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Associations between Epiphytic Bryophyte and Woody Plant Species in a Temperate Deciduous Broad-Leaved Forest

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Abstract: Determining whether epiphytic bryophytes have ecological preferences for woody plants remains difficult. Here, our primary aim in developing the torus-translation test is to evaluate the associations between epiphytic bryophytes and woody plants at the species, genus, or family levels in a 100 m × 100 m forest dynamics plot in a temperate, deciduous broad-leaved forest (China). We collected all the epiphytic bryophyte species on woody plants and recorded the woody plant species in the 1-ha plot in 2020. All the epiphytic bryophytes on the trees from the ground level up to 2 m were collected. We recorded 988 epiphytic bryophyte specimens belonging to 61 species in 254 woody plants. The Torus-translation test showed that 93.44% (57/61), 93.44% (57/61), and 98.36% (60/61) of the bryophyte species were significantly positively associated with the family, genus, and species of woody plants, respectively. A total of 317, 563, and 857 significant positive associations concerning the family, genus, and species of the woody plants were observed among the 61 examined bryophyte species. In addition, few significant negative associations were identified regarding the family, genus, and species of woody plants. More rare bryophyte species were positively correlated with woody plants than dominant bryophyte species. Our study demonstrates that most epiphytic bryophytes exhibit ecological habitat preferences for woody plants. These observations highlight the importance of the species composition of woody plants with respect to the maintenance of epiphytic bryophytes' diversity. Epiphytic bryophytes' growth preference for woody plants, especially rare bryophyte species, should be considered in the process of bryophyte diversity conservation in temperate, deciduous broad-leaved forests.

Keywords: ecological preference; forest dynamics plot; species diversity; temperate deciduous broad-leaved forest; torus-translation test; epiphytic bryophyte; woody plant; forest ecosystems

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1. Introduction

Epiphytic bryophytes are essential to forest biodiversity and are widely used as indicators of forest continuity and naturalness [1,2]. The study of the host specificity of epiphytic bryophytes is a very intensively studied aspect of substratum ecology [3]. Woody plants are one of the most important substrates for bryophytes' growth [4]. Much is known about the relationship of bryophytes to woody plants' diversity [5–7], tree diameters [2,8], and community types [9–11]. Several studies have investigated the host specificity of epiphytic bryophytes by descriptive research [3,12–17]. No ideal approach is available for the associations between epiphytic bryophytes and woody plants. Thus, determining whether epiphytic bryophytes have ecological preferences for woody plants remains difficult.

One manifestation of niche differentiation is habitat specialization, such that different species of bryophytes are best suited to different microhabitats wherein they are competitively dominant [18–20]. Based on this hypothesis, Harms et al. proposed the torus-translation test for assessing associations between woody plants and topography habitats [18]. The advantage of this method is that it excludes spatial autocorrelation and allows for more conservative test results [18,19,21]. Here, torus-translations tests were developed to assess whether the bryophytes' distribution pattern corresponded to random distribution or ecological specialization.

Different bark types have different physiological properties, are related to the ecology of different tree species, and provide different microhabitats for bark-living species [22]. The most important phorophyte attributes in determining species distribution relationships are pH, chemical composition, and the roughness of the bark [13]. Tree bark pH has a considerable effect on epiphytic bryophytes, wherein a high bark pH supports the high richness of bryophytes [2]. The niche partitioning of the physical and chemical properties among the bark types may constitute an important reason for epiphytic bryophytes' diversity.

The sampling scale of a study can influence researchers' ability to quantify species diversity and their coexistence mechanism [23,24]. A large scale can obscure important environmental variations, whereas a small scale can increase noise in the data and reduce the fraction explained [23,24]. Therefore, comparing the results obtained using different sampling scales is useful in the interpretation of the results.

The rare, common, or dominant species have different ecological niches in forest ecosystems [25,26]. Rare species have narrower ecological niches than dominant species [27]. Different groups of epiphytic bryophytes may have different functions in forest ecosystems [28]. Therefore, we hypothesize that a greater number of rare bryophyte species have a greater ecological preference for woody plants than dominant species.

Temperate, deciduous broad-leaved forests are dominated by deciduous trees and show wide variation in their community structure at time and space scales [29]. Epiphytic bryophytes are abundant in these ecosystems [29]. In this study, our primary aim in developing a torus-translation test is to evaluate the associations between epiphytic bryophytes and woody plants at the species, genus, or family levels in a 100 m × 100 m forest dynamics plot in a temperate, deciduous broad-leaved forest.

2. Materials and Methods

2.1. Study Site and Sampling

The study was conducted in a 1 ha (100 m × 100 m) plot in a temperate, deciduous broad-leaved forest in the Baotianman National Nature Reserve, southwest of Henan Province, China (33°25′ N–33°33′ N, 111°53′ E–112°04′ E; Figure 1). The study site has an annual mean temperature of 15.1 °C and annual mean precipitation of 885.6 mm [30]. It is in a transitional region that shifts from a northern subtropical climate to a warm temperate climate [31]. The Baotianman National Nature Reserve has a continental monsoon climate with four distinctive seasons [31]. The soils are dominated by Haplic Luvisol [30], with 27–30% clay, 11–13% slit, and 57–62% sand content and an average depth of 40–60 cm. In the reserve, the vegetation is a transitional type between warm, temperate, broad-leaved deciduous forest and northern subtropical mixed evergreen and deciduous forest [32,33]. The main tree species in the tree layer are *Quercus aliena* Bl. var. *Acuteserrata* Maxim. ex Wenz., *Pinus armandii* Franch., *Quercus variabilis* Bl., and *Quercus serrata* Thunb. The main shrub species are *Lindera glauca* (Sieb. et Zucc.) Bl, *Acer davidii* Franch., and *Rhododendron simsii* Planch. [34]. The plot area was divided into 25 quadrates (20 m × 20 m), and each quadrate was further subdivided into 16 sub-quadrates (5 m × 5 m). All stems ≥1 cm diameters at breast height in the plot were tagged, mapped, and measured. Table S1 shows more detailed community profiles of the plot.

We collected all epiphytic bryophyte species on woody plants and recorded woody plant species in the 1-ha plot in 2020. All epiphytic bryophytes on trees from ground level up to 2 m were collected. Bryophyte specimens were collected with small spatulas and then stuffed into paper envelopes. Specimen collectors had professional training before specimen collection. The training included basic characteristics of bryophytes, field identification of bryophytes, and field specimen collection methods. A total of 988 specimens were collected. All specimens were transported back to the laboratory. Voucher specimens were deposited in the bryophyte herbarium of the Institute of Henan Agricultural University (https://www.henau.edu.cn/, accessed on 1 November 2021).

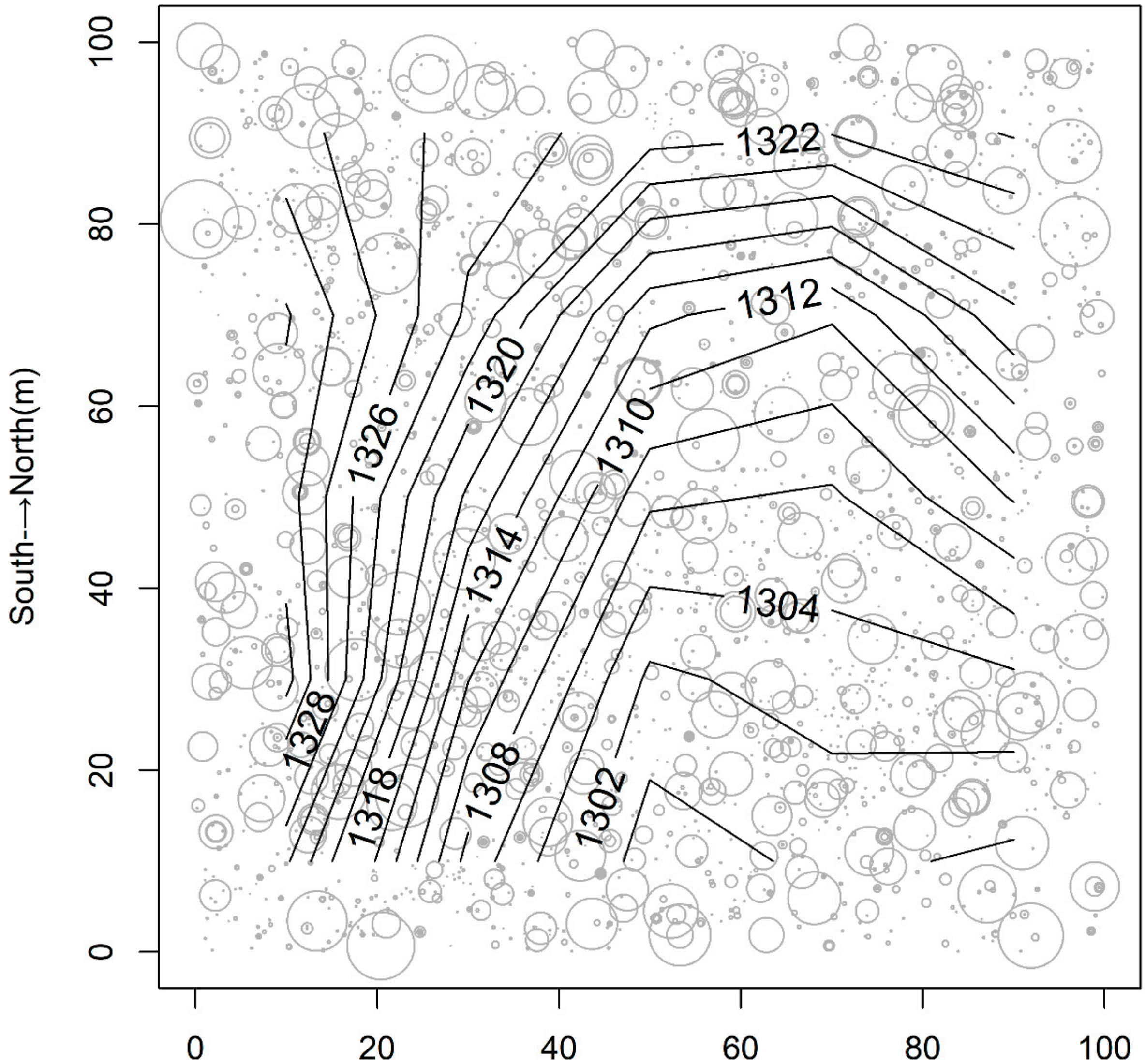

Figure 1. Spatial distribution of woody plant species in the plot. The circle sizes represent the diameter at breast height of the species. The black line shows the plot contours.

2.2. Data Analysis

Rows and columns within the interaction matrix (Tables S1–S3) represent woody plant and bryophyte species, respectively. Each cell in the matrix included the number of bryophytes in which the focal plant–bryophyte association was observed. A correlation network approach was used to visualize the interactions between woody plants and bryophyte species. We evaluated the structure of the plant–bryophyte network using the H_2' metric of specialization and connectance index [35]. The architecture of the plant–bryophyte network was visualized using the 'bipartite' package of R 3.4.0 [36].

Associations of bryophyte species with the woody plants were determined using torus-translation tests, which consider the spatial autocorrelation species distribution [18,19]. The basic concept of the torus-translation test is to calculate distribution probability of a species in each habitat using a model in which the species distribute randomly between habitats [18,19]. In our study, one species, one family, or one genus were considered as a habitat (consisting of 15 families, 20 genera, and 28 species of woody plants). A total of 254 woody plants had individual bryophytes; thus, 254 unique torus-translated habitat maps were initially possible. The torus translation of each original map was performed 254 times. From this, it is possible to generate three original maps (180° rotation, mirror image, and 180° rotation of the mirror image) to continue the torus translation [18]. In total, these procedures provide one real and 1015 translated maps. If the true relative density of a bryophyte species in the focal habitat is greater or smaller than at least 97.5% of the expected relative densities, then it is determined to be statistically positively or negatively associated with the species, family, or genus of a woody plant (α = 0.05 level of significance for a two-tailed test). More detailed descriptions of torus-translation tests can be found in Harms et al. [18].

Three groups, namely, dominant species, common species, and rare species, were constructed to understand the associations between different groups of bryophytes and woody plants. In this study, dominant species were defined as species with occurrences greater than 20, common species were defined as species with occurrences greater than 3 and less than or equal to 20, and rare species were defined as species with occurrences less than 3 in the plot. Table S6 shows more detailed profiles of the rare, common, or dominant species of epiphytic bryophyte in the plot.

3. Results

A total of 3318 woody plants belonging to 75 species were identified in the plot (Table S4). We recorded 988 epiphytic bryophyte specimens belonging to 61 species in 254 woody plants (Table S5). Two hundred and fifty-four woody plants belong to 15 families, 21 genera, and 28 species. The results of the species accumulation curve showed that the sampling area of the plants and bryophytes is sufficient in this study (Figure 2).

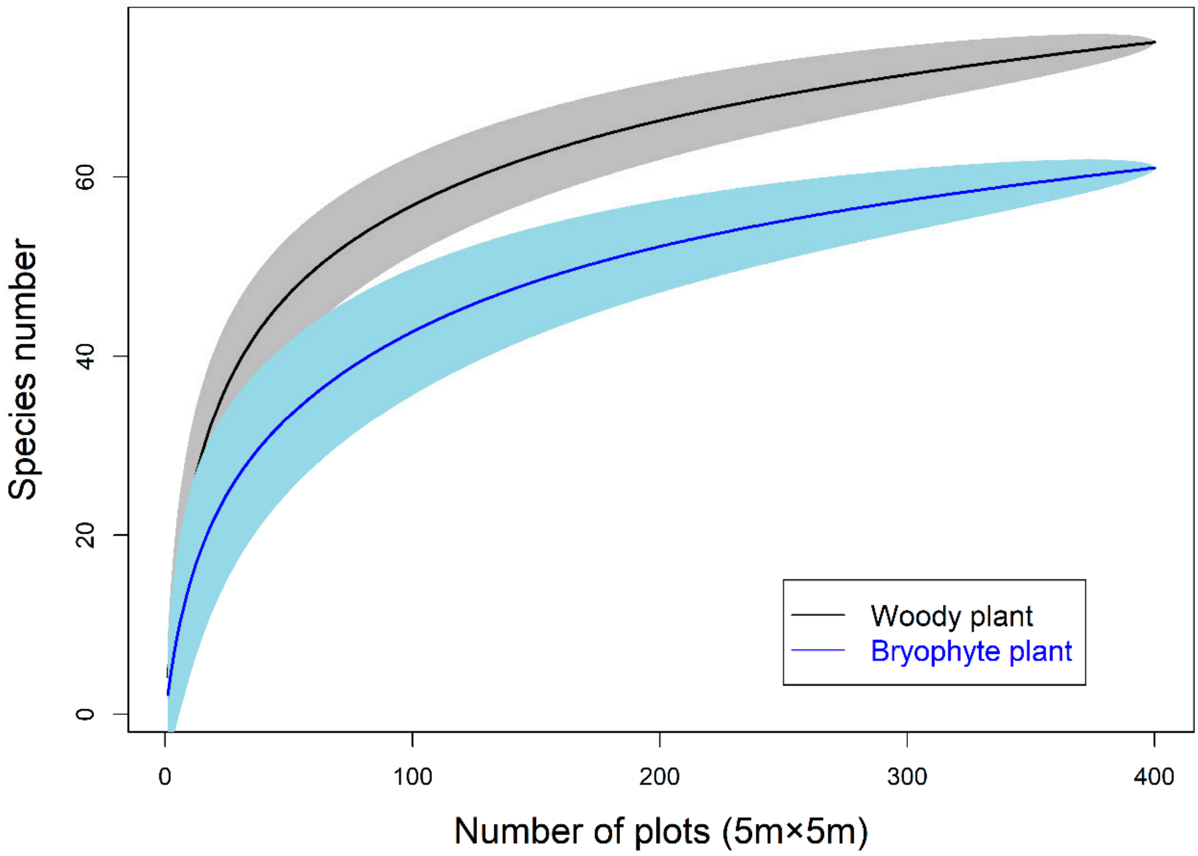

Figure 2. Species accumulation curves of species richness for both woody plant and bryophyte communities. Yellow and blue lines refer to the woody plant and bryophyte species, respectively. Light-colored regions refer to standard deviation.

3.1. Diversity within the Network and Connectance

The network of symbiotic interactions between the plants and bryophytes was highly asymmetric in terms of species richness (Figure 3). It included fewer plant species than bryophyte species, namely, 28 vs. 61, resulting in a mean of 2.18 bryophyte species interacting per plant species. Based on the connectance index, there are 27.10%, 19.59%, and 16.86% of possible interactions occurring in the observed interactions among the bryophytes and the families, genera, and species of woody plants, respectively. The H_2' estimates of interaction specialization were 0.106, 0.114, and 0.123 for the families, genera, and species of woody plants, respectively.

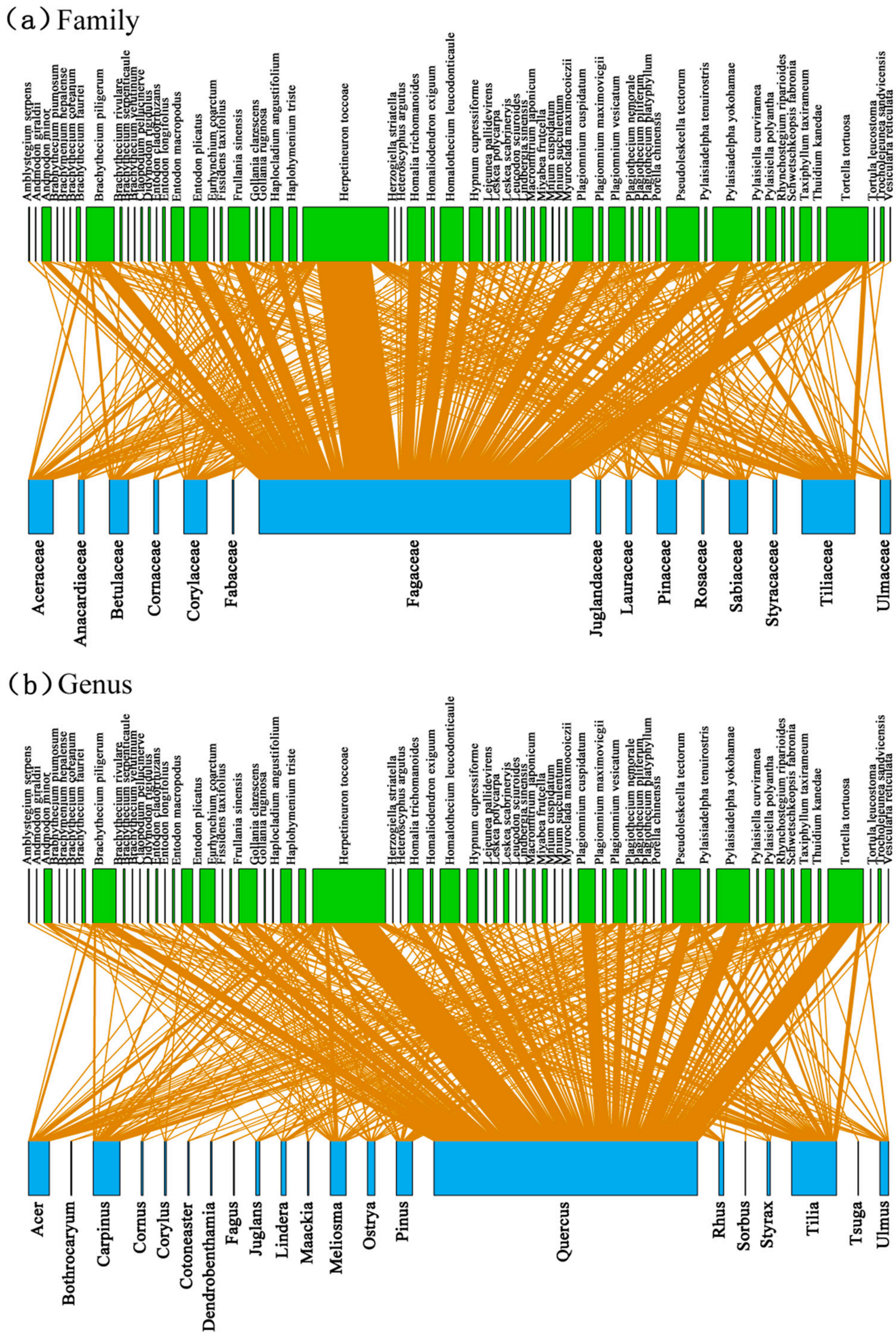

Figure 3. *Cont*.

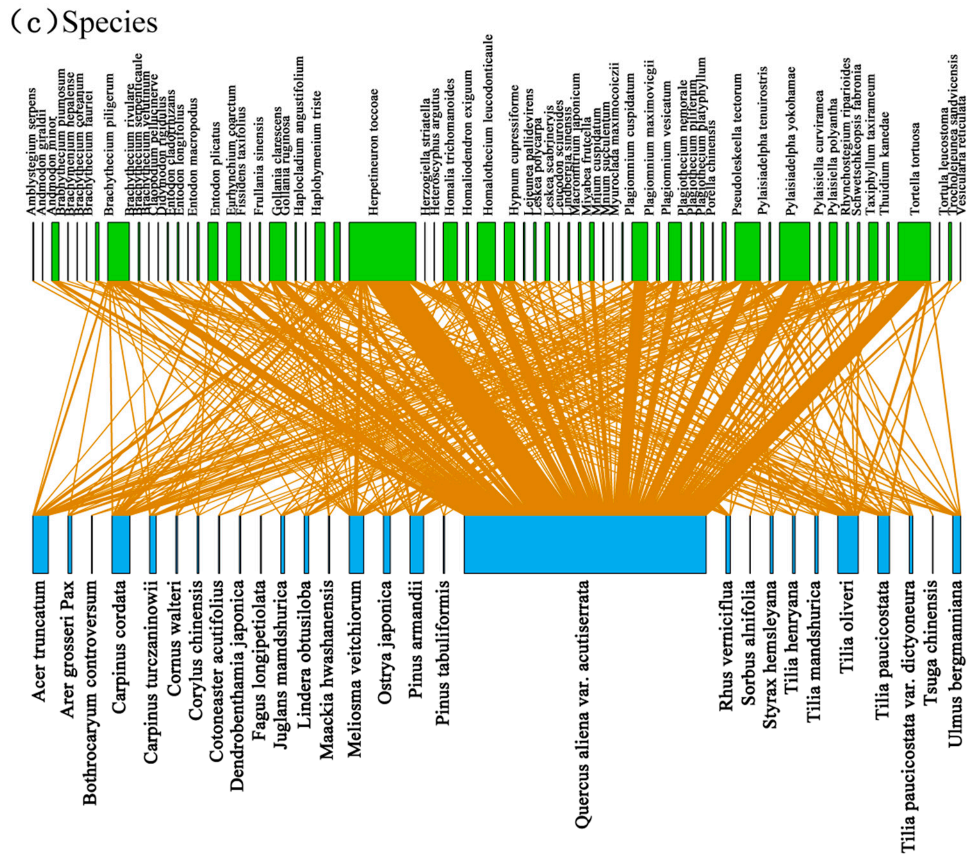

Figure 3. Bipartite display of the plant and bryophytes network. The entire network includes all the 28 woody plant species in 21 genera and 15 families (top) and the 61 bryophyte species (bottom). The thickness of lines and the size of rectangles represent the number of observed associations. (**a**) is at family level, (**b**) is at genus level and (**c**) is at species level.

3.2. Associations between Bryophyte and Plant

The torus-translation test showed that 93.44% (57/61), 93.44% (57/61), and 98.36% (60/61) of the bryophyte species were significantly positively associated with the families, genera, and species of woody plants, respectively (Figure 4). A total of 317, 563, and 857 significant positive associations with the families, genera, and species of woody plants were observed among the 61 examined bryophyte species. A total of 36, 43, and 44 of the bryophyte species examined were positively associated with five, six, and seven or more of the families, genera, and species of woody plants, respectively.

Few significant negative associations were identified with the families, genera, and species of woody plants. *Brachythecium piligerum* Card., *Herpetineuron toccoae* (Sull. and Lesq.) Cardot, *Anomodon minor* Lindb., and *Frullania sinensis* Steph. were not positively associated with the families of the plants. *Brachythecium piligerum*, *Herpetineuron toccoae, Anomodon minor,* and *Homalia trichomanoides* (Hedw.) B. S. G. were not positively associated with the genera of the plants. *Brachythecium piligerum* was not positively associated with the species of the plants (Figure 4).

All the families (15), genera (20), and species (28) of woody plants were positively associated with two or more of the bryophyte species. Fewer bryophyte species were positively associated with *Ostrya japonica* Sarg. (5), *Tilia paucicostata* Maxim. (4), *Carpinus cordata* Bl. (6), *Dendrobenthamia* Hutch (7), *Sorbus* L. (6)*, Maackia* Rupr. (4), *Tsuga* Carr. (3), *Meliosma* Bl. (5), Cornaceae Bercht. and J. Presl (7), Aceraceae Juss. (5), Anacardiaceae R. Br. (6), Leguminosae sp. (4), Corylaceae Mirbel (3), and Juglandaceae DC. ex Perleb (4). The negative associations are also concentrated in these families, genera, or species of woody plants (Figure 4).

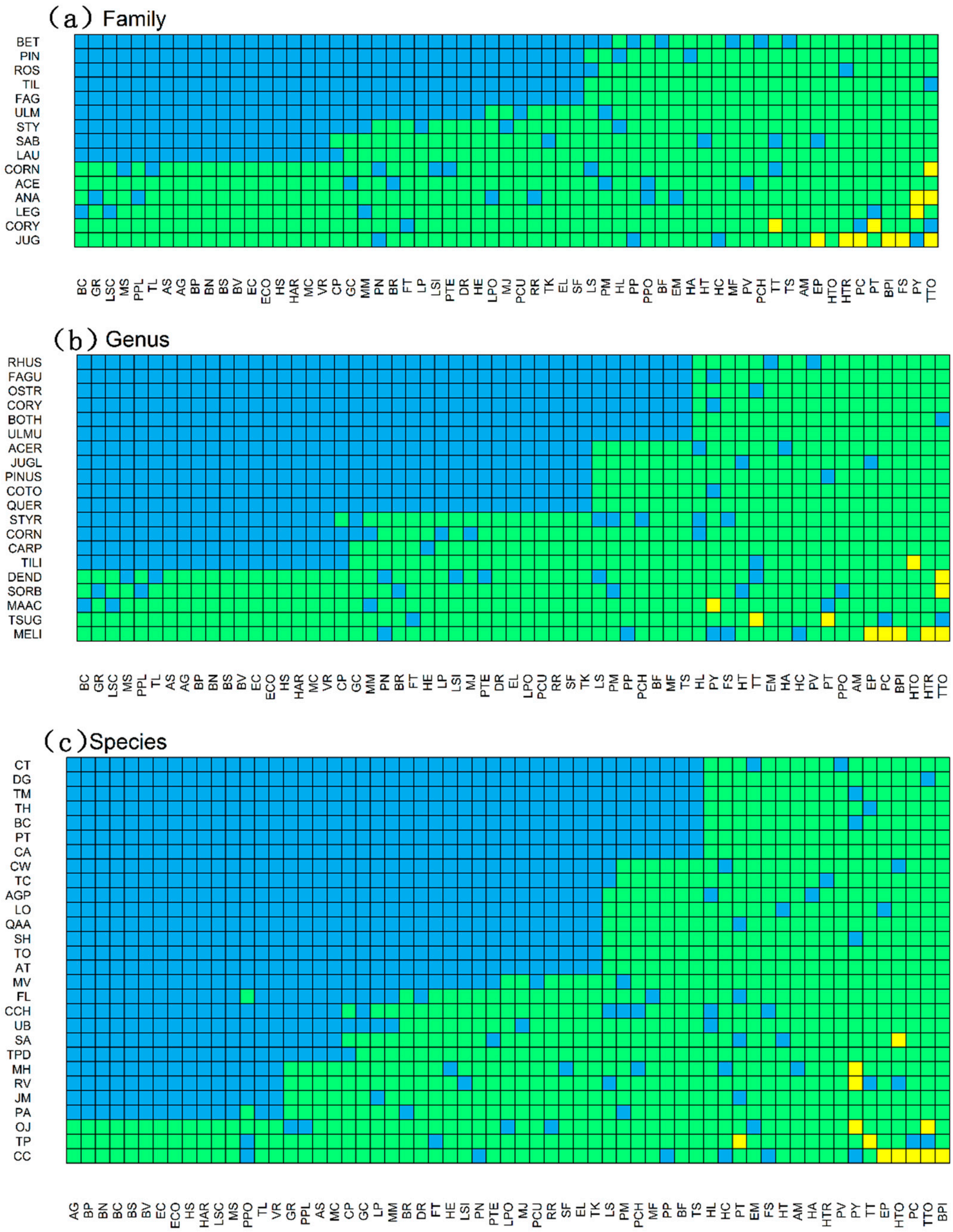

Figure 4. Associations between bryophyte species and woody plants (α = 0.05 level of significance for torus-translation test). Blue squares denote significant positive associations, yellow squares denote significant negative associations, and green squares denote neutral associations. The abbreviations of woody plant and bryophyte species are shown in Tables S4 and S5. (**a**) is at family level, (**b**) is at genus level and (**c**) is at species level.

Based on the results of the torus-translation test, more rare bryophyte species showed positive associations with woody plants than common bryophyte species. The number of dominant bryophyte species positively associated with woody plants was the lowest. More dominant bryophyte species showed neutral associations with woody plants than common and rare bryophyte species (Figure 5).

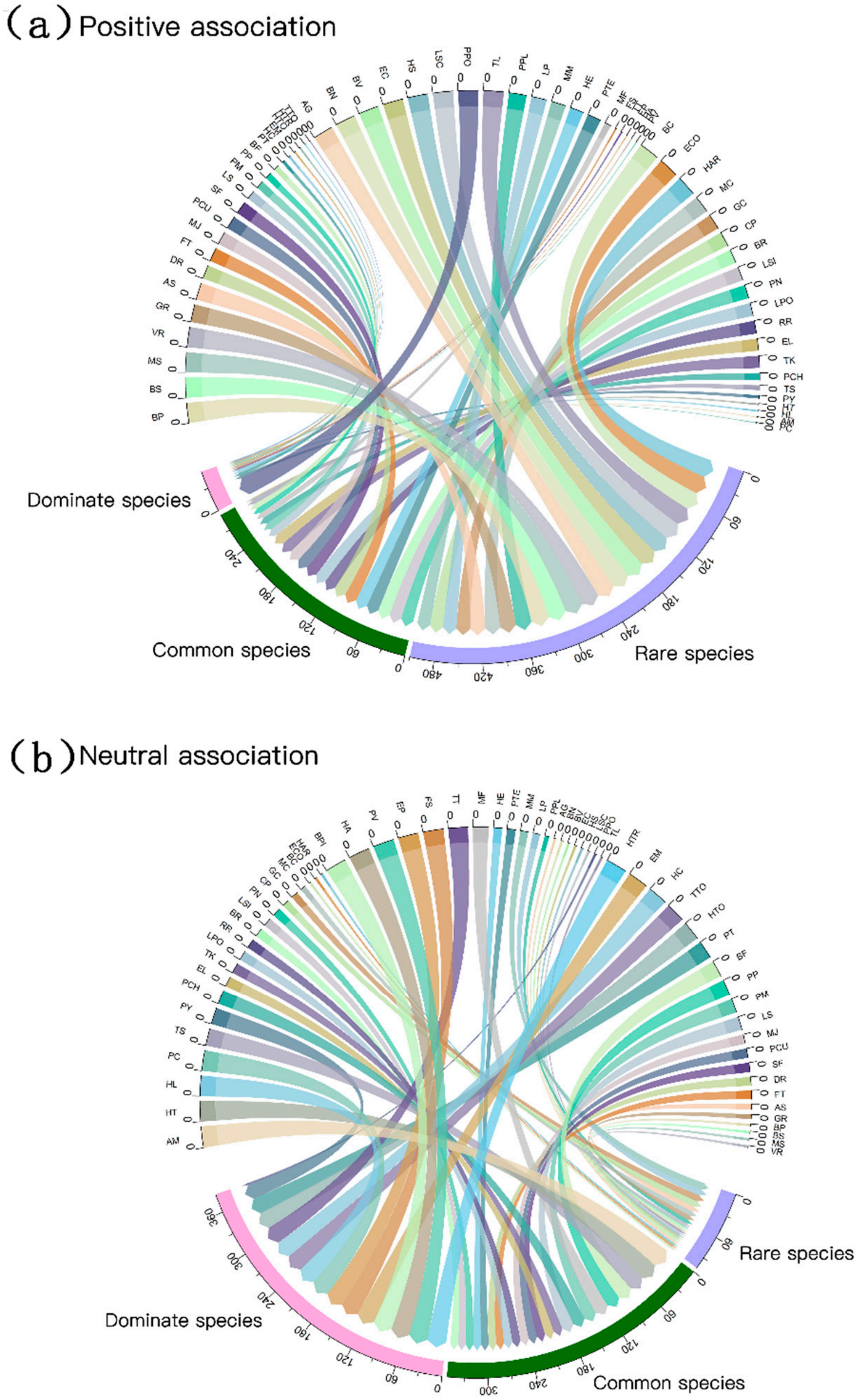

Figure 5. Associations between different groups of bryophytes (rare, common, or dominant species of epiphytic bryophyte) and woody plants based on the results of torus-translation test. The entire network includes all the 28 woody plant species and 61 bryophyte species. There are too few bryophyte species negatively associated with woody plants, so they are not shown here. The abbreviations of woody plants are shown in Table S4. The different groups of bryophytes are shown in Table S6. (**a**) shows the positive correlation, while (**b**) shows the negative correlation.

4. Discussion

The plant–bryophytes network showed that the distribution of bryophytes on the woody plants is specialized and uneven. This characteristic network structure of the plant–bryophyte network may result from the physical (e.g., crack depth, hardness, and roughness) and chemical (e.g., nitrogen, phosphorus, and potassium) property differences among the bark types of different woody plants. However, the organization of the links in the plant–bryophyte networks showed a moderate or relatively low level of modularity [3,14,15]. The H_2' estimate of interaction specialization was from 0.106 to 0.123, which are values as low as those previously reported in plant–fungus networks (0.265) [37], plant–seed disperser networks (0.354) [38], and plant–pollinator networks (0.533) [39]. The reason is that the links in the plant–bryophyte network likely represent the associations between epiphytic bryophytes and woody plants that belong to non-symbiotic systems [40]. Species in non-symbiotic systems should have lower levels of modularity than those in symbiotic systems [37].

The torus-translation test made it possible to evaluate the associations between epiphytic bryophyte and woody plant species. The results showed that most epiphytic bryophytes exhibited ecological habitat preferences for woody plants; without this specific statistical approach, it would be unlikely that such a result would be detected. In the past, the torus-translation test was mainly used for exploring the association between woody plants and topographic habitat factors [18,19]. In our study, 93.44%, 93.44%, and 98.36% of the bryophyte species had significant positive associations with the family, genus, and species of woody plant, respectively. Previous studies have shown that bark with strong acidity is not conducive to the growth of epiphytic bryophytes, and deep cracks in the bark can affect bryophytes' attachment [41,42]. Many of the bryophytes in the study prefer to adhere to individuals of *Quercus aliena* var. *acuteserrata*, perhaps because its bark splits deeper than other woody plants. Few bryophyte species are found on individuals of the *Pinus armandii* species, probably because its bark is more acidic than that of other woody plants [41,43]. Our study demonstrates the importance of niche partitioning of the physical and chemical properties in the bark of different woody plants with respect to the maintenance of local diversity in epiphytic bryophyte communities.

Our result also showed that the epiphytic bryophyte distribution was scale-dependent. Within community ecology, there is extensive evidence for variation in the spatial patterns and processes driving plant diversity at different spatial grains or extents [44–46]. For example, Mills and Macdonald in 2005 [45] found that bryophyte species composition is related to a hierarchy of factors including fine-scale variation in the type and quality of available microsites along with micro-environmental variation at different scales. In our study, the resolution of the sampling unit gradually increased from family to genus to species of woody plant. The results showed that the number of significant associations increased from family to genus to species of the woody plants. These differences provide an insight into the interaction between niche-partitioning processes and the scale of microhabitat heterogeneity. This interaction is useful in determining the scale dependence of epiphytic bryophytes' distribution.

Consistent with our hypothesis, more rare bryophyte species were positively correlated with woody plants than dominant bryophyte species. Dominant bryophytes have a wider ecological niche than rare bryophytes, so they thrive on a wide variety of woody plants [47]. Rare bryophytes may be more sensitive to the changes in the physical and chemical properties of the bark of woody plants and can only adapt to the bark microhabitats of a few woody plants [48]. Considering that rare bryophytes have a stricter demand for microhabitats and fewer individuals, more attention should be paid to rare bryophytes in future conservation.

5. Conclusions

Our study demonstrates that most epiphytic bryophytes exhibit ecological habitat preferences for woody plants in temperate, deciduous broad-leaved forests. These observations highlight the importance of the species composition of woody plants with respect to the maintenance of epiphytic bryophyte diversity. Therefore, the growth preference of bryophytes for woody plants, especially rare bryophyte species, should be considered in the process of bryophytes' diversity conservation. Nevertheless, this study only analyzed the associations of epiphytic bryophytes with the woody plants from a statistical perspective. The direct effects of the bark's physicochemical properties, tree size, and light availability under the canopy on epiphytic bryophytes should be considered in future studies. Our study was conducted in a forest community where *Quercus aliena* var. *acuteserrata* is the dominant species. The relationships between epiphytic bryophytes and woody plants should be explored in more forest communities in future studies.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d14110979/s1, Table S1: Species abundance of bryophytes by families of woody plants; Table S2: Species abundance of bryophytes by genera of woody plants; Table S3: Species abundance of bryophytes by species of woody plants; Table S4: Woody plant composition and abbreviations; Table S5: Bryophyte species composition and abbreviations. Table S6: Rare, common, or dominant species of epiphytic bryophyte in the plot.

Author Contributions: Y.C.: Conceptualization, Writing—original draft, Data curation, Methodology, Software, Funding acquisition, Writing—review and editing, Visualization, Investigation, Formal analysis. S.W.: Visualization, Investigation, Formal analysis. W.L.: Visualization, Investigation, Formal analysis. F.L.: Visualization, Investigation, Formal analysis. Y.S.: Funding acquisition, Resources, Validation, Supervision, Project administration. J.W.: Visualization, Investigation, Formal analysis. Z.Y.: Funding acquisition, Visualization, Investigation, Formal analysis. All authors have read and agreed to the published version of the manuscript.

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Data availability statement: The data presented in this study are available in the article/ Supplementary Material.

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Conflicts of Interest: The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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