

# Niche and Interspecific Association of Terricolous Macrolichens in Tuoli Taste District of Barluk Mountain National Nature Reserve, Xinjiang, China

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## Abstract

Based on investigating 15 sample plots along the altitude gradient, and 25 quadrats (0.5 × 0.5 m) in each of the sample plots, we aimed to analyse interspecific associations and the niche of the 20 main terricolous macrolichens in the Tuoli Taste district of Barluk Mountain National Nature Reserve, Xinjiang, China. We studied these aspects by calculating niche breadth, niche overlap, variance ratio, Pearson correlation coefficient, and Spearman's rank correlation coefficients. The results showed a total of 20 terricolous macrolichen species belonging to 5 genera, with *Cladonia* being the dominant genus (13 species, accounting for 65%). Fruticose lichens were the main growth form (14 species, accounting for 70%). Regarding niche breadth, *C. gracilis subsp. turbinata* had the largest niche breadth (Levins index: 4.609; Shannon-Wiener index: 1.693), while *P. muscigena* had the smallest (Levins index: 1.241; Shannon-Wiener index: 0.434). For niche overlap, the overlap value between species ranged from 0 to 0.94, with 26 species pairs showing no overlap and 46 species pairs having an overlap value less than 0.1. The overall interspecific association of the community was positive ( $VR = 3.653$ ,  $P < 0.05$ ). Spearman's rank correlation analysis indicated that 51% of species pairs were positively associated (3 pairs extremely significant, 10 pairs significant) and 49% were negatively associated. In conclusion, the terricolous macrolichen community in the study area has formed a relatively stable structure through niche differentiation and moderate interspecific associations, which is closely related to their adaptation to the extreme environment.

## Keywords

Forest Ecosystem, Niche, Resource Competition, Species Association,

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## Terricolous Lichen

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### 1. Introduction

The niche of lichens refers to the position and role of lichens in the ecosystem, including the resources they utilize and the environmental conditions they adapt to. Research on lichen niche has mainly focused on the differences in niche breadth and niche overlap among different species, and the relationship between niche characteristics and environmental factors (Giordani et al., 2015; Jin & Tumur, 2017; Rolshausen et al., 2018; Imin et al., 2022). Interspecific association of lichens refers to the interaction between different lichen species. At present, research on interspecific association of lichens has mainly explored the patterns and influencing factors of interspecific relationships through field investigation and statistical analysis (Antoine & McCune, 2004; Imin & Tumur, 2025). However, there are still some deficiencies in the research, such as the lack of in-depth research on the mechanism of interspecific association and the influence of global environmental changes on interspecific association.

Terricolous lichens are a special group of lichens that grow on the soil surface, and they are widely distributed in alpine, arid, and semi-arid regions, and they play a crucial role in nutrient cycling, energy flow, and maintaining biodiversity (Rai et al., 2011, 2012). Previous studies have shown that terricolous macrolichens have different niche characteristics in different environments, and their interspecific associations are also affected by environmental factors.

The Barluk Mountain National Nature Reserve (BMNNR) in Xinjiang, China, is a unique geographical location where the terricolous macrolichens have adapted to the harsh environments such as drought, strong radiation, and large temperature differences through long-term evolution, forming a special ecological community (Mamatali, 2024). Although terricolous macrolichens are a significant component of the forest ecosystem in the BMNNR, they have received limited research. The ground-dwelling macrolichens and their ecological indicator values have been studied (Toksun et al., 2025). But there is a lack of systematic research on the niche and interspecific association of terricolous macrolichens in this nature reserve. Studying the niche and interspecific association of these terricolous macrolichens is of great scientific significance. On the one hand, it helps to understand the adaptation strategies of terricolous macrolichens to the special environment of the reserve, revealing the mechanism of their coexistence and community stability.

The main research objectives of this study were to clarify the niche characteristics of terricolous macrolichens in the BMNNR and to explore the interspecific association relationships among them.

### 2. Material and Methods

#### 2.1. Study Area

The study sites BMNNR are located within latitude 45°42' - 46°03' N and longi-

tude 82°26' - 83°13' E. The conservation area covers an area of 115037.3 km<sup>2</sup> and encompasses a wide range of elevation from 800 to 2800 m asl (Abdushali, 2013). The climate of BMNNR changes from lower to higher altitudes. The average annual temperature is 6.2°C, with extreme maximum and minimum temperatures of 38.6°C and -35.9°C respectively. The annual accumulated temperature  $\geq 10.0^\circ\text{C}$  is 2869°C, the annual precipitation is 289.2 mm, and the annual evaporation is 1882.7 mm (Toksun et al., 2024).

The vegetation types in the reserve are diverse, shows variation depending on altitude and climate types. Including the subalpine zone (above 2300 m altitude), mid-mountain zone (1400 - 2300 m altitude), low-mountain zone (900 - 1400 m altitude) and the piedmont plain area (500 - 900 m altitude) (Liu et al., 2010; Wang & Abdushali, 2011; Abdushali, 2013), which provide a variety of habitats for terricolous macrolichens. The unique geographical location, climate conditions, and vegetation types make the BMNNR an ideal area for studying the niche and inter-specific association of terricolous macrolichens.

## 2.2. Lichen Sample Collection and Identification

Sample plots were set up along the altitude gradient in the Tuoli Tasite district of BMNNR, with a total of 15 sample plots. Each sample plot is 10 × 10 m in area. In each sample plot, a total of 25 quadrats each with size of 0.5 × 0.5 m were designed at intervals of 1 m, set out to investigate terricolous macrolichens. For each quadrat, the following data was collected: species name of terricolous macrolichens, coverage and frequency (Table S1 and Table S2), and growth forms. We conducted the lichen survey between 8 June to 22 July 2024 to ensure that the terricolous macrolichens were in a relatively stable growth period. During the collection process, photographs were taken of the sample plots and quadrats for future reference.

At each site, we identified common species in the field and took voucher specimens of all other lichens. We identified the lichen specimens morphologically and/or by microscopic examination of their ascospores, as well as by chemical-spot tests and responses to UV light (Abbas & Wu, 1998; Brodo et al., 2001; Orange et al., 2010).

## 2.3. Data Analysis

### 2.3.1. Niche Analysis

Niche breadth: the following two indexes were used to calculate the niche breadth of each terricolous macrolichen species.

Levins index ( $B_1$ ) (Zhang, 2004; Hong et al., 2013):

$$B_1 = \frac{1}{\sum_{j=1}^r (P_{ij})^2}$$

where  $B_1$  is the niche breadth of species  $i$ ;  $n$  is the number of sample plots,  $D_i$  is the important value of individuals in  $i$  sample plot.

Shannon-Wiener Index ( $B_2$ ) (Zhang, 2004; Liu et al., 2019):

$$B_2 = -\sum_{j=1}^r (P_{ij} \ln P_{ij})$$

where:  $B_2$  is the niche breadth of species  $i$ ;  $r$  is the number of grades of resources;  $P_{ij}$  is the ratio of the utilization of the  $j$ th resource to the utilization of all resources by species  $i$ . Considering that important values can better reflect the utilization efficiency of lichen species on environmental resources,  $P_{ij}$  is an important value of species when using this index to calculate the niche breadth.

Niche overlap: Pianka index ( $O_{ij}$ ) will be used to calculate the niche overlap between species  $i$  and species  $j$ . The formula is:

$O_{ij} = \sum (P_{ik} P_{jk}) / \sqrt{[\sum (P_{ik})^2 \sum (P_{jk})^2]}$ , where  $P_{ik}$  and  $P_{jk}$  are the important values of species  $i$  and  $j$  in resources  $k$ , respectively (Wang et al., 1984).

### 2.3.2. Interspecific Association Analysis

Overall association test: The overall association was determined using the variance ratio method proposed by Schluter (1984), and the significance of the association was tested using the statistic  $W$  (Ma et al., 2019).

$\chi^2$  test used to test the significance of interspecific association. The contingency table will be established based on the presence or absence of species, and the  $\chi^2$  value will be calculated. If  $\chi^2 > 3.841$ , it indicates a significant association; if  $\chi^2 \leq 3.841$ , it indicates no significant association (Zhao et al., 2018; Li et al., 2017)

Association coefficient (AC): Used to measure the degree of interspecific association. The formula is:  $AC = (ad - bc) / [(a + b)(c + d)(a + c)(b + d)]^{(1/2)}$  when  $ad \geq bc$ ;  $AC = (ad - bc) / [(a + b)(a + c)]$  when  $ad < bc$ , where  $a$  is the number of quadrats with both species present,  $b$  is the number of quadrats with species  $i$  present and species  $j$  absent,  $c$  is the number of quadrats with species  $i$  absent and species  $j$  present, and  $d$  is the number of quadrats with both species absent. The value of AC ranges from  $-1$  to  $1$ , with positive values indicating positive association and negative values indicating negative association (Ma et al., 2019; Xu et al., 2016; Huang et al., 2019). Statistical software's such as SPSS 22.0 and R 4.0.0 were used for data processing and analysis.

## 3. Results

### 3.1. Species Composition and Distribution

As a result of collecting and identifying lichen specimens from Tuoli Tasite, B MNNR, 20 species, in 5 genera were identified. *Cladonia* lichens dominated with a total of 13 species, accounting for 65% of the in terms of growth forms, there are 14 species of fruticose lichens and 6 species of foliose lichens, accounting for 70% and 30% of the total number of terricolous macrolichen species, respectively (Table 1).

### 3.2. Niche Characteristics

#### 3.2.1. Niche Breadth

The niche breadth is related to the environmental adaptability of the species. Species with a larger niche breadth are usually more adaptable to environmental

changes, while species with a smaller niche breadth are more sensitive to environmental changes (Li & Tumur, 2023). In this study, the niche breadth of different terricolous macrolichen species varied. The species with the largest niche breadth was *Cladonia gracilis subsp. turbinata*, with a Levins and Shannon-Weiner index of 4.609 and 1.693 respectively, following that is *Cladonia cornuta*, 3.745 and 1.468 indicating that these two species can utilize a variety of resources and adapt to a wide range of environmental conditions. In contrast, *Physconia muscigena* has a smaller niche breadth (Levins index of 1.241 and Shannon-Weiner index of 0.434), suggesting that it has higher environmental specificity and narrower resource utilization range (Table 2).

**Table 1.** Species composition with respect to the terricolous macrolichen in the Tuoli Taste district of BMNNR.

Numbering	Species	Family	Growth form
1	<i>Anaptychia setifera</i> (Mereschk.) Räsänen	Physciaceae	fruticose
2	<i>Cladonia acuminata</i> (Ach.) Norrl.	Cladoniaceae	fruticose
3	<i>Cladonia cenotea</i> (Ach.) Schaer.	Cladoniaceae	fruticose
4	<i>Cladonia chlorophaea</i> (Flörke ex Sommerf) Speg.	Cladoniaceae	fruticose
5	<i>Cladonia coniocraea</i> (Flk.) Spreng	Cladoniaceae	fruticose
6	<i>Cladonia conista</i> (Nyl.) Robbins	Cladoniaceae	fruticose
7	<i>Cladonia cornuta</i> (L.) Hoffm.	Cladoniaceae	fruticose
8	<i>Cladonia fimbriata</i> (L.) Fr.	Cladoniaceae	fruticose
9	<i>Cladonia humilis</i> (With.) J.R. Laundon	Cladoniaceae	fruticose
10	<i>Cladonia gracilis subsp. turbinata</i> (Ach.) Ahti	Cladoniaceae	fruticose
11	<i>Cladonia pocillum</i> (Ach.) Rich.	Cladoniaceae	fruticose
12	<i>Cladonia phyllophora</i> Ehrh.ex Hoffm.	Cladoniaceae	fruticose
13	<i>Cladonia pyxidata</i> (L.) Hoffm.	Cladoniaceae	fruticose
14	<i>Cladonia scabriuscula</i> (Delise) Nyl.	Cladoniaceae	fruticose
15	<i>Phaeophyscia constipata</i> (Nyl.) Moberg	Physciaceae	foliose
16	<i>Phaeophyscia limbata</i> (Belt) Kashiw.	Physciaceae	foliose
17	<i>Physcia dubia</i> (Hoffm.) Lett.	Physciaceae	foliose
18	<i>Physconia grisea</i> (Lam.) Poelt	Physciaceae	foliose
19	<i>Physconia muscigena</i> (Ach.) Poelt	Physciaceae	foliose
20	<i>Physconia perisidiosa</i> (Erichs.) Mobag.	Physciaceae	foliose

**Table 2.** Species composition and importance value of the terricolous macrolichen in Tuoli Taste district of BMNNR.

Species	Important value	$B_1$	$B_2$
<i>Cladonia gracilis subsp. turbinata</i>	10.92	4.609	1.693
<i>Cladonia cornuta</i>	14.00	3.745	1.468

## Continued

<i>Anaptychia setifera</i>	5.51	3.682	1.586
<i>Cladonia chlorophaea</i>	9.24	3.628	1.563
<i>Phaeophyscia constipata</i>	8.21	3.734	1.353
<i>Cladonia pocillum</i>	5.10	3.397	1.288
<i>Cladonia phyllophora</i>	3.99	3.332	1.361
<i>Cladonia humilis</i>	4.11	3.311	1.356
<i>Physconia grisea</i>	5.26	3.049	1.212
<i>Cladonia pyxidata</i>	4.99	3.033	1.234
<i>Physconia perisidiosa</i>	8.84	2.968	1.197
<i>Cladonia cenotea</i>	6.76	2.934	1.370
<i>Cladonia fimbriata</i>	3.42	2.756	1.159
<i>Physcia dubia</i>	4.82	2.717	1.155
<i>Cladonia acuminata</i>	4.26	2.635	1.257
<i>Cladonia scabriuscula</i>	5.37	1.986	1.026
<i>Cladonia coniocraea</i>	1.78	1.945	0.804
<i>Cladonia conista</i>	1.37	1.878	0.913
<i>Phaeophyscia limbata</i>	5.22	1.578	0.719
<i>Physconia muscigena</i>	3.87	1.241	0.434

The Importance value is an effective indicator for comprehensively measuring the status and role of species in a community. Through the analysis of species important values, we can understand the dynamics of populations in the community. In Tuoli Tasite district of BMNNR the highest importance value for terricolous lichen species is *Cladonia cornuta*, which is 14%, followed by 10.92 of *Cladonia gracilis subsp. turbinata*, which is significantly higher than other lichen species. Meanwhile, we found that the importance values of *Anaptychia setifera* and *Cladonia pocillum*, are rather low, 5.51 and 5.10 respectively, but their niche breadth are higher. We believe that these two species are “broad but not specialized” in resource utilization, so it is natural that their individual numbers, distribution frequencies or biomass in the community are difficult to predict, in contrast, *Cladonia scabriuscula* and *Phaeophyscia limbata* have relatively high importance values but narrow niches. We believe that species with narrow niches usually focus on certain key resources and with long-term adaptation, develop efficient utilization capabilities, this enables them to form high population densities and high dominance in local areas, thus eventually developing high importance values.

### 3.2.2. Niche Overlap

In general, the niche overlap between species in the same habitat is higher than that between species in different habitats. This is because species in the same hab-

itat have similar environmental requirements and thus compete for the same resources (Li & Tumur, 2023).

In Tuoli Tasite district of BMNNR, there is a certain degree of niche overlap among terricolous macrolichen species, the overlap value was between 0 and 0.94 (Table S3). The highest niche overlap occurs between *C. conista* × *C. scabriuscula* (0.94), *C. cenotea* × *C. scabriuscula* (0.93), *C. humilis* × *C. scabriuscula* (0.90), *P. constipata* × *P. muscigena* (0.89), *C. cornuta* × *C. scabriuscula* (0.87), *C. acuminata* × *C. phyllophora* (0.85), *C. conista* × *C. phyllophora* (0.85), *C. acuminata* × *C. coniocraea* (0.83), *P. dubia* × *P. perisidiosa* (0.81); indicating that they have similar resource utilization patterns and may have competitive relationships. For example, most *Cladonia* lichens exhibit the highest niche overlap values, which is related to their similar demands for resources such as soil moisture and light in their habitats. Although *Physcia dubia* and *Physconia perisidiosa* do not belong to the same genus, they share the same growth form and thus utilize habitat resources in the same way, leading to a relatively high niche overlap.

Among them, there is a total of 26 pairs of terricolous lichen species with narrow niche overlap values of 0, indicating that there is no common resource demand and the species are distributed in a specific environment. The niche overlap value of 46 pairs of terricolous lichen are also lower than 0.1, indicating that they also have low niche overlap. In the Tuoli Tasite district of BMNNR, as altitude increases, community species diversity gradually increases, which in turn leads to a decrease in the niche breadth of terricolous macrolichen species and causes changes in niche overlap value.

### 3.2.3. Interspecific Association

The overall association of the terricolous macrolichen community as shown in Table 3, the variance ratio of the overall interspecific association in the community  $VR = 3.653$ ,  $>1$ . This indicates that under the condition of the independent null hypothesis, the overall interspecific relationship shows a positive correlation. The statistical test  $W$  was used to test the significance of  $VR$ , which showed that the interspecific association of macrolichens was significant, and the species distribution was relatively dependent.

**Table 3.** General associativity test among terricolous macrolichen in Tuoli Taste district of BMNNR.

$S_r^2$	$\sigma_r^2$	Variance ratio ( $VR$ )	Test statistic ( $W$ )	$\chi^2$ threshold ( $\chi^2$ 0.95, $\chi^2$ 0.05)	Results
4.548	1.245	3.653	54.79	[6.57, 23.68]	$P < 0.05$

### 3.2.4. Interspecific Correlation

The Pearson correlation coefficient and Spearman's rank correlation coefficient are important indicators reflecting the linear relationship of interspecific covariation between two species, and they can reflect the quantitative change relationship between species (Li et al., 2017; Ma et al., 2019). The Pearson's correlation coeffi-

cient shows that there are 59 pairs of species with a positive correlation, accounting for 31.1% of the total pairs. Among them, 22 pairs have a relatively high correlation coefficient, accounting for 11.6% of the total pairs, and 37 pairs have a moderate association degree, accounting for approximately 19.5% of the total pairs. There are 131 pairs with a negative correlation, accounting for 68.9% of the total pairs, among which 26 pairs are extremely significant with a coefficient of  $-0.14$ , indicating a weak negative correlation. The Pearson's index indicates that different species have a strong degree of independence from each other and their correlation is not close (Table S4).

The Spearman's correlation coefficient shows that, among the 190 species pairs, 97 pairs of species show a positive correlation, accounting for 51% of the total (Table S5). Among them, the correlation of 3 pairs of species are extremely significant ( $P < 0.01$ ) (*C. conista* × *P. grisea*, *C. phyllophora* × *P. muscigena*, *C. scabriuscula* × *C. humilis*), and 10 pairs of species have significantly correlation ( $P < 0.05$ ). There are 93 pairs of species negative associations, accounting for 49% of the total. The correlation between *C. acuminata* × *C. cenotea*, *A. setifera* × *C. pocillum* and *C. gracilis subsp. turbinata* × *P. dubia* are significantly negative. The highest coefficient is 0.98 (*C. conista* × *P. grisea*), and the lowest coefficient is  $-0.54$  (*C. acuminata* × *C. cenotea*), 0.52 (*A. setifera* × *C. pocillum*, *C. gracilis subsp. turbinata* × *P. dubia*). This indicates that the positive association relationships among the 20 terricolous macrolichen species in the study area are stronger than the negative association relationships.

There are significant differences in the detection results of species pairs under different methods (Table 4).

**Table 4.** Interspecific correlation test with different methods on the terricolous macrolichen in BMNNR.

Test method	No of species pair extremely significance ( $P < 0.01$ )		No of species pair significantly ( $P < 0.05$ )		No of species pair no significantly ( $P > 0.05$ )	
	Positive	Negative	Positive	Negative	Positive	Negative
Pearson's correlation coefficient	22	26	37	47	131	117
Spearman's correlation coefficient	13	4	84	89	93	97

#### 4. Discussion

Niche is one of the most crucial concepts and theories in ecology, and it plays a key role in understanding community structure and function, interspecific relationships within communities, biodiversity, dynamic succession of communities, and population evolution, among other aspects (Peterson & Soberon, 2012; Mckane et al., 2002). Interspecific association refers to the mutual correlation between different species in terms of spatial distribution, and it is one of the important quanti-

tative and structural characteristics of communities. Therefore, studying species niches and interspecific associations helps to gain an in-depth understanding of species' ability to utilize resources, the cooperative and competitive relationships between species, as well as the laws of community succession (Coxson & Coyle, 2003). Niche breadth reflects a species adaptability to the environment. The wider the niche breadth of a species, the stronger its ability to adapt to the environment and utilize resources. Similarly, in the BMNR, some terricolous macrolichens have a relatively wide niche breadth and a broad distribution range. For example, *C. gracilis subsp. turbinata*, *C. cornuta*, *C. chlorophaea*, and *P. perisidiosa* are distributed in most of the surveyed sample plots. In contrast, some lichens have a narrow niche breadth. For instance, *P. muscigena* and *P. limbata* have a narrow niche breadth because they are only distributed in specific habitats such as high herb coverage, weak light, and high soil moisture under the ground of broad-leaved forests, and forming a single dominant community.

The degree of niche overlap value reflects the similarity in resource utilization between species (Wang et al., 1984). In BMNR, among them are total of 190 pairs of terricolous lichen species, there is no niche overlap among 26 species pairs, indicating that there is no common resource demand and are distributed in a specific environment. The niche overlap value of 46 pairs of terricolous lichen are lower than 0.1, indicating that they have low niche overlap. This result indicates that in the study area, the available resources for terricolous macrolichens are relatively abundant, and the competition between species is weak. Therefore, the terricolous macrolichens have formed a relatively stable community. In the study area, the niche overlap values are low, and terricolous lichen species exhibit a high degree of niche differentiation; competition among species is not intense, making the community relatively stable. Species with wider niches generally exhibit niche overlap with other species, but the overlap values are low. In contrast, some species with narrower niche breadths, due to their specific habitat requirements, are mostly distributed in undisturbed, high-altitude areas with high humidity, are only recorded in single quadrats, and show high niche overlap values with other species. There is no direct linear relationship between niche overlap and niche breadth.

The interspecific association relationships are important for the formation and development of terricolous macrolichen communities. Positive associations promote the coexistence and development of species, while negative associations regulate the population density of species, preventing excessive reproduction of a single species and maintaining the balance of the community. In this study, the overall interspecific relationship shows a positive correlation. This means that the distribution of different species in the community tends to be consistent, and they have a tendency to appear together in spatial distribution. This may be due to similar adaptation strategies such as similar requirements for habitat conditions like light, moisture, and soil, or mutual promotion in their growth and reproduction. In the Tuoli Tasite district of BMNNR, in suitable habitats, resources are

relatively abundant and can meet the demand of closely related species for the same resources, leading to the aggregated distribution of a large number of closely related species; thus, environmental filtering dominates community assembly. In contrast, in some extreme environments, habitats are relatively harsh and resources are scarce. Due to resource competition, species coexist through niche differentiation, and limiting similarity plays a dominant role in shaping community species composition.

Environmental factors have a significant impact on the niche and interspecific association of macrolichens in the BMNNR (Mamatali, 2024). In this study, we found that altitude, as an important environmental factor, affects the distribution and niche characteristics of terricolous macrolichens through changes in temperature, precipitation, and vegetation types in the Tuoli Tasite district of BMNNR. With the increase of altitude, the niche breadth of some species decreases, and the niche overlap between species also changes. Mamatali (2024) reported that soil moisture and soil pH play an important role in controlling the species composition and community structure of terricolous lichen of BMNNR. This study found that in the Tuoli Tasite district of BMNNR, terricolous macrolichen species adapted to dry soil conditions have a larger niche breadth in areas with low soil moisture, and the interspecific association between them are more likely to be positive. In contrast, species that prefer humid soil conditions have different niche characteristics and interspecific relationships. Therefore, we believe that vegetation coverage affects the light and moisture conditions on the soil surface, thereby influencing the niches and interspecific associations of terricolous macrolichens. Additionally, in areas with high vegetation coverage, the competition for light among terricolous macrolichens is more intense, leading to changes in their niche and interspecific relationships.

There are still some unanswered questions: What is the mechanism behind the niche differentiation of terricolous macrolichens? How do long-term climate changes affect the niche and interspecific association of terricolous macrolichens? Further studies are needed to explore these issues using molecular biology and long-term monitoring methods.

## 5. Conclusion

In summary, this study systematically investigated and analyzed the terricolous macrolichens in the BMNNR, Xinjiang, China, clarifying the niche characteristics and interspecific association relationships of terricolous macrolichens in this region, which provides a key basis for understanding the ecological adaptation mechanisms of lichen communities in arid and semi-arid areas.

In terms of species composition, a total of 20 species of terricolous macrolichens belonging to 5 genera were found in the study area, among which *Cladonia* was dominant (13 species, accounting for 65%), and fruticose lichens were the main type (14 species, accounting for 70%).

Regarding niche characteristics, there are significant differences in niche

breadth among different lichen species. The niche overlap analysis showed that 26 species pairs had an overlap value of 0, and 46 species pairs had an overlap value lower than 0.1, indicating that most species reduce competition through differentiation in resource utilization, while species with high overlap may have potential resource competition relationships.

The analysis of interspecific associations showed that the overall lichen community presented a significant positive association ( $VR = 3.653$ ,  $P < 0.05$ ), indicating that species have a tendency to co-occur in spatial distribution, which may be related to their similar adaptation strategies to environmental conditions (such as requirements for light, soil pH, etc.).

However, the study still has limitations: first, it did not deeply explore the molecular mechanism of niche differentiation; second, there is a lack of long-term monitoring data to evaluate the impact of climate change on interspecific associations. In the future, combining molecular marker technology with long-term positioning observation can further analyze the response mechanism of lichens to environmental changes, providing more accurate scientific support for the protection and management of the Barluk Mountain ecosystem.

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## Conflicts of Interest

The authors declare no conflict of interest regarding the publication of this paper.

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## Appendix

**Table S1.** Relative coverage of 20 terricolous lichens on 15 sampling plots.

	Sp1	Sp2	Sp3	Sp4	Sp5	Sp6	Sp7	Sp8	Sp9	Sp10	Sp11	Sp12	Sp13	Sp14	Sp15	Sp16	Sp17	Sp18	Sp19	Sp20
P1	0.00	0.00	12.15	0.00	0.00	0.00	1.79	0.00	6.91	0.00	0.00	0.00	0.00	68.03	0.00	0.00	11.13	0.00	0.00	0.00
P2	1.02	0.00	0.00	70.33	0.00	0.00	7.03	0.00	0.00	12.02	0.00	1.36	0.00	0.00	0.00	6.86	0.00	0.00	1.36	0.00
P3	0.00	6.49	0.00	0.00	0.00	3.32	0.00	0.00	8.80	0.00	11.54	0.00	0.00	2.16	0.00	0.00	0.00	49.78	0.00	17.89
P4	7.05	0.00	3.70	10.08	5.60	0.00	0.00	0.00	0.00	0.00	0.00	0.00	47.14	0.00	23.74	0.00	2.69	0.00	0.00	0.00
P5	0.00	2.71	0.00	0.00	0.00	0.00	0.00	6.44	0.00	14.01	0.00	0.00	0.00	0.00	0.00	76.84	0.00	0.00	0.00	0.00
P6	0.00	0.00	6.12	0.00	0.00	9.14	9.21	7.37	21.52	0.00	16.21	2.43	1.77	4.27	0.00	0.00	0.00	15.55	6.41	0.00
P7	7.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	27.16	0.00	0.00	0.00	1.21	0.00	0.00	0.00	0.00	0.00	64.59
P8	6.69	7.09	0.00	3.55	19.57	0.00	12.12	0.00	0.00	1.95	0.00	0.87	0.00	0.00	4.38	0.00	0.00	0.00	43.78	0.00
P9	0.00	0.00	0.00	18.65	0.00	0.00	0.00	18.89	0.00	0.00	26.85	0.00	18.57	0.00	0.00	0.00	17.04	0.00	0.00	0.00
P10	8.44	14.67	0.00	0.00	0.00	7.11	0.00	0.00	0.00	0.00	0.00	49.78	0.00	0.00	0.00	0.00	0.00	20.00	0.00	0.00
P11	0.00	0.00	29.57	24.57	0.00	0.00	0.00	0.00	9.72	8.54	0.00	0.00	2.89	14.59	0.00	3.15	0.00	0.00	0.00	5.65
P12	0.00	0.00	0.00	0.00	0.00	0.00	48.73	0.00	0.00	0.00	33.13	0.00	0.00	0.00	18.14	0.00	0.00	0.00	0.00	0.00
P13	0.81	0.00	24.02	12.96	9.05	0.46	0.00	15.32	10.48	12.42	0.00	4.80	0.00	2.01	0.00	0.00	0.00	6.46	1.20	0.00
P14	16.25	10.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	19.50	0.00	0.00	53.75
P15	0.00	0.00	9.82	48.55	0.00	0.00	4.12	0.00	0.00	2.02	0.00	0.00	20.51	0.00	11.04	3.94	0.00	0.00	0.00	0.00

**Table S2.** Relative frequency of 20 terricolous lichens on 15 sampling plots.

	Sp1	Sp2	Sp3	Sp4	Sp5	Sp6	Sp7	Sp8	Sp9	Sp10	Sp11	Sp12	Sp13	Sp14	Sp15	Sp16	Sp17	Sp18	Sp19	Sp20
P1	0.00	0.00	23.08	0.00	0.00	0.00	28.21	0.00	12.82	0.00	0.00	0.00	0.00	15.38	0.00	0.00	20.51	0.00	0.00	0.00
P2	5.00	0.00	0.00	30.00	0.00	0.00	7.50	0.00	0.00	30.00	0.00	7.50	0.00	0.00	0.00	7.50	0.00	0.00	12.50	0.00
P3	0.00	12.82	0.00	0.00	0.00	7.69	0.00	0.00	15.38	0.00	12.82	0.00	0.00	7.69	0.00	0.00	0.00	12.82	0.00	30.77
P4	21.43	0.00	10.71	3.57	3.57	0.00	0.00	0.00	0.00	0.00	0.00	0.00	17.86	0.00	35.71	0.00	7.14	0.00	0.00	0.00
P5	0.00	10.34	0.00	0.00	0.00	0.00	0.00	17.24	0.00	48.28	0.00	0.00	0.00	0.00	0.00	24.14	0.00	0.00	0.00	0.00
P6	0.00	0.00	14.81	0.00	0.00	3.70	22.22	1.85	5.56	0.00	5.56	7.41	3.70	7.41	0.00	0.00	0.00	9.26	18.52	0.00
P7	26.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	40.00	0.00	0.00	0.00	13.33	0.00	0.00	0.00	0.00	0.00	20.00
P8	21.43	22.62	0.00	1.19	7.14	0.00	5.95	0.00	0.00	13.10	0.00	3.57	0.00	0.00	9.52	0.00	0.00	0.00	15.48	0.00
P9	0.00	0.00	0.00	11.11	0.00	0.00	0.00	14.81	0.00	0.00	18.52	0.00	11.11	0.00	0.00	0.00	44.44	0.00	0.00	0.00
P10	13.33	20.00	0.00	0.00	0.00	6.67	0.00	0.00	0.00	0.00	0.00	26.67	0.00	0.00	0.00	0.00	0.00	33.33	0.00	0.00
P11	0.00	0.00	8.57	5.71	0.00	0.00	0.00	0.00	20.00	17.14	0.00	0.00	14.29	11.43	0.00	8.57	0.00	0.00	0.00	14.29
P12	0.00	0.00	0.00	0.00	0.00	0.00	58.33	0.00	0.00	0.00	8.33	0.00	0.00	0.00	33.33	0.00	0.00	0.00	0.00	0.00
P13	3.70	0.00	14.81	9.26	5.56	1.85	0.00	9.26	5.56	22.22	0.00	9.26	0.00	5.56	0.00	0.00	0.00	7.41	5.56	0.00
P14	16.67	11.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	13.89	0.00	0.00	58.33
P15	0.00	0.00	15.28	8.33	0.00	0.00	33.33	0.00	0.00	19.44	0.00	0.00	4.17	0.00	13.89	5.56	0.00	0.00	0.00	0.00

**Table S3.** Niche overlap value of terricolous macrolichen in Tuoli Taste district of Barluk Mountain National Nature Reserve.

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
2	0.68																		
3	0.12	0																	
4	0.19	0.02	0.49																
5	0.64	0.83	0.41	0.18															
6	0.26	0.61	0.29	0.02	0.05														
7	0.06	0.06	0.34	0.23	0.06	0.09													
8	0.05	0.21	0.35	0.24	0.19	0.16	0.02												
9	0.03	0.14	0.79	0.16	0.1	0.46	0.1	0.2											
10	0.36	0.24	0.35	0.45	0.16	0.03	0.08	0.41	0.17										
11	0	0.11	0.1	0.13	0	0.31	0.64	0.39	0.32	0									
12	0.57	0.85	0.21	0.2	0.16	0.85	0.04	0.81	0.19	0.18	0.05								
13	0.5	0	0.55	0.42	0.21	0.05	0.09	0.24	0.18	0.18	0.22	0.01							
14	0.11	0.84	0.93	0.09	0.04	0.94	0.87	0.08	0.9	0.21	0.08	0.03	0.07						
15	0.36	0.08	0.28	0.21	0.21	0	0.15	0	0	0.13	0.7	0.01	0.51	0					
16	0.03	0.49	0.18	0.29	0	0	0.05	0.15	0.09	0.3	0	0.02	0.09	0.03	0.04				
17	0.34	0.18	0.35	0.2	0.04	0	0.07	0.49	0.25	0	0.43	0	0.4	0.42	0.06	0			
18	0.27	0.7	0.22	0.03	0.07	0.16	0.04	0.14	0.63	0.07	0.3	0.22	0.02	0.12	0	0	0		
19	0.64	0.66	0.24	0.31	0.76	0.29	0.14	0.14	0.32	0.34	0.13	0.16	0.03	0.07	0.89	0.73	0	0.16	
20	0.04	0.46	0.08	0.03	0	0.17	0	0	0.26	0.41	0.1	0	0.03	0.15	0	0.01	0.81	0.24	0

**Table S4.** Pearson's correlation coefficient.

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
2	0.87																		
3	-0.15	-0.23																	
4	-0.09	-0.18	0.13																
5	0.85	0.83	0.25	-0.02															
6	-0.19	-0.11	0.06	-0.19	-0.1														
7	0.48	0.53	-0.22	0.07	0.53	0.08													
8	-0.17	-0.2	0.73	0.08	0.21	0.16	-0.21												
9	-0.22	-0.21	0.7	-0.07	0.11	0.74	-0.07	0.62											
10	0	-0.11	0.65	0.51	0.27	-0.16	-0.1	0.55	0.34										
11	-0.31	-0.2	-0.19	-0.15	-0.21	0.39	0.25	0.32	0.18	-0.36									
12	0.04	0.04	0.59	0.08	0.29	0.2	-0.08	0.54	0.49	0.48	-0.17								
13	0.02	-0.23	-0.09	0.09	-0.12	-0.14	-0.22	0.04	-0.22	-0.3	0.15	-0.26							
14	-0.21	-0.17	0.17	-0.16	-0.11	-0.01	-0.16	-0.07	0.16	-0.13	-0.14	-0.1	-0.18						
15	0.42	0.21	-0.15	-0.02	0.31	-0.22	0.43	-0.27	-0.31	-0.28	-0.06	-0.24	0.67	-0.23					

