studies revealed that biotic interactions triggering niche partitioning in resource use [70,71] could explain the niche packing within a functional volume. Additionally, although the approach of the null model comparing the expected and observed patterns of functional diversity was widely used in many studies, it has fallen short in delivering generalizable conclusions [72]. For instance, clustering of species in functional traits could also emerge from hierarchical competition [73], in addition to environmental filtering. Therefore, it is necessary to build more mechanistic, dynamic models of community assembly to contrast the different ecological theories and processes [72,74,75] in future research.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/f13081206/s1, Figure S1: Geographical distribution of the 250 plots. Plots were taken from five forest sites in subtropical China. At each site, 50 plots with an area of $20 \text{ m} \times 20 \text{ m}$ were randomly established.

Author Contributions: R.Z. conceived this project. C.H. and Y.X. conducted the field investigation and collected the data. C.H. performed the statistical analyses and wrote the first draft with Y.X. All the authors contributed to improving the quality of the manuscript. All authors have read and agreed to the published version of the manuscript.

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