RESEARCH ARTICLE

Microgeographic distribution and mycobiont–photobiont associations in Arctic *Umbilicaria* lichens

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Abstract

Lichen symbioses are shaped by interactions between mycobionts and photobionts, yet how these relationships are structured at extremely small spatial scales in polar ecosystems remains poorly understood. Here, we investigated mycobiont–photobiont associations in *Umbilicaria* lichens collected from two isolated boulders in Ny-Ålesund, Svalbard, using ITS rDNA sequencing of both symbiotic partners and analyses of group I introns in mycobiont SSU rDNA. We identified five co-occurring *Umbilicaria* taxa across the two boulders, with four taxa occurring on each boulder. These taxa displayed pronounced horizontal and vertical segregation associated with rock orientation and surface position, revealing strong ecological structuring at the within-boulder scale. In contrast, all photobionts belonged to *Trebouxia jamesii* and showed low genetic differentiation, forming four weakly structured haplotype groups that were not correlated with host species or microhabitat. This pattern indicates weak sorting amongst local *T. jamesii* lineages and extensive photobiont sharing across mycobiont species and microhabitats. In addition, group I introns at the SSU rDNA 1769 insertion site were detected in two *Umbilicaria* lineages and occurred as short and long variants with highly conserved catalytic core structures. Their lineage-specific distribution and structural conservation provide additional information on mycobiont evolutionary history and may be relevant to stress responses, although their functional and adaptive significance remains to be experimentally evaluated. Together, our results demonstrate that Arctic *Umbilicaria* communities combine high fungal diversity and fine-scale spatial niche partitioning with broad photobiont sharing. This dual strategy of ecological differentiation and symbiotic flexibility may facilitate lichen persistence in extreme polar environments.

To access the supplementary material, please visit the article landing page

Keywords

Lichen symbiosis; *Trebouxia jamesii*; group I introns; rDNA sequencing; symbiotic flexibility; Svalbard

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Abbreviations

CTAB: cetyltrimethylammonium bromide
ITS: internal transcribed spacer
LSU: large subunit
ME: minimum evolution
NCBI: National Center for Biotechnology Information
PCR: polymerase chain reaction
SSU: small subunit region

Introduction

Lichens are symbiotic organisms that comprise mycobionts and algae or cyanobacteria, which are photobionts (Asplund & Wardle 2017). Like vascular plants, lichens have a long evolutionary history (Nelsen et al. 2020). Lichenization comprises five main stages: (1) pre-contact; (2) contact; (3) envelopment; (4) incorporation; and (5) differentiation, during which the algal cells and the fungus combine to form a complex thallus (Pichler et al. 2023), sometimes accompanied by a switch to a different photobiont (Ohmura et al. 2019). Photobionts provide a carbon source to support the growth of lichens through photosynthesis, whilst mycobiont hyphae form a "miniature greenhouse" that protects photobionts from harsh environmental stressors such as strong radiation and drought. Special symbiotic structures help lichens adapt to extreme environments. As a result, lichens are widely distributed, covering a wide variety of extreme environments. However, multiple studies of lichen distribution have shown that lichens typically exhibit regional endemism (Davydov et al. 2024), which may be attributed to

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historical, ecological and biological factors (Lücking et al. 2017).

Patterns of association between lichen-forming fungi and photobionts are commonly described in terms of specificity and selectivity (Muggia et al. 2018). Here, specificity refers to the taxonomic breadth of compatible partners, whereas selectivity refers to non-random or unequal association frequencies amongst compatible partners (Yahr et al. 2004, 2006; Leavitt et al. 2015). Mycobiont–photobiont pairings may be shaped by reciprocal compatibility, local partner availability and environmental filtering and therefore should not be interpreted as a unidirectional choice by either symbiont. Flexibility in partner associations may broaden the ecological amplitude of lichens and facilitate their persistence in harsh and nutrient-poor environments (Piercey-Normore 2006; Peksa & Skaloud 2011; Williams et al. 2017). Such association flexibility may be particularly relevant in Arctic habitats exposed to low temperatures, intense radiation and other environmental stresses (Nelsen et al. 2021). Patterns of partner association may also influence the ecological and evolutionary diversification of lichen-forming fungi (Fernández-Mendoza et al. 2011; del Campo et al. 2013). Several studies have reported correlations between the photobiont genotype and the geographical and ecological distribution of the lichen (Leavitt et al. 2015; Dal Grande et al. 2018; Jüriado et al. 2019; Garrido-Benavent et al. 2020; Rolshausen et al. 2020).

Umbilicaria is a primarily saxicolous lichen genus that can be readily distinguished from other lichen genera. As of 3 August 2026, the Catalogue of Life (https://www.gbif.org/taxon/84R8) recognizes 95 accepted species of *Umbilicaria*. Under the broad phylogenetic classification, the genus comprises approximately 100 species and eight subgenera (Davydov et al. 2017). The foliose thalli of this genus usually grow on rocks and are attached to the substratum at a single point by a short strand called an umbilicus. The thalli of *Umbilicaria* specimens can reach sizes of 1–30 cm in diameter or more (Krzewicka & Smykla 2004). *Umbilicaria* is widespread and is found in abundance in both the Arctic and Antarctic (Sancho et al. 1998; Krzewicka & Smykla 2004; Krzewicka & Maciejowski 2008; Davydov et al. 2017).

To further investigate the Arctic distribution of *Umbilicaria* and examine fine-scale mycobiont–photobiont association patterns and their relationship with the spatial structure of the community of Arctic lichens, we collected thalli from *Umbilicaria* samples and identified their mycobiont and photobiont components on Blomstrandhalvøya, across the fjord from the research settlement of Ny-Ålesund, in Svalbard. This study further examined the local distribution of lichen populations and the selectivity of regional mycobionts and photobionts with the aim of exploring the origin of the complexity and diversity of lichen symbiotic relationships.

Materials and methods

Study area and sampling

Sampling was conducted in July 2012 near London, on the southern part of Blomstrandhalvøya, an island in Kongsfjorden, Svalbard (approximately 78°58′N, 12°04′E; Fig. 1). The site was situated on low-elevation terrain that descended gently southward towards Kongsfjorden and was covered by sparse, low tundra vegetation. A small pond occupied the central part of the sampling area.

A total of 115 *Umbilicaria* thalli were collected from two isolated boulders located on opposite sides of the pond, hereafter referred to as Stone A and Stone K. Their positions were approximately 0.15 km apart. Stone A was situated on the northern and slightly higher side of the pond. It was an irregular, approximately block-shaped boulder measuring about 2.5 m in length, more than 1.5 m at its widest point and about 2 m at its highest point. Stone K was situated on the southern side of the pond and was slightly smaller and irregularly shaped, measuring approximately 1.5 m in both length and width and nearly 2 m at its highest point. These dimensions are approximate field estimates.

Of the 115 thalli, 92 were collected from Stone A using a sampling design covering four aspects, south-west, north-west, north-east and south-east, and two vertical zones. For sampling purposes, the upper and lower zones were separated visually at approximately half of the exposed height of the boulder, corresponding to about 1 m above the ground level. This operational division was used to standardize sampling positions and did not represent a measured environmental threshold. The remaining 23 thalli were collected from Stone K. Information for all specimens is provided in Supplementary Table S1.

The Kongsfjorden region has a maritime High-Arctic climate. At the nearby Ny-Ålesund meteorological station, the 1991–2020 mean annual air temperature was approximately −4°C, and annual precipitation is approximately 460 mm. Seasonal snowmelt generally begins in May or June, and July and August are usually snow-free at the meteorological station.

DNA extraction and Sanger sequencing

Total DNA was extracted from mycobionts and photobionts using a modified CTAB method (Zhou et al. 2006). The mycobiont ITS segments were then

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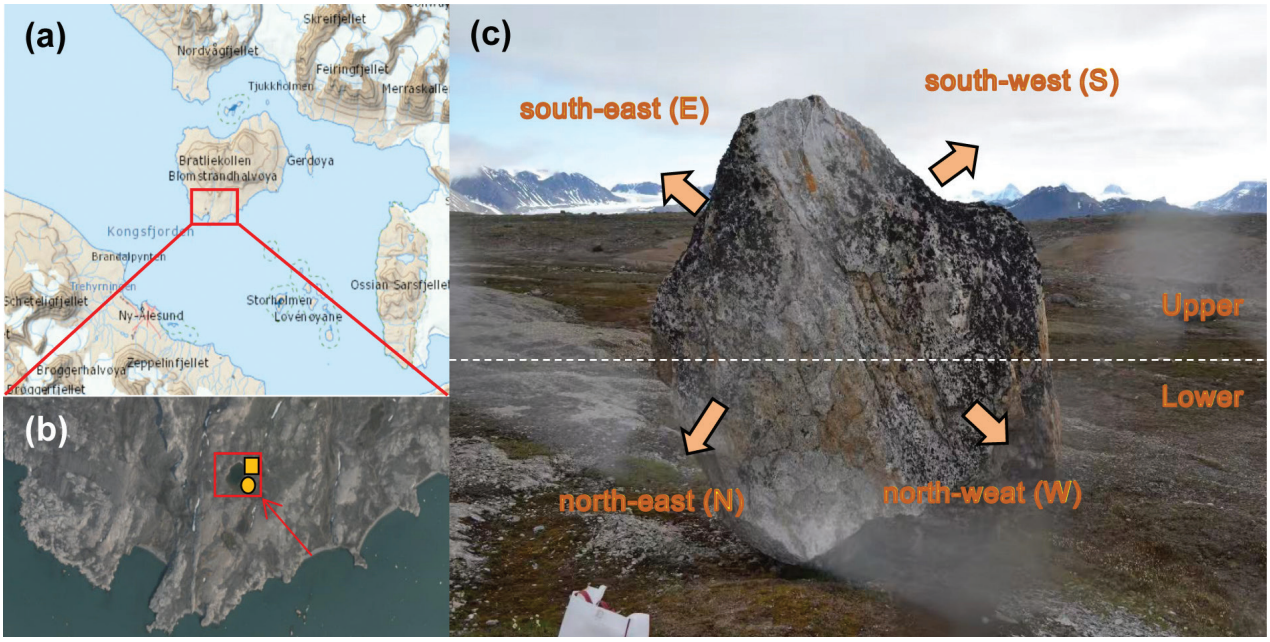


Fig. 1 (a) The sampling area on Blomstrandhalvøya in Kongsfjorden and (b) the location of the collection sites: Stone A (square) and Stone K (dot). In total, 115 *Umbilicaria* samples were collected from the two stones, 92 of which were collected from (c) eight positions on Stone A.

amplified using the specific fungal primer pair ITS4 (5′-TCCTCCGCTTATTGATATGC-3′) and ITS5 (5′-GGAAGTAAAAGTCGTAACAAGG-3′; White et al. 1990). For the photobiont ITS sequences, the algal-specific primer pair nr-SSU-1780-5′ (5-CTGCGGAAGGA TCATTGATTC-3′) and nrLSU-0012-3′ (5-AGTTCAGC GGGTGGTCTTG-3′) were employed (Piercey-Normore & DePriest 2001). PCR amplification was performed as follows: initial denaturation at 95°C for five minutes, followed by 35 amplification cycles at 95°C for 30 seconds, 53°C for 45 seconds and 72°C for one minute and a final extension at 72°C for five minutes.

Following PCR, dideoxy-mediated chain-termination sequencing reaction electrophoresis was conducted using the 3730XL DNA Sequencing Analyzer (Applied Biosystems). The sequencing primers utilized were the same as those employed for PCR. Double-directional sequence data were obtained for both mycobionts and photobionts. Finally, these data were checked and assembled using the SEQMAN programme in the Lasergene v7.1 software package (DNAStar Inc.).

Data analysis and phylogenetic tree construction

ITS sequences were successfully obtained for both symbiotic partners from all 115 thalli, and all samples were included in the corresponding phylogenetic analyses. All sequences generated in this study have been submitted to the NCBI, and their accession numbers are listed in Supplementary Table S1. The mycobiont sequences varied considerably in length, ranging 534–999 bp. Potential introns were initially recognized as discrete additional sequence blocks within the conserved SSU rDNA alignment. Insertions occurring at previously documented SSU rDNA group I intron sites were provisionally treated as candidate group I introns (DePriest & Been 1992; Gargas et al. 1995). Their identity was subsequently confirmed by the presence of conserved group I intron core elements and by reconstruction of the characteristic P1–P9 secondary structure, as described later. To determine the standardized insertion positions, we retrieved the 18S rRNA gene sequence of *Saccharomyces cerevisiae* (GenBank accession Z75578) and the 16S rRNA sequence of *Escherichia coli* from GenBank and aligned these reference sequences with our data. The sequences analysed in this study were divided into three data sets: the mycobiont ITS data set, the group I intron data set and the photobiont ITS data set. The group I introns, SSU and LSU rDNA were removed from the mycobiont matrix before phylogenetic analysis was performed. For the mycobiont and the photobiont ITS data sets, preliminary alignment was conducted using the ClustalW algorithm in MEGA11 software (Tamura et al. 2021).

During the alignment of group I introns from mycobionts, the secondary structures were constructed prior to alignment, and the alignment was conducted using ClustalW in MEGA with default parameters (Thompson

et al. 1994; Tamura et al. 2021). Manual adjustments were performed to ensure that the conserved elements remained properly aligned within the sequences, and alignment gaps were treated as missing data. The phylogenetic trees for mycobionts, photobionts and group I introns were constructed using the ME method in MEGA7.

Group I intron secondary structure prediction

We utilized the BioChen online platform (https://www.biochen.org/cn/tools/transform_sequence) to convert the group I introns into RNA sequences. Analysis was conducted to identify conserved sequences of group I intronic sequences, after which the secondary structures of group I introns were visualized in Adobe Illustrator 2021 (Adobe Systems Inc.).

Results

Phylogenetic analyses of mycobiont ITS rDNA

The ME tree of mycobionts based on ITS rDNA sequences displayed five distinct monophyletic groups: *Umbilicaria decussata*, *U. krascheninnikovii*, *U. lyngei*, *U. arctica* and *Umbilicaria* cf. *polaris* (Fig. 2; Supplementary Figs. S1–S3). *Umbilicaria* cf. *polaris*, *U. lyngei* and *U. arctica* were strongly supported, whilst the *U. decussata* group was supported at 74% and the *U. krascheninnikovii* at 67% (Fig. 2; Supplementary Figs. S1–S3).

Phylogenetic analyses conducted on 115 *Umbilicaria* individuals identified 53 of them as belonging to *U. arctica*, 23 belonging to *U. decussata*, 19 belonging to *U. krascheninnikovii*, 18 belonging to *U. lyngei* and two as *U.* cf. *polaris*. The ME tree of mycobionts and the regularities of distribution revealed a correlation between the growth tendency of the species and the upper or lower parts of Stone A. Of the 92 samples collected from Stone A, all samples identified as *U. decussata* and *U. krascheninnikovii* were distributed on the lower part of the sample stone. In contrast, *U. lyngei* and *U. arctica* were distributed on both the lower and upper parts of Stone A, although nearly all *U. arctica* samples were collected from the upper part of the stone.

Phylogenetic analysis demonstrated that *U. decussata* formed a monophyletic group with a bootstrap support of 74%, consisting of three individuals collected from the south-west of Stone A, nine from the north-west, two from the north-east, eight from the south-east and one from Stone K. *Umbilicaria krascheninnikovii* also formed a monophyletic group with 67% bootstrap support that consisted of nine individuals collected from the south-west of Stone A, one from the north-west, one from the north-east, four from the south-east and four from Stone K. *Umbilicaria lyngei* formed a well-supported monophyletic group with 99% bootstrap support, comprising three individuals collected from the south-west of Stone A, two from the north-west, nine from the north-east and four from the south-east. The *U. lyngei* group could be further divided into three distinct monophyletic subgroups. The first sub-group consisted of one individual collected from the south-east of Stone A, with 62% bootstrap support with another sequence (AF297669) from NCBI, whilst the second subgroup consisted of two individuals from the north-east, with 64% bootstrap support. Umbilicaria *arctica* was represented by the largest number of individuals and constituted a well-supported monophyletic group with 98% bootstrap support, consisting of eight individuals collected from the south-west of Stone A, 11 from the north-west, 12 from the north-east, six from the south-east and 16 from Stone K. The *U. arctica* group could be further divided into two distinct monophyletic subgroups, of which the smaller sub-group comprised two individuals collected from the north-east of Stone A and was supported by a bootstrap value of 99%.

Two specimens were designated *Umbilicaria* cf. *polaris* because their ITS sequences showed the closest affinity to reference sequences of *U. polaris*, whereas the available thalli lacked sufficiently clear diagnostic morphological characters for an unequivocal species-level identification. The qualifier "cf." was therefore retained to indicate this uncertainty.

Phylogenetic analyses of photobiont ITS rDNA

In the present study, we obtained ITS rDNA sequences from 115 photobionts and constructed an ME tree (Fig. 3; Supplementary Fig. S4). The analysis identified all photosynthetic partners as *Trebouxia jamesii*.

Although the ME tree indicated that *T. jamesii* exhibited low genetic diversity, the 115 individuals could be divided into four clades. Clade I contained 69 individuals, clade II comprised seven individuals, 37 individuals belonged to clade III and two individuals were assigned to clade IV. Photobiont genotypes were unrelated to geographical location or even the host mycobiont species. No mycobiont species showed a clear preferential association with a particular *T. jamesii* clade, indicating extensive sharing of closely related photobiont lineages within the sampled community. This finding suggests the existence of shared algal pools in these habitats.

Group I intron analyses

Sequence alignment revealed that 20 of 115 *Umbilicaria* individuals harboured a group I intron (Fig. 2), 18 of which were identified as belonging to *U. lyngei* and two belonged to *Umbilicaria* cf. *polaris*. The splicing site of

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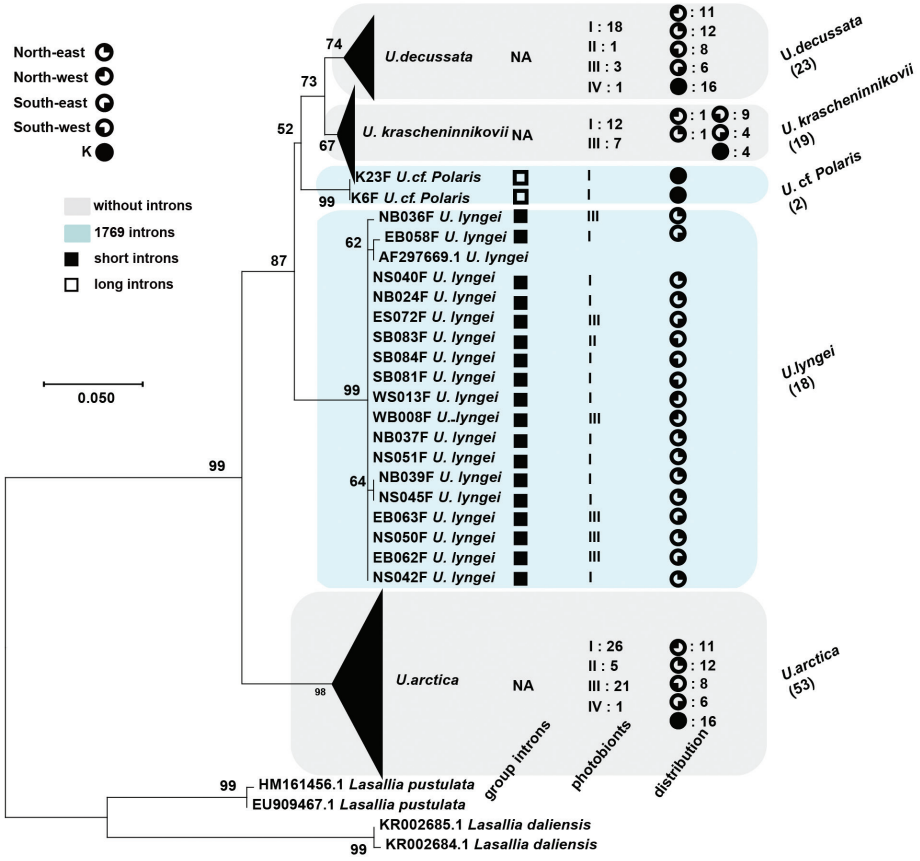


Fig. 2 ME tree of mycobionts based on ITS rDNA sequences. The ME tree displays bootstrap support values (1000 replications), where numbers <50 are not shown. Pie charts indicate the collection site, where the number beside each pie chart represents the number of individuals collected from each location. Amongst the position, 1769 introns found in the mycobiont sequences, a grey background indicates none of the 1769 introns; a blue background represents the presence of the 1769 introns; filled black squares denote short introns; and empty squares indicate long introns. The same branch without introns is folded, and the details of these branches are shown in Supplementary Figs. S1–S3.

group I introns is characterized by the conserved nucleotide 5′ -U↓……G↓3, and the insertion site was determined to be 1769 based on the SSU rDNA sequence of *S. cerevisiae* (GenBank no. Z75578); using the SSU rDNA sequence of *E. coli* as a reference yielded a site of 1506 (Friedl et al. 2000; Bhattacharya et al. 2002; Del Campo et al. 2009; Nyati et al. 2013).

The group I introns were classified into two groups on the basis of their lengths (Gutiérrez et al. 2007), including the "short 1769 group" (150–300 bp) and the "long 1769 group" (300–450 bp). All individuals from *U. lyngei* contained 1769 short introns, whereas *Umbilicaria* cf. *polaris* contained 1769 long introns. However, none of the 1769 introns was detected in other *Umbilicaria* individuals.

Previous research indicates that the secondary structure of group I introns from the same insertion site is conserved, and most of the conserved nucleotides are located in the elements P, Q, R and S (Burke et al. 1987; Del Campo et al. 2009). Group I introns generally have base pairing regions designated as P1 through P9, amongst which the P4 region is formed by P and Q, whereas the P7 region consists of R and S. The results of the present study clearly demonstrated that these conserved elements displayed high similarity in the three clades, as shown in Table 1 and Fig. 4, whereas P3 and P4 were not completely consistent. Figure 4B depicts the secondary structure of the Clade 2 1769 long intron group, which harbours a larger P8.

Discussion

Mycobiont and photobiont diversity

High regional *Umbilicaria* diversity has been reported from polar environments. For example, nine *Umbilicaria*

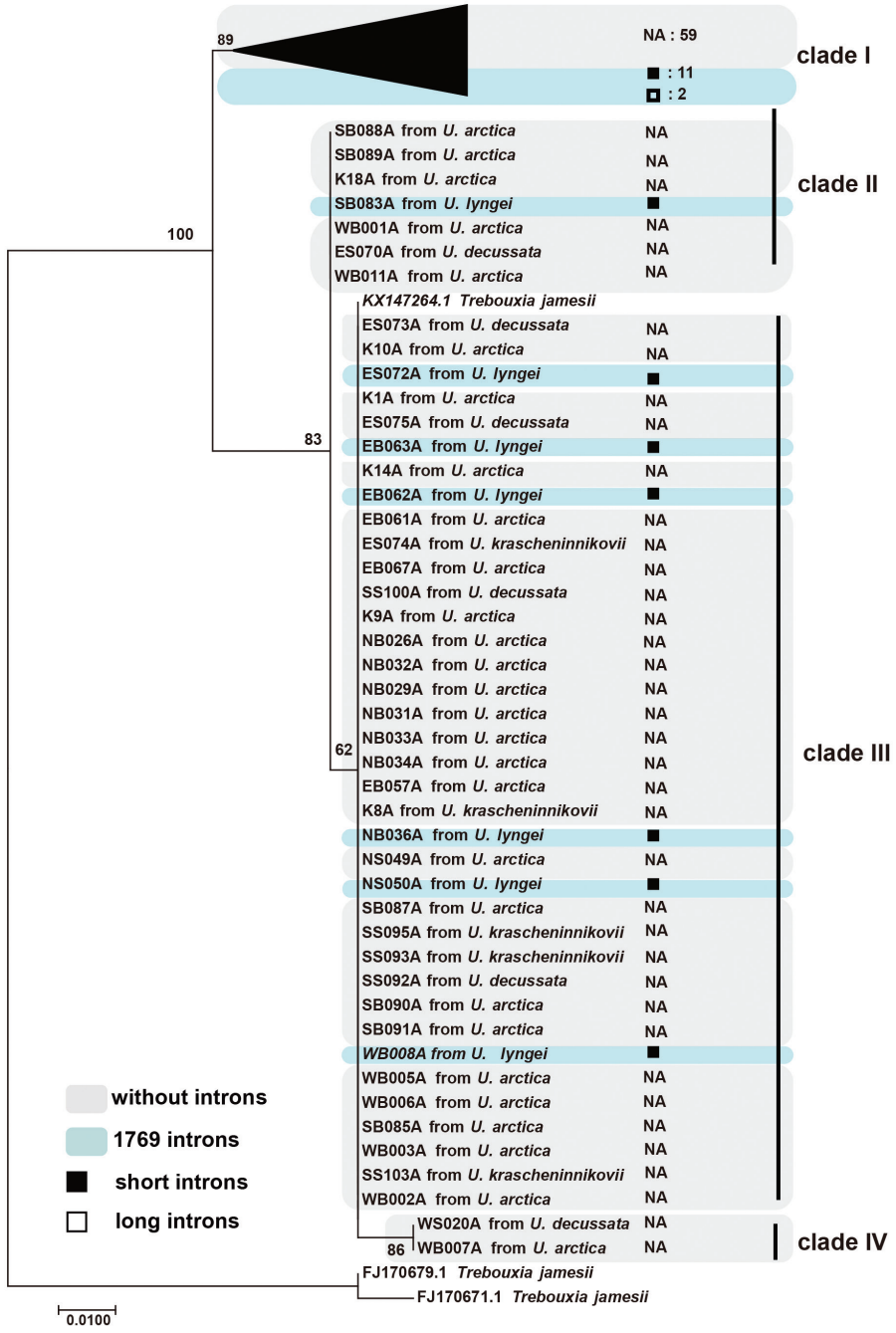


Fig. 3 ME tree of photobionts based on ITS rDNA sequences. The ME tree displays bootstrap support values (1000 replications), where numbers <50 are not shown. Based on the phylogenetic tree, the symbiotic algae can be divided into four haploid types: haplotype I (69 individuals; the branch is folded; details in Supplementary Fig. S4), haplotype II (seven individuals), haplotype III (37 individuals) and haplotype IV (two individuals).

species were documented around Admiralty Bay on King George Island in the maritime Antarctic (Krzewicka & Smykla 2004), and regional lichen surveys have also documented *Umbilicaria* diversity in Svalbard (Krzewicka & Maciejowski 2008).

The phylogenetic diversity of mycobionts that we observed near a pond on Blomstrandhalvøya, Svalbard, was high, despite the restricted geographic area investigated. High diversity was observed even at a very small scale: five taxa across the two boulders, with four taxa occurring on each boulder.

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Table 1 Conserved core sequences of *Umbilicaria* group I introns at the 1769 site on SSU rDNA.

	P3	P4	P4'	P7	P3'	P7'
		P	Q	R		S
Clade 1	TAGGCA	TGCTGG	CCAGCA	CCCGG	GGCCT	CCGGG
Clade 2	GTATAG	TGCTGG	CCAGCA	CCCGG	CTATAC	CCGGG

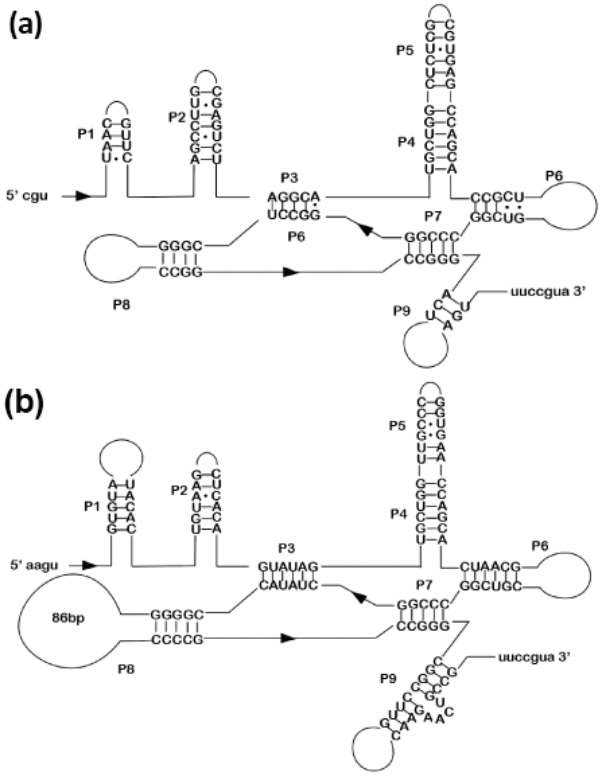


Fig. 4 Schematic diagram of the secondary structure of group I introns at the SSU rDNA 1769 site from *Umbilicaria*. The conserved sequences in the helix region are shown with bases. (a) Secondary structure of the short 1769 group, with a smaller P8 region. (b) Secondary structure of the long 1769 group.

This study analysed 115 samples collected from two stones. Except for *U. arctica*, all mycobiont groups exhibited distinct distribution preferences (Fig. 5). Umbilicaria *decussata* preferentially occurred in the south-eastern and north-western sectors of Stone A; *U. krascheninnikovii* was mostly found towards the south-western sector, whereas *U. lyngei* was predominantly distributed in the north-eastern sector (Fig. 5a). Figure 5b shows the distribution patterns of four photobiont clades. Amongst the 92 samples from Stone A, *U. arctica* was evenly distributed around all stone sides, predominantly on the upper portion. *Umbilicaria decussata* showed a preference for the south-eastern and north-western sectors (as noted above), whereas *U. krascheninnikovii* tended towards the south side, and *U. lyngei* predominantly occurred on the north-east side, with the latter evenly covering both upper and lower stone portions (Fig. 6).

Comparable species richness has also been documented in other cold, rocky environments. Twenty *Umbilicaria* species have been documented in the Polish Tatra Mountains, indicating that high diversity within this genus is not restricted to polar regions (Krzewicka 2004). Nevertheless, the present study differs markedly in spatial scale: rather than surveying a broad mountain region, it documents the coexistence and spatial segregation of multiple *Umbilicaria* species within a very small area. Therefore, the notable feature of our results is not only the number of species detected but also their distinct distribution patterns at the scale of individual rock surfaces.

In addition, observations showed that lichens on the upper part of Stone A were generally larger than those on the lower part. However, because snow-cover duration and relevant microclimatic variables were not measured, the environmental causes of this pattern remain uncertain.

Photobionts were relatively less diverse than mycobionts, and all photobionts belonged to the genus *Trebouxia*. This is the most common and abundant photobiont genus, and lichens capable of surviving in extreme environments are often associated with *Trebouxia* species that can adapt to diverse ecosystems (De Carolis et al. 2022). Consistent with previous studies, all lichen photobionts in our study were identified as *T. jamesii*. To further explore the selectivity of the mycobionts and photobionts, we divided the 115 *T. jamesii* specimens into four clades.

Mycobiont–photobiont association patterns and partner sharing

Summarizing the associations between the five mycobiont taxa and the four photobiont clades (Fig. 7) revealed that *U. decussata* and *U. arctica* formed symbioses with all four photobiont clades, *U. lyngei* was paired with three clades and *U. krascheninnikovii* was paired with two clades. Because *Umbilicaria* cf. *polaris* was represented by only two specimens, its association pattern should be interpreted cautiously. Overall, no clear tendency for particular mycobiont species to associate with a specific photobiont clade was detected. The four *T. jamesii* clades were shared amongst multiple mycobiont species, indicating limited host-related partitioning and the presence of a broadly shared local photobiont pool.

Notably, the association flexibility observed in this study occurred amongst closely related lineages within a single photobiont species—*T. jamesii*—rather than amongst

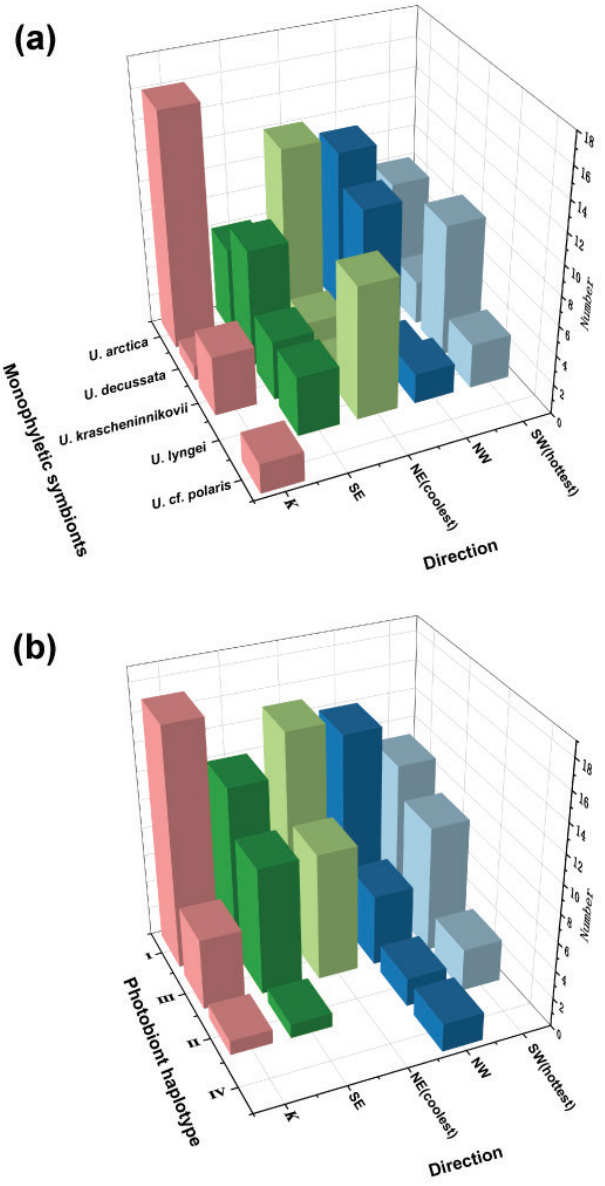


Fig. 5 Three-dimensional bar charts of (a) mycobiont and (b) photobiont distribution on Stone A (represented with the abbreviations for four directions) and Stone K (represented by K).

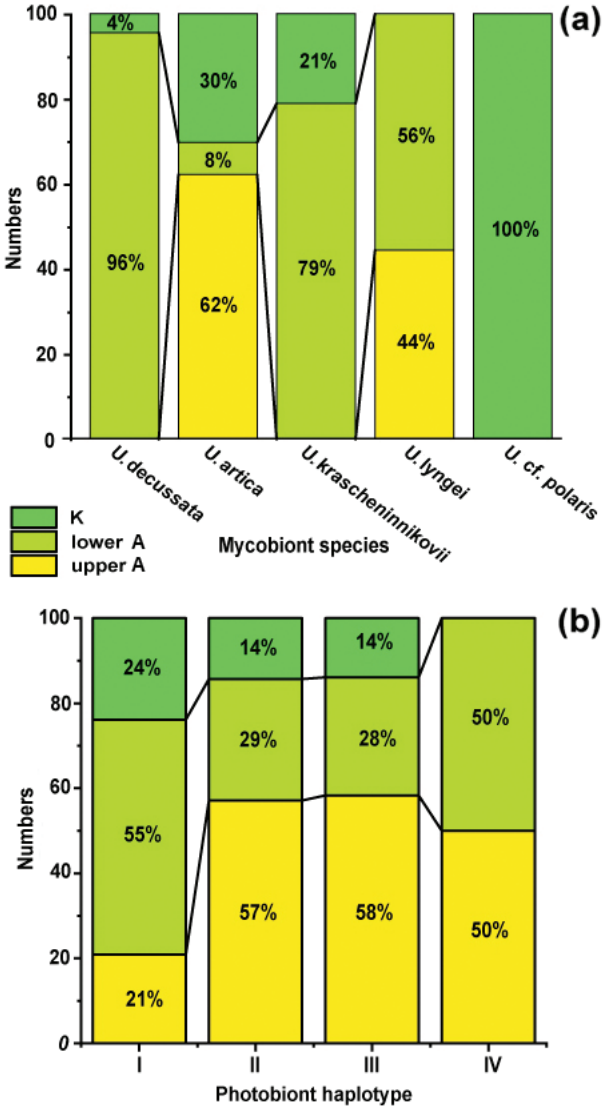


Fig. 6 Stacked bar chart of the vertical distribution of (a) mycobiont species and (b) photobiont clades on Stone K and the upper and lower parts of Stone A.

distantly related photobiont species. Lichen symbiotic associations may be influenced jointly by reciprocal compatibility and selectivity between the partners, the local availability of compatible algae and environmental filtering (Yahr et al. 2004, 2006; Peksa & Škaloud 2011; De Carolis et al. 2022). The ability of several *Umbilicaria* mycobionts to associate with multiple locally available *T. jamesii* lineages may increase their opportunities to establish and maintain symbioses under heterogeneous Arctic conditions. However, because the present study analysed photobionts recovered from established lichen thalli and did not characterize free-living environmental algae or experimentally test partner compatibility, our results demonstrate realized partner sharing but cannot determine the mechanism responsible for the observed associations. Therefore, broad photobiont sharing should be interpreted as a potential component of symbiotic flexibility rather than as direct evidence that low selectivity itself caused adaptation to environmental stress.

Evolutionary information reflected by group I introns

Group I introns are widespread in protists, plants, eubacteria, archaea and even mycobionts and photobionts

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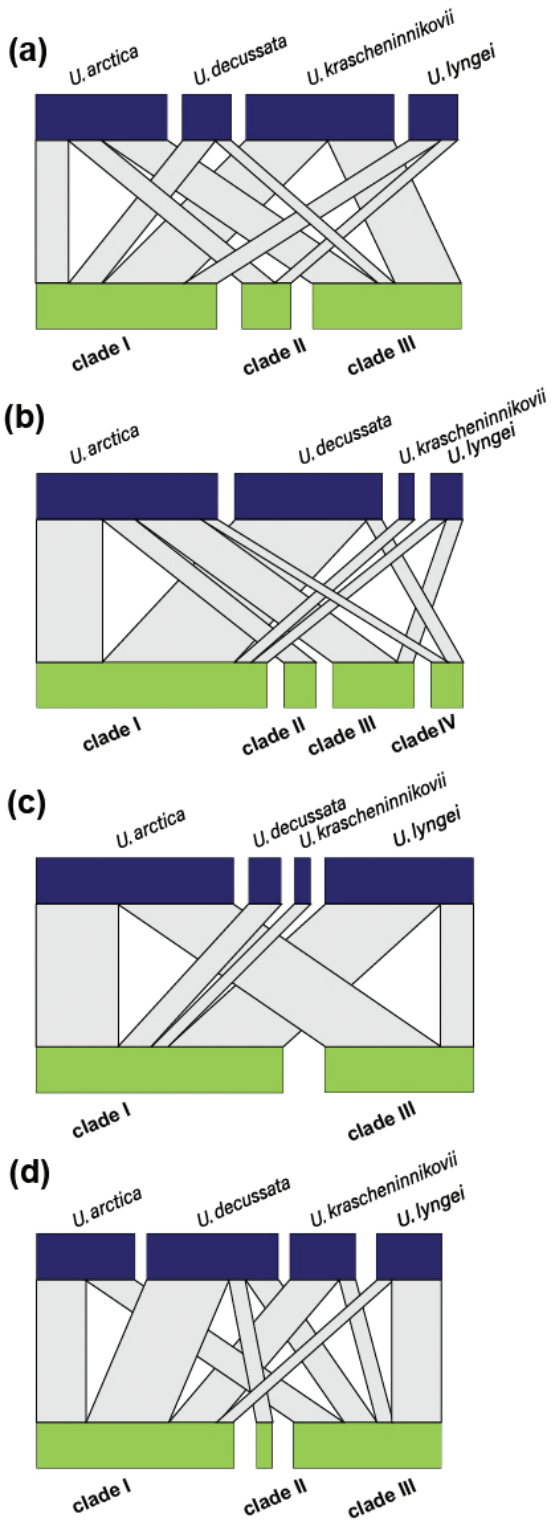


Fig. 7 Interaction network structure between photobiont clades and mycobiont species based on bipartition network analysis, depicting the degree of selectivity of mycobionts collected from the (a) south-west, (b) north-west, (c) north-east and (d) south-east sides of Stone A. Algal clades are shown on the bottom, and mycobiont species are shown on the top.

(Del Hoyo et al. 2018; Nawrocki et al. 2018; Corsaro & Venditti 2020; Liu & Pyle 2024) and were first discovered in *Tetrahymena thermophila* (Cech et al. 1981). Much research has focused on the structural properties of group I introns (Müller 2017; Furulund et al. 2022; Lian et al. 2022; Gomes et al. 2024). Previous studies have demonstrated that the secondary structure of the group I introns is more conserved than that of the primary structure. Studies have shown that group I introns are divided into three domains: the P1–P2 domain, P4–P6 domain and P3–P9 domain (including P3, P7, P8 and P9). The P4–P6 and P3–P9 domains constitute the catalytic centre of the intron ribozyme (Cech et al. 1994; Damberger & Gutell 1994; Adams et al. 2004; Woodson 2005; Zhang et al. 2010). In mycobionts, multiple group I introns may exist in the SSU rDNA of an individual (Bhattacharya et al. 2002). Group I introns have also been previously reported in the nuclear SSU rDNA of *Umbilicaria*. Researchers have identified typical group I introns at position 1506 of the nuclear SSU rDNA, reconstructed a consensus secondary structure for these introns and demonstrated that their sequences provided molecular information complementary to the ITS- and LSU-based phylogenies (Krzewicka et al. 2009). The previous study provides a direct precedent for characterizing *Umbilicaria* group I introns on the basis of both their insertion positions and conserved secondary structures. Against this background, our detection of two intron length groups in Arctic *U. lyngei* and *Umbilicaria* cf. *polaris* extends the available information on the distribution and structural variation of group I introns within the genus. In our study, the group I intron at position 1769 was detected in all *U. lyngei* and *Umbilicaria* cf. *polaris* specimens, and these introns were divided into two groups according to their length. The RNA secondary structures were predicted to clarify the conserved domain and its characteristics (Fig. 4). The P8 element represented the main difference between the short group and the long group. However, the P8 element is not a conserved domain in group I introns and is more likely to undergo mutation or loss without affecting the function of group I introns. It is worth mentioning that the P4 and P7 elements of all introns in this study exhibit extreme conservation. The conservation of the P4 and P7 elements observed in our sequences is consistent with the conserved catalytic core reported for *Umbilicaria* group I introns, whereas variation in the peripheral P8 element appears to account for much of the structural difference between the short and long intron groups identified here (Krzewicka et al. 2009).

Previous studies suggest that group I introns may influence fungal stress resistance via regulating rRNA splicing (Müller 2017). Given that lichenized fungi in extreme environments often face oxidative stress,

desiccation and temperature fluctuations, the presence of group I introns in mycobionts may be of interest in the context of fungal stress responses. However, whether these introns influence rRNA processing, ribosome assembly or stress tolerance remains to be experimentally determined, particularly in Arctic and Antarctic lichen symbioses.

Conclusion

Together, our results indicate that Arctic *Umbilicaria* communities combine fine-scale spatial differentiation amongst mycobionts with broad photobiont sharing. These patterns may contribute to the persistence of lichen symbioses under heterogeneous Arctic conditions, although their adaptive significance and underlying functional mechanisms require further investigation.

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Disclosure statement

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Data availability

The sequences generated for this study were deposited in GenBank. See Supplementary Table S1 for accession numbers.

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