Postprint: Ecological Niche Analysis of Bryophytes Based on Two Different Resource Axes

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Abstract

Using community type and substrate type (including corticolous, saxicolous, and terricolous) as resource axes, the niche characteristics of bryophytes in 56 quadrats of the Xiaoqinling Mountains were analyzed and compared. The results showed that: (1) There were certain differences in the niche characteristics of bryophyte species on the two resource axes, and the ranking of niche breadth of bryophyte species changed to some extent across different resource axes. On both resource axes, Brachythecium had relatively large niche breadth, while Oxystegus and Jungermania showed considerable differences in niche breadth across different resource axes. (2) Comparing the niche overlap values on the two resource axes, those on substrate type were significantly higher than those on community type; the ranking of niche overlap values for individual species also changed markedly across different resource axes. Homaliodendron and Pylaisiella showed completely opposite results on the two resource axes. (3) Similar to vascular plants, bryophyte species with larger niche breadth had high niche overlap values, and those with small niche breadth also exhibited considerable niche overlap.

Full Text

Preamble

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Ecological Niche of Bryophytes Based on Two Resource Axes

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Abstract: Bryophytes are relatively primitive species among higher plants and constitute an important component of biodiversity. The ecological adaptability of species varies based on resource space. This study was conducted in the Xiaoqinling Mountains Nature Reserve, located in Lingbao, western Henan Province (34°23 –34°31 N, 110°23 –110°44 E), an area rich in plant resources. Using stratified sampling, fifty-six 20 m × 20 m representative sample plots were established. Trees, shrubs, herbs, and bryophytes were surveyed and sampled. The multiple regression tree method was applied to the 56 plots, with elevation, slope, and aspect as independent variables, and 405 vascular plants in the 56 plots used to determine importance values for community classification. The 56 sample plots were divided into five cluster types defined as different resource bases. Based on the determination of bryophyte epiphytic substrates, which were divided into trees and rocks, characteristic of different resource niches. In two different resource axes, 15 types of importance values were selected, including the order Jungermanniales. Mosses included both acrocarpous and pleurocarpous types. The niche breadth and overlap values of the 15 selected groups were determined using the Shannon-Wiener niche index and Levins niche overlap value. The effects of association between substrate types (trees, rock, and soil) as resource axes on the niche characteristics of bryophytes were examined and compared among the 56 sites.

The results showed: (1) The niche characteristics of bryophytes differed between the two resource axes. On different resource axes, breadth varied among bryophyte species. In particular, the breadth of *Jungermannia* was greater. The breadths of *Brachythecium* in the two types of resource axes differed. In the two resource axes, *Brachythecium* had a larger niche breadth, ecological adaptability, and environmental utilization ability, whereas the niche width of *Oxystegus* was smaller, narrower, and exhibited weaker ecological adaptability. Niche widths differed between the resource axes. (2) The niche overlap values of the substrate for the two resource axes were significantly higher than those of association types. The niche overlap order of individual species on different resource axes also differed. *Pylaisiella* showed opposite results. (3) Similar to that observed in vascular plants, in bryophyte species, niche overlap was high with large niche breadth. Bryophyte species with small niche breadth could also exhibit large niche overlap. For example, *Fissidens* had a large niche breadth, whereas other species had large niche overlap values. However, *Homaliodendron* exhibited niche widths that were small, although they still exhibited large niche overlap values, thereby demonstrating that a certain degree of similarity existed in the use of both resources.

Keywords: bryophyte; association types; growth base types; niche characteristics

Introduction

Niche theory and its applications have been a research focus among scholars both domestically and internationally, widely applied in exploring scientific questions such as community succession, community structure, and interspecific relationships [1-3]. Due to factors such as interspecific competition, species rarely occupy their entire fundamental niche in biological communities. Theoretically, the maximum niche a species can occupy is called the fundamental niche [4-6]. As intraspecific and interspecific correlations within communities change, species niches also change [7].

Bryophytes are small, spore-reproducing higher plants that are the second largest plant group after angiosperms and constitute an important component of biodiversity [8-9]. The growth of bryophyte species is greatly influenced by communities, and they are also an important component of forest ecosystems. Bryophyte community structure differs significantly among different communities. Previous studies on bryophytes in major ecosystems found that ground bryophytes had the highest richness under dark coniferous forests [10]. Guo and Cao found that epiphytic bryophytes had the highest richness and diversity in the transition zone between mixed Korean pine-broadleaf forests and dark coniferous forests in Changbai Mountain [10]. In studies of ground bryophytes in Douglas-fir forests, Rambo and Muir found that the more broadleaf species in the forest and the larger the forest gaps, the higher the diversity of bryophytes [11]. Király et al. [12] and Guo and Cao [10] respectively pointed out that bryophyte richness is also affected by shrub and herb layers, and that habitat has a strong influence, with some bryophyte species having specific habitat preferences. Cao and Guo found in their study of bryophytes in different habitat types in the Changbai Mountain region that rock-dwelling bryophytes were the most species-rich, followed by rotten wood-dwelling and epiphytic species, with soil-dwelling species being fewer and aquatic species the least [13]. Liang et al. found in their investigation of bryophytes in the Helan Mountain region that rock-dwelling mosses were the most numerous, followed by soil-dwelling mosses, with wood-dwelling mosses being the least [14].

Research on the niches of vascular plants, especially woody plants, has matured, but research on bryophytes is still in the preliminary exploration stage. Unlike vascular plants, bryophytes are not only sensitive to their own micro-growth environment, but the larger community environment also has certain impacts on them [15]. Therefore, studying the population niches of bryophytes can help us gain a deeper understanding of intraspecific and interspecific competition among bryophyte populations and is helpful for understanding the status and role of bryophyte populations in the entire forest community. Although considerable work has been done on the ecology of bryophytes, most niche studies on bryophytes have been conducted in single habitats such as epiphytic or soil-dwelling [16-17]. There have been no reports on differences in niche characteristics of bryophyte species in different habitat substrates, nor on research related to the effects of forest community macro-environments and bryophyte micro-growth substrate environments on bryophytes. Therefore, this study investigates the niches of bryophytes under different association types and different growth substrate types in the Xiaoqinling region, aiming to reveal the niche characteristics of bryophytes on different resource axes and their ability to utilize resources and environments, thereby providing a scientific theoretical basis for further research and conservation of bryophyte resources and species diversity in this region.

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1 Study Area Overview

The Xiaoqinling National Nature Reserve is located at the border of Henan and Shaanxi provinces in Lingbao City, western Henan Province, with geographical coordinates of 34°23 –34°31 N, 110°23 –110°44 E. The reserve extends 31 km east-west and 12 km north-south, covering an area of 15,160 hm^2. The main peak, Laoyachan' ao, on the northern slope of the Xiaoqinling Mountains, has an elevation of 2,413.8 m. The region has good vegetation cover with a forest coverage rate of 81.2% [18-20]. The climate belongs to the warm temperate continental monsoon semi-arid type, with annual average temperature of 11.2-14.2°C, extreme maximum temperature of 42.7°C, extreme minimum temperature of -17°C, frost-free period of 210 days, and annual precipitation of 612 mm, concentrated in summer and autumn [21]. The reserve' s strata belong to the Archean Taihua Group, with igneous rocks and thin-layer acidic lithosol soil. The soil pH is 6.2-7.0.

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2 Research Methods

2.1 Data Collection

In July 2015, sample plots were established along elevation gradients in representative communities within the study area. Fifty-six 20 m × 20 m representative plots were set up. In each plot, all trees with DBH 1 cm were surveyed. Additionally, 5 m × 5 m shrub subplots and 1 m × 1 m herb subplots were established in each tree plot. A total of 405 vascular plant species were surveyed. Trees were dominated by Pinaceae, Anacardiaceae, and Rosaceae; shrubs were dominated by Oleaceae, Celastraceae, and Salicaceae; herbs were dominated by Cyperaceae, Gramineae, and Compositae.

All bryophytes in each plot were collected, including rock-dwelling, soil-dwelling, and epiphytic mosses on all woody plants. When multiple moss species grew interwoven, each species was collected separately into paper bags. Different moss clumps were bagged separately. After bagging, the plot number and habitat substrate were recorded. Specimens were brought back to the laboratory for identification using *Flora Bryophytarum Sinicorum* and *Catalogue of Life China*

[23-24]. A total of 2,160 bryophyte specimens were collected and deposited in the Herbarium of Henan Agricultural University.

2.2 Resource Axis Division

To better study bryophyte niche characteristics and explore the effects of different association types and substrate types on bryophyte niches, this study used two resource axis divisions:

1. **Association type axis**: The 56 plots were classified into five association types using multiple regression tree method with elevation, slope, and aspect as independent variables and importance values of 405 vascular plants in the 56 plots as dependent variables [22]. The five association types were:
   - *Euptelea pleiospermum-Acer grosseri-Glechoma longituba* (Ass.)
   - *Poa acroleuca* (white-topped early bluegrass)
   - *Pinus armandii-Betula utilis-Salix phylicifolia-Carex siderosticta* (Ass.)
   - *Quercus mongolica-Rosa bella* (Ass.)
   - *Pinus armandii-Pinus tabuliformis-Acer grosseri-Oplismenus undatifolius* (Ass.)
   - *Cayerus compressus-Forsythia suspensa* (Ass.)
2. **Substrate type axis**: Based on collection substrates, bryophytes were divided into three substrate types: rock-dwelling, soil-dwelling, and tree-dwelling (epiphytic). Each resource state included all bryophytes growing on that substrate. For mosses growing at substrate boundaries, they were assigned based on the substrate type where their rhizoids attached.

2.3 Important Value Calculation

Important value is an indicator of a species' importance or dominance in a community, reflecting its relative importance and optimal habitat [25-27]. Due to their small size and limited distribution ranges, traditional point sampling reduces bryophyte species diversity [13,28]. Considering bryophyte spore dispersal characteristics and the significance of large-scale niche studies, this study conducted complete surveys in 20 m × 20 m plots rather than traditional sampling.

For bryophyte abundance calculation, the number of occurrences of a moss species in one plot was used as its abundance in that plot. Frequency was calculated as the ratio of plots where the species occurred to total plots. Important value was calculated using relative abundance and relative frequency [30]:

$$\text{Important Value} = \frac{\text{Relative Abundance} + \text{Relative Frequency}}{2} \times 100\%$$

Where: - Relative Abundance = (Abundance of a bryophyte species in a plot / Total abundance of all bryophytes in the plot) × 100% - Relative Frequency =

(Frequency of a bryophyte species / Total frequency of all bryophyte species) × 100%

2.4 Niche Breadth Calculation

Niche breadth reflects the degree of resource utilization by species. This study analyzed niche breadth from two perspectives: 1. Using association types as a one-dimensional resource axis, reflecting bryophyte resource utilization in the macro-environment of forest community types 2. Using substrate types as a resource axis, reflecting bryophyte resource utilization in their micro-growth environment

The Shannon-Wiener niche index was used to calculate niche breadth [31]:

$$B_i = -\sum_{j=1}^{r} P_{ij} \ln P_{ij}$$

Where: - B_i = Shannon-Wiener niche breadth of species i - P_{ij} = Proportion of resource j used by species i relative to all resources used - $P_{ij} = n_{ij}/Y_i$ - n_{ij} = Importance value of species i in resource state j - Y_i = Sum of importance values of species i across all resource states

2.5 Niche Overlap Calculation

Niche overlap refers to the degree of shared utilization of a resource state by two species [7,32]. Based on data characteristics, the Levins formula was used [33-34]:

$$C_{ih} = \sum_{j=1}^{r} P_{ij} P_{hj}$$

$$L_{hi} = \frac{C_{ih}}{B_L(h)} \quad L_{ih} = \frac{C_{ih}}{B_L(i)}$$

Where: - L_{ih} = Niche overlap value of species i on species h - L_{hi} = Niche overlap value of species h on species i - $B_L(i)$ and $B_L(h)$ = Levins niche breadth indices - The domain of L_{hi} and L_{ih} is [0,1]

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3 Results

3.1 Important Value Analysis of Bryophyte Genera

Important values were calculated under both association type and substrate type resource axes. Fifteen genera were analyzed, including *Jungermannia* (a liverwort genus) and moss genera containing both acrocarpous and pleurocarpous species. Under both resource divisions, *Brachythecium* and *Plagiomnium* had significantly higher important values than others, indicating their dominant status in the bryophyte community of this region.

Important values of bryophytes in different association types

Important values of bryophytes under different substrate types

3.2 Niche Breadth Analysis

Niche breadth primarily reflects species' utilization of surrounding resources. When using different association types as the resource axis, the ranking of niche breadth was: *Brachythecium* > *Plagiomnium* > *Entodon* > *Taxiphyllum* > *Thuidium* > *Minum* > *Pylaisiadelpha* > *Eurhynchium* > *Anomodon* > *Jungermannia* > *Pylaisiella* > *Atrichum* > *Fissidens* > *Homaliodendron* > *Oxystegus*.

When using different substrate types as the resource axis, the ranking was: *Brachythecium* > *Plagiomnium* > *Entodon* > *Minum* > *Eurhynchium* > *Thuidium* > *Taxiphyllum* > *Anomodon* > *Jungermannia* > *Pylaisiadelpha* > *Fissidens* > *Oxystegus* > *Atrichum* > *Homaliodendron* > *Pylaisiella*.

Brachythecium had the largest niche breadth under both axes, indicating the widest ecological adaptation range and strong environmental resource utilization ability. *Homaliodendron* had relatively small niche breadth, indicating narrow ecological adaptation range and weak adaptability. The ranking of bryophyte niche breadth differed between the two axes, particularly for *Oxystegus* and *Jungermannia*, suggesting these genera have strong adaptation to their micro-growth environments but different adaptation abilities to forest community macro-environments.

[Figure 1: see original paper] Niche breadth of bryophytes in two resource axes

3.3 Niche Overlap Analysis

When using association types as the resource axis, among 105 species pairs, 51 pairs (48.57%) had niche overlap values $L < 0.10$, 42 pairs (40.00%) had $0.10 < L < 0.20$, 10 pairs (9.52%) had $0.20 < L < 0.30$, and 2 pairs (1.90%) had $L > 0.30$.

When using substrate types as the resource axis, 0 pairs had $L < 0.10$, 30 pairs (28.57%) had $0.10 < L < 0.20$, 62 pairs (59.05%) had $0.20 < L < 0.30$, and 13 pairs (12.38%) had $L > 0.30$.

[Figure 2: see original paper] Niche overlap value of cluster type
[Figure 3: see original paper] Niche overlap value of substrate type

In both methods, species pairs with larger niche breadth showed relatively high niche overlap values, indicating that populations with wide niches are more likely to overlap due to similar resource utilization. However, species with small niche breadth could also show large niche overlap. For example, *Atrichum* and *Oxystegus* had large niche overlap values despite their small niche breadths.

Niche overlap values differed between the two methods. When using substrate types as the resource axis, overlap values were significantly higher than when using association types, indicating that most bryophyte species have similar requirements in their micro-growth environment but differ in resource utilization in the forest community macro-environment. Notably, *Homaliodendron* and *Pylaisiella* showed completely opposite patterns: under association types, their overlap values were the smallest (L_{ih} and L_{hi} = 0.034-0.038), but under substrate types, their overlap values were among the largest (L_{ih} and L_{hi} = 0.33). Conversely, *Taxiphyllum* and *Pylaisiella* had large overlap under association types (L_{ih} and L_{hi} = 0.15) but small overlap under substrate types. These opposite patterns may result from differences in biological characteristics and resource utilization at different environmental scales, which is beneficial for species coexistence.

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4 Discussion

Niche breadth reflects the degree of environmental resource utilization and adaptation status of species, characterizing ecological adaptability and distribution range—the larger the niche breadth, the stronger the environmental adaptability [35]. The Shannon-Wiener niche breadth formula applied to both association and substrate resource axes revealed differences in niche breadth. The two resource axes represent different resource dimensions for bryophyte growth.

Brachythecium had the largest niche breadth under both axes, indicating the widest ecological adaptation range. *Thuidium* also had relatively large niche breadth, showing strong environmental adaptability. In contrast, *Oxystegus* and *Jungermannia* showed large differences between the two axes, possibly due to weaker adaptability under different association types. For example, these two genera were absent in Association Type 1 (*Pinus armandii-Pinus tabuliformis-Acer grosseri-Oplismenus undatifolius*), but showed strong adaptability across different substrate types. This aligns with Lin et al.' s [36] conclusion that main populations in mixed conifer-broadleaf forests have different ecological adaptabilities in different resource spaces.

Niche overlap refers to the phenomenon where two or more species jointly utilize or occupy the same resource factor [37]. Larger niche overlap values between two populations indicate similar resource utilization or similarity in certain ecological factor relationships. Niche overlap values differed significantly between the two resource axes, with substrate type showing significantly higher values than association type, indicating that most bryophyte species have similar requirements in their micro-growth environment but show greater differentiation in forest community macro-environment resource utilization. This pattern is consistent with Chen et al.' s [38] findings on ground mosses and reflects Guo and

Cao' s [17] research on ground bryophytes under three forest types in Changbai Mountain.

In bryophytes, similar to vascular plants, species with large niche breadth tend to have large niche overlap values, but species with small niche breadth may also have large overlap values. Small niche differentiation on growth substrates may not favor bryophyte coexistence, but differences in adaptation among different communities increase niche differentiation, reducing competition for the same resources and facilitating overall coexistence. As resource axes increase, niche differentiation among species may gradually increase, possibly explaining why more species can coexist in resource-rich environments, though the specific mechanisms require further study.

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5 Conclusion

This study applied niche theory to investigate and compare niche breadth and overlap values of bryophytes in the Xiaoqinling region along two resource axes. The results showed:

1. Bryophyte niche characteristics differed significantly between the two resource axes. *Brachythecium* showed wide niche breadth on both axes, while other bryophytes showed varying degrees of difference, particularly *Oxystegus* and *Jungermannia*.
2. The principle that species with larger niche breadth also have larger niche overlap values applies to bryophyte populations on both resource axes.
3. Studies on bryophyte niches using association types and habitat types are important for revealing interspecific relationships and ecological adaptability of bryophytes, and provide insights into the mechanisms of bryophyte existence in forest environments.

These results contribute to understanding bryophyte biology and provide a scientific basis for conservation of bryophyte resources and species diversity in the Xiaoqinling region.

References

[1] Modern niche theory in contemporary ecology. *Advances in Ecology*, 1988, 5(2): 77-84.
[2] Elton C S. *Animal Ecology*. Chicago: University of Chicago Press, 2001.
[3] Leibold M A. The niche concept revisited: mechanistic models and community context. *Ecology*, 1995, 76(5): 1371-1382.
[4] Niche state theory and expansion hypothesis. *Acta Ecologica Sinica*, 1997, 17(3): 324-332.

[5] May R M. *Theoretical Ecology*. Beijing: Science Press, 1980: 58-64.
[6] Curtis J T, McIntosh R P. An upland forest continuum in the prairie-forest border region of Wisconsin. *Ecology*, 1951, 32(3): 476-496.
[7] Discussion on niche definition and improvement of niche overlap measurement formulas. *Acta Ecologica Sinica*, 1984, 4(2): 119-127.
[8] Schofield W B. *Introduction to Bryology*. New York: Macmillan Publishing Company, 1985.
[9] Diversity of bryophytes. *Biodiversity Science*, 1999, 7(4): 332-339.
[10] Guo S, Cao T. Relationship between epiphytic bryophyte distribution and environment in Changbai Mountain forest ecosystems. *Acta Ecologica Sinica*, 2000, 20(6): 922-931.
[11] Rambo T R, Muir P S. Forest floor bryophytes of *Pseudotsuga menziesii-Tsuga heterophylla* stands in Oregon: influences of substrate and overstory. *The Bryologist*, 1998, 101(1): 116-130.
[12] Király I, Nascimbene J, Tinya F, Ódor P. Factors influencing epiphytic bryophyte and lichen species richness at different spatial scales in managed temperate forests. *Biodiversity and Conservation*, 2013, 22(1): 209-223.
[13] Cao T, Guo S. Bryophyte diversity in different habitat types in Changbai Mountain region. *Biodiversity Science*, 2000, 8(1): 50-59.
[14] Liang et al. Bryophyte species diversity in Helan Mountain. *Journal of Inner Mongolia University (Natural Science Edition)*, 1998, 29(1): 118-124.
[15] Bryophyte biology. Beijing: Science Press, 1998.
[16] Epiphytic bryophyte niches in Shanghai. *Chinese Journal of Ecology*, 2006, 25(11): 1338-1343.
[17] Guo S, Cao T. Niche studies of ground bryophytes in main ecosystems of Changbai Mountain. *Acta Ecologica Sinica*, 2001, 21(2): 231-236.
[18] Scientific expedition collection of Henan Xiaoqinling Nature Reserve. Beijing: Science Press, 2004.
[19] Bird survey of Xiaoqinling National Nature Reserve. *Northwest Plant Journal*, 2011, (24): 38-38.
[20] Comparison of community characteristics between planted and natural secondary *Pinus armandii* forests in Huoditang forest region of Qinling Mountains. *Acta Botanica Boreali-Occidentalia*, 2009, 29(11): 2301-2311.
[21] Causes of *Abies chensiensis* death in Xiaoqinling Nature Reserve. *Acta Ecologica Sinica*, 2016, 36(7): 1936-1945.
[22] Quantitative classification, ordination and vertical patterns of diversity in Xiaoqinling forest communities. *Acta Ecologica Sinica*, 2014, 34(8): 2068-2075.
[23] *Flora Bryophytarum Sinicorum*. Beijing: Science Press, 2010.
[24] *Catalogue of Life China*. Beijing: Science Press, 2013.
[25] Species diversity and community dynamics in several deciduous broadleaf forests in warm temperate zones. *Chinese Journal of Plant Ecology*, 2001, 25(3): 283-290.
[26] Measurement methods for biological community diversity. *Chinese Journal of Plant Ecology*, 1986, 10(3): 161-170.
[27] Principles and methods for biodiversity research. Beijing: China Science and Technology Press, 1994: 141-165.

[28] Effects of quadrat size on bryophyte ecological indicators. *Journal of Shanxi University (Natural Science Edition)*, 2011, 31(2): 198-203.
[29] Jia H. [D]. 2015.
[30] Issues regarding important value calculation methods. *Journal of Ecology*, 1992, 11(2): 44-49, 35-35.
[31] Mathematical methods in niche theory research. *Chinese Journal of Applied Ecology*, 1994, 5(3): 331-337.
[32] Colwell R K, Futuyma D J. On the measurement of niche breadth and overlap. *Ecology*, 1971, 52(4): 567-576.
[33] Hurlbert S H. The measurement of niche overlap and some relatives. *Ecology*, 1978, 59(1): 67-77.
[34] Niche analysis of dominant species in Guandishan Shenweigou. *Wuhan Botanical Research*, 2002, 20(3): 203-208.
[35] Multidimensional niche characteristics of main populations in mixed conifer-broadleaf forests. *Acta Ecologica Sinica*, 1994, 14(1): 32-39.
[36] Lin S, et al. Multidimensional niche breadth measurement. *Chinese Journal of Applied Ecology*, 2005, 16(1): 39-43.
[37] Niche theory and coexistence mechanisms. *Acta Ecologica Sinica*, 2002, 22(6): 962-968.
[38] Chen Y, et al. Ground moss niches in Shanghai. *Chinese Journal of Ecology*, 2010, 33(2): 312-316.

Note: Figure translations are in progress. See original paper for figures.