Diversity and distribution of lichens in recently deglaciated areas of southeastern Spitsbergen

Wojciech Maciejowski¹, Piotr Osyczka², Jerzy Smykla³, Wiesław Ziaja⁴, Krzysztof Ostafin⁴, Beata Krzewicka⁵*

¹ Institute of the Middle and Far East, Jagiellonian University, Gronostajowa 3, 30-387 Cracow, Poland
² Institute of Botany, Jagiellonian University, Gronostajowa 3, 30-387 Cracow, Poland
³ Institute of Nature Conservation, Polish Academy of Sciences, Mickiewicza 33, 31-120 Cracow, Poland
⁴ Institute of Geography and Spatial Management, Jagiellonian University, Gronostajowa 7, 30-387 Cracow, Poland
⁵ W. Szafer Institute of Botany, Polish Academy of Sciences, Lubicz 46, 31-512 Cracow, Poland

* Corresponding author. Email: b.krzewicka@botany.pl

Abstract

The diversity and distribution of lichen species were investigated in recently deglaciated areas of the borderland between Sørkapp Land and Torell Land (southeastern Spitsbergen, Svalbard). A total of 15 sites representing various habitat types specific to the area were evaluated. Sampling sites were characterized by a very diverse composition of lichens and species richness ranging from as few as two species to as many as 53. None of the species was ubiquitous among the investigated sampling sites; conversely, most were recorded only once or twice indicating a high heterogeneity in species distribution. Eighty species are reported for the first time from southeastern Spitsbergen. The terricolous lichen Verrucaria xyloxena is reported for the first time from the Svalbard archipelago. The influence of the selected abiotic and biotic environmental factors on the occurrences and distributions of lichen species is discussed in this paper.

Keywords

Arctic; Svalbard; Sørkapp Land; Torell Land; lichenized fungi; spontaneous succession; ice-free areas

Introduction

Spitsbergen is the largest island of the Svalbard archipelago in the Norwegian Arctic. The southeastern part of the island encompasses the mountainous areas of the borderland between Sørkapp Land and Torell Land (Fig. 1) that sharply descend to the coast of the Barents Sea. This part of Spitsbergen is characterized by a much colder climate with more sunshine and lower humidity compared to that in the western coast of the island [1]. Weather conditions, e.g., insolation, wind direction, and near-ground temperature are significantly affected by the local orography [2]. The harsh climate is primarily the result of strong and gusty winds from the east, the presence of the cold East Spitsbergen Current, and extensive inland glaciation [3]. Consequently, the area experiences a very short growing season and its soils are commonly poorly developed. The landscape is mostly barren and devoid of continuous vegetation, which is limited only to few small “oases” [4,5]. The limited vegetation and dominance of cryptogams, mainly lichens and mosses, is typical for the high Arctic polar deserts [3,6].
During the Little Ice Age, the area was almost entirely covered by glaciers [5,7]. However, from the beginning of the twentieth century, it has experienced rapid changes in climate and intense deglaciation [8–10]. Glaciers covered 129 km² (83%) of the study area in 1900 and their coverage had been reduced to only 73 km² (47%) of the area) by 2016 (data based on Wassiliew [7] and Copernicus Sentinel satellite images from 2016). A completely new landscape was created in vast areas, which were relatively suddenly freed of ice. New landforms, progressive soil-forming processes, and changing water relations have accelerated a spontaneous succession process in the last few decades [5].

New landforms, gradual soil development and changing water relations result in the relaxation of environmental constraints and the development of a variety of ice-free habitats suitable for the existence of a terrestrial biota. These habitats are colonized by different groups of organisms, including cyanobacteria, lichens, bryophytes, and vascular plants, thus, providing excellent opportunities for investigating environmental changes and ecosystem development processes during a relatively short period [11–13]. However, compared to the western coast of Sørkapp Land, our study area is much less accessible and covered with pack-ice during most of the year. The knowledge of the area’s ecosystems and how they have or might have changed is very limited, because of the difficulties associated with performing field studies. Studies of the initial vegetation succession processes in the northeastern Sørkapp Land were performed as recently as 2005 [3]. During the first expedition, only 48 lichen species were recorded [14]; for comparison, ca. 200 species of lichens were reported from the western part of Sørkapp Land [15–18], whereas a total of 742 species are known from the entire Svalbard archipelago [6]. Detailed knowledge on the occurrence and species richness of lichen on the east coast of Spitsbergen is relatively limited, because of the remoteness and low accessibility of the region.

The main purpose of our study was to obtain a clear idea of the current diversity of lichen in this poorly investigated but rapidly changing region. Moreover, to provide insights into the factors controlling species distribution and lichen diversity, we analyzed spatial patterns of species richness and distribution in relation to different types of deglaciated habitats that are typical for the southeastern Spitsbergen.

**Material and methods**

**Field survey and sampling**

The Fieldwork and sampling were carried out in July and August 2016 during a research expedition organized by the Institute of Geography and Spatial Management of Jagiellonian University as part of the project “Southeastern Spitsbergen landscape-seascape and biodiversity dynamics under current climate warming”.

A total of 15 sites (Fig. 1) were surveyed:

1. Northern slopes of the Ostoogadskijfjella mountain massive: λ = 16°53′09.7″ E, φ = 77°02′13.3″ N (Fig. 2A);
2. Peripheries of the Sykorabreen glacier: λ = 17°03′51.2″ E, φ = 77°02′15.2″ N;
3. Eastern slopes of the Kamtoppane mountain: λ = 17°10′21.8″ E, φ = 77°01′01.5″ N (Fig. 2B);
4. Fore-fields of the Bevanbreen glacier: λ = 17°13′02.4″ E, φ = 77°00′08.1″ N (Fig. 2C);
5. Fore-fields close to the front of the Bevanbreen glacier: λ = 17°12′51.7″ E, φ = 76°59′56.8″ N;
6. Western slopes of the Geologtoppen mountain: λ = 17°10′30.2″ E, φ = 76°58′52.4″ N;
7. Foot of the Geologtoppen mountain: λ = 17°15′35.8″ E, φ = 76°59′19.0″ N;
8. Foot of the Twillingtoppen mountain: λ = 17°16′38.2″ E, φ = 76°58′41.9″ N (Fig. 2D);
9. Eastern slopes of the Twillingtoppen mountain: λ = 17°15′49.8″ E, φ = 76°58′42.6″ N (Fig. 2E);
10. Summit of the Twillingtoppen mountain: λ = 17°14′57.5″ E, φ = 76°58′35.0″ N;
11. Slopes above the former lake Davislaguna: λ = 17°16′07.7″ E, φ = 76°58′07.5″ N;
12. Summit of the Hedgehogfjellet mountain: λ = 17°14′58.9″ E, φ = 76°57′52.0″ N (Fig. 2F);
13. Vicinity of the Daudbjørnpynten headland: \( \lambda = 17^\circ 15'35.2'' \) E, \( \varphi = 76^\circ 56'26.5'' \) N (Fig. 2G);
14. The Daudbjørnpynten headland: \( \lambda = 17^\circ 15'40.3'' \) E, \( \varphi = 76^\circ 56'22.1'' \) N;
15. Coast at the foot of the Koval'skijjella mountain ridge: \( \lambda = 17^\circ 17'17.0'' \) E, \( \varphi = 77^\circ 03'37.0'' \) N (Fig. 2H).

The selected sites represented a broad range of arbitrarily determined habitats differing in physiognomic types of tundra, geomorphology, and microclimate. Their brief characteristics are provided in Tab. 1.

Species identification

Identification in the field was practiced only when taxonomically nonproblematic specimens were concerned. However, specimens of all the observed taxa were collected for detailed taxonomic evaluation in the laboratory. The collected specimens were identified using routine microscopic and laboratory techniques based on the following keys and taxonomic treatments: Thomson [19, 20], Brodo et al. [21], Øvstedal et al. [6], Smith et al. [22], and Wirth [23]. In addition, chemical analyses of lichen substances were also
Fig. 2 General view of selected sampling sites. (A) Northern slopes of the Ostrogradskijfjella mountain massive (site No. 1); (B) eastern slopes of the Kamtoppane mountain (site No. 3); (C) fore-fields of the Bevanbreen glacier (site No. 4); (D) foot of the Twillingtoppen mountain (site No. 8); (E) eastern slopes of the Twillingtoppen mountain (site No. 9); (F) summit of the Hedgehogfjellet mountain (site No. 12); (G) vicinity of the Daudbjørnpynten headland (site No. 13); (H) coast at the foot of the Kovaškjifjella mountain ridge (site No. 15). Characteristics of sampling sites are provided in Tab. 1.
### Tab. 1 Location and characteristics of the study sites.

| Sampling site | Locality | Brief characteristics of environment |
|---------------|----------|--------------------------------------|
| 1             | Northern slopes of the Ostrogradskijfella mountain massive (Sørkapp Land), 120–160 m a.s.l. | Multisize grained material (from the Hambergbreen glacier’s recession at the turn of the twenty-first century), in many places with the dominance of big rocky blocks. A varied mosaic of habitats. Cryosols covered by large patches of mosses (Fig. 2A) are developed in the wettest loamy-and-debris hollows (with dead ice in bedrock). There are Regosols covered by small mosses clumps and single vascular plants (mainly Saxifraga caespitosa, S. cernua, Cerastium arcticum) at the drier rocky-and-debris bedrock. Extremely dry and poor habitats are formed by boulders with epilithic lichens. |
| 2             | Peripheries of the Sykorabreen glacier (Sørkapp Land), 10–15 m a.s.l. | Multisize grained material (from the Sykorabreen glacier’s recession in the period 2005–2016), with the dominance of fine-grained material, mainly sandy or clayey, with muddy patches. Very moist habitats due to dead ice in bedrock. Noticeable beginnings of the development of soils and vegetation, but very poor in species. |
| 3             | Eastern slopes of the Kamtoppane mountain (Sørkapp Land), 45–60 m a.s.l. | Multisize grained material of the former lateral moraine of the Hambergbreen glacier (recessed at the beginning of the 20th century) dropping down very steeply to the coast. There are individual depressions with periodically small lakes in places. Shallow soils (mainly Regosols). Patches of mosses in humid places. Succession of single vascular plants (e.g., Saxifraga caespitosa, S. nivalis, Cerastium arcticum, Papaver dahlianum, Draba sp.) is visible on a dry fine-grained bedrock. Lichens only grow on rock debris (Fig. 2B). |
| 4             | Fore-fields of the Bevanbreen glacier (Sørkapp Land), 1–4 m a.s.l. | Coastal plain and fore-field of the Bevanbreen glacier shaped since 1936, after the glacier’s recession. Fine-grained moraine material, washed (and episodically flooded) by melt-water flowing from the aforementioned glacier’s tongue. The landscape is varied by hollows with fine-grained (silty or clayey) material and small hills of ground moraine (glacial till) with poor ornithogenic fertilization (they are used as observation points by Arctic skuas Stercorarius parasiticus). Succession of tundra vegetation (Fig. 2C) with mosses, lichens, and clumps of vascular plants (e.g., Puccinella vahlana, Oxyria digyna). The lower parts are sporadically flooded by the sea during storms. |
| 5             | Fore-fields close to the front of the Bevanbreen glacier (Sørkapp Land), 65–75 m a.s.l. | Rampart of the Bevanbreen glacier’s front moraine formed during the last 25–30 years. It is composed of mixed-up multisize grained rock crumbs with the dominance of coarse-grained material. Significantly diverse morphology (hills and hollows) determines variable humidity conditions. |
| 6             | Western slopes of the Geologtoppen mountain (Sørkapp Land), 475–480 m a.s.l. | Gentle slope of the Geologtoppen massif, exposed to the west, covered by coarse-grained layer of debris, dry. Lack of soil. Very poor habitat. |
| 7             | The foot of the Geologtoppen mountain (Sørkapp Land), 2–25 m a.s.l. | Fore-field of the Coryelbreen glacier built of glaciﬂuvial and marine material, systematically superimposed by a glaciﬂuvial cone. Many hills of ground moraine and a large lateral moraine ridge are on the edge of this site. The lowest parts are sporadically flooded by sea water. A varied mosaic of habitats. Very moist patches in the bottom of the periodically flooded lake and loamy moraine depressions are covered by lush mosses and in some places by vascular plants (mainly Puccinella vahlana). There is a complete lack of vegetation on the dry and gravel bedrock. |
| 8             | The foot of the Tvillingtoppen mountain (Sørkapp Land), 25–40 m a.s.l. | Former lateral moraine of the Hambergbreen glacier, from the beginning of the twentieth century, built of multisize grained material (mainly debris and small rocky blocks) with dead ice mostly already melted in bedrock (Fig. 2D). Very dry. Slow development of soils (Regosols) covered by clumps of vegetation with mosses and vascular plants (mainly Luzula confusa). |
| 9             | Eastern slopes of the Tvillingtoppen mountain (Sørkapp Land), 110–225 m a.s.l. | Wide flattening of the Tvillingtoppen slope which passes up into the high (almost vertical) rock wall exposed to the east. On the surface, a thick cover of rock rubble of various fractions, from silt to large rocky blocks (Fig. 2E). Very dry, soil-forming processes are very slow. Individual bundles of mosses grow in the hollows and rock crevices. Epilithic lichens dominate. More luxuriant vegetation grows only in a few patches, near the rock walls with very small bird colonies. |
| 10            | Summit of the Tvillingtoppen mountain (Sørkapp Land), 525–532 m a.s.l. | High-located slope of the Tvillingtoppen massif, exposed to the west, covered by dusty and fine-grained debris weathering material. Dry and lack of soils. Very poor habitat, only with epilithic lichens. |
conducted when necessary and according to the method summarized by Orange et al. [24]. Taxonomic classification and nomenclature follow the Index of Fungorum [25] and MycoBank [26]. The collected specimens were deposited in the herbarium of the W. Szafer Institute of Botany, Polish Academy of Sciences in Cracow (KRAM-L).

Habitat variability

To evaluate the degree of habitat environmental variability across sampling sites, the following ten factors were estimated using a 4-grade scale. The environmental characteristics were estimated based on the field observations, available topographic maps, and published data [3,4,14], and are summarized in Tab. 2. Selected factors and their scalings are provided below:

- Time since deglaciation (Ice-1: ca. 30–50 years; Ice-2: ca. 60–80 years; Ice-3: over 100 years; Ice-4: not glaciated during the Little Ice Age);
- Distance from the shoreline (Dis-1: 0–10 m, direct impact of sea waves, strong abrasion, and material accumulation; Dis-2: 10–100 m, moderate impact of waves and seawater; Dis-3: 100–500 m, low impact of waves, humid air supply only; Dis-4: >500 m, no direct impact of waves);
- Elevation (Alt-1: up to 5 m a.s.l.; Alt-2: 5–150 m a.s.l.; Alt-3: 150–500 m a.s.l.; Alt-4: >500 m a.s.l.);
- Substrate texture (Sub-1: sand and fine gravel; Sub-2: thick gravel and small rock blocks; Sub-3: massive rock blocks; Sub-4: substrate with highly variable texture);
- Intensity of geomorphological processes (Geo-1: no visible changes; Geo-2: small intensity of changes mostly due to wind and frost movements; Geo-3: intensive changes due to destructive hydrological impacts and mass movements; Geo-4: very strong and notorious changes);

| Sampling site | Locality | Brief characteristics of environment |
|---------------|----------|-------------------------------------|
| 11            | Slopes above the former lake Davislaguna (Sørkapp Land), 35–85 m a.s.l. | Steep rock-waste talus cone at the foot of the Hedgehogfjellet massif, which passes up into the vertical rock wall exposed to the east. There are visible development of soils (Lithic Leptosols, Regosols) and succession of vascular plants (mainly Cerastium arcticum, Saxifraga cernua, Oxyria digyna) in the rock crevices and silty-loamy hollows. Weak ornithogenic fertilization. |
| 12            | Summit of the Hedgehogfjellet mountain (Sørkapp Land), 600–615 m a.s.l. | Narrow mountain ridge covered with a layer of the weathered rock debris (a boulder-field), mainly with small and medium-size rocky blocks (Fig. 2F). Only epilithic vegetation (mainly lichens). |
| 13            | Vicinity of the Daudbjørnpynten headland (Sørkapp Land), 45–145 m a.s.l. | Wide valley and concave slope flattening which form an extensive Arctic oasis, unglaciated during the Little Ice Age. There are steep slopes with bird colonies above them. The rocky-weathered cover with well-developed soils (Histosols, Regosols) dominates there. Very strong fertilization from bird colonies (Alle alle and Cepphus grylle). The variability of soil moisture affects the diversity of habitats (Fig. 2G). A very well developed moss-lichen tundra (mainly Aulacomnium turgidum), with a significant share of vascular plants (mainly Salix polaris, Saxifraga rivularis, Poa alpina, Papaver dahlianum), grows very on wet places. In drier places, an increase of ground lichens is visible, and Luzula confusa dominates among vascular plants. Numerous epilithic lichens grow on large rocky blocks. |
| 14            | The Daudbjørnpynten headland (Sørkapp Land), 0–2 m a.s.l. | The foot of the sea cliff with a narrow beach, varied by large rocky blocks. The area is very often destroyed and flooded by sea waves during storms. |
| 15            | Coast at the foot of Koval’skjelljella mountain ridge (Torell Land), 25–30 m a.s.l. | Multisize grained material of the former lateral moraine of the Hambergbreen glacier with a well-developed soil and relatively high humidity of bedrock (melting dead ice). Luxuriant moss-lichen tundra (Fig. 2H) with a large share of vascular plants (e.g., Oxyria digyna, Ranunculus pygmaeus, Cochlearia groenlandica, Poa alpina). Intensive ornithogenic fertilization by multithousand bird colonies (mainly Uria lomvia and Larus hyperboreus). |
Species occurrences across habitat classes

Seriation of an absence–presence (0/1) matrix using the algorithm described by Brower and Kile [27] was used to analyze the occurrences of lichen species across particular habitat classes. A constrained optimization algorithm was applied and all recorded species were included in seriation. In addition, the number of species in all habitat classes was calculated to reveal differences in species richness between the classes and to determine the direction of changes in biodiversity.

Results

A total of 114 lichen species (γ diversity) were recorded in 14 of the 15 study sites. The site containing no lichen species (i.e., site No. 14, which is regularly modified by the
sea) was excluded from further consideration. The complete list of species and their distribution across the sites are provided in Table 3. Species richness (α diversity) was highly variable among sites and ranged from (0) 2 to 53 species (mean ±SD = 21.5 ±13.2), although sites most commonly exhibited richness in the range of 18 to 31 species (50% of sites). Only two sites were characterized by a greater number of lichen species: site No. 15 at the foot of the Koval’skijfjella mountain ridge in Torell Land (39 species) and site No. 13 in the vicinity of the Daudbjørnpynten headland (53 species). Both sites had similar habitat conditions; however, they differ in terms of glacier retreat (Table 1, Table 2). At present, these two localities have a well-developed soil that is covered by moss-lichen tundra and host a diverse flora of vascular plants (e.g., Oxystyla digyna, Poa alpina, Papaver dahlium, Salix polaris, Saxifraga rivularis, Cochlearia groenlandica, Luzula confusa, Draba sp.). The lichens at both sites displayed different stages of thalli development ranging from initial to well-developed forms. Species of the genus Umbilicaria were particularly abundant on stone blocks, and dense cushions of terricolous lichens were observed growing on the soil among mosses. Despite the high lichen richness observed at these two sites, only a few species were exclusively recorded, such as Cladonia mitis, C. pocillum, Flavocetraria nivalis, and Rhizoplaca melanophthalma. The rest of the species found at these sites were also found at other sampling sites. The site with the smallest number of species (site No. 2) was located on the periphery of the Sykorabreen glacier and was only uncovered in the last decade. Only two species of Stereocaulon were recorded there: Stereocaulon glareosum, found exclusively at this locality, and S. capitellatum, which was also noted at other localities. Their juvenile forms were found on a soil film on stable rock blocks.

Differences in species compositions among the sites (β diversity) were also considerable (Table 3). Most species were recorded only once (46 species) or twice (35 species) and none of the species was found at all sampling sites. This indicates high heterogeneity in species distribution. Among the observed species were reputedly rare species, for example, Staurothele arctica, which has only been reported in Spitsbergen twice, including in this study, and Caloplaca tornoeensis, which has been sporadically recorded from Svalbard. Furthermore, the terricolous lichen Verrucaria xyloxaena is reported here for the first time from the Svalbard archipelago. Only 10 species were relatively widely distributed in the study area (number of occurrences is shown in parentheses): Candelariella vitellina (7), Cladonia borealis (7), Lecanora polytropa (13), Lecidea atrobrunnea (7), Porpidia tuberculosa (9), Rhizocarpon geographicum (11), Tremolecia atrata (13), Umbilicaria cylindrica (12), U. hyperborea (10), and U. torrefacta (7). From the above species, Lecanora polytropa and Tremolecia atrata are considered to occur frequently across the entire study area, being absent only in extremely harsh habitats, such as areas notoriously flooded by the sea or areas recently freed from ice (see Fig. 3). Analyses of the seriation graphs (Fig. 3) demonstrate that the aforementioned common species occurred across most of the sampling sites, suggesting they exhibit wide ecological tolerances. Similarly, some of the more uncommon lichens also demonstrate a tolerance of variation in some environmental factors. These species were observed in habitats spanning all the scale degrees of the specified habitat factor. Cladonia macrosceras occurred in habitats of all four classes of Veg factor, Ionaspis lacastris in habitats of all classes of Alt, Sub, Veg, Cov, Moi, and Win factors, Lecidea auriculata in habitats of all classes of Ice, Sub, Moi, and Win, Psilotelia lucida in habitats of all classes of Ice, Stereocaulon capitellatum in habitats of all classes of Ice and Sub, Umbilicaria arctica in habitats of all classes of Ice, Veg, Cov, Fer, and Moi and U. virginis in habitats of all classes of Fer and Moi. Conversely, other species were associated with specific habitat parameters (see Fig. 3).

Most species (90% of listed lichens) were found in habitats 100–500 m from the coast (Dis-3) and at elevations ranging from 5–150 m a.s.l. (Alt-2). None of the lichens was observed at sites directly by the sea (Dis-1) (Fig. 3A). A minute intensity of geomorphological processes (Geo-2) was preferred by 92 lichen species. A stable rocky substrate and substrates of varied textures (Sub-2 and Sub-4) were preferred by almost 100% of the recorded lichens. The more common species and/or terricolous lichens (around 20% of all species) sporadically occurred in habitats whose substrates were classified into the two other substrate categories (Sub-1 and Sub-3). Humidity (Moi) and wind factor (Win) appear to be the least important parameters in determining lichen distribution (Fig. 3B). The amount of time since glacier retreat (Ice) turned out to be an important
| No. | Species name                                      | Abbrev. | Substrate | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 |
|-----|--------------------------------------------------|---------|-----------|---|---|---|---|---|---|---|---|---|----|----|----|----|----|----|
| 1   | Acarospora badiusfusca (Nyl.) Th. Fr.            | Aca bad | L         |   |   |   |   |   |   |   |   |   |    |    |    |    |    |
| 2   | Acarospora molybdina (Wahlenb.) A. Massal.       | Aca mol | L         |   |   |   |   |   |   |   |   |   |    |    |    |    |    |
| 3   | Acarospora rugulosa Körb.                        | Aca rug | L         |   |   |   |   |   |   |   |   |   |    |    |    |    |    |
| 4   | Acarospora sinopica (Wahlenb.) Körb.             | Aca sin | L         |   |   |   |   |   |   |   |   |   |    |    |    |    |    |
| 5   | Acarospora veronensis A. Massal.                 | Aca ver | L         |   |   |   |   |   |   |   |   |   |    |    |    |    |    |
| 6   | Acarospora verruciformis H. Magn.                | Aca verr| L         |   |   |   |   |   |   |   |   |   |    |    |    |    |    |
| 7   | Amandinea coniops (Wahlenb.) M. Choisy          | Ama con | L         |   |   |   |   |   |   |   |   |   |    |    |    |    |    |
| 8   | Arthrorhaphis alpina (Schaer.) R. Sant.          | Art alp | G         |   |   |   |   |   |   |   |   |   |    |    |    |    |    |
| 9   | Arthrorhaphis citrinella (Ach.) Poelt            | Art cit | G         |   |   |   |   |   |   |   |   |   |    |    |    |    |    |
| 10  | Aspicilia circularis (H. Magn.) Oxner           | Asp cir | L         |   |   |   |   |   |   |   |   |   |    |    |    |    |    |
| 11  | Aspicilia culcis (Lyngge) Thomson                | Asp cul | L         |   |   |   |   |   |   |   |   |   |    |    |    |    |    |
| 12  | Aspicilia mashiginensis (Zahlbr.) Oxner          | Asp mas | L         |   |   |   |   |   |   |   |   |   |    |    |    |    |    |
| 13  | Bacidia bagliettoana (Massal. & de Not.) Jatta  | Bac bag | B         |   |   |   |   |   |   |   |   |   |    |    |    |    |    |
| 14  | Baemlycales rufus (Huds.) Rebenh.                | Bae ruf | G         |   |   |   |   |   |   |   |   |   |    |    |    |    |    |
| 15  | Bellemerea subsorediza (Lyngge) R. Sant. cf.     | Bel sub | L         |   |   |   |   |   |   |   |   |   |    |    |    |    |    |
| 16  | Bueellia insignis (Naeg. ex Hepp) Th. Fr.       | Bue ins | B         |   |   |   |   |   |   |   |   |   |    |    |    |    |    |
| 17  | Caloplaca exsecuta (Nyl.) Dalla Torre & Sarnth.  | Cal exs | L         |   |   |   |   |   |   |   |   |   |    |    |    |    |    |
| 18  | Caloplaca tornoënsis H. Magn.                   | Cal tor | B         |   |   |   |   |   |   |   |   |   |    |    |    |    |    |
| 19  | Candelariella aurella (Hoffm.) Zahlbr.           | Can aur | L         |   |   |   |   |   |   |   |   |   |    |    |    |    |    |
| 20  | Candelariella vitellina (Ehrh.) Müll. Arg.      | Can vit | L         |   |   |   |   |   |   |   |   |   |    |    |    |    |    |
| 21  | Cetraria ericetorum Opiz                         | Cet cri | G         |   |   |   |   |   |   |   |   |   |    |    |    |    |    |
| 22  | Cetraria islandica (L.) Ach.                    | Cet isl | G         |   |   |   |   |   |   |   |   |   |    |    |    |    |    |
| 23  | Cetraria islandica ssp. crispiformis            | Cet cri | G         |   |   |   |   |   |   |   |   |   |    |    |    |    |    |
| 24  | Cetraria nigricans (Retz.) Nyl.                 | Cet nig | G         |   |   |   |   |   |   |   |   |   |    |    |    |    |    |
| 25  | Circinaria caesioinerea (Nyl.) A. Nordin, S. Savic & Tibell | Cir cae | L         |   |   |   |   |   |   |   |   |   |    |    |    |    |    |
| 26  | Cladonia borealis S. Stenroos                  | Cla bor | G         |   |   |   |   |   |   |   |   |   |    |    |    |    |    |
| 27  | Cladonia chlorophaea (Hörk.) Spreng.            | Cla chl | G         |   |   |   |   |   |   |   |   |   |    |    |    |    |    |
| 28  | Cladonia macroceras (Delise) Hav.               | Cla mac | G         |   |   |   |   |   |   |   |   |   |    |    |    |    |    |
| 29  | Cladonia macrophyllodes Nyl.                    | Cla des | G         |   |   |   |   |   |   |   |   |   |    |    |    |    |    |
| No. | Species name                        | Abbrev. | Substrate | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 |
|-----|------------------------------------|---------|-----------|----|---|---|---|---|---|---|---|---|----|----|----|----|----|----|
| 30  | *Cladonia mitis* Sandst.           | Cla mit | G         |    |   |   |   |   |   |   |   |    |    |    |    |    |    |
| 31  | *Cladonia pocillum* (Ach. O. J. Rich. | Cla poc | G/B       |    |   |   |   |   |   |   |   |    |    |    |    |    |    |
| 32  | *Cladonia pyxidata* (L.) Hoffm.    | Cla pyx | G         |    |   |   |   |   |   |   |   |    |    |    |    |    |    |    |
| 33  | *Cladonia stricta* (Nyl.) Nyl.     | Cla str | G         |    |   |   |   |   |   |   |   |    |    |    |    |    |    |    |
| 34  | *Cladonia subulata* (L.) Wigg.    | Cla sub | G         |    |   |   |   |   |   |   |   |    |    |    |    |    |    |    |
| 35  | *Flavocetraria nivalis* (L.) Kärnefelt & Thell | Fla niv | G         |    |   |   |   |   |   |   |   |    |    |    |    |    |    |    |
| 36  | *Fuscia gothoburgensis* (H. Magn.) Wirth & Vězda | Fus got | L         |    |   |   |   |   |   |   |   |    |    |    |    |    |    |    |
| 37  | *Gowardia nigricans* (Ach.) Halonen, Myllys | Gow nig | G         |    |   |   |   |   |   |   |   |    |    |    |    |    |    |    |
| 38  | *Ionaspis lacustris* (With.) Lutzoni | Ion lac | L         |    |   |   |   |   |   |   |   |    |    |    |    |    |    |    |
| 39  | *Lecanora handeli* Steiner        | Lec han | L         |    |   |   |   |   |   |   |   |    |    |    |    |    |    |    |
| 40  | *Lecanora intricata* (Ach.) Ach.  | Lec int | L         |    |   |   |   |   |   |   |   |    |    |    |    |    |    |    |
| 41  | *Lecanora polytropa* (Hoffm.) Rabenh. | Lec pol | L         |    |   |   |   |   |   |   |   |    |    |    |    |    |    |    |
| 42  | *Lecanora torrida* Vain.         | Lec tor | L         |    |   |   |   |   |   |   |   |    |    |    |    |    |    |    |
| 43  | *Lecidea atrorubens* (Ram. ex Lam. & DC) Schar. | Lec atr | L         |    |   |   |   |   |   |   |   |    |    |    |    |    |    |    |
| 44  | *Lecidea auriculata* Th. Fr.      | Lec aur | L         |    |   |   |   |   |   |   |   |    |    |    |    |    |    |    |
| 45  | *Lecidea confluentia* (Web.) Ach. | Lec con | L         |    |   |   |   |   |   |   |   |    |    |    |    |    |    |    |
| 46  | *Lecidea lapicida* (Ach.) Ach.    | Lec lap | L         |    |   |   |   |   |   |   |   |    |    |    |    |    |    |    |
| 47  | *Lecidea plana* (J. Lahm) Nyl.    | Lec pla | L         |    |   |   |   |   |   |   |   |    |    |    |    |    |    |    |
| 48  | *Lecidea tessellata* Flörke       | Lec tes | L         |    |   |   |   |   |   |   |   |    |    |    |    |    |    |    |
| 49  | *Lecidella effugiens* (B. Nilsson) Knoph & Hertel | Lec eff | L         |    |   |   |   |   |   |   |   |    |    |    |    |    |    |    |
| 50  | *Leidoma demissum* (Rutstr.) G. Schneid. & Hertel | Lec dem | B         |    |   |   |   |   |   |   |   |    |    |    |    |    |    |    |
| 51  | *Lepraria eburnea* J. R. Laundon  | Lep ebu | B         |    |   |   |   |   |   |   |   |    |    |    |    |    |    |    |
| 52  | *Lepraria neglecta* (Nyl.) Lettau  | Lep neg | B         |    |   |   |   |   |   |   |   |    |    |    |    |    |    |    |
| 53  | *Lepraria rigidula* (de Lesd.) Tønsberg | Lep rig | G         |    |   |   |   |   |   |   |   |    |    |    |    |    |    |    |
| 54  | *Lepraria svalbardensis* Tønsberg | Lep sva | G         |    |   |   |   |   |   |   |   |    |    |    |    |    |    |    |
| 55  | *Micarea incrassata* Hedl.        | Mic inc | B         |    |   |   |   |   |   |   |   |    |    |    |    |    |    |    |
| 56  | *Myrionoma smagida* (Wahlenb.) Nägeli ex Uloth | Myr sma | L         |    |   |   |   |   |   |   |   |    |    |    |    |    |    |    |
| 57  | *Ochrolechia androgyina* (Hoffm.) Arnold | Och and | B/G       |    |   |   |   |   |   |   |   |    |    |    |    |    |    |    |
| 58  | *Ochrolechia frigida* (Sw.) Lyngre | Och fri | B/G       |    |   |   |   |   |   |   |   |    |    |    |    |    |    |    |
| 59  | *Orphnispora mariopsis* (Massal.) D. Hawksw. | Orp mor | L         |    |   |   |   |   |   |   |   |    |    |    |    |    |    |    |
| No. | Species name                                      | Abbrev. | Substrate |
|-----|--------------------------------------------------|---------|-----------|
| 60  | Parmelia saxatilis (L.) Ach.                    | Par sax | B         |
| 61  | Peltigera canina (L.) Willd.                    | Pel can | G         |
| 62  | Peltigera malacea (Ach.) Funck.                 | Pel mal | G         |
| 63  | Phaeophyscia endococcina (Körb.) Moberg         | Pha end | L         |
| 64  | Phaeophyscia nigricans (Förk.) Moberg           | Pha nig | L/B       |
| 65  | Physcia caesia (Hoffm.) Fürn.                   | Phy cae | L         |
| 66  | Physcia dubia (Hoffm.) Lettau                   | Phy dub | L         |
| 67  | Physcia tenella (Scop) DC.                      | Phy ten | L         |
| 68  | Polyblastia septentrionalis Lyne                | Pol sep | L         |
| 69  | Polysporina simplex (Davies) Vězda              | Pol sim | L         |
| 70  | Porphidia flavocruenta Fryday & Buschbom       | Por fla | L         |
| 71  | Porphidia melinodes (Körb.) Hertel              | Por mel | L         |
| 72  | Porphidia thomsonii Gowan                      | Por tho | L         |
| 73  | Porphidia tuberculosa (Sm.) Hertel & Knoph     | Por tub | L         |
| 74  | Pseudephebe minuscula (Nyl.) Brodo & D. Hawksw.| Pse min | L/G       |
| 75  | Pseudephebe pubescens (L.) M. Choisy            | Pse pub | L/G       |
| 76  | Psileuclea lucida (Ach.) M. Choisy              | Psi luc | L         |
| 77  | Rhizocarponatroflavescens Lyne                  | Rhi atr | L         |
| 78  | Rhizocarpon copelandii (Körb.) Th. Fr.          | Rhi cop | L         |
| 79  | Rhizocarpon eupetraeum (Nyl.) Arnold            | Rhi eup | L         |
| 80  | Rhizocarponexpallens Th. Fr.                    | Rhi exp | L         |
| 81  | Rhizocarpon guminatum Körb.                    | Rhi gem | L         |
| 82  | Rhizocarpon geographicum (L.) DC.               | Rhi geo | L         |
| 83  | Rhizocarpon hochstetteri (Körb.) Vainio        | Rhi hoc | L         |
| 84  | Rhizocarpon inarense (Vain.) Vain.              | Rhi ina | L         |
| 85  | Rhizocarpon intermediellum Räsänen              | Rhi int | L         |
| 86  | Rhizocarpum polycarpum (Hepp) Th. Fr.           | Rhi pol | L         |
| 87  | Rhizoplaca melanophthalma (Ram.) Leuckert & Poelt| Rhi mel | L         |
| 88  | Sphaerophorus globosus (Huds.) Vainio           | Sph glo | L         |
| 89  | Staurothele arctica Lyne                        | Sta arc | L         |
| No. | Species name                           | Abbrev. | Substrate | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 |
|-----|---------------------------------------|---------|-----------|---|---|---|---|---|---|---|---|---|----|----|----|----|----|----|
| 90  | Stereocaulon alpinum Laur.            | Ste alp | G         |   |   |   |   |   |   |   |   |   |    |    |    |    |    |    |
| 91  | Stereocaulon arcticum Lynege          | Ste arc | L         |   |   |   |   |   |   |   |   |   |    |    |    |    |    |    |
| 92  | Stereocaulon botryosum Ach. em. Frey  | Ste bot | L         |   |   |   |   |   |   |   |   |   |    |    |    |    |    |    |
| 93  | Stereocaulon capitellatum H. Magn.    | Ste cap | G         | * | * | * | * |   |   |   |   |   |    |    |    |    |    |    |
| 94  | Stereocaulon glareosum (Savicz) H. Magn. | Ste gla | G         |   |   |   |   |   |   |   |   |   |    |    |    |    |    |    |
| 95  | Stereocaulon rivulorum H. Magn.       | Ste riv | G         |   |   |   |   |   |   |   |   |   |    |    |    |    |    |    |
| 96  | Tremolecia atrata (Ach.) Hertel       | Tre atr | L         | * | * | * | * | * | * | * | * | * |    |    |    |    |    |    |
| 97  | Umbilicaria aprina Nyl.               | Umb apr | L         |   | * |   |   |   |   |   |   |   |    |    |    |    |    |    |
| 98  | Umbilicaria arctica (Ach.) Nyl.       | Umb arc | L         | * | * | * | * |   |   |   |   |   |    |    |    |    |    |    |
| 99  | Umbilicaria crustulosa (Ach.) Frey    | Umb cru | L         |   |   |   |   |   |   |   |   |   |    |    |    |    |    |    |
| 100 | Umbilicaria cylindrica (L.) Delise    | Umb cyl | L         | * | * | * | * | * | * | * | * | * |    |    |    |    |    |    |
| 101 | Umbilicaria decussata (Vill.) Frey    | Umb dec | L         |   |   |   |   | * | * | * | * | * |    |    |    |    |    |    |
| 102 | Umbilicaria hyperborea (Ach.) Hoffm   | Umb hyp | L         | * | * | * | * | * | * | * | * | * |    |    |    |    |    |    |
| 103 | Umbilicaria lyngei Scholander         | Umb lyn | L         |   |   |   |   |   |   |   |   |   |    |    |    |    |    |    |
| 104 | Umbilicaria nylanderiana (Zahlbr.) H. Magn. | Umb nyl | L         | * |   |   |   |   |   |   |   |   |    |    |    |    |    |    |
| 105 | Umbilicaria torrefacta (Lightf.) Schrad. | Umb tor | L         | * | * | * | * | * | * | * | * | * |    |    |    |    |    |    |
| 106 | Umbilicaria velloa (L.) Ach.          | Umb vel | L         | * |   |   |   |   |   |   |   |   |    |    |    |    |    |    |
| 107 | Umbilicaria virginis Schaefer         | Umb vir | L         | * | * |   |   |   |   |   |   |   |    |    |    |    |    |    |
| 108 | Usnea sphacelata R. Br.               | Usn sph | L         |   | * |   |   |   |   |   |   |   |    |    |    |    |    |    |
| 109 | Verrucaria sp.                        | Ver sp. | L         |   | * |   |   |   |   |   |   |   |    |    |    |    |    |    |
| 110 | Verrucaria aethiobola Wahlenb.         | Ver aet | L         | * |   |   |   |   |   |   |   |   |    |    |    |    |    |    |
| 111 | Verrucaria margareta (Wahlenb.) Wahlenb. | Ver mar | L         | * |   |   |   |   |   |   |   |   |    |    |    |    |    |    |
| 112 | Verrucaria xyloxea Norman              | Ver xyl | G         | * |   |   |   |   |   |   |   |   |    |    |    |    |    |    |
| 113 | Xanthoria elegans (Link) Th. Fr.      | Xan ele | L         | * |   |   |   |   |   |   |   |   |    |    |    |    |    |    |
| 114 | Xanthoria sorediata (Vain.) Poelt     | Xan sor | L         | * |   |   |   |   |   |   |   |   |    |    |    |    |    |    |
|     | Total                                 |         |           | 12| 2 | 31| 22| 22| 18| 9 | 23| 24| 8 | 15| 19| 53| 0 | 39|
| Species  | Habitat  | Location  | Age Class |
|----------|----------|-----------|-----------|
| Species A | Habitat A | Location A | Age Class A |
| Species B | Habitat B | Location B | Age Class B |
| Species C | Habitat C | Location C | Age Class C |
| Species D | Habitat D | Location D | Age Class D |

Table showing the distribution of lichen species across different habitats and locations in southeastern Spitsbergen.
factor influencing the quantitative and qualitative diversity of lichens that determines the development of various communities (Fig. 3A). Only 10% of the recorded lichens were exclusively noted in sites classified into the Ice-1 and Ice-2 categories. Seventy lichen species were noted in areas classified into the Ice-3 category, including 18 species occurring exclusively in Ice-3 habitats. Similarly, 77 lichen species were noted in sites classified into the Ice-4 category, including 29 species occurring exclusively in these habitats. The biotic factors, including vegetation cover (Cov), ornithogenic fertilization intensity (Fer), and dominant vegetation type (Veg) mainly grouped the lichen species into two classes (Class 1 and Class 4). The lichen species found in habitats classified into either Class 2 or Class 3 of Cov, Fer, and Veg were observed sporadically (Fig. 3B).

Fig. 4 shows variation in patterns of species richness across the considered environmental variables. The most pronounced changes in species richness appear to be related to variation in abiotic factors, including the time since deglaciation (Ice), distance from the shoreline (Dis), elevation (Alt), and intensity of geomorphological and hydrological processes (Geo). For instance, species richness clearly increased as time since glacier retreat also increased. Patterns related to the distance of habitats from the sea coast and habitat elevation indicate that mountain ridges and slopes up to the altitude of 150 m a.s.l. hosted considerably larger numbers of species than lower, coastal areas or steeper mountain slopes and peaks. Other factors were also important and often strongly affected species richness. Unstable sands and fine gravels were poorly colonized by lichens. Contrasting patterns were identified in the effects of biotic factors on lichen richness, as extreme values of ornithogenic fertilization, moisture, and the abundance of mosses and vascular plants seemingly promoted lichen species richness, while lower species richness were associated with habitats exhibiting less extreme values.

![Fig. 3](image-url) Association matrices of lichen species and 4-grade-scaled habitat factors. Abbreviations indicate: (i) Ice – time since deglaciation; Dis – distance from the shoreline; Alt – elevation; Sub – substrate texture; Geo – intensity of geomorphological processes; (ii) Veg – dominant vegetation; Cov – vegetation cover; Fer – ornithogenic fertilization intensity; Moi – moisture; Win – wind exposure. For variable specifications and lichen species acronyms see “Material and methods” and Tab. 3.

![Fig. 4](image-url) Lichen species richness in 4-grade scale for particular habitat factors. For abbreviation see Fig. 3 caption. For variable specifications see "Material and methods".
**Discussion**

Taking into account the number of lichen taxa known from the Svalbard archipelago (>740) [6] and the ca. 200 taxa reported from the western part of Sørkapp Land [15–18], a total species richness of 128 species (114 reported in the current study and 14 species previously reported by Krzewicka and Maciejowski [14] but not recorded here) can be considered as relatively low. However, it is worth noting that the relatively low lichen species richness in the study area is analogous to prior reports on the diversity of vascular plants, which reported richness of only 20–25 species [3] (also personal data). In contrast, 82 species are known from western Sørkapp Land [28,29]. These patterns of low diversity are likely related to differences in glaciation history between study areas, with the current study area being almost completely covered by glaciers during the Little Ice Age but having recently been the subject of considerable deglaciation [3,5]. Increases in the severity of climatic conditions are also likely an important factor limiting biological colonization and ecosystem development processes [1].

One of the goals of our study was to provide insights into the factors that are responsible for the local distribution and diversity of lichens. Therefore, the sampling design covered a broad range of habitats that are typical for the deglaciated areas of southeastern Spitsbergen. Significant differences in the environmental characteristics of the sampling sites are related primarily to their geological and climatological history [5,30]. From a lichenological point of view, the foot of Koval’škijfjella and areas in the vicinity of the Daudbjørnpynten headland are the most interesting since both sites are characterized by high lichen diversity (39 and 53 species, respectively). These sites are generally similar in terms of their environmental conditions, including distance from the sea, elevation, intensity of geomorphological processes, moisture content, and ornithogenic fertilization (see Tab. 2). Nevertheless, the sites differed considerably in their glaciation history. The Daudbjørnpynten headland was ice-free during the Little Ice Age while the site at the foot of Koval’škijfjella was covered by ice until the beginning of the twentieth century when the glacier began to retreat [3,8]. In spite of this, both sites are, at present, overgrown by a well-developed moss-lichen tundra with a large number of vascular plants. This is likely due to the high moisture regime and strong ornithogenic fertilization at these sites, both of which are crucial factors in the development of nutrient-rich soil [31,32].

The rich lichen biota of both sites, in addition to numerous epilithic taxa, also consists of epigeic and epiphytrophic species, among which patches of *Flavocetraria nivalis, Cetraria islandica, Sphaerophorus globosus*, and *Cladonia* spp. were the most common. Whereas on rocks and boulders, *Umbilicaria* spp., foliose lichens common in some polar and alpine regions [33,34], grow abundantly forming the main visual component of the epilithic biota. High variation in the stages of lichen thallus development is symptomatic among encountered lichens. This variability is often associated with older deglaciation events and substratum stability, which appear to be decisive factors controlling lichen development in Svalbard [6,18,35].

Many species were found across the other sampling sites, and only a few, i.e., *Cladonia mitis, C. pocillum, Flavocetraria nivalis, and Rhizoplaca melanophthalma*, seemed to be restricted in their distribution. All of these species are either foliose or fruticose macrolichens and also occur frequently on the opposite side of the island on its west coast [6]. The species richness of Koval’škijfjella and areas in the vicinity of Daudbjørnpynten is comparable with that of some areas of the west coast, for example 43 species of lichens were noted on the Longyearbreen moraine and 60 on the Irenebreen moraine [18].

Considering the importance of glaciation history in determining lichen species distribution and richness, it is not surprising that the lowest species richness is associated with recently deglaciated habitats (i.e., Sykorabreen peripheries) or the recent presence of permanent snowfields (i.e., Tvillingtoppen summit). On the other hand, substratum instability due to intensive geomorphological and/or hydrological processes (i.e., at the Daudbjørnpynten headland and the foot of Geologtoppen) are responsible for the limitation of the development of lichen biotas.

It should be mentioned that a remarkable number of the recorded species appeared to be seemingly rare in the investigated area. Unfortunately, inaccessible but important habitats, such as vertical rock cliffs, can be accidentally omitted during field research. Thus, the actual species richness in the area can still be considerably underestimated.
Considering the current rapid climate change and related ecological implications, further targeted studies are needed to provide a complete assessment of tundra vegetation diversity and a baseline for the monitoring of environmental changes in the area.

Conclusions

- One hundred fourteen species of lichen were identified in the study area and 80 of them are reported for the first time from southeastern Spitsbergen.
- The terricolous species *Verrucaria xyloxena* has been recorded for the first time from Svalbard.
- The species richness at sampling sites is highly variable. None of the lichens was recorded from every site while most of them were recorded only once or twice. This indicates a high heterogeneity in species distribution.
- Comparisons between lichenological data from 2005 and 2016 provide evidence for the phenomenon of rapid succession in the lichen biotas of the studied area.
- Local abiotic environmental factors have the greatest impact on the occurrence of some patterns of lichens. The most important are: geomorphological processes (including cryogenic, frost, slope, wind, and marine-coastal processes), proprieties of bedrock (mainly granulation and degree of soil formation, usually conditioned by intensity of ornithogenic fertilization), as well as the amount of time since deglaciation.

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