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Distribution Pattern of Woody Plants in a Mountain Forest Ecosystem Influenced by Topography and Monsoons

Xiayan Zhou [1,†], Zhao Wang [1,†], Wenxin Liu [1], Qianjin Fu [2], Yizhen Shao [1], Fengqin Liu [1], Yongzhong Ye [1], Yun Chen [3,*] and Zhiliang Yuan [1,*]

1 College of Life Sciences, Henan Agricultural University, No. 63 Agricultural Road, Zhengzhou 450002, China; 15077797441@163.com (X.Z.); wz15037627157@163.com (Z.W.); liuwenxin0805@163.com (W.L.); shaoyizhen@126.com (Y.S.); zkfengqin@outlook.com (F.L.); yeyzh@163.com (Y.Y.)
2 Wumasi Forestry Centre, Luoyang 471000, China; zhp20208090@163.com
3 Scientific Observation and Research Station of Forest Ecosystem in the North-South Transition Zone of Funiu Mountain, Zhengzhou 450052, China
* Correspondence: cyecology@163.com (Y.C.); yzlsci@163.com (Z.Y.)
† These authors contributed equally to this work.

Abstract: Many areas are affected by the monsoon because of different sea and land positions. At the same time, the blocking effect of a mountain range forms different habitats on both sides of the mountain range. However, the distribution mechanism of woody plants is unclear in mountain forest ecosystems influenced by topography and monsoons. In this study, 10 plots, each with an area of 1 hm^2 (100 m $\times$ 100 m), were randomly established on the south and north aspects of a mountain forest. We examined community structure differences and distribution preferences of woody plants on both sides of the mountain. Our findings were as follows: (1) The characteristics of woody plant assemblages differed among various aspects. (2) Network analysis showed that specialization index was 0.186 and modularity index was 0.235, and the torus translation test showed that a total of 45 species were detected to be associated with at least one of the habitats (45/106, 42.45%). (3) The community stability of the south aspect was higher than that of the north aspect. Our findings suggest that the distribution of woody plants among different aspects was specialized and not random in alpine forest ecosystems. This study contributes to a clear understanding of the distribution mechanism of woody plants in mountain forest ecosystems influenced by topography and monsoons.

Keywords: different aspects; habitat specialization; environmental heterogeneity; forest dynamic plot; species diversity

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1. Introduction

Many areas are affected by the monsoon due to different sea and land positions. At the same time, the blocking effect of a mountain range forms different habitats on both sides of the mountain range. For example, the south aspect of the Himalayas is characterized by abundant rainfall and lush vegetation, while the north aspect has less rainfall and sparse vegetation [1]. Differences are observed in temperature and precipitation between the western and eastern sides of the central mountain range in Taiwan [2]. A vast arid, semi-arid region is on the western side of the southeastern mountains in Australia [3]. However, the distribution mechanism of woody plants is unclear in mountain forest ecosystems influenced by topography and monsoons.

Many studies have shown that the distribution of woody plants on a large scale is mainly affected by climate factors such as temperature and precipitation [4–7]. The distribution of woody plants on a small scale is mainly affected by topography, as well as soil's physical and chemical properties [8–10]. At the regional scale, the distribution mechanisms of woody plants in alpine forest ecosystems may be more complex than those at large and small scales. The spread of woody plants may be affected by the isolation of high mountains on either side of the mountain [11,12]. Due to the influence of the monsoon, precipitation on the windward side of the mountain is usually significantly greater than that on the leeward side [13–15]. Therefore, two habitats with huge environmental differences are formed in a relatively small spatial distance in mountain forest ecosystems.

Habitat specialization is the process by which species physiologically adapt to grow in their particular abiotic environment and outcompete other plants that are not closely suited to the local conditions [16]. Habitat heterogeneity greatly influences plant diversity [17,18]. As an important topographic factor, the aspect significantly influences microclimate conditions such as precipitation and wind speed [19–21], as well as soil properties such as organic matter content, chemical property, and soil texture [22–24]. A mountain ecosystem is a hotspot for biodiversity conservation because of its complex environmental conditions. Whether the species distribution is random or follows habitat specialization on both sides of the mountain in mountain forest ecosystems remains to be elucidated.

The Funiu mountain range, which is affected by the East Asian monsoon, is located in the transition zone between subtropical and warm temperate climates. This mountain range has the highest average elevation in Henan Province, China, and it obstructs the monsoon and forms various microhabitats on both sides of the mountain [25–27]. The Funiu mountains are known as a World Biosphere Reserve and a national nature reserve, as well as an ideal site for mountain forest ecosystem research.

In this study, we pose the question of whether the distribution of species is random or specialized on both sides of the mountain influenced by topography and monsoons. We examined community structure differences and the species–aspect relationships in the Funiu mountain range to have a clear understanding of the distribution mechanism of woody plants in mountain forest ecosystems influenced by topography and monsoons.

2. Materials and Methods

2.1. Study Site

The Funiu mountain range is located in the transition zone between the warm temperate and north subtropical zones (110°30′–113°30′ E, 32°45′–34°20′ N, China) (Figure 1). The main axis of the mountain range is aligned in a northwest-southeast direction, forming an important dividing line between the north and south climatic regions of China. The study area has an average elevation of 1000 m and covers an area of 5600 km^2. The weather is hot and rainy in summer under the influence of the southeast monsoon, and cold and dry in winter under the influence of the northwest monsoon [28–30].

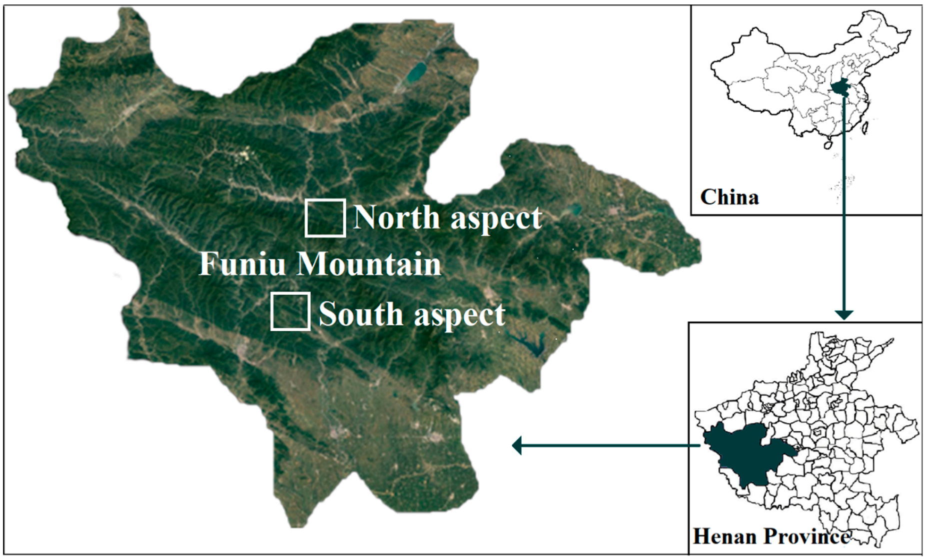

Figure 1. Location of north and south aspects of Funiu mountain range, Henan province, China.

The annual average temperature on the south aspect is 14.6 °C, with annual precipitation of 885.6 mm and forest coverage of 89%. The annual average temperature on the north aspect is 12.4 °C, with annual precipitation of 546 mm and forest coverage of 98.5% [29,31].

In the reserve, the vegetation is a transitional type between warm temperate broad-leaf deciduous forest and northern subtropical mixed evergreen and deciduous forest [31,32]. The main tree species in the tree layer are *Quercus acuidentata*, *Quercus variabilis*, and *Quercus glandulifera*. The main shrub species are *Lindera glauca*, *Acer davidii*, and *Rhododendron simsii* [33].

2.2. Sampling Design and Data Collection

The temperate deciduous forest, which is less affected by human activities, was selected as the survey plots on the south and north aspects of the Funiu mountain range. Five 1 hm^2 (100 m × 100 m) plots were randomly established on each aspect, the south and north respectively, with a total of 10 hm^2 (Table S2). Each plot was divided into 25 quadrates (20 m × 20 m). All woody plant stems ≥ 1 cm diameter at breast height (DBH) in the plot were tagged, measured, and mapped [34], including DBH, coordinates, status and specimen collection, etc. The plots were established and data were collected following the plot standards of the Center for Tropical Forest Science network [35]. Based on the Flora of China (http://www.iplant.cn/frps, accessed on 1 September 2020) and the Chinese Virtual Herbarium (https://www.cvh.ac.cn, accessed on 1 September 2020), specimens of woody plants were identified, and woody plants were divided into trees and shrubs.

2.3. Data Analysis

Based on the important value (IV), the dominant species of trees and shrubs in two habitats were statistically analyzed to understand the community structure of woody plants in a different aspect. The calculation formula [36] is as follows: important value (IV) = (relative abundance (%) + relative frequency (%) + relative diameter at breast height (%))/3. To prove the reasonableness of sampling, the species accumulation curves of woody plants in two habitats were drawn using the specaccum function in the vegan package in R software [37]. Kruskal–Wallis method was applied to compare the differences in species richness and abundance between the two habitats ($p < 0.05$ level of significance) [38].

The species composition and distribution of each habitat were visualized by using the circlize R package [39]. PCoA analysis of the abundance of woody plants based on Bray–Curtis distance matrix was used to test the effects of habitat partitioning on the beta diversity of woody plants, and ANOVA was conducted to test how these distances differ among habitats. This analysis was completed by using vegan package in R software [36,37,40].

The specificity of woody plants to different habitats at the community level was examined using network analysis. The network structure of woody plants and different habitats were implemented in the Java programming language using Gephi [41]. Modular and specialization indexes were used to evaluate the network relationship between habitats and species. The modular index was calculated using Gephi. The specialization index was calculated using the bipartite v.2.04 package of R [42].

The species distribution preferences of the two habitats at the species level were analyzed using torus translation tests. To improve the accuracy of the test results, species with ≥10 individuals were tested in the entire 10 hm^2 plot, including 106 plants, 69 trees, and 37 shrubs. In our study, based on the 20 m × 20 m quadrates of 10 hm^2 plots in two habitats, which gave one real and 999 torus translated habitat maps under the torus translation tests. A species was considered significantly positively associated with a habitat if its relative density in the true habitat map was ≥95% of the values obtained from torus translated maps (α = 0.05 level of significance for a one-tailed test). If ≤5%, the species is considered to be negatively associated with the habitat. If >5% and <95%, then no association exists between species and habitat. Further details on this method are provided by Harms et al. [43]. Torus translation test analyses were conducted in R 3.4.0.

In addition to topographic factors, interspecific relationships may also be an important factor affecting species distribution. Therefore, we used Gephi in the Java programming language to analyze Spearman's correlation coefficients of species in different habitats, and the network layout was completed using the ForceAtlas2 algorithm [41]. Finally, the network node, links, modularity index, average clustering coefficient, and average path length were used to describe the complex interaction patterns among woody plants. A specific summary of all the methods is summarized in Table S1.

3. Results

3.1. Species Composition of Two Habitats

A total of 159 species of woody plants, including 93 trees and 66 shrubs, were found on the south aspect. On the north aspect, 106 species of woody plants were found, including 63 trees and 43 shrubs. Differences were observed in the composition of dominant species in various habitats (Table S3). The number of species of trees was more than that of shrubs in two habitats (Figure 2A,B). Furthermore, the number of species increased quickly between 0 and 2000 m^2, and then began to stabilize (Figure 2C,D).

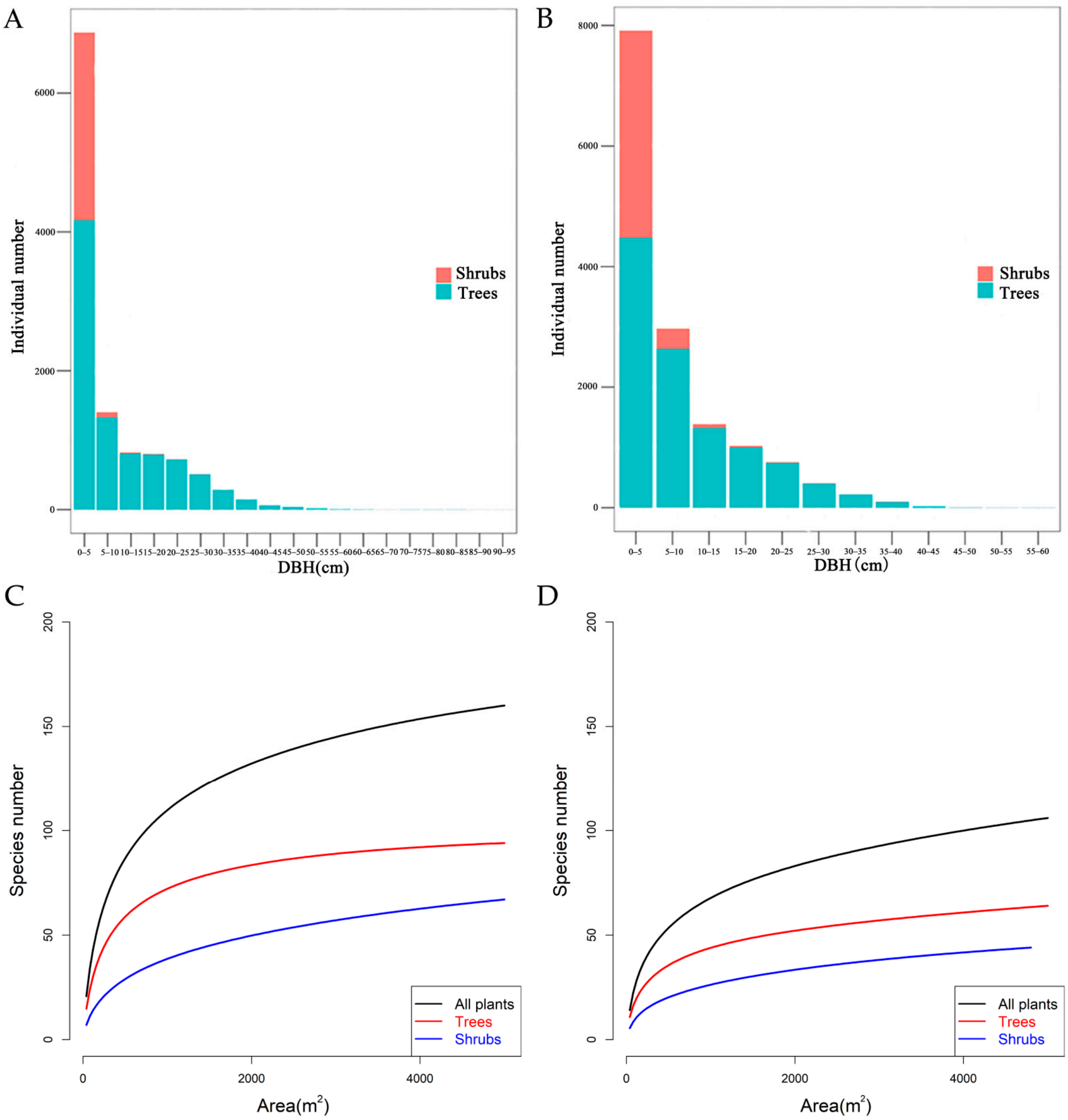

Figure 2. DBH ((**A**): south aspect, (**B**): north aspect) and species accumulation curves ((**C**): south aspect, (**D**): north aspect) of woody plants in north and south aspects of Funiu mountain range.

Significant differences were observed in the abundance and richness of woody plants (all plants, trees, and shrubs) between the two habitats ($p \leq 0.05$) (Figure 3A–F). The abundance of species was higher on the north aspect, where *Quercus aliena* var. *acutiserrata* was the most abundant woody plant and *Forsythia suspensa* was the most abundant shrub (Table S3 and Figure 4A–C). Significant differences were observed in the distribution of woody plants between the two habitats (all plants: F = 5.2595, $p < 0.05$; trees: F = 14.013, $p < 0.001$; shrubs: F = 7.684, $p < 0.01$) (Figure 4D–F).

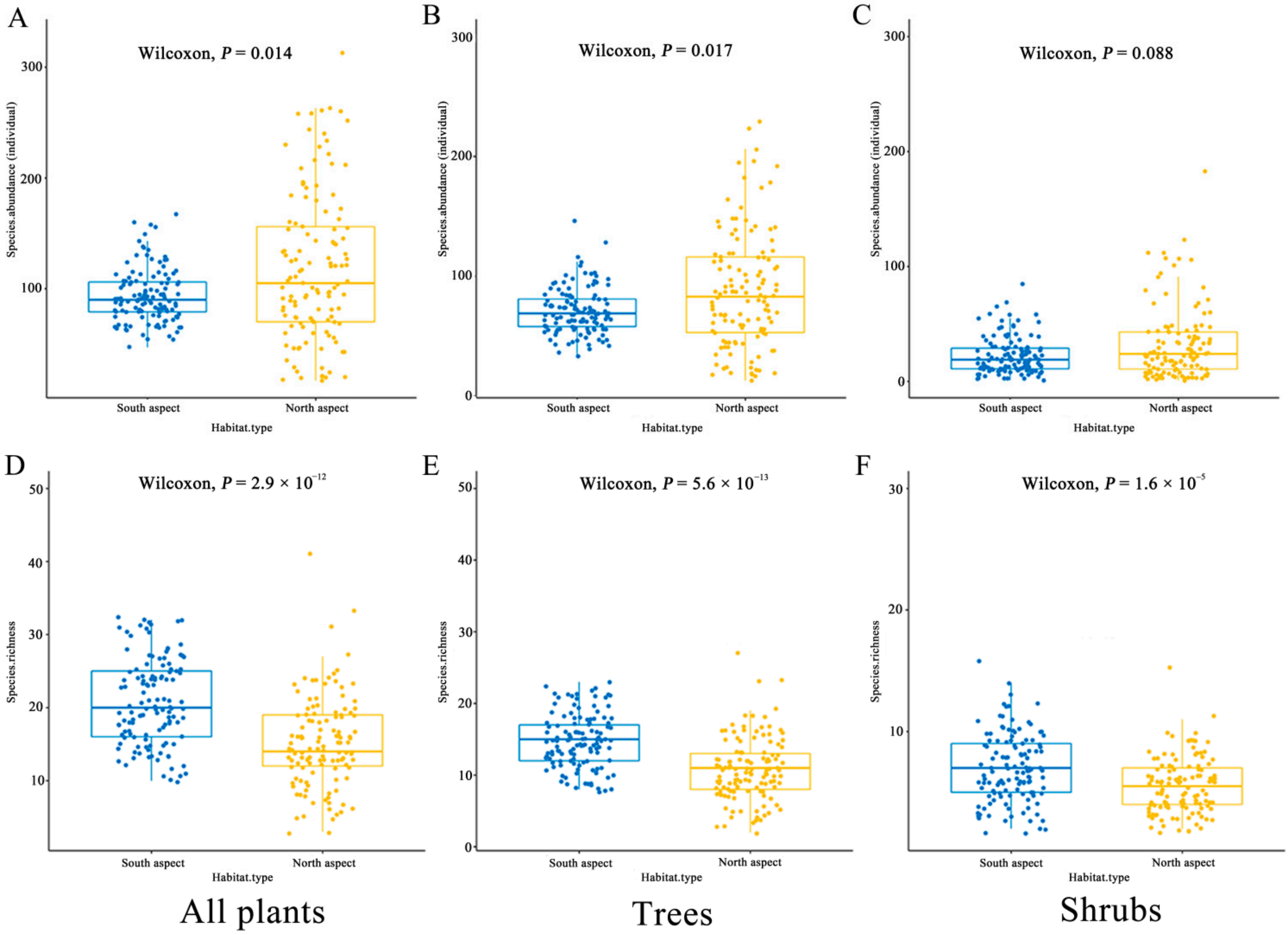

Figure 3. Differences in abundance and richness of all plants, trees, and shrubs in north and south aspects of Funiu mountain range. Using the Kruskal–Wallis method to test for significant differences ($p \leq 0.05$ level of significance). (**A**,**D**) showed abundance and richness of all plants, respectively. (**B**,**E**) represented abundance and richness of trees, respectively. (**C**,**F**) represented abundance and richness of shrubs, respectively.

3.2. Associations between Species and Habitats

The network analysis shows that the specialization index (all plants) was 0.186 and modularity index was 0.235. The modularity and specialization indexes of shrubs were higher than those of trees (Figure 5).

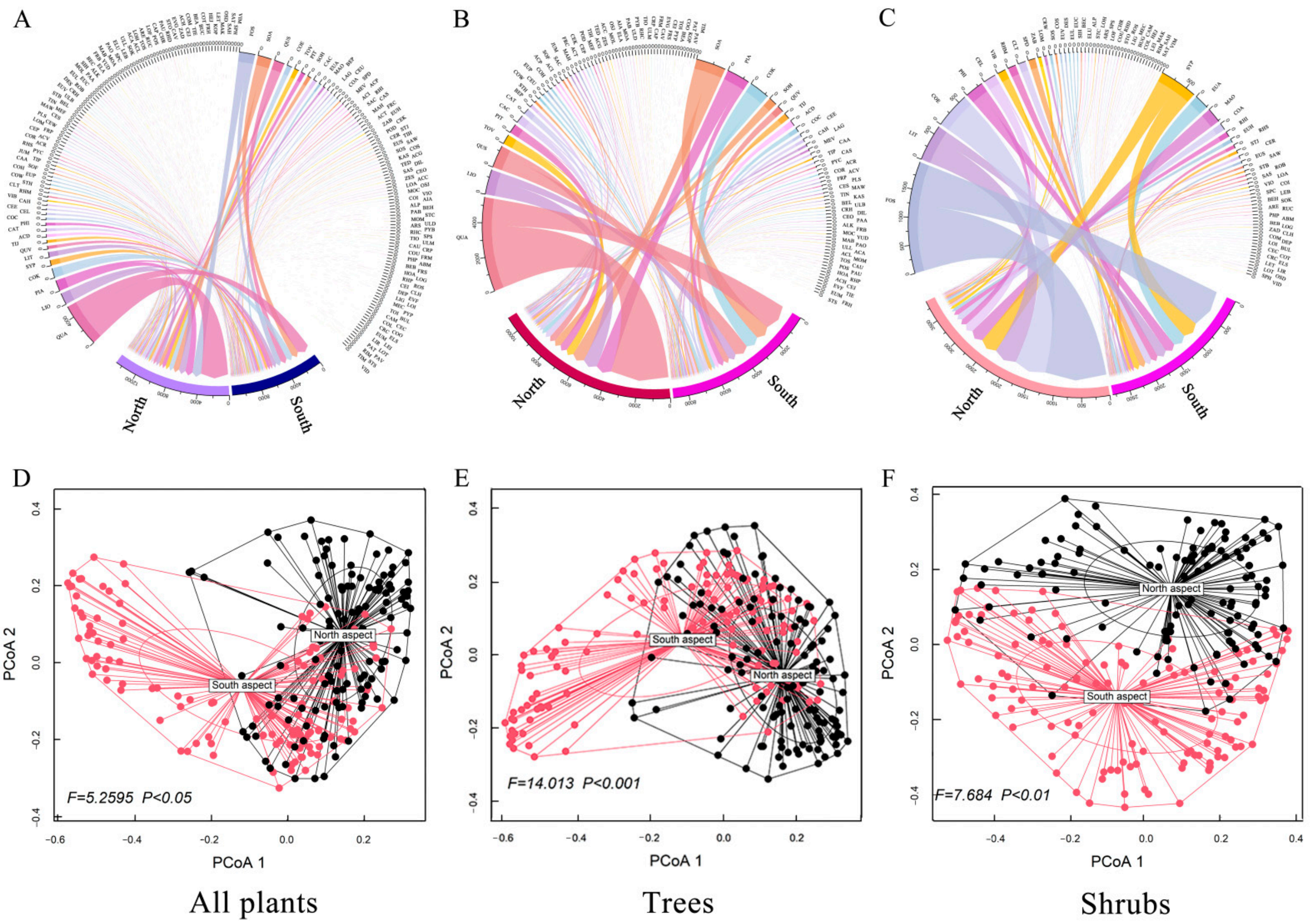

Figure 4. Proportion of species composition and distribution ratio in north and south aspects of Funiu mountain range ((**A**): all plants, (**B**): trees, and (**C**): shrubs). Effect of habitat types on beta diversity of the woody plant by running the betadisper function. PCoA1 and PCoA2 were two principal coordinate components in the "PCoA" analysis ((**D**): all plants, (**E**): trees, and (**F**): shrubs).

Based on the torus translation test, a total of 45 species were detected to be associated with at least one of the habitats (45/106, 42.45%), in which 39 positive and 25 negative associations were observed. The association proportion on the south aspect (38.68%) was higher than that on the north aspect (21.70%). The proportion of species positively associated with the south aspect (25.47%) was higher than that with the north aspect (11.32%) (Figure 6A).

The association proportion between shrubs and habitats (59.46%) was higher than that of trees (39.13%) (Figure 6B,C). The proportion of negative association between shrubs and the north aspect was higher than that of positive association, accounting for 18.92% (Figure 6B,C).

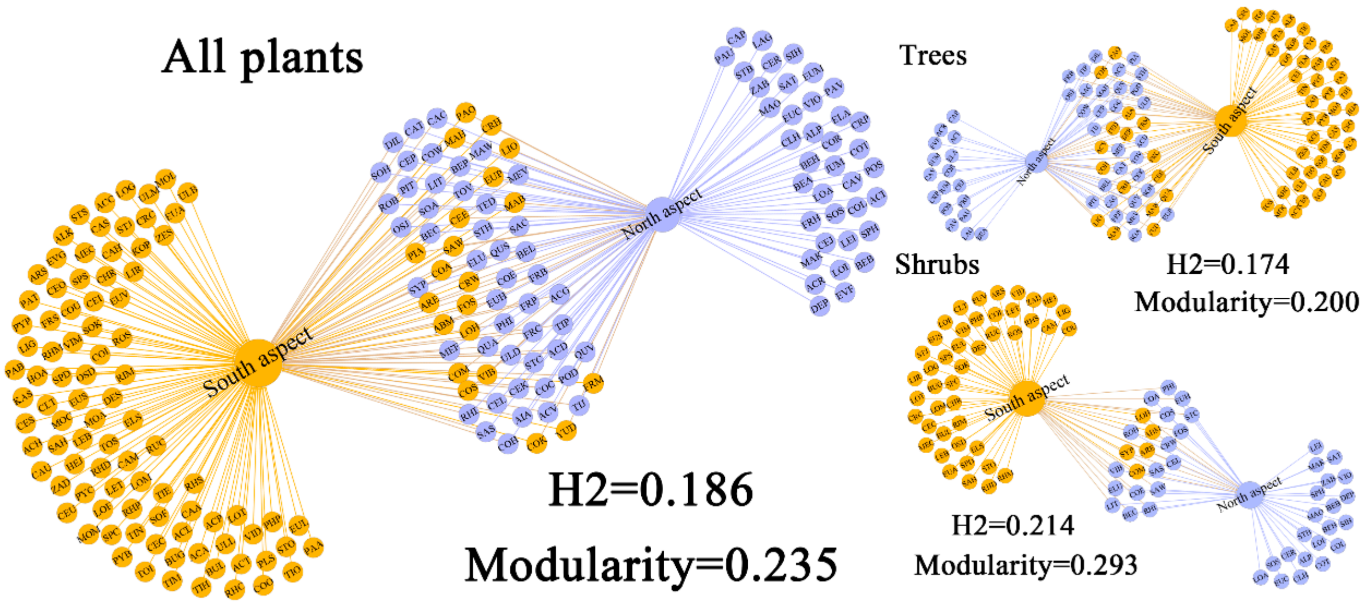

Figure 5. Network analysis of species composition among north and south aspects of Funiu mountain range. The dot size indicates the abundance of species, and the edges represent the relationship between species and habitats.

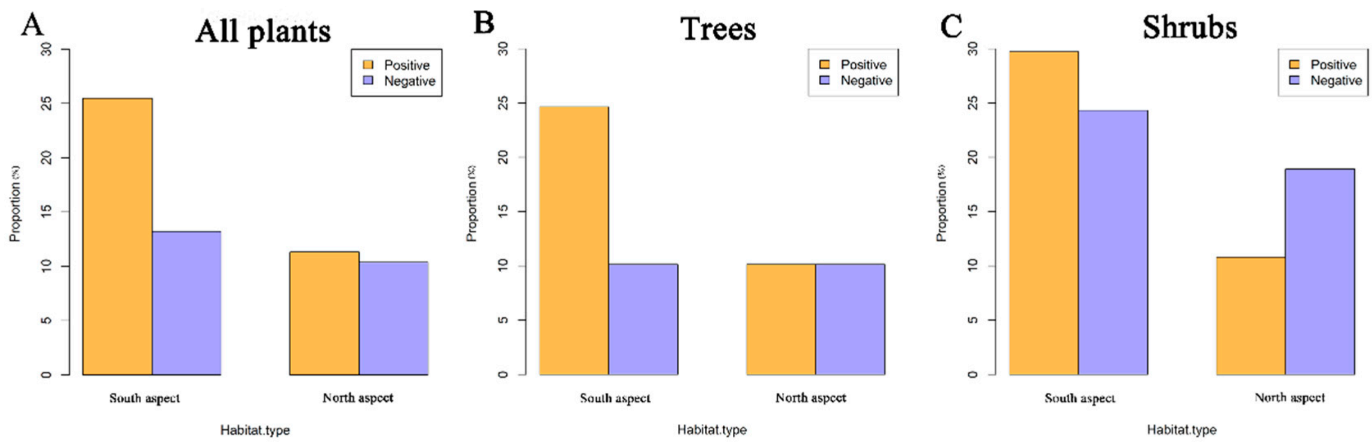

Figure 6. Associations between all plants (**A**), trees (**B**), and shrubs (**C**) and two habitats of Funiu mountain based on torus translation test ($p \leq 0.05$).

3.3. Co-Occurrence Network Analysis of Species

The modularity index, mean path length, and mean clustering coefficient of the south aspect were higher than those of the north aspect (Figure 7C–E). The network nodes and links of the north aspect were higher than those of the south aspect (Figure 7F,G). A few species were negatively associated with the south aspect (Figure 7A,B). Evidently, the abundance of important nodes (such as QUA, QUV, and LIO) in the network graph on the south aspect was higher. The abundance of important nodes (such as MAK, EVF, and BEB) in the network graph on the south aspect was lower.

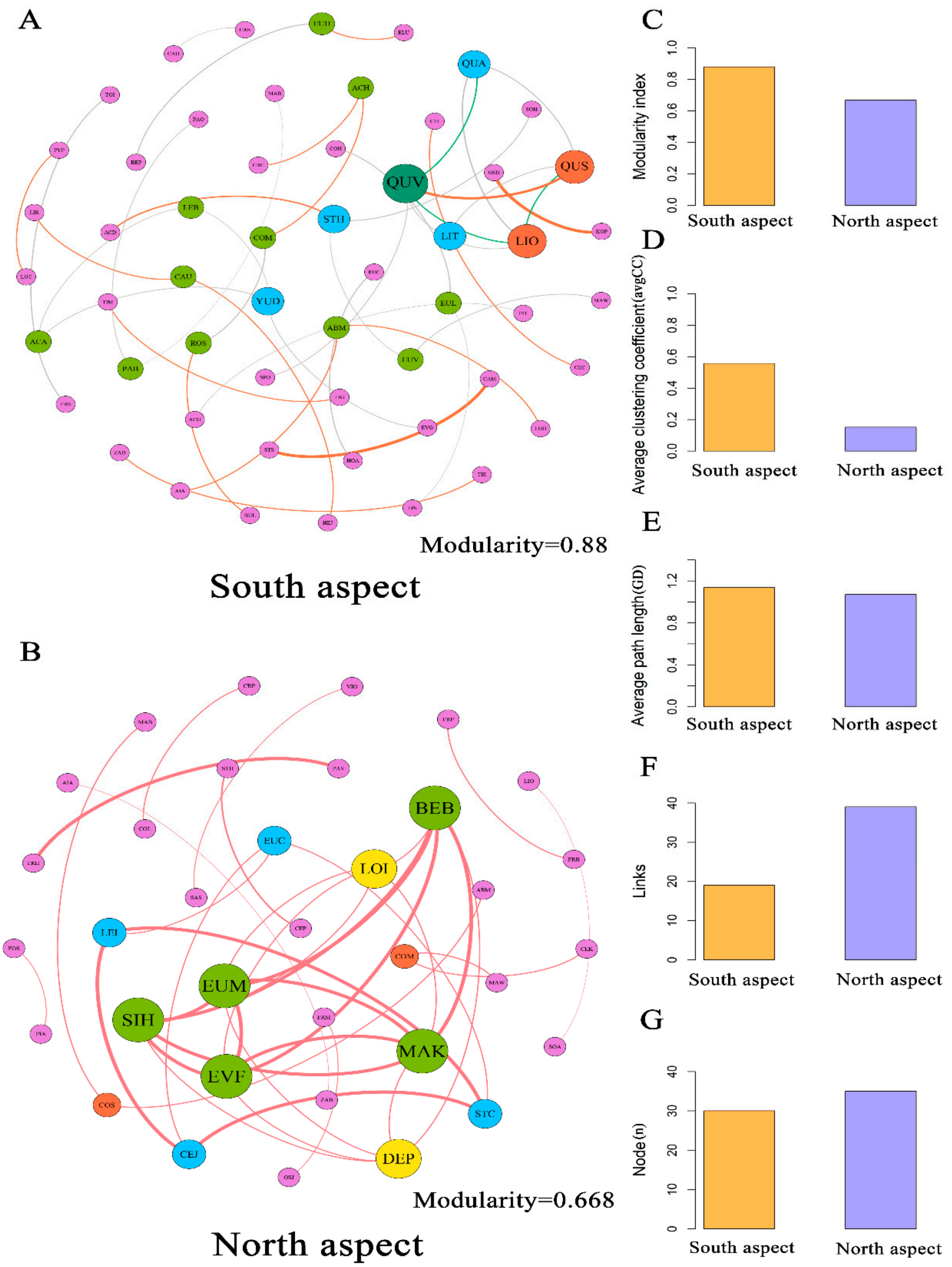

Figure 7. Impact of different aspects on network interactions of species at Funiu mountain range. A node represents a species. The size of each node is proportional to the number of connections (that is, degree). The thickness of the line indicates the degree of association between species. Red edges represent significant positive relationships and blue edges represent significant negative relationships ($p < 0.05$). The gray line indicates that the interspecific relationship is not significant. (**A**): co-occurrence network of species on the south aspect, (**B**): co-occurrence network of species on the north aspect, (**C**): modularity index, (**D**): average clustering coefficient, (**E**): average path length, (**F**): species degree (links), and (**G**): number of related species (Node (n)).

4. Discussion

Our findings indicate that many woody plant species have strong associations with different aspects of the mountain forest ecosystem (Figure 5). The modularity index of woody plants was 0.235 (Figure 5), which was higher than the biota network index (0.185) of the previously reported plant-gypsum soils [44] and lower than the plant-seed disperser network index (0.323) [45]. The network structure of species and aspects may be determined by the habitat conditions, including terrain, climate, and other factors [36,37,46]. Due to the influence of monsoon climate, the south aspect was windward aspect and the north aspect was leeward, and the rainfall on the south aspect was higher than that on the north aspect in the Funiu mountain range [47–50]. The south-facing aspect received more than the amount of solar radiation than the north-facing aspect in the northern hemisphere [51]. Differences in temperature, humidity, and other natural factors were observed in different aspects, and formed different microhabitats in different aspects [52,53]. Thus, the distribution of woody plants among different aspects was specialized and not random.

In our study, the characteristics of woody plant assemblages differed between different aspects. Different woody plants showed different aspect preferences in the forest with various aspects. One possible reason was that high mountains formed a barrier between the two aspects, thereby limiting the dispersal and reproduction of species for a long time [54–56]. Another possible reason was that different species had different physiological requirements for the environment in which they grow [10]. For example, in this study, *Lindera obtusilobum* is suitable for high temperature and rainy climates, and is a common species in the subtropical region [57]. *Betula platyphylla* for humid climate is a common species in the cold temperate zone [58]. Our study demonstrates the importance of different aspects in maintaining local diversity in the woody plant community [31,47].

In our study, differences were observed in species co-occurrence networks in different aspects. The modularity index and average clustering coefficient of the south aspect were higher than those of the north aspect, indicating that the community stability of the south aspect was higher than that of the north aspect (Figure 7) [59,60]. The number of individual woody plants on the north aspect was higher than that on the south aspect, but the diversity of woody plants on the south aspect was higher than that on the north aspect (Figure 3). This result may indicate that forest ecosystems on the north aspect of Funiu mountain are more vulnerable to environmental change than those on the south aspect [61,62].

Consistent with our hypothesis, shrubs showed higher specialization than trees in different aspects. In addition, more shrubs had specific preferences than trees with respect to forests in different aspects. On a large scale, the distribution of trees was mainly influenced by climate conditions such as temperature and precipitation [63]. Shrubs generally have shallower roots than trees, so they are more susceptible to local environmental factors such as soil and precipitation [64,65]. In addition to topography and soil's physical and chemical properties, canopy structure also influenced shrubs [66]. Therefore, more shrubs exhibited distinct distribution preferences than trees in various aspects of the forest ecosystem.

5. Conclusions

Our study found that the distribution of woody plants among different aspects was specialized and not random in Alpine forest ecosystems influenced by topography and monsoons at the regional scale. More shrubs exhibited distinct distribution preferences than trees in different aspects of the forest ecosystem. In terms of resource protection and biodiversity maintenance, we should adopt different conservation strategies according to the distribution characteristics and preferences of woody plants in Alpine forest ecosystems influenced by topography and monsoons at the regional scale.

Supplementary Materials: The following supporting informationcan be downloaded at: https://www.mdpi.com/article/10.3390/f13060957/s1, Table S1: An overview of all of the methods; Table S2: Stand features of each plot on the north and south aspects of Funiu mountain; Table S3: Dominant species in north and south aspects of Funiu mountain range. The important values were calculated as follows: important value = (relative abundance (%) + relative frequency (%) + relative basal area at breast height (%))/3.

Author Contributions: Conceptualization, X.Z. and Z.W.; Methodology, X.Z.; Software, Z.W.; Validation, Y.C.; Formal Analysis, X.Z; Investigation, X.Z. and Q.F.; Resources, Z.W.; Writing—Original Draft Preparation, X.Z.; Writing—review and editing, X.Z., Z.W., W.L., F.L., Y.Y., Y.S., Z.Y., Y.C. and Q.F.; Visualization, X.Z.; Supervision, Y.C. and Z.Y.; Project administration, Z.W.; Funding acquisition, Z.W. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement: The data that support this study will be shared upon reasonable request to the corresponding author.

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