Postprint: A Study on Lichen Ecological Niche Characteristics in the Dabancheng Mountainous Area, Urumqi

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Abstract

To reveal the utilization status of habitat resources and competition intensity among lichens in the Dabancheng mountainous area, this study established 30 quadrats in the field and surveyed species coverage data, employing niche breadth, niche overlap indices, and ordination analysis to investigate the niche characteristics and environmental influencing factors of lichens in this region. The results indicated: (1) Rusavskia elegans and Circinaria contorta exhibited the widest niches in the Dabancheng mountainous area, demonstrating strong adaptability to various environments, whereas other lichen species possessed relatively narrow niche breadths with low utilization of environmental resources. (2) Niche overlap values among species were generally low, with very few species pairs displaying high overlap; lichen species showed a high degree of niche differentiation, and interspecific competition was not intense. (3) Species with broader niches exhibited niche overlap with most other species, but the overlap values remained low; conversely, some species with narrow niche breadths showed relatively high niche overlap values with other species; no direct linear relationship existed between niche overlap and niche breadth. (4) Lichen species distribution differed along the altitudinal gradient, with altitude, light intensity, humidity, wind speed, and disturbance being the dominant environmental factors driving differences in niche characteristics of lichen community species in this region. In summary, lichen species in the Dabancheng mountainous area occupied distinct niches due to competition for habitat resources, resulting in niche differentiation; the community was relatively stable; and differences in habitat conditions along the altitudinal gradient constituted an important reason for the differential distribution of species. This study can provide a theoretical basis for research on lichen community assembly and holds great significance for the conservation of lichen species diversity and habitats in this region.

Full Text

Preamble

Niche Characteristics of Lichen Species in the Dabancheng Mountainous Area, Urumqi

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Abstract

To reveal the status of habitat resource utilization and the degree of competition among lichens in the Dabancheng mountainous area, this study established 30 sample plots in the field and investigated species coverage data. Using niche width, niche overlap indices, and ordination analysis, we examined the niche characteristics of lichens and their environmental driving factors. The results showed: (1) *Rusavskia elegans* and *Circinaria contorta* had the broadest niches in the Dabancheng mountainous area, demonstrating strong adaptability to different environments, while other lichen species exhibited narrow niche widths and low utilization of environmental resources. (2) Niche overlap values between species were generally low, with very few species pairs showing high overlap, indicating high niche differentiation and weak interspecific competition. (3) Species with broader niches overlapped with many other species but at low values; some narrow-niche species showed high overlap with others, revealing no direct linear relationship between niche overlap and niche width. (4) Lichen species distribution varied along the altitudinal gradient, with altitude, light intensity, humidity, wind speed, and disturbance being the dominant environmental factors influencing niche characteristics. In summary, through competition for habitat resources, lichen species in the Dabancheng mountainous area occupy distinct niches, forming niche differentiation and relatively stable communities. Differences in habitat conditions along altitudinal gradients represent an important cause of species distribution patterns. This study provides a theoretical basis for research on lichen community assembly and is significant for the conservation of lichen diversity and habitats in the region.

Keywords: lichen, niche width, niche overlap, altitudinal gradient, Dabancheng mountainous area

Introduction

Niche theory has long been a mainstream concept in community ecology, and studies on species niche characteristics can reflect their status and role within communities. Johnson (1910) first used the concept of "niche" without formally defining it, while Grinnell (1917) formally defined niche as the positional characteristics occupied by different species or subspecies in different environments. Subsequent scholars systematically studied niche definitions and quantitative measurement methods (Gause, 1934; Keddy, 1992; Vannette & Fukami, 2014), elaborating and validating niche theory from multiple perspectives and establishing that niche differentiation forms the basis of species coexistence. Despite numerous challenges in defining, quantifying, and measuring niches during the development of ecological research, niche theory has achieved substantial results in community ecology (Sales et al., 2021; Niu et al., 2022) and remains an important framework for studying mechanisms of species coexistence and diversity maintenance.

Quantitative niche research primarily involves calculating niche width and niche overlap values to reflect species' resource utilization capabilities and similarity (Pang et al., 2022). Currently, numerous studies both domestically and internationally have quantitatively analyzed the spatial ranges and habitat resource utilization capabilities of species in communities to explore niche mechanisms underlying species coexistence, focusing mainly on herbaceous, shrub, arboreal, and moss communities (Chen et al., 2009; Sun et al., 2021; Cao et al., 2021; Pang et al., 2022). Early research on lichen community ecology primarily focused on traditional species diversity indices to explore distribution patterns. Additionally, due to their unique structure and high sensitivity to environmental and climate changes, some studies have assessed pollution levels, climate change, and disturbance in forests, cities, and protected areas by examining relationships between lichen diversity and air pollution, environmental change, and disturbance (Lubek et al., 2018; Koch et al., 2019; Lucheta et al., 2019). With the widespread application of quantitative niche methods in higher plants, these approaches have gradually been applied to lichens, though such studies remain limited (Anwar et al., 2012; Giordani et al., 2015; Jin & Anwar, 2017; Rolshausen et al., 2018; Li et al., 2021; Tian & Anwar, 2021). Tian et al. (2021) analyzed niche characteristics of lichens on the northern slope of Bogda Peak by calculating niche width and overlap, finding that differences in resource utilization capabilities led to niche differentiation. Baihetinisha et al. (2022) analyzed niche characteristics of saxicolous lichens at Tianshan No. 1 Glacier, indicating small differences in resource utilization capabilities and widespread competitive relationships among species. These studies suggest that lichen niches may be influenced by interspecific competition and environmental factors, but they did not analyze niche characteristics in combination with specific environmental factors. However, population niches are affected by both biotic factors such as human activity and abiotic environmental factors (Sun et al., 2022), and given that lichens are highly sensitive to environmental changes, environmental factors may significantly influence lichen niches.

The Dabancheng mountainous area is a severely arid and semi-arid region with strong light exposure and abundant exposed rocks compared to other study areas. Lichens are considered pioneers in desert ecosystems and play important roles in early plant community succession. In this region, lichens dominate the vegetation, particularly covering rock surfaces where higher plants cannot grow, making them ecologically significant. Therefore, this study quantitatively analyzed lichen niche characteristics in the Dabancheng mountainous area by calculating niche width and overlap values in combination with environmental factors to address two scientific questions: (1) What are the niche characteristics of lichen species? (2) How do environmental factors influence species niche characteristics? Based on traditional lichen diversity and distribution patterns, this study explores mechanisms underlying lichen diversity maintenance from a niche perspective, providing more comprehensive information on species-environment relationships, interspecific interactions, and species traits. This research provides a basis for lichen diversity conservation and is significant for studying and protecting the unique desert habitats of Dabancheng.

1.1 Study Area Overview

The Dabancheng District is located between the western and eastern Tianshan Mountains at the southern foot of Bogda Peak, the highest peak in the eastern Tianshan range, on the southern outskirts of Urumqi, approximately 86 km from the city center. It forms a semi-enclosed valley surrounded by mountains on three sides. The northern mountainous area of Dabancheng District lies on the southern slope of Bogda Peak, covering about one-third of the total district area, with geographical coordinates of 88°19 -88°32 E, 44°21 -44°38 N. The terrain is complex, with mountains rising from southwest to northeast, and climate varies significantly with altitude. Due to structural differences in the mountains, areas below 1800 m in the Dabancheng mountainous region experience severe desert influence and belong to a mid-temperate continental arid climate zone with dry conditions and little rainfall throughout the year. This severely arid and semi-arid region represents a typical desert and semi-desert area in the Eurasian hinterland and serves as an important ecological barrier and restoration zone for Urumqi. These special climatic conditions have led to unique desert climate adaptation mechanisms in local organisms (Thomas et al., 2003; Ren et al., 2011).

1.2.1 Field Survey and Sampling

Field surveys were conducted at six sites in the Dabancheng District. Between 1500 m and 3500 m altitude, we selected 30 plots measuring 20 m × 20 m. Within each plot, five 1 m × 1 m quadrats were randomly established. All lichen species within the quadrats were identified, and substrate types were recorded. A 50 cm × 50 cm grid was used to count the number of grids occupied by each lichen species, and average coverage for each species in the plot was calculated based on grid occupancy proportions. According to lichen and vegetation distribution patterns, the sampling area was divided into four altitudinal zones: low altitude (<2000 m, 9 quadrats), mid-low altitude (2000–2500 m, 9 quadrats), mid-high altitude (2500–3000 m, 3 quadrats), and high altitude (>3000 m, 9 quadrats). Collected lichens were brought to the laboratory for specimen preparation and identified using morphological and anatomical characteristics combined with chemical spot tests. Species identification followed *Lichens of Xinjiang* (Abdulla & Wu, 1998), *Conspectus of Chinese Lichens*

(2nd edition), *Lichens of North America*, and recent literature. All specimens are stored in the Lichen Herbarium of Xinjiang University (XJU-L).

1.2.2 Niche Width Calculations

Levins (1968) niche width and Shannon-Wiener niche width (Zhang, 2004) were calculated as:

$$B_i = \frac{1}{\sum_{j=1}^{r} P_{ij}^2}$$

$$B_\alpha = -\sum_{j=1}^{r} (P_{ij} \ln P_{ij})$$

where B_i is the Levins niche width for species i, B_α is the Shannon-Wiener niche width for species i, $P_{ij} = n_{ij}/N_i^+$ represents the proportion of individuals of species i in resource state j relative to the total number of individuals of that species, n_{ij} is the quantity of resource state j utilized by population i (represented by species coverage of species i in quadrat j), N_i is the total quantity of population i, and r is the number of quadrats.

1.2.3 Niche Overlap Calculation

Pianka (1974) niche overlap (Zhang, 2004) was calculated as:

$$O_{ik} = \frac{\sum_{j=1}^{r} P_{ij} P_{kj}}{\sqrt{\sum_{j=1}^{r} P_{ij}^2 \sum_{j=1}^{r} P_{kj}^2}}$$

where O_{ik} is the niche overlap value between species i and k, with a value range of [0,1]; $P_{kj} = n_{kj}/N_k^+$ represents the proportion of individuals of species k in resource state j relative to the total number of individuals of that species, and n_{kj} is the quantity of resource state j utilized by population k.

The total mean of all niche overlap values among populations in the plot = total number of niche overlap values among all populations in the plot / total number of species pairs.

1.2.4 Diversity Indices

Species richness (S), Shannon-Wiener diversity index (H) (Shannon & Wiener, 1949), Simpson index (D) (Simpson, 1949), and Pielou evenness index (J) (Pielou, 1975) (Zhang, 2004) were calculated as:

$$S = \text{number of species in the quadrat}$$

$$H = -\sum_{i=1}^{S} P_i \ln P_i$$

$$D = 1 - \sum_{i=1}^{S} P_i^2$$

$$J = \frac{H}{\ln S}$$

where S is species richness, P_i represents the abundance proportion of the ith species, i.e., $P_i = N_i/N_0$; N_i is the total quantity of population i, and N_0 is the sum of quantities for all S species.

1.2.5 Statistical Analysis

Calculations of niche width values, niche overlap values, and species diversity indices, as well as cluster analysis, were performed using the "spaa" and "cluster" packages in R 4.0.2 software. Canonical correspondence analysis (CCA), redundancy analysis (RDA) ordination, and principal coordinates analysis (PCoA) of niche characteristics and environmental factors were conducted using CANOCO 5.0 software.

2.1 Niche Width of Lichens in the Dabancheng Mountainous Area

The trends for Levins and Shannon-Wiener niche width values of lichen species in the Dabancheng mountainous area were consistent (Table 1). The species with the broadest Levins niche width was *Circinaria contorta* (Levins $B_\alpha = 12.0934$, Shannon-Wiener $B_i = 2.6007$), while the species with the broadest Shannon-Wiener niche width was *Rusavskia elegans* (Levins $B_\alpha = 11.6655$, Shannon-Wiener $B_i = 2.6929$). These two species exhibited the widest niches, occurring in most surveyed quadrats with broad distribution ranges and full utilization of environmental resources. Species with relatively broad niches included *Lecanora argopholis*, *Lecidea tessellata*, *Xanthoparmelia wyomingica*, *Acarospora rosulata*, *Lobothallia alphoplaca*, and *Protoparmeliopsis peltata*, which had relatively wide adaptive ranges and could sufficiently utilize habitat resources.

Thirty-eight species exhibited narrow niches, including *Acarospora bullata*, *A. stapfiana*, *Xanthoparmelia coreana*, *Cladonia mitis*, *C. humilis*, etc., with Levins and Shannon-Wiener niche widths of $B_\alpha = 1$ and $B_i = 0$, respectively. These species were recorded in only one quadrat during the survey, indicating narrow ecological adaptation ranges.

Statistical analysis of species numbers across different niche width categories revealed 64 species with Levins niche width $B_\alpha < 2$ and 69 species with Shannon-Wiener niche width $B_i < 1$ (Table 2), indicating that most lichens in the Dabancheng mountainous area have narrow niche widths, limited ecological adaptation ranges, and weak resource utilization capabilities. These species were distributed in individual quadrats within different environmental zones, with relatively concentrated distributions resulting in low niche width indices.

2.2 Niche Overlap Among Lichens in the Dabancheng Mountainous Area

Niche overlap values between lichen species in the Dabancheng mountainous area were generally low. Species pairs with overlap values less than 0.1 accounted for 80.07% of all pairs, with 66.81% showing zero overlap. Species pairs with overlap values between 0.1 and 0.5 represented 15.51% of all pairs, while those between 0.5 and 1.0 comprised only 4.42%. This indicates low similarity in resource utilization among different lichen populations, with species differing in their adaptation to habitat resources, forming niche differentiation and weak interspecific competition (Supplementary Table 1).

Generally, species with broader niches have wider distributions and greater opportunities to overlap with other species. *Circinaria contorta*, with the broadest Levins niche width, overlapped with 77 species, but all overlap values were less than 0.65. *Rusavskia elegans*, with the broadest Shannon-Wiener niche width, overlapped with 94 species, with the highest overlap value of 0.84 with *Lichinella nigritella*, but relatively low values with other species. Narrow-niche species overlapped with few other species but showed high overlap values when they did. This demonstrates that broad-niche species have higher probabilities of overlapping with others but not necessarily higher overlap values, while narrow-niche species have lower probabilities of overlap but may exhibit higher values when overlap occurs.

Cluster analysis and ordination based on niche overlap values for the 111 lichen species surveyed in the Dabancheng mountainous area, combined with PCoA results, divided these species into three ecological groups (Figure 1 [Figure 1: see original paper]).

The first ecological group included 55 lichen species such as *Rusavskia elegans*, *Circinaria contorta*, *Lecanora argopholis*, *Candelariella rosulans*, and *Acarospora pulvinata*, which were distributed across quadrats in different altitudinal zones with relatively wide distribution ranges. The two species with the broadest Levins and Shannon-Wiener niche widths (*R. elegans* and *C. contorta*) belonged to this group, overlapping with most other lichen species. The second ecological group comprised 27 species including *Dimelaena oreina*, *Aspicilia subcaesia*, *A. persica*, and *A. verrucigera*, which were mainly distributed in high-altitude regions above 3000 m with no human disturbance, strong winds, high humidity, and weak light on shaded slopes. The third ecological group included 29 species such as *Lecidea tessellata*, *Protoparmeliopsis peltata*, *Umbilicaria virginis*, *Candelariella aurella*, and *Sporastatia asiatica*, which were primarily distributed in mid-high altitude regions of 2500–3000 m with weak human disturbance and high humidity.

These results indicate that lichen species distribution differs among altitudinal zones in the Dabancheng mountainous area, primarily due to differences in habitat conditions across these zones. Low-altitude regions are relatively dry with strong light, while humidity increases with altitude, providing more niches for species survival.

2.3 Species Distribution Across Different Altitudinal Gradients

Based on vegetation distribution patterns and plot locations in the Dabancheng mountainous area, the sampling region was divided into four altitudinal zones at 500 m intervals to analyze lichen diversity and distribution patterns across different altitude ranges.

Using coverage data for 111 species from 30 quadrats in the Dabancheng mountainous area, Bray-Curtis distances between plots were calculated and PCoA ordination was performed (Figure 2 [Figure 2: see original paper]). The first and second axes explained 34% of the total variance, with quadrats from different altitudes arranged sequentially along these axes. Low-altitude quadrats showed greater dispersion, while high-altitude quadrats were relatively clustered, indicating greater variation in lichen community composition among low-altitude plots. However, quadrats were ordered along axis 1 from low to high altitudes, demonstrating differences in lichen community species between high and low altitudinal gradients.

Diversity indices were calculated for lichen species in different altitudinal zones and analyzed using one-way ANOVA (Figure 3 [Figure 3: see original paper]). Species richness was highest in high-altitude regions above 3000 m and lowest in low-altitude regions (<2000 m). Shannon-Wiener diversity index, Simpson index, and Pielou index were higher in mid-high altitude regions (2500–3000 m) and lower in low-altitude (<2000 m) and high-altitude (>3000 m) regions. One-way ANOVA indicated significant differences in Pielou evenness index between regions above 3000 m and below 2500 m ($P < 0.05$), while other diversity indices showed no significant differences among altitudinal zones ($P > 0.05$) (Figure 3).

2.4 Environmental Interpretation of Niche Characteristics

DCA analysis was performed on the relationship between niche width and niche overlap values of lichen community species and environmental factors across different quadrats. The gradient length of the first ordination axis for niche width was between 3 and 4, and the cumulative variance explained by the first four axes of RDA ordination was greater than that of CCA, so RDA was used to analyze the relationship between niche width and environmental factors. The gradient length of the first ordination axis for niche overlap was greater than 4, so CCA ordination was selected and displayed in a two-dimensional projection (Figure 4 [Figure 4: see original paper]).

The RDA ordination for niche width showed positive correlations with altitude, wind speed, and humidity, and negative correlations with light intensity, disturbance, and slope aspect. In the CCA ordination for niche overlap, light intensity and disturbance showed positive correlations, while altitude, humidity, wind speed, and slope aspect showed negative correlations. Overall, altitude was the most strongly correlated environmental factor with both niche width and niche overlap, followed by light intensity, wind speed, humidity, disturbance, and slope aspect, with slope aspect having non-significant effects on niche characteristics.

3 Discussion and Conclusion

Niche width quantitatively reflects the degree of diversification or specialization in habitat resource utilization and differences in environmental adaptation among species (Nie et al., 2021). In other words, broader niche width indicates stronger resource utilization capability and often leads to dominant species in communities (Sun et al., 2022). This study found that *Rusavskia elegans* is widely distributed on rock surfaces across different altitudes and habitats, showing strong adaptability to various environments and serving as a dominant species in the region. This is related to the high environmental tolerance of *R. elegans*, which exhibits high accumulation capacity for pollutant elements and tolerance to harsh habitats, resulting in high generalization and full utilization of habitat resources (Zhao et al., 2019). Additionally, *Circinaria contorta* also showed relatively broad niche width, possibly because the study treated each sampling plot as a resource state, reflecting comprehensive resource utilization status (Luo et al., 2021). Although *C. contorta* had low abundance, it could utilize different habitat resources across most plots, indicating that these two species have low habitat requirements and can adapt to the harsh conditions of the region, playing important roles in lichen community assembly. Most lichens in this region exhibited narrow niche widths, closely related to local habitat conditions. Low-altitude areas experience severe desertification with drought-tolerant saxicolous lichens, while high-altitude areas have significantly higher proportions of foliose lichens. The aggregated distribution of species with similar ecological requirements in different habitats leads to high specialization and low resource utilization.

Niche overlap primarily reflects the degree of intersection in resource utilization among species in space, as well as the similarity of biological and ecological characteristics, which can explain symbiotic and competitive relationships to some extent (Xiao et al., 2021). Higher niche overlap indicates more similar resource requirements and more intense interspecific competition. The generally low niche overlap values among lichen species pairs in this region indicate widespread niche differences, high niche differentiation, weak interspecific competition, and relatively stable communities. Although the study area is overall arid with low habitat heterogeneity, the extremely small size of lichen thalli makes microhabitats critically important. Lichens occupy unique microhabitats, maintaining coordinated and stable interspecific relationships. Gause (1934) argued that niche overlap is merely a non-essential prerequisite for competition; in other words, whether competition exists between species depends on specific habitat conditions. Only when resources are scarce or insufficient does niche overlap lead to competitive exclusion. The overall harsh environment and relative resource scarcity in this region suggest that lichen species experienced intense competition during early colonization, but subsequently occupied their suitable ecological resource niches, forming niche differentiation that resulted in generally low overlap values. On the other hand, treating survey quadrats as comprehensive habitat resource states with high species distribution overlap also contributes to low niche overlap values (Zong et al., 2021).

Species with broad niches and wide distribution ranges are more likely to overlap with other species (Jing et al., 2020). Most lichen species in this region are saxicolous crustose lichens with strong environmental adaptability, distributed across different altitudinal zones, resulting in high probabilities of niche overlap with other species. For example, broad-niche species such as *Circinaria contorta* and *Rusavskia elegans* overlapped with many species but at low values. In contrast, some narrow-niche species such as *Cladonia mitis*, *C. humilis*, *Calogaya pusilla*, *Caloplaca cerina*, and *Circinaria maculata*, due to their specific habitat requirements, were mainly distributed in undisturbed, high-humidity, high-altitude regions and were recorded in only single quadrats, yet showed high niche overlap with other species. This aligns with some studies finding no direct linear relationship between niche overlap and niche width (Sun et al., 2021), possibly related to species' biological and ecological characteristics (Guo et al., 2009), leading to complementary resource utilization or resulting from co-occurrence in the same quadrat.

Differences in niche characteristics result from the combined effects of various environmental factors. Previous studies have shown that lichen distribution is related to light, humidity, temperature, altitude (Baniya et al., 2010; Sahu et al., 2019; Nascimento et al., 2021), and other environmental factors. The Dabancheng mountainous area suffers severe desertification with dry habitats and scarce resources. Ordination analysis revealed altitude as an important factor influencing lichen niche characteristics. With increasing altitude, humidity increases and human disturbance decreases, creating more suitable conditions for species colonization. Additionally, increased water availability facilitates the growth of foliose and fruticose lichens with higher water requirements (Gauslaa, 2014), resulting in highest species diversity in the mid-high altitude region of 2500–3000 m. Lichen diversity decreased at high altitudes, mainly due to harsh habitat conditions and strong winds that may be unfavorable for lichen growth (Pottier et al., 2013). This study found that altitude, humidity, and light intensity significantly influenced lichen niche characteristics, primarily because altitude affects humidity and light conditions. Therefore, differences in habitat conditions along altitudinal gradients lead to species niche differentiation. Overall, lichen species distribution varies along altitudinal gradients in the Dabancheng mountainous area, with niche differentiation formed through habitat resource competition, resulting in relatively stable communities. However, due to the relatively harsh habitat conditions, these communities are fragile and sensitive to external disturbance, which may affect lichen diversity and ecosystem stability. Therefore, avoiding significant human disturbance is crucial for ecological conservation in this region.

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Supplementary Table 1 Niche Overlap of Lichens in the Dabancheng Mountainous Area

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

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