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ORIGINAL RESEARCH PAPER

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

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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].

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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 km^2 (83%) of the study area in 1900 and their coverage had been reduced to only 73 km^2 (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 Ostrogradskijfjella 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 Tvillingtoppen mountain: λ = 17°16′38.2″ E, φ = 76°58′41.9″ N (Fig. 2D);
9. Eastern slopes of the Tvillingtoppen mountain: λ = 17°15′49.8″ E, φ = 76°58′42.6″ N (Fig. 2E);
10. Summit of the Tvillingtoppen 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);

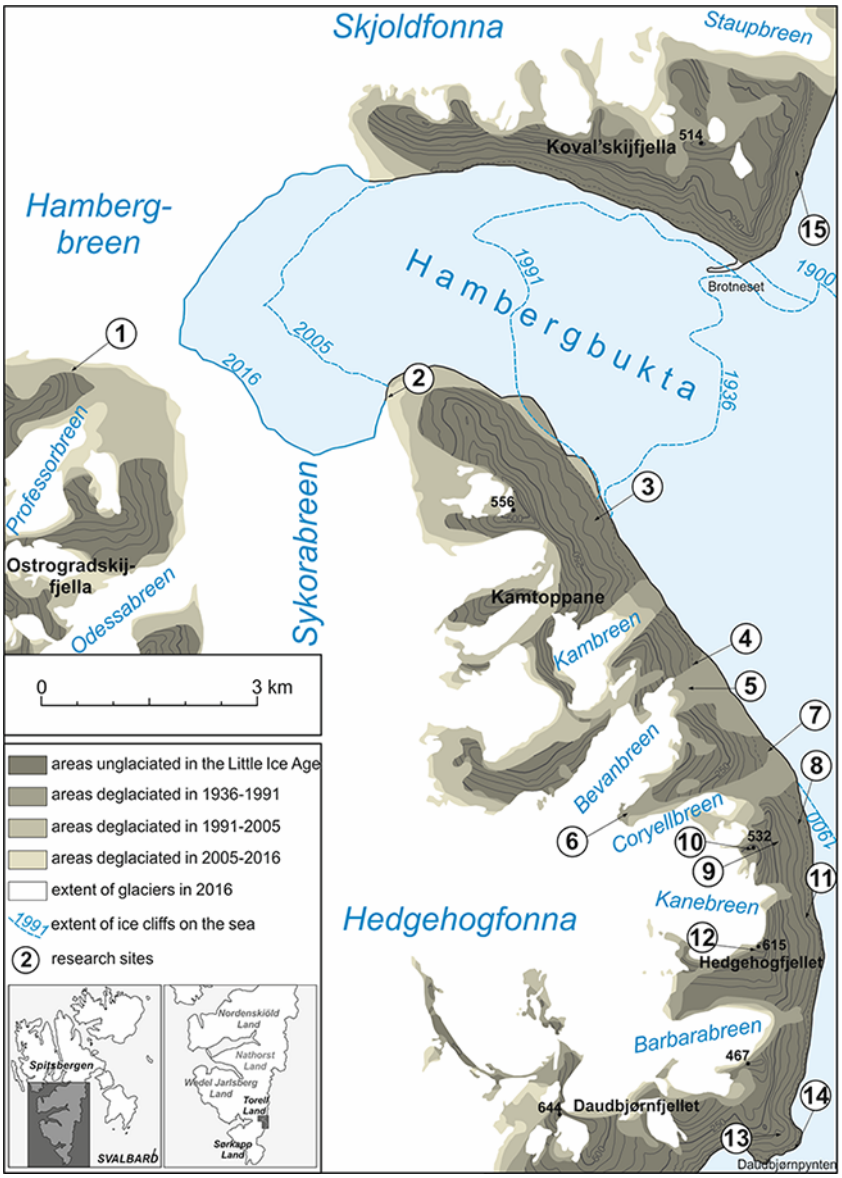

Fig. 1 Map of northeastern Sørkapp Land (Spitsbergen) showing locations of the sampling sites and the extent of glaciers in 1900, 1936, 1991, 2005, and 2016.

13. Vicinity of the Daudbjørnpynten headland: λ = 17°15′35.2″ E, φ = 76°56′26.5″ N (Fig. 2G);
14. The Daudbjørnpynten headland: λ = 17°15′40.3″ E, φ = 76°56′22.1″ N;
15. Coast at the foot of the Koval'skijfjella mountain ridge: λ = 17°17′17.0″ E, φ = 77°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 Tvillingtoppen mountain (site No. 8); (**E**) eastern slopes of the Tvillingtoppen 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 Koval'skijfjella 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 Ostrogradskijfjella 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 are 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 vahliana*, *Oxyria dygina*). The lowest 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 Coryellbreen 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 vahliana*). 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.

Tab. 1 Continued

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 dygina*) 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 with *Aulacomnium turgidum*), with a significant share of vascular plants (mainly *Salix polaris*, *Saxifraga rivularis*, *Poa alpina*, *Papaver dahlianum*), grows on very 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'skijfjella 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 dygina*, *Ranunculus pygmaeus*, *Cochlearia groenlandica*, *Poa alpina*). Intensive ornithogenic fertilization by multithousand bird colonies (mainly *Uria lomvia* and *Larus hyperboreus*).

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);

Tab. 2 Environmental characteristics of the study sites.

Sampling site	Locality	Habitat variability
1	Northern slopes of the Ostrogradskijfjella mountain massive	Ice-1, Dis-4, Alt-3, Sub-4, Geo-2, Veg-2, Cov-2, Fer-2, Moi-3, Win-2
2	Periphery of the Sykorabreen glacier	Ice-1, Dis-2, Alt-2, Sub-1, Geo-2, Veg-1, Cov-1, Fer-1, Moi-4, Win-2
3	Eastern slopes of the Kamtoppane mountain	Ice-3, Dis-3, Alt-2, Sub-4, Geo-2, Veg-2, Cov-1, Fer-1, Moi-2, Win-3
4	Fore-fields of the Bevanbreen glacier	Ice-2, Dis-2, Alt-1, Sub-2, Geo-3, Veg-3, Cov-2, Fer-2, Moi-3, Win-3
5	Fore-fields close to the front the Bevanbreen glacier	Ice-1, Dis-3, Alt-2, Sub-4, Geo-2, Veg-2, Cov-1, Fer-1, Moi-3, Win-2
6	Western slopes of the Geologtoppen mountain	Ice-2, Dis-4, Alt-3, Sub-2, Geo-2, Veg-1, Cov-1, Fer-1, Moi-1, Win-2
7	The foot of the Geologtoppen mountain	Ice-3, Dis-2, Alt-1, Sub-4, Geo-3, Veg-3, Cov-2, Fer-2, Moi-3, Win-3
8	The foot of the Tvillingtoppen mountain	Ice-3, Dis-3, Alt-2, Sub-2, Geo-2, Veg-2, Cov-1, Fer-1, Moi-1, Win-3
9	Eastern slopes of the Tvillingtoppen mountain	Ice-4, Dis-4, Alt-3, Sub-4, Geo-4, Veg-1, Cov-1, Fer-2, Moi-1, Win-2
10	Summit of the Tvillingtoppen mountain	Ice-4, Dis-4, Alt-4, Sub-1, Geo-2, Veg-1, Cov-1, Fer-1, Moi-1, Win-1
11	Slopes above the former lake Davislaguna	Ice-4, Dis-3, Alt-2, Sub-4, Geo-3, Veg-3, Cov-2, Fer-3, Moi-2, Win-3
12	Summit of the Hedgehogfjellet mountain	Ice-4, Dis-4, Alt-4, Sub-2, Geo-1, Veg-1, Cov-1, Fer-1, Moi-2, Win-1
13	Vicinity of the Daudbjørnpynten headland	Ice-4, Dis-3, Alt-2, Sub-2, Geo-2, Veg-4, Cov-4, Fer-4, Moi-4, Win-4
14	The Daudbjørnpynten headland	Ice-4, Dis-1, Alt-1, Sub-3, Geo-4, Veg-1, Cov-1, Fer-1, Moi-2, Win-3
15	Coast at the foot of the Koval'skijfjella mountain ridge	Ice-3, Dis-3, Alt-2, Sub-4, Geo-1, Veg-4, Cov-4, Fer-4, Moi-4, Win-4

Abbreviations: (***i***) Ice – time since glacier retreat; Dis – distance to the sea coast; Alt – elevation; Sub – substrate texture; Geo – intensity of geomorphological processes; (***ii***) Veg – dominant type of vegetation; Cov – vegetation cover; Fer – ornithogenic fertilization intensity; Moi – moisture; Win – wind exposure. For class descriptions see "Material and methods".

- Dominant vegetation (Veg-1: cryptogams only; Veg-2: mainly cryptogams, vascular plants rare; Veg-3: cryptogams with scattered patches of vascular plants; Veg-4: lush arctic tundra with a high proportion of vascular plants);
- Vegetation cover (Cov-1: 0–25%; Cov-2: 25–50%; Cov-3: 50–75%; Cov-4: 75–100%);
- Ornithogenic fertilization intensity (Fer-1: no ornithogenic impacts; Fer-2: low fertilization; Fer-3: moderate fertilization; Fer-4: strong fertilization);
- Moisture content (Moi-1: very dry; Moi-2: dry; Moi-3: wet; Moi-4: very wet);
- Wind exposure (Win-1: windless; Win-2: small; Win-3: large; Win-4: strong winds).

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 Tab. 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 (Tab. 1, Tab. 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., *Oxyria digyna*, *Poa alpina*, *Papaver dahlianum*, *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 (Tab. 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 tornoënsis*, which has been sporadically recorded from Svalbard. Furthermore, the terricolous lichen *Verrucaria xyloxena* 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 macroceras* occurred in habitats of all four classes of Veg factor, *Ionaspis lacustris* 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, *Psilolechia 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

Tab. 3 Occurrence of lichen species at the sampling sites in the region of northeastern Sørkapp Land (southeastern Spitsbergen). Abbreviation and symbols: • – present; B – epibryophytic lichen; G – terricolous lichen; L – epilithic lichen; 1–15 – sampling sites.

No.	Species name	Abbrev.	Substrate	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	*Acarospora badiofusca* (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 culicis* (Lynge) Thomson	Asp cul	L			•			•									
12	*Aspicilia mashiginensis* (Zahlbr.) Oxner	Asp mas	L	•		•	•											
13	*Bacidia bagliettoana* (Massal. & de Not.) Jatta	Bac bag	B															•
14	*Baeomyces rufus* (Huds.) Rebent.	Bae ruf	G												•	•		
15	*Bellemerea subsorediza* (Lynge) R. Sant. cf.	Bel sub	L											•	•			
16	*Buellia 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 eri	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 caesiocinerea* (Nyl.) A. Nordin, S. Savic & Tibell	Cir cae	L											•				
26	*Cladonia borealis* S. Stenroos	Cla bor	G			•	•			•	•	•				•		•
27	*Cladonia chlorophaea* (Flörke) Spreng.	Cla chl	G								•					•		
28	*Cladonia macroceras* (Delise) Hav.	Cla mac	G				•				•					•		•
29	*Cladonia macrophyllodes* Nyl.	Cla des	G				•											

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Tab. 1 Continued

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	*Fuscidea 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 handelii* 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 atrobrunnea* (Ram. ex Lam. & DC) Schaer.	Lec atr	L	•		•	•	•				•		•				•
44	*Lecidea auriculata* Th. Fr.	Lec aur	L			•		•	•			•	•			•		
45	*Lecidea confluens* (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	*Lecidoma 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	*Myriospora smaragdula* (Wahlenb.) Nägeli ex Uloth	Myr sma	L								•							
57	*Ochrolechia androgyna* (Hoffm.) Arnold	Och and	B/G			•	•											•
58	*Ochrolechia frigida* (Sw.) Lynge	Och fri	B/G			•									•	•		•
59	*Orphniospora moriopsis* (Massal.) D. Hawksw.	Orp mor	L						•							•		

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Tab. 1 Continued

No.	Species name	Abbrev.	Substrate	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
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* (Flörke) Moberg	Pha nig	L/B				•											•
65	*Physcia caesia* (Hoffm.) Fürnr.	Phy cae	L				•									•		
66	*Physcia dubia* (Hoffm.) Lettau	Phy dub	L				•											•
67	*Physcia tenella* (Scop) DC.	Phy ten	L													•		
68	*Polyblastia septentrionalis* Lynge	Pol sep	L															•
69	*Polysporina simplex* (Davies) Vězda	Pol sim	L			•												
70	*Porpidia flavocruenta* Fryday & Buschbom	Por fla	L			•			•									
71	*Porpidia melinodes* (Körb.) Hertel	Por mel	L												•			
72	*Porpidia thomsonii* Gowan	Por tho	L								•							•
73	*Porpidia 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	*Psilolechia lucida* (Ach.) M. Choisy	Psi luc	L			•	•	•	•		•	•						
77	*Rhizocarpon atroflavescens* Lynge	Rhi atr	L								•							
78	*Rhizocarpon copelandii* (Körb.) Th. Fr.	Rhi cop	L									•						
79	*Rhizocarpon eupetraeum* (Nyl.) Arnold	Rhi eup	L								•	•			•			•
80	*Rhizocarpon expallescens* Th. Fr.	Rhi exp	L	•							•							
81	*Rhizocarpon geminatum* 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	G						•							•		•
89	*Staurothele arctica* Lynge	Sta arc	L										•			•		

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Tab. 1 Continued

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* Lynge	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 vellea* (L.) Ach.	Umb vel	L											•				
107	*Umbilicaria virginis* Schaerer	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 margacea* (Wahlenb.) Wahlenb.	Ver mar	L			•												
112	*Verrucaria xyloxena* 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

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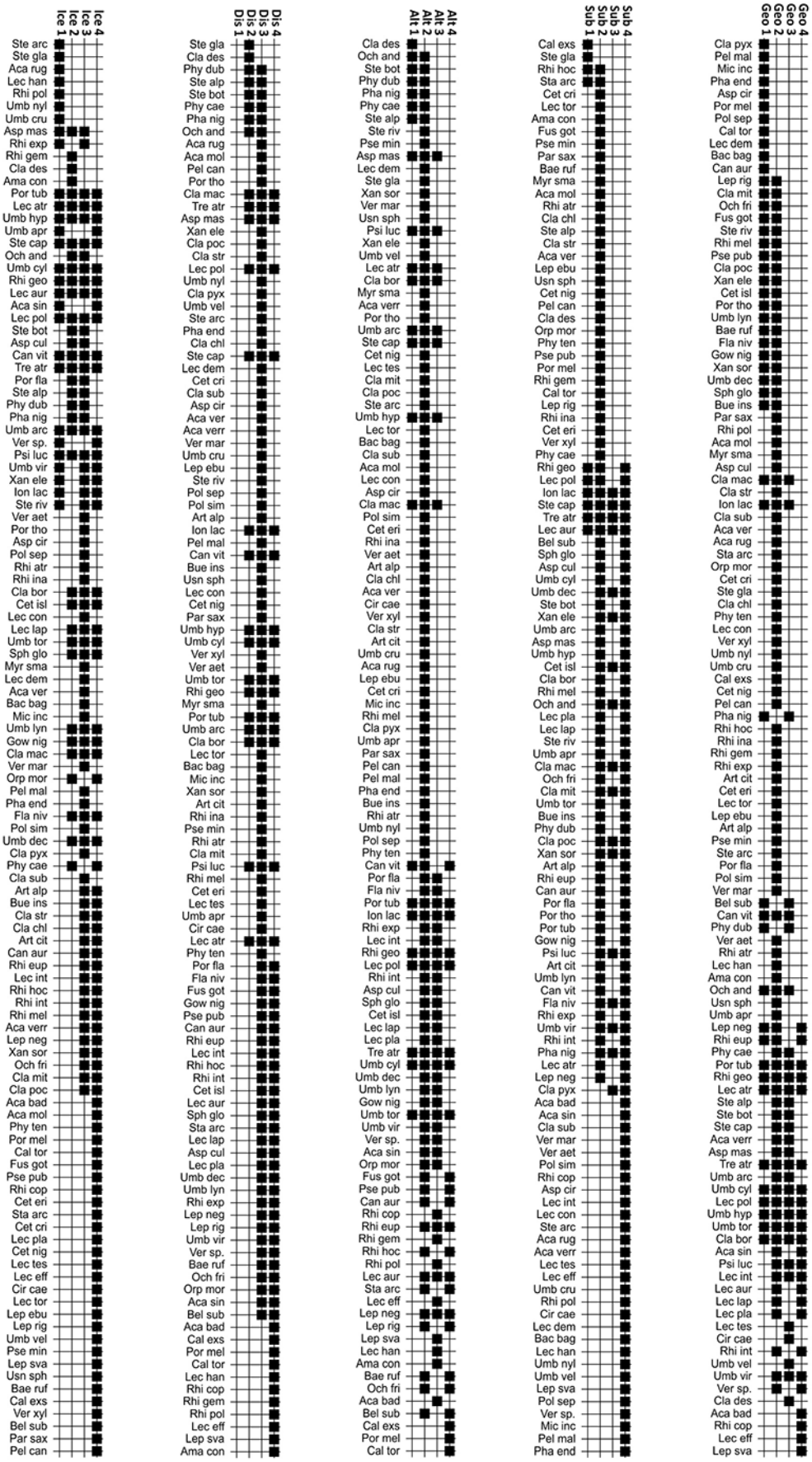
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Lec tor
Lep ebu
Lep rig
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Pse min
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Umb nyl
Cla pyx
Umb vel
Ste arc
Pha end
Cla chl
Ste cap
Lec dem
Cet cri
Cla sub
Asp cir
Aca ver
Aca verr
Ver mar
Umb cru
Lep ebu
Ste riv
Pol sep
Pol sim
Art alp
Ion lac
Pel mal
Can vit
Bue ins
Usn sph
Lec con
Cet nig
Par sax
Umb hyp
Umb cyl
Ver xyl
Ver aet
Umb tor
Rhi geo
Myr sma
Por tub
Umb arc
Cla bor
Lec tor
Bac bag
Mic inc
Xan sor
Art cit
Rhi ina
Pse min
Rhi atr
Cla mit
Psi luc
Rhi mel
Cet eri
Lec tes
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Cir cae
Lec atr
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Sta arc
Lec lap
Asp cul
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Umb dec
Umb lyn
Rhi exp
Lep neg
Lep rig
Umb vir
Ver sp.
Bae ruf
Och fri
Orp mor
Aca sin
Bel sub
Aca bad
Cal exs
Por mel
Cal tor
Lec han
Rhi cop
Rhi gem
Rhi pol
Lec eff
Lep sva
Ama con
Alt 1
Alt 2
Alt 3
Alt 4
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Och and
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Pha nig
Phy cae
Ste alp
Ste riv
Pse min
Asp mas
Lec dem
Ste gla
Xan sor
Ver mar
Usn sph
Psi luc
Xan ele
Umb vel
Lec atr
Cla bor
Myr sma
Aca verr
Por tho
Umb arc
Ste cap
Cet nig
Lec tes
Cla mit
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Cla chl
Aca ver
Cir cae
Ver xyl
Cla str
Art cit
Umb cru
Aca rug
Lep ebu
Cet cri
Mic inc
Rhi mel
Cla pyx
Umb apr
Par sax
Pel can
Pel mal
Pha end
Bue ins
Rhi atr
Umb nyl
Pol sep
Phy ten
Can vit
Por fla
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Por tub
Ion lac
Rhi exp
Lec int
Rhi geo
Lec pol
Rhi int
Asp cul
Sph glo
Cet isl
Lec lap
Lec pla
Tre atr
Umb cyl
Umb dec
Umb lyn
Gow nig
Umb tor
Umb vir
Ver sp.
Aca sin
Orp mor
Fus got
Pse pub
Can aur
Rhi cop
Rhi eup
Rhi gem
Rhi hoc
Rhi pol
Lec aur
Sta arc
Lec eff
Lep neg
Lep rig
Lep sva
Lec han
Ama con
Bae ruf
Och fri
Aca bad
Bel sub
Cal exs
Por mel
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Sub 1
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Sub 3
Sub 4
Cal exs
Ste gla
Rhi hoc
Sta arc
Cet cri
Lec tor
Ama con
Fus got
Pse min
Par sax
Bae ruf
Myr sma
Aca mol
Rhi atr
Cla chl
Ste alp
Cla str
Aca ver
Lep ebu
Usn sph
Cet nig
Pel can
Cla des
Orp mor
Phy ten
Pse pub
Por mel
Rhi gem
Cal tor
Lep rig
Rhi ina
Cet eri
Ver xyl
Phy cae
Rhi geo
Lec pol
Ion lac
Ste cap
Tre atr
Lec aur
Bel sub
Sph glo
Asp cul
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Asp mas
Umb hyp
Cet isl
Cla bor
Rhi mel
Och and
Lec pla
Lec lap
Ste riv
Umb apr
Cla mac
Och fri
Cla mit
Umb tor
Bue ins
Phy dub
Cla poc
Xan sor
Art alp
Rhi eup
Can aur
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Por tho
Por tub
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Art cit
Umb lyn
Can vit
Fla niv
Rhi exp
Umb vir
Rhi int
Pha nig
Lec atr
Lep neg
Cla pyx
Aca bad
Aca sin
Cla sub
Ver mar
Ver aet
Pol sim
Rhi cop
Asp cir
Lec int
Lec con
Ste arc
Aca rug
Aca verr
Lec tes
Lec eff
Umb cru
Rhi pol
Cir cae
Lec dem
Bac bag
Lec han
Umb nyl
Umb vel
Lep sva
Pol sep
Ver sp.
Mic inc
Pel mal
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Cla pyx
Pel mal
Mic inc
Pha end
Asp cir
Por mel
Pol sep
Cal tor
Lec dem
Bac bag
Can aur
Lep rig
Cla mit
Och fri
Fus got
Ste riv
Rhi mel
Pse pub
Cla poc
Xan ele
Cet isl
Por tho
Umb lyn
Bae ruf
Fla niv
Gow nig
Xan sor
Umb dec
Sph glo
Bue ins
Par sax
Rhi pol
Aca mol
Myr sma
Asp cul
Cla mac
Cla str
Ion lac
Cla sub
Aca ver
Aca rug
Sta arc
Orp mor
Cet cri
Ste gla
Cla chl
Phy ten
Lec con
Ver xyl
Umb nyl
Umb cru
Cal exs
Cet nig
Pel can
Pha nig
Rhi hoc
Rhi ina
Rhi gem
Rhi exp
Art cit
Cet eri
Lec tor
Lep ebu
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Por fla
Pol sim
Ver mar
Bel sub
Can vit
Phy dub
Ver aet
Rhi atr
Lec han
Ama con
Och and
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Umb apr
Lep neg
Rhi eup
Phy cae
Por tub
Rhi geo
Lec atr
Ste alp
Ste bot
Ste cap
Aca verr
Asp mas
Tre atr
Umb arc
Umb cyl
Lec pol
Umb hyp
Umb tor
Cla bor
Aca sin
Psi luc
Lec int
Lec aur
Lec lap
Lec pla
Lec tes
Cir cae
Rhi int
Umb vel
Umb vir
Ver sp.
Cla des
Aca bad
Rhi cop
Lec eff
Lep sva

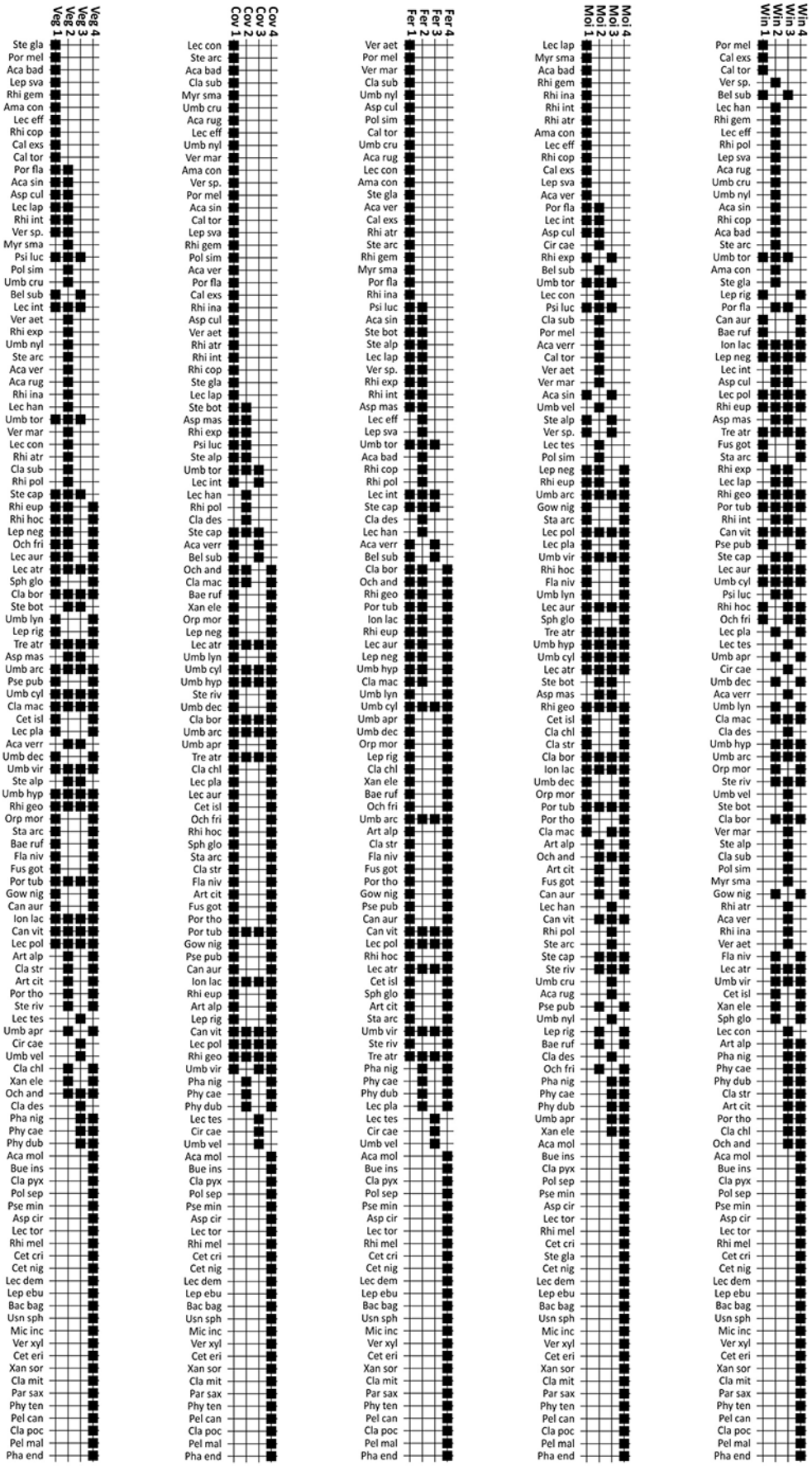
Veg 1 Veg 2 Veg 3 Veg 4
Ste gla Por mel Aca bad Lep sva Rhi gem Ama con Lec eff Rhi cop Cal exs Cal tor Por fla Aca sin Asp cul Lec lap Rhi int Ver sp. Myr sma Psi luc Pol sim Umb cru Bel sub Lec int Ver aet Rhi exp Umb nyl Ste arc Aca ver Aca rug Rhi ina Lec han Umb tor Ver mar Lec con Rhi atr Cla sub Rhi pol Ste cap Rhi eup Rhi hoc Lep neg Och fri Lec aur Lec atr Sph glo Cla bor Ste bot Umb lyn Lep rig Tre atr Asp mas Umb arc Pse pub Umb cyl Cla mac Cet isl Lec pla Aca verr Umb dec Umb vir Ste alp Umb hyp Rhi geo Orp mor Sta arc Bae ruf Fla niv Fus got Por tub Gow nig Can aur Ion lac Can vit Lec pol Art alp Cla str Art cit Por tho Ste riv Lec tes Umb apr Cir cae Umb vel Cla chl Xan ele Och and Cla des Pha nig Phy cae Phy dub Aca mol Bue ins Cla pyx Pol sep Pse min Asp cir Lec tor Rhi mel Cet cri Cet nig Lec dem Lep ebu Bac bag Usn sph Mic inc Ver xyl Cet eri Xan sor Cla mit Par sax Phy ten Pel can Cla poc Pel mal Pha end
Cov 1 Cov 2 Cov 3 Cov 4
Lec con Ste arc Aca bad Cla sub Myr sma Umb cru Aca rug Lec eff Umb nyl Ver mar Ama con Ver sp. Por mel Aca sin Cal tor Lep sva Rhi gem Pol sim Aca ver Por fla Cal exs Rhi ina Asp cul Ver aet Rhi atr Rhi int Rhi cop Ste gla Lec lap Ste bot Asp mas Rhi exp Psi luc Ste alp Umb tor Lec int Lec han Rhi pol Cla des Ste cap Aca verr Bel sub Och and Cla mac Bae ruf Xan ele Orp mor Lep neg Lec atr Umb lyn Umb cyl Umb hyp Ste riv Umb dec Cla bor Umb arc Umb apr Tre atr Cla chl Lec pla Lec aur Cet isl Och fri Rhi hoc Sph glo Sta arc Cla str Fla niv Art cit Fus got Por tho Por tub Gow nig Pse pub Can aur Ion lac Rhi eup Art alp Lep rig Can vit Lec pol Rhi geo Umb vir Pha nig Phy cae Phy dub Lec tes Cir cae Umb vel Aca mol Bue ins Cla pyx Pol sep Pse min Asp cir Lec tor Rhi mel Cet cri Cet nig Lec dem Lep ebu Bac bag Usn sph Mic inc Ver xyl Cet eri Xan sor Cla mit Par sax Phy ten Pel can Cla poc Pel mal Pha end
Fer 1 Fer 2 Fer 3 Fer 4
Ver aet Por mel Ver mar Cla sub Umb nyl Asp cul Pol sim Cal tor Umb cru Aca rug Lec con Ama con Ste gla Aca ver Cal exs Rhi atr Ste arc Rhi gem Myr sma Por fla Rhi ina Psi luc Aca sin Ste bot Ste alp Lec lap Ver sp. Rhi exp Rhi int Asp mas Lec eff Lep sva Umb tor Aca bad Rhi cop Rhi pol Lec int Ste cap Cla des Lec han Aca verr Bel sub Cla bor Och and Rhi geo Por tub Ion lac Rhi eup Lec aur Lep neg Umb hyp Cla mac Umb lyn Umb cyl Umb apr Umb dec Orp mor Lep rig Cla chl Xan ele Bae ruf Och fri Umb arc Art alp Cla str Fla niv Fus got Por tho Gow nig Pse pub Can aur Can vit Lec pol Rhi hoc Lec atr Cet isl Sph glo Art cit Sta arc Umb vir Ste riv Tre atr Pha nig Phy cae Phy dub Lec pla Lec tes Cir cae Umb vel Aca mol Bue ins Cla pyx Pol sep Pse min Asp cir Lec tor Rhi mel Cet cri Cet nig Lec dem Lep ebu Bac bag Usn sph Mic inc Ver xyl Cet eri Xan sor Cla mit Par sax Phy ten Pel can Cla poc Pel mal Pha end
Moi 1 Moi 2 Moi 3 Moi 4
Lec lap Myr sma Aca bad Rhi gem Rhi ina Rhi int Rhi atr Ama con Lec eff Rhi cop Cal exs Lep sva Aca ver Por fla Lec int Asp cul Cir cae Rhi exp Bel sub Umb tor Lec con Psi luc Cla sub Por mel Aca verr Cal tor Ver aet Ver mar Aca sin Umb vel Ste alp Ver sp. Lec tes Pol sim Lep neg Rhi eup Umb arc Gow nig Sta arc Lec pol Lec pla Umb vir Rhi hoc Fla niv Umb lyn Lec aur Sph glo Tre atr Umb hyp Umb cyl Lec atr Ste bot Asp mas Rhi geo Cet isl Cla chl Cla str Cla bor Ion lac Umb dec Orp mor Por tub Por tho Cla mac Art alp Och and Art cit Fus got Can aur Lec han Can vit Rhi pol Ste arc Ste cap Ste riv Umb cru Aca rug Pse pub Umb nyl Lep rig Bae ruf Cla des Och fri Pha nig Phy cae Phy dub Umb apr Xan ele Aca mol Bue ins Cla pyx Pol sep Pse min Asp cir Lec tor Rhi mel Cet cri Ste gla Cet nig Lec dem Lep ebu Bac bag Usn sph Mic inc Ver xyl Cet eri Xan sor Cla mit Par sax Phy ten Pel can Cla poc Pel mal Pha end
Win 1 Win 2 Win 3 Win 4
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Fig. 3 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.

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.

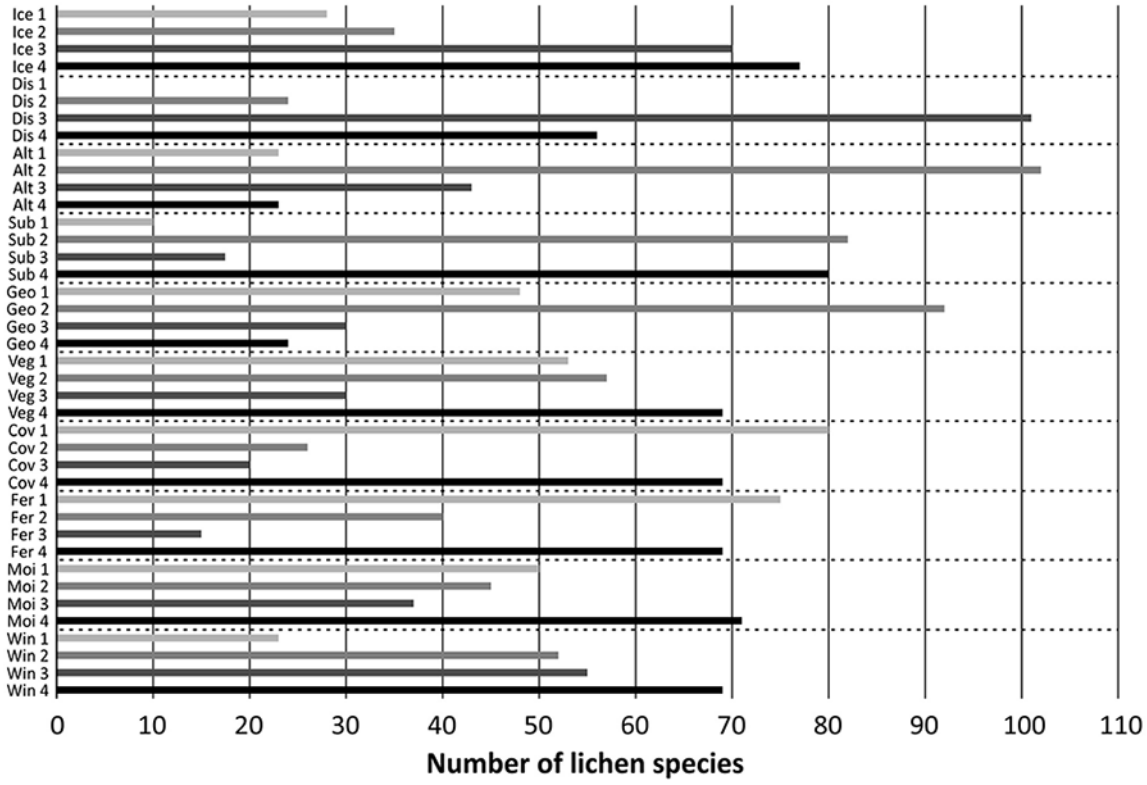

Fig. 4 Lichen species richness in 4-grade scale for particular habitat factors. For abbreviation see Fig. 3 caption. For variable specifications see "Material and methods".

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'skijfjella 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'skijfjella 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 epibryophytic 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 thalli 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'skijfjella 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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