

Article

The Relationship between Trait-Based Functional Niche Hypervolume and Community Phylogenetic Structures of Typical Forests across Different Climatic Zones in China

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Abstract: Functional traits are pivotal for understanding the functional niche within plant communities. Yet, the relationship between the functional niches of typical forest plant communities across different climatic zones, as defined by functional traits, and their association with community and phylogenetic structures remains elusive. In this study, we examined 215 woody species, incorporating 11 functional traits spanning leaf economy, mechanical support, and reproductive phenology, gathered from forests in four climatic zones from tropical, subtropical, warm-temperate to cold-temperate zones in China and supplemented by the literature. We quantified the functional niche hypervolume (FNH), reflecting the multidimensional functional niche variability. We then probed into the correlation between the FNH and community and phylogenetic structures of forests. Our findings reveal that species richness significantly influences the geographic variance of functional niche space in forest vegetation across different climatic zones. Specifically, a community's species richness correlates positively with the functional niche breadth occupied by the community species. The FNH of woody plants across diverse forest types shows significant associations with both the mean phylogenetic distance (MPD) and the mean nearest phylogenetic taxon distance (MNTD) of the communities. There is a progressive increase in tropical rainforest (TF), subtropical evergreen deciduous broad-leaved mixed forest (SF), and warm-temperate coniferous broad-leaved mixed forest (WF), followed by a decline in the cold-temperate coniferous forest (CF). This pattern suggests potential environmental filtering in CF, which may constrain the spatial extent of plant functional niches. Our research underscores the substantial variability in the FNH across China's typical forest vegetation, highlighting the complex interplay between functional traits, community richness, and phylogenetic distance.

Keywords: woody plant; functional traits; Chinese typical forest; phylogenetic characteristics; geographical differentiation



Citation: Huang, J.; Yu, R.; Ding, Y.; Xu, Y.; Yao, J.; Zang, R. The Relationship between Trait-Based Functional Niche Hypervolume and Community Phylogenetic Structures of Typical Forests across Different Climatic Zones in China. *Forests* **2024**, *15*, 954. <https://doi.org/10.3390/f15060954>

Received: 29 April 2024

Revised: 22 May 2024

Accepted: 29 May 2024

Published: 30 May 2024



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1. Introduction

The examination of functional traits and their diversity under varying environmental conditions forms the foundational pillar of functional biogeography [1]. Functional diversity encapsulates the range and value of species or organisms' functional traits that influence ecosystem functions [2–4]. It serves not only as a marker for niche availability within a community [5] but also mirrors the resilience and disturbance resistance of the forest community [3,6]. Furthermore, functional diversity and its performance are key

to bolstering ecosystem stability [7]. In habitats under stress, plants adapt through conservative functional strategies—characterized by a lower specific leaf area, a reduced leaf nutrient content, and a higher specific stem density [8]. Nonetheless, under certain circumstances, plants enhance their adaptability to local stressors (e.g., drought, low temperatures, and significant disturbances) through expedited resource acquisition strategies, such as a higher specific leaf area and nutrient content, coupled with a lower specific stem density in deciduous species, thereby enriching the community functional diversity [9]. However, excessive disturbances typically diminish the community functional diversity, ultimately eroding the ecosystem stability [6].

The functional niche intricately mirrors the adaptive strategies of plants across varied environments, thereby playing a crucial role in deciphering community mechanisms and forecasting species distributions along environmental gradients [10,11]. Defined by the species' relative positioning on the functional axis within a multidimensional niche space, crafted from species' functional traits [12–14], the functional niche can be quantified through the conceptualization of the functional niche space. A novel methodology, predicated on the variation of intraspecific traits, facilitates the calculation of this functional niche space [15]. The functional space of plant communities is shaped by an amalgamation of biotic and abiotic influences. These filters selectively act on functional traits, dictating species establishment [16]. Thus, alterations in species' functional niche space, rooted in plant functional traits, are intrinsically tied to these dual factors [17]. Despite the proliferation of research on the spatial dynamics of plant form and function and their influencing factors [18], with a predominant focus on abiotic elements such as temperature, precipitation, and soil nutrients—for instance, the notable expansion of functional trait space with increasing mean annual temperature at lower altitudes within and across mountainous terrains [19]—the impact of biotic factors, including community phylogenetic structures on plant functional niche space, have been relatively underexplored.

It is commonly held that communities with higher species richness exhibit higher functional diversity, encompass a larger functional niche space, and are better equipped to access survival resources in dynamic environments [20]. Nonetheless, certain studies have indicated that within plant communities, the magnitude of the plant functional space and species diversity does not always show a uniform pattern of change [21]. For instance, a negative correlation was observed between the extent of the community functional space and species richness in the forest of northeast Spain [22]. This suggests that the correlation between functional diversity and species diversity might hinge on the breadth of the species trait pool and the manner in which species delineate the functional niche space they inhabit. Conversely, in some regions, a positive correlation has been noted [23], underscoring the need for more robust scientific inquiry into how community structure impacts the plant functional niche space. The influence of community structures on the plant functional niche space in different forest vegetation types remains to be fully elucidated.

Evolutionary processes are posited to foster niche complementarity and resource partitioning [24]. Investigating plant community lineages can shed light on how species evolution, or phylogeny, influences community assembly processes. Research has substantiated the significance of phylogeny in the evolution of plant functional traits [25,26]. For instance, Baraloto et al. evaluated the relationship between the utility of plant functional traits and phylogenetic characteristics in forecasting community assembly processes, utilizing the most extensive trait and phylogenetic database to date for any collection of species-rich communities [27]. Donovan et al. investigated the influence of phylogeny on the global leaf economic spectrum [28]. Hu et al. discovered that phylogeny significantly affects the flowering phenology of plants in Gutian Mountain, with adaptations manifesting as thick, involute, hairy leaves in colder climates versus thin leaves with distinct surface structures in warmer climates [29]. Unique trait clusters were associated with the driest and most seasonal climates. For example, picophyll, fleshy, and succulent leaves were prevalent in arid climates, while leptophyll, linear, dissected, and revolute or involute leaves were common in regions with highly seasonal rainfall. In wetter climates, various trait clusters

emerged, such as microphyll leaves that are moderately thick, patent, and entire or notophyll leaves that are waxy and dark green. The limited plasticity of leaf size, shape, color, and other morphological traits in response to climate suggests that apparent changes along climate gradients reflect plant responses to environmental conditions at a community level, driven by species turnover. Leveraging information on leaf morphological traits, which is readily available in floras, could enhance the predictive capabilities of models of species distribution as well as vegetation function [30].

The concept of a plant functional niche delineates a species' positioning along a functional axis within a multidimensional niche space, which is defined by the species' functional traits [12–14]. Since plant functional traits are influenced by community phylogeny, it stands to reason that plant functional niches, when based on these traits, might also bear a strong relation to phylogeny. Delving into plant functional niches within communities, while taking phylogenetic characteristics into account, can enhance our comprehension of niche dynamics in community assembly. A fundamental premise in community phylogeny is the hypothesis of phylogenetic conservatism, which suggests that species with close phylogenetic relationships tend to exhibit similar functional traits [31]. Underpinning this hypothesis, ecologists postulate that the functional niche of species exhibits conservatism; in other words, species sharing closer phylogenetic ties tend to have overlapping functional niches [32]. Intriguingly, environmental filtering can lead to distantly related species converging upon similar functional niches, indicative of the periodicity of functional niches. This phenomenon is attributed to the convergent evolution of morphological structures among species that have adapted to identical environmental conditions over prolonged periods [33].

Previously, we unveiled significant functional niche differentiation among different forest vegetation types across various climatic regions of China, including tropical rainforest (TF), subtropical evergreen deciduous broad-leaved mixed forest (SF), warm-temperate coniferous broad-leaved mixed forest (WF), and cold-temperate coniferous forest (CF), based on plant functional traits [34]. Furthermore, we revealed that the sizes and overlaps of their functional niche hypervolumes (FNHs) exhibit geographical differentiation, highlighting primary climatic factors [35]. However, to date, it remains unclear how community structural characteristics relate to the size of trait-based ecological niche hypervolume. Therefore, in this study, we computed the functional niche space for these four forest types and evaluated the impact of community self-structures on the FNH under different climatic conditions. Our methodology primarily involved calculating species richness, individual abundance, potential maximum plant height (MPH), and diameter at breast height (DBH) area, followed by examining the interplay between these four community structure indicators and the dimensions of the functional niche space. The study aims to address two key questions: (1) Is there a discernible connection between the functional niche hypervolume and the forest vegetation community structure? (2) Does a relationship exist between the functional niche hypervolume and the phylogenetic structure of forest communities?

2. Materials and Methods

2.1. Study Area

The research was conducted in four distinct forest vegetation areas spanning tropical, subtropical, warm-temperate, and cold-temperate climatic zones across China. These included the TF, SF, WF, and CF, located in Bawangling Nature Reserve in Hainan, Mulinzi and Xingdoushan Nature Reserve in Hubei, Xiaolongshan Nature Reserve in Gansu, and Kanas Nature Reserve in Xinjiang, respectively (Figure 1). These locations represent quintessential examples of China's forest vegetation. Bawangling boasts one of China's most pristine tropical rainforests [36], which is particularly noted for its extensive coverage of tropical mountain rainforest within the reserve. The SFs of Mulinzi and Xingdoushan are characterized by pronounced seasonal variations, typically featuring a first forest layer of deciduous broad-leaved trees, underpinned by a second layer of evergreen broad-

leaved trees. Xiaolongshan's WF is uniquely situated at the convergence of four natural vegetation zones, offering a unique combination of geographic location and environmental conditions [36]. This forest vegetation straddles the southern edge of the temperate zone, embodying characteristics of the warm-temperate climate [36]. Kanas's cool temperate coniferous forest stands as a distinctive exemplar of the southern boreal forests of the West Siberian Mountains within China and globally [36,37].



Figure 1. The typical forest vegetation types from the four climatic zones across China. (A), tropical rainforest (TF) in Bawangling Nature Reserve in Hainan; (B), subtropical evergreen deciduous broad-leaved mixed forest (SF) in Mulinzi Nature Reserve in Hubei; (C), warm-temperate coniferous broad-leaved mixed forest (WF) in Xiaolongshan Nature Reserve in Gansu; (D), cold-temperate coniferous forests (CF) in Kanas Nature Reserve in Xinjiang.

2.2. Plots and Species

For the study, forest dynamics plots (FPDs) were established randomly within each of the four forest vegetation types, adhering to the standard methodologies of the Center for Tropical Forest Science (CTFS) [38] between April 2018 and July 2019. A total of 200 plots, each measuring 20 m × 20 m, were set up. Within each plot, every woody plant (trees and shrubs) with a DBH of 1 cm or greater was investigated, tagged, measured, and documented. This included the species identification, DBH, and coordinates within the plot. Identification of all the woody plant species was performed with assistance from local botanists, and the Latin scientific names were standardized according to the Flora of China (<http://efloras.org/> (accessed on 1 December 2021)).

2.3. Functional Traits

We evaluated and gathered data on 11 functional traits, categorized into 4 leaf economic traits, 3 mechanical support traits, and 4 reproductive phenological traits (Table S1). The leaf economic traits and mechanical support traits were directly measured from the field samples, and the reproductive traits were derived from the Flora of China, with supplementary data obtained through a literature review and local flora resources. In this study, functional traits from 215 plants spanning 56 families and 116 genera were compiled.

Trait sampling was conducted during the peak growing seasons from June to September. All the procedures, from field sampling to laboratory analyses, adhered to standardized protocols across the four study locations. To ensure the accuracy of the functional trait data and secure an ample number of healthy samples for measurement and statistical analysis, only woody plant species with an abundance greater than 20 within the sample plots were selected. These species accounted for over 90% of the woody plant individuals in each plot. The measurement of the functional traits followed the established guidelines for plant functional traits [39]. Mature and healthy canopy leaves were collected from trees, with sun-exposed leaves selected from shrubs. For each species, samples from 10 individual plants were taken, including 5 leaves and a 10 cm twig per plant.

Reproductive phenological traits for each species were also compiled, utilizing the Flora of China and supplemented by relevant literature reviews. The first and last flowering months of each species, as listed in the Flora of China, were converted to Julian dates to calculate the FLT, FLD, FRT, and FRD [40]. While the plant reproductive phenological traits sourced from databases were not measured in the study's plots, thus potentially leading to variability in the data collection standards across species or plots, previous research indicates that such data remain a reliable basis for quantifying changes in plant reproductive phenology [40–42].

2.4. Phylogenetic Data Generation

We utilized Phylomatic 3.0 software to construct the phylogenetic tree based on the APG classification system. Given that the species list in this study was derived according to the Flora of China, which uses the Engler system for classification, it was necessary to update this list to the APGIII version of the family, genus, and species list for the 215 species from four sample plots across different climatic regions into the “taxa =” box in the Phylomatic 3.0 software. We selected “zanne 2014” for the “storedtree =”, set “clean =” to “true”, and clicked “send” to generate the phylogenetic tree with branches (<http://phylodiversity.net/phylomatic/> (accessed on 31 December 2021)).

2.5. Index

We analyzed the community structure characteristics of different forest vegetation types and organized the survey data from the four study areas. We counted the number of families, genera, species, and individuals of woody plants in each of the 50 quadrats per vegetation type. Here, the number of species indicated the species richness and individual abundance was measured by the total number of plants. We calculated the plant density per quadrat, which was the number of plants per unit area. The diameter class structure of the community species was analyzed using 5 cm as the classification unit. First, the overall diameter class structure of forest vegetation and woody plants in different climate areas was calculated, followed by separate statistics for each vegetation type. We then examined the relationship between the community structure characteristics and the functional niche space of the forest vegetation in different climatic regions. The four fundamental community structure characteristics calculated in each 20 × 20 m quadrat included species richness, individual abundance, mean MPH, and DBH area, using the community weighted mean for the latter two metrics. The three community phylogenetic characteristics calculated were phylogenetic diversity (PD), mean phylogenetic distance (MPD), and mean nearest phylogenetic taxon distance (MNTD) for all species pairs within each quadrat.

2.6. Data Analysis

We applied the “PCA of PCA” method to calculate the functional niche values (i.e., species load values) of the species along the PC1, PC2, and PC3 axes derived from the functional niche spaces of the forest vegetation (FNSF) in various climatic zones. Then, the n-dimensional hypervolume method [17] was used to calculate the functional niche space for each 20 m × 20 m quadrat. Pearson correlation tests were employed to evaluate the relationship between the community structure characteristics and the FNSF. Regression

analysis was then performed to assess how the community structure characteristics impact the geographical differentiation of the functional niche space across different climatic zones. Using Phylocom, the “Phylocom PD > pd.output.txt” command was used to obtain the PD results, and “Phylocom comlist > comlist.output.txt” was used to obtain the MPD and MNTD results. The Kruskal Wallis nonparametric test was utilized to determine if significant differences existed in the diversity of the forest vegetation communities across different climatic regions. Linear regression was conducted to explore the relationship between community lineage diversity and latitude and to assess potential geographic patterns. Data analysis and plotting were performed in R version 3.6.0 [43]. The community weighted Mean (CWM) was calculated by the “FD” package, while Pearson correlation analysis and regression analysis employed the “stats” package, and plotting utilized the “ggplot2” package.

3. Results

3.1. Relationship between Functional Niche Space and Community Structure Characteristics

The characteristics of the community structure significantly influence the geographical differentiation of the functional niche space among different forest vegetation types. This is demonstrable between various aspects of the community structure (Table 1). Species richness showed a positive correlation with individual abundance and a negative correlation with both the MPH and DBH area ($p < 0.001$). Likewise, the individual abundance within the community was significantly negatively correlated with the MPH and DBH area ($p < 0.001$). There existed a robust relationship between the community structure characteristics and the functional niche space of the forest vegetation. Specifically, the functional niche space was significantly related to the species richness ($p < 0.001$), with a correlation coefficient of 0.610. However, it showed no significant relationship with the individual abundance, MPH, or DBH area. The functional niche space of the forest vegetation exhibited a pattern of geographical differentiation correlated with species richness (Figure 2), suggesting that a higher species richness within forest vegetation is associated with larger functional niche spaces.

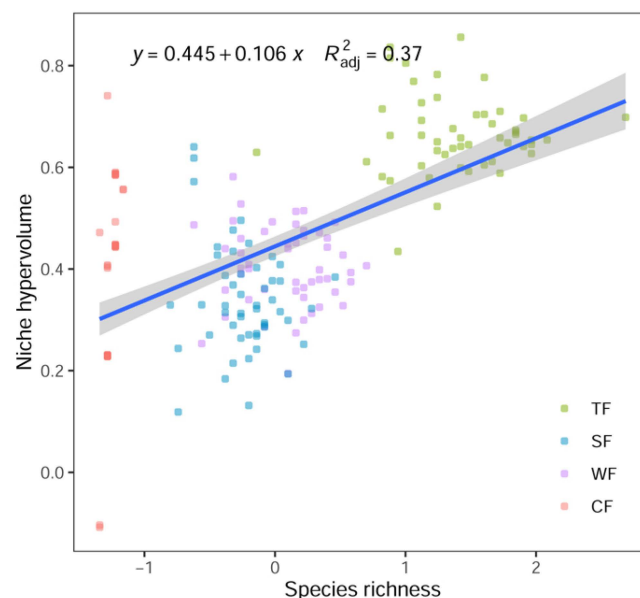


Figure 2. Relationship between functional niche space for woody plants in different forest vegetation types and species richness. Note: p value is less than 0.01. TF—tropical rainforest; SF—subtropical evergreen deciduous broad-leaved mixed forest; WF—warm-temperate coniferous broad-leaved mixed forest; CF—cold-temperate coniferous forest.

Table 1. Correlations of functional niche space for woody plants in different forest types and community structure characteristics.

	Niche Hypervolume	Abundance	Richness	MPH	Area_DBH
Abundance	0.053	1			
Richness	0.610 ***	0.581 ***	1		
MPH	−0.118	−0.800 ***	−0.578 ***	1	
Area_DBH	0.029	−0.766 ***	−0.410 ***	0.971 ***	1

Note: *** describes a significant correlation at the 0.001 level.

3.2. Relationship between FNH of Woody Plants in Different Forest Vegetation Types and Community Phylogenetic Characteristics

The community phylogenetic characteristics significantly influence the geographic differentiation of the FNH of woody plants in different forest vegetation types (Figure 3). The FNH in these forests showed a strong correlation with the MNTD of community species (Figure 3A, $p < 0.001$) and a significant correlation with the MPD of community species (Figure 3B, $p < 0.05$). Notably, the results showed that the MNTD had a more pronounced impact on the FNH across these vegetation types. The hypervolume exhibited a unimodal distribution with the changes in the MNTD, with a declining trend starting from the CF. In the TF, SF, and WF, the FNH significantly expanded as the MNTD increased. Conversely, in the CF, it decreased with an increase in the MNTD.

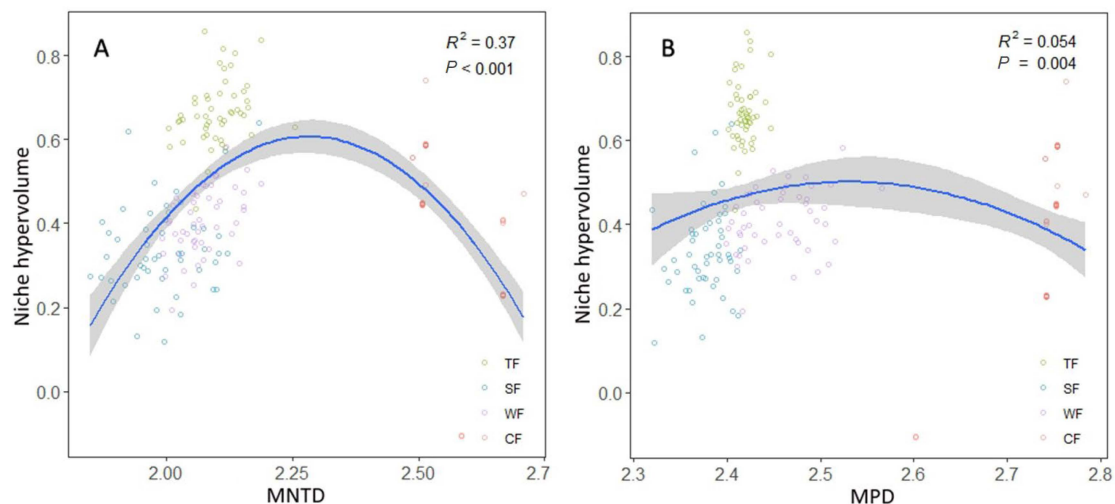


Figure 3. Relationships between hypervolumes of functional niches for woody plants in different forest vegetation types and community phylogenetic characteristics. Note: (A), Relationship between hypervolumes of functional niches and MNTD; (B), Relationship of hypervolumes of functional niches and MPD. MNTD—mean nearest phylogenetic taxon distance; MPD—mean phylogenetic distance; TF—tropical rainforest; SF—subtropical evergreen deciduous broad-leaved mixed forest; WF—temperate coniferous broad-leaved mixed forest; CF—cold-temperate coniferous forest.

4. Discussion

4.1. Community Structure Characteristics and Their Differences in Different Forest Vegetation Types

Understanding the current state of community species diversity, including community composition and structural characteristics, is central to biodiversity research [44]. We analyzed the basic community structure characteristics of forest vegetation across different climatic zones in China. These forests are distributed from south to north across tropical, subtropical, warm-temperate, and cold-temperate zones, each exhibiting distinct geographical differences in community structure. The TF, in particular, displays extremely high species richness with a rich and diverse plant composition, significantly surpassing other

forest types. It has long been recognized that species richness increases towards the tropics, with numerous hypotheses proposed to explain this latitudinal diversity gradient [45]. High diversity in the tropics is often attributed to minimal environmental stress, optimal year-round temperatures, adequate rainfall, and abundant, well-balanced nutrients. Changes in the ecological niche space are likely intertwined with species dispersal and evolution.

With increasing latitude, the species diversity of vegetation communities in different climatic regions shows a declining trend. In the northernmost CF, the diversity is the lowest, featuring only 6 species from 6 genera and 4 families, reflecting the response of different vegetation communities to geographical environmental changes. Interestingly, despite having the most species, the TF does not have the highest plant density. Both the SF and the WF exhibit higher plant densities, possibly due to a higher proportion of small trees filling gaps in the forest. Specifically, the proportion of small-diameter plants in subtropical forests reaches 88.09%. The plant density in cold-temperate coniferous forests is very low at 0.146 plants/m², indicating sparse vegetation with large gaps.

The diameter class structure of woody plants across different climatic zones exhibits a universal inverted “J” shape, with the highest proportion of small-diameter plants ($1 \leq \text{DBH} < 10$ cm). As the plant diameter class expands, the number of plants significantly decreases, indicating that few individual tree species enter the main forest layer in mature virgin forests. Although they are few, these large DBH trees form the backbone of the community and are the main carriers of community biomass, warranting focused attention [46]. Compared to the TF, SF, and WF, the number of individuals in the CF decreases more slowly with increasing diameter class, suggesting a relatively small within-community diameter class difference, with medium and large diameter trees having a quantitative advantage.

4.2. Effects of Community Structure Characteristics on the Geographical Differentiation of the Functional Niche Space

Our study explores how the characteristics of the community structure influence the geographical differentiation of the functional niche space of woody plants in different forest vegetation areas from a biological perspective. The findings offer crucial insights into the mechanism driving biodiversity models across large-scale climatic gradients. We discovered that among the four indicators of community structure—species richness, individual abundance, MPH, and DBH area—though interrelated, only species richness had a significant effect on the functional niche space of woody plants in various forest vegetation types. There is a positive relationship between species richness and the functional niche space occupied by forest vegetation; as the species richness increases, the functional niche space also expands. This observation aligns with prior research. The impact of environmental conditions on the changes in fern functional traits is indirect, with species richness being the primary driver that fills the functional niche space of plants [47].

Why does higher species richness in a community correlate with a larger functional niche space? One plausible explanation is that as species richness increases, the community may evolve in two ways: by densely packing species within the existing functional niche space or by expanding the resource space to accommodate more species. In the former scenario, the functional distance between the species decreases, while in the latter, the spatial volume of the functional niche occupied by all the species increases. According to the niche differentiation theory, species sharing identical niches cannot coexist without niche differentiation, which is essential for community stability. This differentiation results in coexisting species developing distinct functional traits to occupy a broader functional niche space. Therefore, communities with a greater number of species exhibit a wider range of plant functional traits and, consequently, a larger functional niche space [48]. Generally, in communities with high species richness, the functional diversity is also greater, suggesting that the geographical differentiation of the functional niche space of woody plants in forest vegetation in different climatic zones likely stems from species differences. Additionally, the limited functional space occupied by community species might indicate the underutilization

of some resources within the community. Hence, in forest vegetation with favorable natural conditions, communities with lower species richness may harbor potential niches worth exploring [49]. Nonetheless, some studies have identified no correlation or a negative correlation between the spatial size of the plant functional niche and species richness, as the relationship is subject to external disruptions [50]. When a community undergoes disturbances, the relationship between the changes in the community functional space and the species diversity fluctuates [50]. For instance, in riparian forest communities affected by high-intensity disturbances, although the species richness increases, the plant functional space contracts because the disturbance leads to the predominance of species with similar functional traits [51].

4.3. Diversity and Distinction among Different Forest Vegetation Communities

According to the niche theory, each species within a community occupies a unique niche, ensuring that no two long-standing species share the same niche. Various species achieve stable coexistence by mitigating resource competition through niche differentiation [52–54]. For instance, plants exhibit high differentiation among different tree species to efficiently allocate light resources [55]. The lineage diversity of a community reflects the differentiation in the functional niches of species based on their phylogenetic relationships. Communities with a higher lineage diversity typically exhibit more complex species compositions, greater differentiation of functional niches, and more stable structures [56–58]. Forest vegetation community diversity varies significantly across different climatic regions. TFs display the highest diversity, while CFs show the lowest diversity, suggesting simpler species compositions in colder climates. This pattern aligns with previous research findings. Tropical regions, in comparison to other climatic zones, generally boast a higher community lineage diversity [59,60].

In SFs, species diversity is lower than in temperate coniferous broad-leaved mixed forests. This may explain why the species diversity of woody plants in subtropical forests is marginally higher than in temperate forests, yet the functional niche volume they occupy is slightly smaller. The functional niche volume occupied by community species appears to correlate more strongly with community lineage diversity than with species diversity alone. The diversity of forest vegetation communities varies regularly along geographical gradients. Generally, as the latitude increases, the diversity of the forest vegetation communities tends to decrease. Some studies suggest that the impact of large-scale geographical gradients on community lineage diversity is primarily driven by environmental filtering [61]. Therefore, studying the variation in lineage diversity along environmental gradients is crucial for understanding the environmental processes involved in community assembly.

4.4. Effects of Community Phylogenetic Characteristics on the Geographical Differentiation of the Functional Niche of Woody Plants

The functional niche volume of woody plants across various climatic regions' forest vegetation is significantly correlated with both the average nearest phylogenetic distance and the average phylogenetic distance of community species. This correlation indicates that the genetic relationship distance among community species profoundly impacts their functional niche volume. Generally, the greater the genetic distance among woody plants within a community, the larger the functional niche volume they occupy. Among different forest types, the community phylogenetic distance is shortest in SFs, followed by TFs, WFs, and CFs. This sequence suggests that species in subtropical communities are genetically closest, whereas those in cold-temperate coniferous forests are farthest apart, which includes a mix of gymnosperms and angiosperms with diverse origins and distant genetic relationships. Despite the high species count in TFs, functional redundancy is always higher [62].

It is important to note that the influence of genetic relationship distance on the geographic differentiation of the functional niche volume in different forest vegetation types is not absolute. The relationship between the community phylogenetic distance and func-

tional niche volume is not linear, and the regression fitting line trend starting from the cold-temperate coniferous forests indicates that the forest with the farthest community phylogenetic distance does not possess the largest functional niche space for woody plants. The restrictive environmental conditions of the cold-temperate zone, characterized by long winters and extremely low temperatures, likely limit the functional niche of coniferous forest plants through environmental filtration, hindering the expansion of their functional niche space [63,64].

Currently, on the spatiotemporal scale of biogeography, climate and geomorphological changes are the determining factors for the patterns of taxonomic diversity. At the community level and on shorter time scales, current environmental conditions and interspecific relationships play a more significant role. The exact impact of environmental filtration on the functional niche space of community species remains undetermined. Two hypotheses are proposed: one suggests that the environment initially influences the lineage, selecting species with similar phylogenetic relationships (and similar evolutionary histories) because these species share similar functional traits, thereby impacting the functional niche space. Another hypothesis posits that environmental conditions and the lineage relationships of species within a community affect the functional niche space jointly but independently. In fact, we usually find some areas with significant taxonomic variability because of the combinations of these two kinds of factors. These issues offer rich avenues for further exploration and discussion in future studies.

5. Conclusions

Our research innovatively reveals the relationship between the FNH and community and phylogenetic structures of forests in four climate regions. (1) Species richness significantly influences the geographic differentiation of the functional niche space of woody plants in different climatic regions. Communities with a higher species richness occupy larger functional niche volumes. (2) The FNH of woody plants is significantly correlated with both the MNTD and MPD of community species. Additionally, the FNH exhibits a unimodal pattern with respect to the phylogenetic distance of community species. It increases in the TF, SF, and WF and decreases in the CF. This trend suggests the presence of environmental filtration in cold-temperate coniferous forests, which may be limiting the spatial extent of plant functional niches.

Supplementary Materials: The following supporting information can be downloaded at <https://www.mdpi.com/article/10.3390/f15060954/s1>, Table S1: Functional traits and their assigned strategies within plant functional niche dimensions; Table S2: The matrices of phylogenetic characteristics and functional niche hypervolumes based on functional traits for all plots.

Author Contributions: R.Z. and J.H. conceptualized this research project. R.Y., J.H., Y.D., Y.X. and J.Y. conducted the fieldwork. R.Y., Y.D., Y.X. and J.Y. analyzed the data. J.H. and R.Y. drafted the manuscript. All the authors reviewed and approved the final submission. All authors have read and agreed to the published version of the manuscript.

Funding: This work was funded by the National Key R&D Program of China (grant 2023YFE0112800), the National Natural Science Foundation of China (grants 41771059 and 32071648) and the Fundamental Research Funds of CAF (grant CAFYBB2019ZA002).

Data Availability Statement: The datasets generated for this study are available upon request from the corresponding author.

Acknowledgments: We deeply appreciate the support and efforts of those who contributed to the extensive field investigations and sampling within the four forest biomes. Special thanks go to Wendong Wang, Alim, Zhongjun Guo, and Zhiqiang Bai from the Xinjiang Forestry Academy, Wenzhen Liu, Anmin Li, and Shiyun Yuan from the Forestry Science Research Institute of Xiaolongshan Forestry Experimental Bureau, and Xunru Ai from Hubei University for Nationalities. We acknowledge any research not conducted by our team and declare that all funding sources and any direct financial benefits potentially resulting from publication have been disclosed.

Conflicts of Interest: The authors have no conflicts of interest to disclose.

References

- Violle, C.; Reich, P.B.; Pacala, S.W.; Enquist, B.J.; Kattge, J. The emergence and promise of functional biogeography. *Proc. Natl. Acad. Sci. USA* **2014**, *111*, 13690. [[CrossRef](#)] [[PubMed](#)]
- Petchey, O.L.; Gorman, E.J.O.; Dan, F.B.F. *A Functional Guide to Functional Diversity Measures*; Oxford University Press: Oxford, UK, 2009.
- Webb, C.T.; Hoeting, J.A.; Ames, G.M.; Pyne, M.I.; Leroy Poff, N. A structured and dynamic framework to advance traits-based theory and prediction in ecology. *Ecol. Lett.* **2010**, *13*, 267–283. [[CrossRef](#)]
- Violle, C.; Enquist, B.J.; McGill, B.J.; Jiang, L.; Albert, C.H.; Hulshof, C.; Jung, V.; Messier, J. The return of the variance: Intraspecific variability in community ecology. *Trends Ecol. Evol.* **2012**, *27*, 244–252. [[CrossRef](#)] [[PubMed](#)]
- Lamanna, C.; Blonder, B.; Violle, C.; Kraft, N.J.B.; Sandel, B.; Šimová, I.; Donoghue, J.C.; Svenning, J.-C.; McGill, B.J.; Boyle, B.; et al. Functional trait space and the latitudinal diversity gradient. *Proc. Natl. Acad. Sci. USA* **2014**, *111*, 13745–13750. [[CrossRef](#)] [[PubMed](#)]
- Mouillot, D.; Graham, N.A.J.; Villéger, S.; Mason, N.W.H.; Bellwood, D.R. A functional approach reveals community responses to disturbances. *Trends Ecol. Evol.* **2013**, *28*, 167–177. [[CrossRef](#)] [[PubMed](#)]
- Hallett, L.M.; Stein, C.; Suding, K.N. Functional diversity increases ecological stability in a grazed grassland. *Oecologia* **2017**, *183*, 831–840. [[CrossRef](#)]
- Spasojevic, M.J.; Grace, J.B.; Harrison, S.; Damschen, E.I. Functional diversity supports the physiological tolerance hypothesis for plant species richness along climatic gradients. *J. Ecol.* **2014**, *102*, 447–455. [[CrossRef](#)]
- Gherardi, L.A.; Sala, O.E. Enhanced interannual precipitation variability increases plant functional diversity that in turn ameliorates negative impact on productivity. *Ecol. Lett.* **2015**, *18*, 1293–1300. [[CrossRef](#)] [[PubMed](#)]
- Maynard, D.S.; Leonard, K.E.; Drake, J.M.; Hall, D.W.; Crowther, T.W.; Bradford, M.A. Modelling the multidimensional niche by linking functional traits to competitive performance. *Proc. R. Soc. Biol. Sci.* **2015**, *282*, 20150516. [[CrossRef](#)]
- Jiang, F.; Xun, Y.; Cai, H.; Jin, G. Functional traits can improve our understanding of niche- and dispersal-based processes. *Oecologia* **2018**, *186*, 783. [[CrossRef](#)]
- Blonder, B. Hypervolume concepts in niche- and trait-based ecology. *Ecography* **2018**, *41*, 1441–1455. [[CrossRef](#)]
- Li, Y.; Shipley, B.; Price, J.N.; Dantas, V.d.L.; Tamme, R.; Westoby, M.; Siefert, A.; Schamp, B.S.; Spasojevic, M.J.; Jung, V.; et al. Habitat filtering determines the functional niche occupancy of plant communities worldwide. *J. Ecol.* **2018**, *106*, 1001–1009. [[CrossRef](#)]
- Raffard, A.; Santoul, F.; Blanchet, S.; Cucherousset, J. Linking intraspecific variability in trophic and functional niches along an environmental gradient. *Freshw. Biol.* **2020**, *65*, 1401–1411. [[CrossRef](#)]
- Violle, C.; Jiang, L. Towards a trait-based quantification of species niche. *J. Plant Ecol.* **2009**, *2*, 87–93. [[CrossRef](#)]
- Lebrija-Trejos, E.; Pérez-García, E.A.; Meave, J.A.; Bongers, F.; Poorter, L. Functional traits and environmental filtering drive community assembly in a species-rich tropical system. *Ecology* **2010**, *91*, 386–398. [[CrossRef](#)] [[PubMed](#)]
- Blonder, B.; Lamanna, C.; Violle, C.; Enquist, B.J. The n-dimensional hypervolume. *Glob. Ecol. Biogeogr.* **2014**, *23*, 595–609. [[CrossRef](#)]
- Diaz, S.; Kattge, J.; Cornelissen, J.H.C.; Wright, I.J.; Lavorel, S.; Dray, S.; Reu, B.; Kleyer, M.; Wirth, C.; Colin Prentice, I.; et al. The global spectrum of plant form and function. *Nature* **2016**, *529*, 167–171. [[CrossRef](#)] [[PubMed](#)]
- Zhang, L.; Liu, X.; Sun, Z.; Bu, W.; Bongers, F.J.; Song, X.; Yang, J.; Sun, Z.; Li, Y.; Li, S.; et al. Functional trait space and redundancy of plant communities decrease toward cold temperature at high altitudes in Southwest China. *Sci. China Life Sci.* **2023**, *66*, 1674–7305. [[CrossRef](#)]
- Lei, L.; Kong, D.; Li, X.; Guo, Z.; Li, G. Plant functional traits, functional diversity, and ecosystem functioning: Current knowledge and perspectives. *Biodivers. Sci.* **2016**, *24*, 922–931. [[CrossRef](#)]
- Diaz, S.; Cabido, M.; Zak, M.; Martínez Carretero, E.; Aranibar, J. Plant functional traits, ecosystem structure and land-use history along a climatic gradient in central-western Argentina. *J. Veg. Sci.* **1999**, *10*, 651–660. [[CrossRef](#)]
- De Bello, F.; Lepš, J.; Sebastià, M.T. Variations in species and functional plant diversity along climatic and grazing gradients. *Ecography* **2006**, *29*, 801–810. [[CrossRef](#)]
- Diaz, S.; Cabido, M. Vive la différence: Plant functional diversity matters to ecosystem processes. *Trends Ecol. Evol.* **2001**, *16*, 646–655. [[CrossRef](#)]
- Atkinson, C.L.; Van Ee, B.C.; Pfeiffer, J.M. Evolutionary history drives aspects of stoichiometric niche variation and functional effects within a guild. *Ecology* **2020**, *101*, e03100. [[CrossRef](#)]
- Du, Y.; Mao, L.; Queenborough, S.A.; Freckleton, R.P.; Chen, B.; Ma, K. Phylogenetic constraints and trait correlates of flowering phenology in the angiosperm flora of China. *Glob. Ecol. Biogeogr.* **2015**, *24*, 928–938. [[CrossRef](#)]
- Wills, J.; Herbohn, J.; Wells, J.; Marangui Moreno, M.O.; Ferraren, A.; Firn, J. Seedling diversity in actively and passively restored tropical forest understories. *Ecol. Appl.* **2021**, *31*, e02286. [[CrossRef](#)] [[PubMed](#)]
- Baraloto, C.; Hardy, O.J.; Paine, C.E.T.; Dexter, K.G.; Cruaud, C.; Dunning, L.T.; Gonzalez, M.-A.; Molino, J.-F.; Sabatier, D.; Savolainen, V.; et al. Using functional traits and phylogenetic trees to examine the assembly of tropical tree communities. *J. Ecol.* **2012**, *100*, 690–701. [[CrossRef](#)]

28. Donovan, L.A.; Maherali, H.; Caruso, C.M.; Huber, H.; de Kroon, H. The evolution of the worldwide leaf economics spectrum. *Trends Ecol. Evol.* **2011**, *26*, 88–95. [[CrossRef](#)]
29. Hu, X.; Chang-Yang, C.H.; Mi, X.; Du, Y.; Chang, Z. Influence of climate, phylogeny, and functional traits on flowering phenology in a subtropical evergreen broad-leaved forest, East China. *Biodivers. Sci.* **2015**, *23*, 601–609. [[CrossRef](#)]
30. Wang, H.; Wang, R.; Harrison, S.P.; Prentice, I.C. Leaf morphological traits as adaptations to multiple climate gradients. *J. Ecol.* **2022**, *110*, 1344–1355. [[CrossRef](#)]
31. Webb, C.O.; Ackerly, D.D.; McPeck, M.A.; Donoghue, M.J. Phylogenies and community ecology. *Annu. Rev. Ecol. Syst.* **2002**, *33*, 475–505. [[CrossRef](#)]
32. Losos, J.B. Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. *Ecol. Lett.* **2008**, *11*, 995–1003. [[CrossRef](#)] [[PubMed](#)]
33. Winemiller, K.O.; Fitzgerald, D.B.; Bower, L.M.; Pianka, E.R. Functional traits, convergent evolution, and periodic tables of niches. *Ecol. Lett.* **2015**, *18*, 737–751. [[CrossRef](#)] [[PubMed](#)]
34. Yu, R.; Huang, J.; Xu, Y.; Ding, Y.; Zang, R. Plant functional niches in forests across four climatic zones: Exploring the periodic table of niches based on plant functional traits. *Front. Plant Sci.* **2020**, *11*, 00841. [[CrossRef](#)] [[PubMed](#)]
35. Huang, J.; Yu, R.; Zang, R. Differences in functional niche hypervolume among four types of forest vegetation and their environmental determinants across various climatic regions in China. *Front. Plant Sci.* **2023**, *14*, 1243209. [[CrossRef](#)] [[PubMed](#)]
36. *Investigation and Planning Institute of the Ministry of Forestry: Mountain forests in China*; China Forestry Publishing House: Beijing, China, 1981.
37. *Xinjiang Forest Editorial Committee: Xinjiang Forest Xinjiang People's Publishing House*; China Forestry Publishing House: Urumqi/Beijing, China, 1989.
38. Condit, R. Research in Large, Long-Term Tropical Forest Plots. *Trends Ecol. Evol.* **1995**, *10*, 18–22. [[CrossRef](#)] [[PubMed](#)]
39. Pérez-Harguindeguy, N.; Diaz, S.; Garnier, E.; Lavorel, S.; Poorter, H.; Jaureguiberry, P.; Bret-Harte, M.S.; Cornwell, W.K.; Craine, J.M.; Gurvich, D.E.; et al. New handbook for standardised measurement of plant functional traits worldwide. *Aust. J. Bot.* **2013**, *61*, 167–234. [[CrossRef](#)]
40. Laughlin, D.C.; Leppert, J.J.; Moore, M.M.; Sieg, C.H. A multi-trait test of the leaf-height-seed plant strategy scheme with 133 species from a pine forest flora. *Funct. Ecol.* **2010**, *24*, 493–501. [[CrossRef](#)]
41. Mo, F.; Zhang, J.; Wang, J.; Cheng, Z.-G.; Sun, G.-J.; Ren, H.-X.; Zhao, X.-Z.; Cheruiyot, W.K.; Kavagi, L.; Wang, J.-Y.; et al. Phenological evidence from China to address rapid shifts in global flowering times with recent climate change. *Agric. For. Meteorol.* **2017**, *246*, 22–30. [[CrossRef](#)]
42. Rafferty, N.E.; Nability, P.D. A global test for phylogenetic signal in shifts in flowering time under climate change. *J. Ecol.* **2017**, *105*, 627–633. [[CrossRef](#)]
43. R Core Team, T.R. *A Language and Environment for Statistical Computing*; R Foundation for Statistical Computing: Vienna, Austria, 2019.
44. Garnier, E.; Navas, M.L.; Grigulis, K. *Plant Functional Diversity: Organism Traits, Community Structure, and Ecosystem Properties*; Oxford University Press: Oxford, UK, 2016.
45. Brown, J.H. Why are there so many species in the tropics? *J. Biogeogr.* **2014**, *41*, 8–22. [[CrossRef](#)]
46. Zang, R.; Yang, Y.; Jiang, Y. Community structure and tree species diversity characteristics in a tropical montane rain forest in Bawangling Nature Reserve, Hainan Island. *Acta Phytotocol. Sin.* **2001**, *25*, 270–275.
47. Aros-Mualin, D.; Noben, S.; Karger, D.N.; Carvajal-Hernández, C.I.; Kessler, M. Functional diversity in Ferns is driven by species richness rather than by environmental constraints. *Front. Plant Sci.* **2021**, *11*, 615723. [[CrossRef](#)] [[PubMed](#)]
48. Kraft, N.J.B.; Godoy, Levine, J.M. Plant functional traits and the multidimensional nature of species coexistence. *Proc. Natl. Acad. Sci. USA* **2015**, *112*, 797–802. [[CrossRef](#)]
49. Gauzere, P.; Morin, X.; Violle, C.; Caspeta, I.; Ray, C.; Blonder, B. Vacant yet invisable niches in forest community assembly. *Funct. Ecol.* **2020**, *34*, 1945–1955. [[CrossRef](#)]
50. Mayfield, M.M.; Boni, M.F.; Daily, G.C.; Ackerly, D. Species and functional diversity of native and human-dominated plant communities. *Ecology* **2005**, *86*, 2365–2372. [[CrossRef](#)]
51. Biswas, S.R.; Mallik, A.U. Disturbance effects on species diversity and functional diversity in riparian and upland plant communities. *Ecology* **2010**, *91*, 28–35. [[CrossRef](#)]
52. Huang, L.; Xue, W.; Herben, T. Temporal niche differentiation among species changes with habitat productivity and light conditions. *J. Veg. Sci.* **2019**, *30*, 438–447. [[CrossRef](#)]
53. Sapijanskas, J.; Paquette, A.; Potvin, C.; Kunert, N.; Loreau, M. Tropical tree diversity enhances light capture through crown plasticity and spatial and temporal niche differences. *Ecology* **2014**, *95*, 2479–2492. [[CrossRef](#)]
54. Silvertown, J. Plant coexistence and the niche. *Trends Ecol. Evol.* **2004**, *19*, 605–611. [[CrossRef](#)]
55. Tao, S.L.; Guo, Q.H.; Li, C.; Wang, Z.H.; Fang, J.Y. Global patterns and determinants of forest canopy height. *Ecology* **2016**, *97*, 3265. [[CrossRef](#)]
56. Cadotte, M.W.; Dinnage, R.; Tilman, D. Phylogenetic diversity promotes ecosystem stability. *Ecology* **2012**, *93*, S223–S233. [[CrossRef](#)]
57. Flynn, D.F.B.; Mirotchnick, N.; Jain, M.; Palmer, M.I.; Naeem, S. Functional and phylogenetic diversity as predictors of biodiversity-ecosystem-function relationships. *Ecology* **2011**, *92*, 1573–1581. [[CrossRef](#)] [[PubMed](#)]

58. Huang, M.; Liu, X.; Cadotte, M.W.; Zhou, S. Functional and phylogenetic diversity explain different components of diversity effects on biomass production. *Oikos* **2020**, *129*, 1185–1195. [[CrossRef](#)]
59. Nagalingum, N.S.; Knerr, N.; Laffan, S.W.; González-Orozco, C.E.; Thornhill, A.H.; Miller, J.T.; Mishler, B.D. Continental scale patterns and predictors of fern richness and phylogenetic diversity. *Front. Genet.* **2015**, *6*, 132. [[CrossRef](#)]
60. Qian, H.; Jin, Y.; Ricklefs, R.E. Phylogenetic diversity anomaly in angiosperms between eastern Asia and eastern North America. *Proc. Natl. Acad. Sci. USA* **2017**, *114*, 11452–11457. [[CrossRef](#)] [[PubMed](#)]
61. Weigelt, P.; Daniel Kissling, W.; Kisel, Y.; Fritz, S.A.; Karger, D.N.; Kessler, M.; Lehtonen, S.; Svenning, J.-C.; Kreft, H. Global patterns and drivers of phylogenetic structure in island floras. *Sci. Rep.* **2015**, *5*, 12213. [[CrossRef](#)] [[PubMed](#)]
62. Zhang, S.; Zang, R. Tropical forests are vulnerable in terms of functional redundancy. *Biol. Conserv.* **2021**, *262*, 109326. [[CrossRef](#)]
63. Myers, J.A.; Chase, J.M.; Jiménez, I.; Jørgensen, P.M.; Araujo-Murakami, A.; Paniagua-Zambrana, N.; Seidel, R. Beta-diversity in temperate and tropical forests reflects dissimilar mechanisms of community assembly. *Ecol. Lett.* **2013**, *16*, 151–157. [[CrossRef](#)]
64. Yao, L.; Ding, Y.; Xu, H.; Deng, F.; Yao, L.; Ai, X.; Zang, R. Patterns of diversity change for forest vegetation across different climatic regions—A compound habitat gradient analysis approach. *Glob. Ecol. Conserv.* **2020**, *23*, e01106. [[CrossRef](#)]

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