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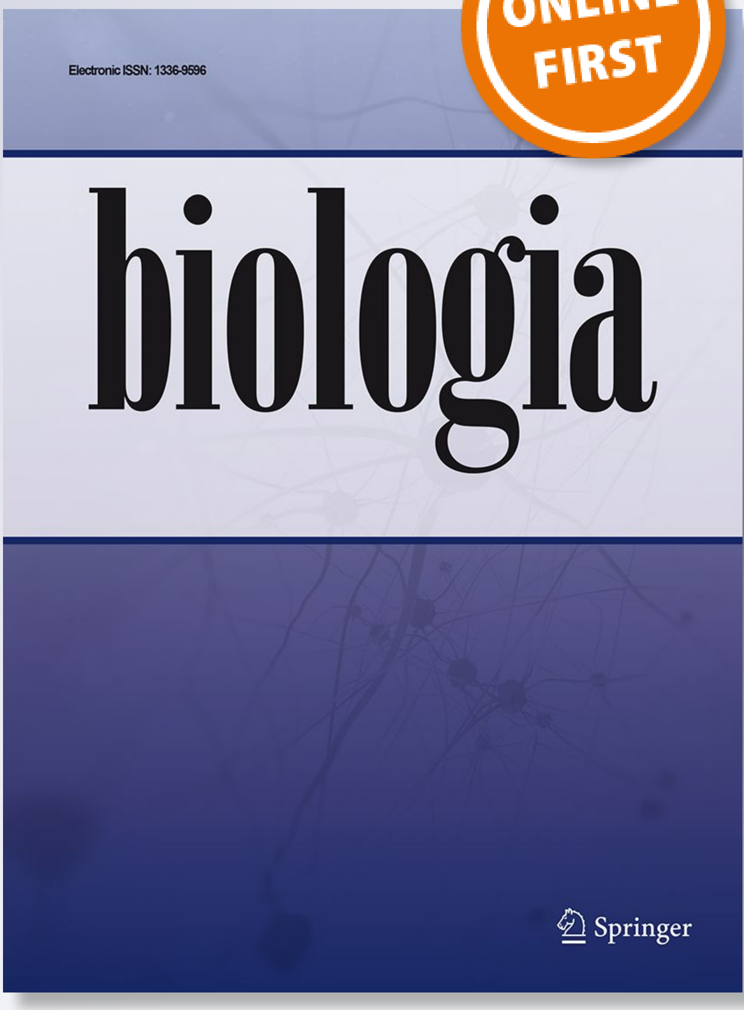

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ORIGINAL ARTICLE

Epiphytic and epixylic lichens in forests of the Šumava mountains in the Czech Republic; abundance and frequency assessments

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Abstract

Extensive sampling of lichen diversity in forest habitats in the Šumava mountains consisted of 128 plots with 824 sampled objects (single trees, snags, logs, etc.). The survey enabled assessment of regional abundance and frequency of epiphytic and epixylic lichen species. 240 species were recorded with frequencies (i.e. number of plots in which each species was recorded) ranging from 1 to 123 and with total abundance scores (i.e. sum of abundances from all objects) ranging from 1 to 1304. Using the total abundance scores, each species was classified as either: rare (129 species), common (68) or abundant (43). We recognised six types of forest, one formed by human activity and five natural ones. Species richness in the natural forests were in decreasing order: beech forests (167 species), bog and waterlogged forests (147), montane spruce forests (124), ash-alder alluvial forests (92) and ravine forests (68). The relative order of the first four kinds is probably real, but the low number of species in ravine forests is a result of insufficient sampling. All species were characterized by their fidelity and specificity to each forest type. Each natural forest category has a group of species with high fidelity. Many species were recorded in only a single category of forest, which demonstrates that a rich regional lichen biota requires variability in forest types. Forest habitats formed by human impact, mostly plantations of coniferous trees, have fewer species, and distinctly fewer species with high fidelity, than any natural forest category. Throughout the region, mature spruce trees in montane spruce forests have been dying at a rapid rate for over 20 years. This has probably resulted in a decline in those lichens that require high humidity, and an increase of some epixylic lichens, especially nitrophilous species. We did not encounter all species previously recorded in forests in the region, but most of the species missing from our list are either rare or have specialised habitat requirements. In the Red List of the Czech Republic, we suggested changes in categories for 32 species.

Keywords Fidelity · Habitats · Lichen diversity monitoring · Montane spruce forests · Regional rarity

Introduction

Quality of red lists and any species-based conservation activities are dependent on reliable quantitative information about species frequencies and abundances. Such information is largely missing for epiphytic and epixylic lichens of temperate forests. Some data are provided by ecological studies on a local scale (e.g. Bässler et al. 2016; Király et al. 2013; Moning et al. 2009; Nascimbene et al. 2010; Wolseley et al. 2017), or for particular forest types (e.g. Hofmeister et al. 2016; Holien 1997; Jönsson et al. 2011), or are restricted to a particular lichen group, e.g. calicioid lichens (Hardman et al. 2017, Lõhmus and Lõhmus 2011). However, attempts to assess abundances of a whole range of lichen species on a regional scale are scarce and usually based on sources of unequal reliability (Lõhmus 2003; Nascimbene et al. 2013). Here we provide regional-scale quantitative data (abundance and frequency assessments) for forest lichens in the Czech part of the Šumava mountains with a territory more than 1600 Km^2. Our data are not based on literature extractions, but on the field plot-based research performed within two months in 2017.

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Our first priority was to determine which species are common and which are rare and, especially for the rarer ones, which are restricted to particular forest types. As well as of being of immediate relevance to conservation, this information also provides a base-line against which future changes (and sometimes the past state) in the region can be monitored, and it facilitates comparisons with other regions. For the latter purpose, our dataset will be better than most of those obtained recently in the Czech Republic, as it includes information on frequency and abundance, not merely presence/absence.

Our second objective was to evaluate lichen biodiversity in five types of natural forest, and also in plantations. Knowing which habitats support particular species of lichens, and whether some habitats are richer in lichens overall, has obvious applications to conservation.

Third, aware that almost all montane spruce forests in the Šumava mountains have suffered severe mortality of spruce trees over the last 25 years (Kindlmann et al. 2012), which has increased irradiance of trunks below the canopy, lowered humidity, reduced the availability of bark as a lichen substrate while increasing that of wood in various states of decaying, and which is sure to lead to major changes in the lichen biota in the near future, we wished to establish baseline data against which those future changes can be compared. "True" baseline data would have had to be obtained in unharmed forests in the 1990s, but unfortunately it was not and our baseline is the best that can now be obtained: for that reason we can not compare the present state with that before changes began.

Our dataset has following specifics. First, the extensive sampling across various forest types means that the data is relevant to the whole region. Second, the data permits meaningful comparisons between different species, because abundances were recorded and the species lists are comprehensive. Third, we sampled all the kinds of organic substrate present in plots (except organic soil), so we recorded most of the epiphytic lichens present in the plots. The dataset does have some limitations: ravine forests were not sampled extensively, and a few rare forest types were not sampled at all (Table 1). Also, the random sampling resulted in most plots being in forests with some degree of human influence: well-preserved and primeval natural forest types are not well represented. These limitations probably resulted in some rare and/or niche-specific species of lichens being poorly represented in, or absent from, the dataset.

We had two priority aims: (1) assessment of frequencies and abundances of epiphytic lichens in the Šumava mountains; (2) evaluation of specificity and fidelity of epiphytic species to the main forest types.

Methods

Geographic scope and design of plots

Our field investigations were performed in the context of the biodiversity project "Silva Gabreta monitoring" and were supported and permitted by the administration of the National park Šumava (Vimperk, Czech Republic). Lichen biodiversity data were collected from 128 permanent plots on the Czech side of the Šumava mountains (see Fig. 1 for the pattern). Plot design followed Bässler et al. (2015) who did complex biodiversity research on the German side of the Šumava mountains. Plots on the Czech side were designed to cover the main forest types proportionally to their area (Zenáhlíková et al. 2015). Permanent plots are circles 12.62 m in radius, i.e. 500 m^2 in area. Their locations were selected from the grid of points

Table 1 Forest types in the Šumava mountains and their area and percentage. Calculated for the territory of the National park plus Landscape protected area Šumava. Data provided by the Nature Conservation Agency of the Czech Republic (AOPK ČR 2017). Codes of habitats reflect Chytrý et al. (2010)

Forest type	Included habitats	area (km^2)	percentage	number of plots and their altitudinal range
Forest habitats formed by human impact	X9, X10, X12	518.2	47.63%	17 (726–983 m)
Beech forests	L5.1, L5.2, L5.4	268.2	24.63%	33 (597–1178 m)
Montane spruce forests	L9.1, L9.3	139.4	12.73%	28 (995–1341 m)
Bog and waterlogged forests	L9.2, L10.1, L10.2, L10.4	126.4	11.62%	37 (728–1152 m)
Ash-alder alluvial forests	L2.1, L2.2	27,5	2.52%	11 (665–862 m)
Raised bogs with *Pinus mugo*	R3.2	5.7	0.53%	not sampled
Boreo-continental pine forests	L8.1	2,2	0.21%	not sampled
Ravine forests	L4	0.9	0.08%	2 (905–1017 m)
Alder carrs	L1	0.2	0.02%	not sampled
Oak forests	L7.1, L7.2	0,2	0.02%	not sampled
Pinus mugo scrubs	A7	0,04	0.01%	not sampled

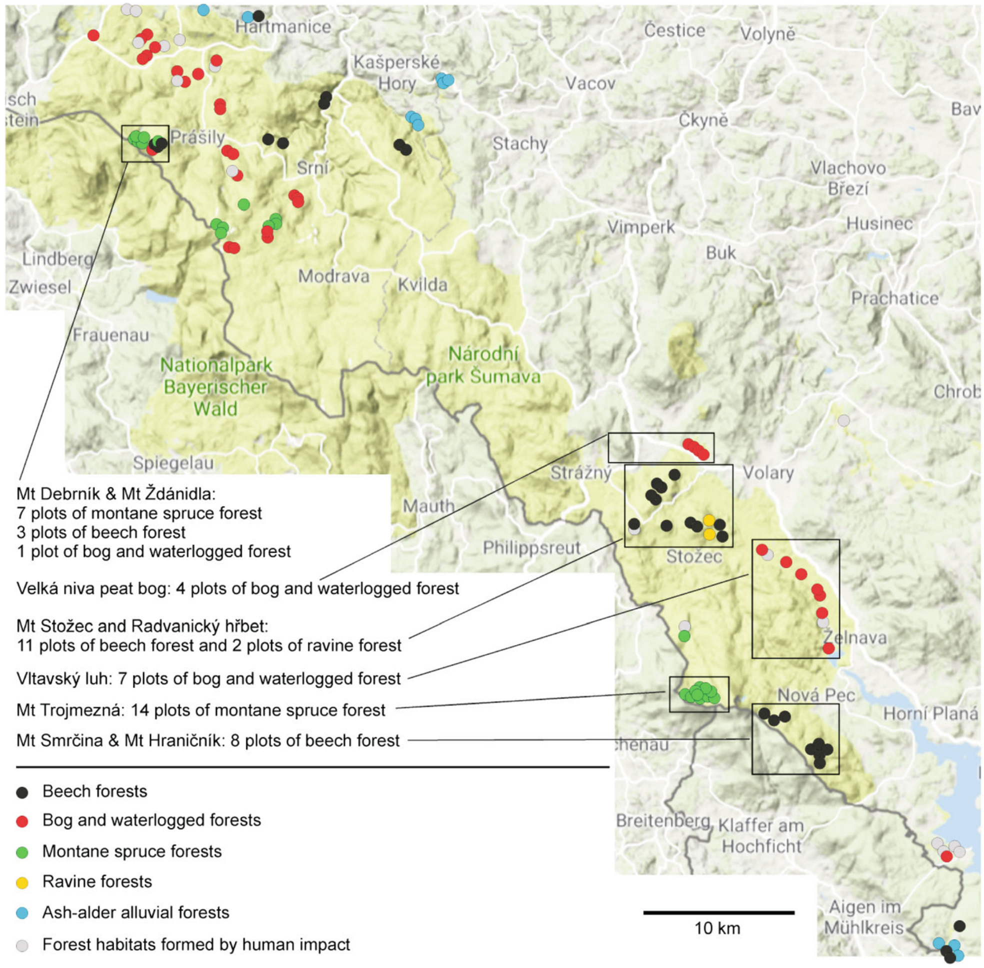

Fig. 1 Sampling pattern on the Czech side of the Šumava mountains. Borderline with Austria and Germany in grey; territory of the National park Šumava in green

separated by 353.55 m (ÚHÚL 2007) to be equally distributed along the altitudinal gradient. The plot design weighted by an area of forest types inevitably resulted in an unequal coverage: bog and waterlogged forests are most strongly represented, by 37 plots, but ravine forests are only present in two plots (see below for more details).

Sampling in plots

All the field work was done by the first author in August–September 2017. Epiphytic and epixylic lichens were recorded from as many organic substrata as possible (but excluding organic soil), including: trunks (up to 2 m height), lower twigs of living and dead trees, snags, stumps, logs and blow-downs. Inorganic substrates were ignored. At least six objects (object = single tree, stump, log, etc.) were selected in each plot with an aim to maximize recorded diversity. The number of investigated objects was increased (up to ten) when the local lichen diversity was supposed to be higher. All lichens observed on the selected objects were recorded. Each species on each object was assigned an abundance category: 1, one to three thalli present; 2, four to ten thalli; 3, more than ten thalli. Sampling per plot was not restricted by time. The study of a plot finished when no additional lichens could be observed on the selected objects.

Identification of lichens, voucher deposition, nomenclature

Well known species were identified in the field and vouchers were not taken. However 220 specimens of 111 species were collected and are deposited in PRA (numbers JV18701–18745, JV18778–18789, JV18878–19041). Thin layer chromatography was done on specimens of *Fuscidea pusilla*, *Lecanora expallens*, *L. norvegica*, *L. sarcopidoides*, *Lecidella subviridis*, *Lepraria ecorticata*, *Ochrolechia* spp., and on selected specimens of *Loxospora*, *Pycnora* and *Ropalospora*. Some species were not recognized in the study, such as *Lepraria elobata* which cannot be distinguished from *L. incana* in the field. Nomenclature of species follows Liška and Palice (2010).

Classification of forest types in the Šumava mountains

Our classification is based on the catalogue of habitats (Chytrý et al. 2010), but we merged the habitats into larger categories according to factors that substantially influence epiphytic lichen communities: phorophyte composition, altitude, humidity and human impact. Forest types and their frequency in the Šumava mountains are listed in Table 1. Areas were calculated from the layer of habitat mapping (AOPK ČR 2017) and were provided by the Nature Conservation Agency of the Czech Republic. Six types of forests were sampled (see below). Most habitats with percentage below 1% (Table 1) were not sampled and are not included within the following forest types.

(1) **Beech forests.** (33 plots) Three habitats included: acidophilous beech forests (20), montane sycamore-beech forests (6) and herb-rich beech forests (7). Predominant phorophytes: *Fagus sylvatica*, *Abies alba*, *Picea abies* and *Acer pseudoplatanus*.
(2) **Bog and waterlogged forests** (37 plots) Included: Bog and waterlogged spruce forests (26), pine mire forests with *Vaccinium* (3), *Pinus rotundata* bog forests (5) and Birch mire forests (3). Predominant phorophytes: *Picea abies*, *Pinus sylvestris*, *P. rotundata*, *Betula carpatica* and *Vaccinium uliginosum*.
(3) **Montane spruce forests** (28 plots). Included: montane *Calamagrostis* spruce forest (23) and montane *Athyrium* spruce forests (5). Predominant phorophytes: *Picea abies* and *Sorbus aucuparia*.
(4) **Ravine forests** (2 plots). Single habitat. Phorophytes present on plots: *Acer pseudoplatanus*, *Fagus sylvatica* and *Picea abies*.
(5) **Ash-alder alluvial forests** (11 plots). Single habitat. Predominant phorophytes: *Alnus glutinosa*, *A. incana*, *Fraxinus excelsior*, *Acer pseudoplatanus*.
(6) **Forest habitats formed by human impact** (17 plots) Included: Plantations of coniferous trees (9), plantations of deciduous trees (1), forest clearings (3) and stands of early successional woody species (4). Predominant phorophytes: *Picea abies*, *Pinus sylvestris*, *Betula pendula*, *Fagus sylvatica*, *Salix aurita* s. lat. and *S. caprea*.

Calculations applied to primary data

The frequency of a species is the number of plots containing that species. It was counted both for the whole dataset and for each category of forest. The specificity of a species to a particular type of forest is the number of plots of that forest type in which the species occurs divided by the total number of plots for that forest category. Abundance was estimated for each species on each object, using the 1–3 scale defined above. The total abundance score for a species was defined as the sum of its abundances in the whole dataset, and the partial abundance score was the corresponding sum for a particular forest category. The fidelity of a species to a category of forest is its partial abundance score divided by its total abundance score. Following Dufrêne and Legendre (1997), we calculated indicator value as fidelity * specificity * 100. For each pair of forest categories, the number of shared species was determined and Sørensen's index of similarity (Sørensen 1948) was calculated.

Calculating of accumulation curves

Species accumulation curves (SAC) were calculated according to Colwell et al. (2004). SAC are a series of means and standard deviations of number of species for increasing number of sampling sites. We used the method "exact" implemented in the *specaccum* function, package 'vegan' for R (R developmental core team 2016). Unlike the "random" method using a manually defined number of permutations, and therefore providing different results from repeated runs, the 'exact' method uses an exhaustive search and repeated runs give identical results.

Species richness estimates

Lists of species from each plot serve as incidence data usable for estimates of species richness in the forest types. We used the estimator Chao2 (Chao 1987) implemented in the *specpool* function, package 'vegan' for R (R developmental core team 2016).

Results

Frequency and abundance of forest lichens in the Šumava mounains (Czech part)

We recorded 240 species on 824 objects in 128 plots. Frequencies ranged from 1 to 123 and total abundance scores ranged from 1 to 1304. Fig. 2 shows, for each species, its

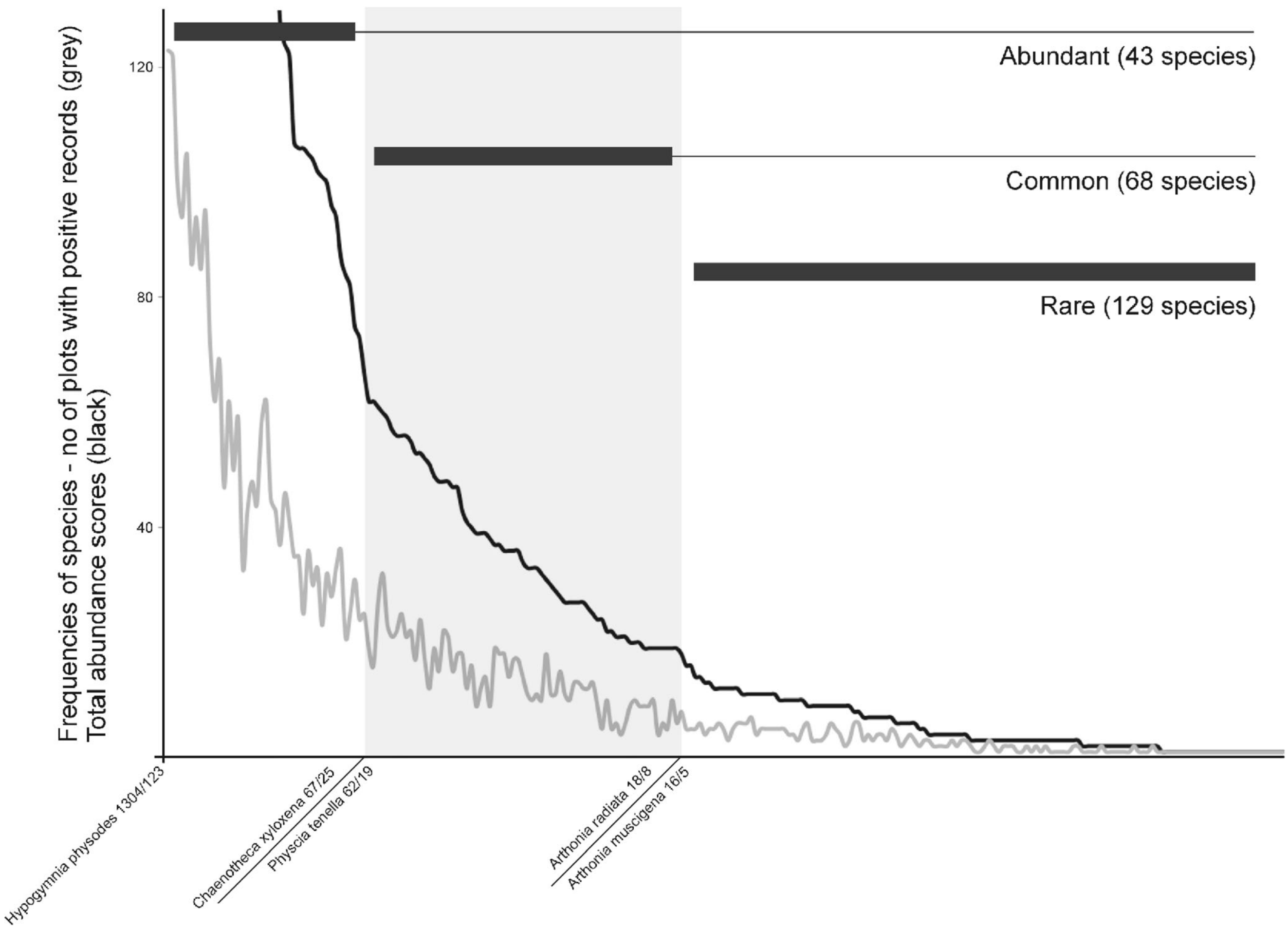

Fig. 2 Frequencies and abundance scores of lichen species recorded from 128 plots in the Šumava mountains (see sampling details in Methods). Species are divided into three groups of regional abundance according to critical points in slope of the abundance curve (black). Marginal species in the groups are pointed out with their abundance score and frequency

frequency and total abundance score; the species are in order of decreasing abundance. We used cutoff values of 65 and 17 to divide the total abundance curve into three parts. The leftmost part, in which the curve drops rapidly, has values above 65 and corresponds to regionally abundant species (43 species). The middle part, in which the curve drops less rapidly, has values between 17 and 65 and corresponds to regionally common species (68 species). The rightmost part, in which the curve declines only slowly, has values below 17 and corresponds to regionally rare species (129 species, i.e. more than half of the species recorded). Appendices 1 & 2 list the details.

Assessment of lichen diversities in each forest type

Among well sampled forest types, beech forests have highest species richness (Table 2). Beech forests also have the highest number of specific species (see "specificity" above), and the plots with the higher numbers of species (Table 2). Seventeen species had high fidelity (above 0.65) to beech forests (Fig. 4). Table 3 shows indicator values and other characteristics of species with high fidelity. Both fidelities and indicator values of some species would decrease if ravine forests were more extensively sampled, because there is substantial species overlap (Table 4; of the 68 species detected in ravine forests 62 also occur in beech forests).

Bog and waterlogged forests and montane spruce forests are most similar in species composition (Table 4). This is because coniferous trees dominate both categories, so the same common acidophilous lichen species flourish in both. Bog and waterlogged forests have slightly higher species richness (see the accumulation curves in Fig. 3), but some plots in bog and waterlogged forests, especially those dominated by birch, are poor in species (with a minimum as low as 13 species per plot). Plots in montane spruce forests have rather

Table 2 Species richness characteristics in the six categories of forest in the Šumava mountains. Based on data from research on 128 plots (see Methods)

Forest category / number of plots	All recorded species	Species richness estimated by Chao2	Species in only single forest category	Average species richness per plot	Minimum species richness per plot	Maximum species richness per plot
Beech forests / 33	167	265 ± 33	37	28	11	53
Bog and waterlogged forests / 37	147	201 ± 20	17	28	13	45
Montane spruce forests / 28	124	166 ± 18	5	32	23	39
Ravine forests / 2	68	not available	2	41	37	45
Ash-alder alluvial forests / 11	92	114 ± 10	8	28	18	36
Forest habitats formed by human impact / 17	86	121 ± 15	4	21	11	27

uniform species richness, all in the range 23–39 (Table 2). Seventeen species were recorded only in bog and waterlogged forests and fourteen species with high fidelity to this forest type are pointed out in Fig. 4. Only five species were recorded solely in montane spruce forests, but twelve species have fidelity above 0.65 (Fig. 4). In both categories, some species with high fidelities also have high indicator values (Table 3); in other words, the two categories are well separated by indicator species despite the overlap in species.

The low number of species recorded (92) in ash-alder alluvial forests may be caused in part by the small sample size, but the shape of the species accumulation curve suggests that this type does indeed have slightly lower species richness than montane spruce forests (Fig. 3). Eight species were recorded solely in this category and another seven species have high fidelity (Fig. 4). However, indicator values of the species with high fidelity are low, because all of them have low frequencies and low abundance scores (Table 3). Species overlap with other forest categories is between 45 and 69; the highest overlap is with beech forests (Table 4).

Ravine forests are diverse in tree species, microhabitats and microclimatic conditions and could have the highest species richness of lichens (Table 2 and Fig. 3), but as this forest type is rare in the Šumava mountains (Table 1), and was sampled in only two plots, the conclusion is tentative.

Forest habitats formed by human impact, mostly plantations of conifers, have significantly fewer species than any type of natural forests (Fig. 3, Table 2). The only species with fidelity above 0.65 is *Lecanora persimilis* (Fig. 4), but it has very low frequency and correspondingly low indicator value, 4.06 (see Table 3 for comparison).

Discussion

Relevance of observed rarity of species

More than half of the species recorded (129 of 240) are here classified as "rare", but a few of them are probably not rare in reality. Lichens that usually occur on twigs in the canopy (e.g. *Arthonia puncriformis*, *Arthopyrenia punctiformis*, *Ramalina farinacea*) and nitrophilous species preferring twigs (e.g. *Catillaria nigroclavata*, *Lecania naegelii*) were rarely recorded because canopies were not adequately sampled.

A few tiny species, such as *Scoliciosporum curvatum,* are easy to overlook and may also have been under-sampled. Some "rare" species may be quite common in habitats for which we had few or no plots: *Absconditella sphagnorum,* which is linked to organic substrata in peat bogs, may be an example. A few normally epilithic species that occur only occasionally on bark or wood (e.g. *Baeomyces rufus*, *Chrysothrix chlorina*, *Psilolechia lucida*) are here classified as "rare", though they may be common on their usual substrate. However, most of the 129 "rare" species are genuinely rare. Some of them, such as *Chaenotheca sphaerocephala* or *Sclerophora peronella*, are very substrate/habitat specific too.

Many of what we are calling "rare species" would more accurately be termed regionally rare. Although rare in the Šumava mountains they may be common in other regions or at lower altitudes (e.g. *Lecidella elaeochroma, Micarea denigrata*). Some species are regionally rare because their substrate is rare in the Šumava mountains (e.g. *Macentina abscondita* or *Piccolia ochrophora*, which prefer *Sambucus* bark).

Undetected species = rare species

About two hundred species known to be present in the Šumava mountains are not present in our dataset. This estimate is based on published floristic data (e.g. Palice 1999; Malíček and Palice 2015; Malíček et al. 2014) and data from herbarium databases of Zdeněk Palice, Jiří Malíček and Jan Vondrák. Most of them are very rare and their distribution is far from random. They may only inhabit a few objects, e.g. specifically modified old trunks, in well-preserved parts of suitable forest types. The sampling method used in this study is unlikely to detect them. Some are restricted to forest types that were not sampled (boreo-continental pine forests and

Table 3 Lichen species with highest fidelities (>0.65) to the five types of natural forests in the Šumava mountains. Ordered according to indicator values in each category. See the methods for definitions of the five characteristics

Forest category	Proposed indicator species	Frequency in particular forest type	Partial abundance score	Fidelity	Specificity	Indicator value
Beech forests	*Graphis scripta*	16	37	0.77	0.48	37
	Parmelia saxatilis	15	76	0.79	0.45	36
	Biatora efflorescens	13	42	0.81	0.39	32
	Biatora chrysantha	12	29	0.78	0.36	28
	Agonimia repleta	9	23	0.85	0.27	23
	Pertusaria amara	9	23	0.85	0.27	23
	Porina aenea	9	44	0.71	0.27	19
	Japewia 'dasaea'	6	21	1	0.18	18
	Biatora fallax	5	10	1	0.15	15
	Lecanora argentata	6	9	0.82	0.18	15
	Thelotrema lepadinum	7	20	0.67	0.21	14
	Lopadium disciforme	4	9	1	0.12	12
	Biatora helvola	3	9	1	0.09	9
	Trapelia corticola	3	9	1	0.09	9
	Opegrapha varia	4	9	0.75	0.12	9
	Trapeliopsis viridescens	4	6	0.75	0.12	9
	Pyrenula nitida	4	8	0.73	0.12	9
	Calicium salicinum	3	6	0.67	0.09	9
Bog and waterlogged forests	*Lecidea nylanderi*	25	142	0.67	0.75	51
	Imshaughia aleurites	19	79	0.79	0.57	45
	Pycnora sorophora	9	34	0.83	0.27	23
	Usnea hirta	6	19	1	0.18	18
	Tuckermannopsis chlorophila	7	15	0.79	0.21	17
	Micarea melaena	5	24	1	0.15	15
	Calicium trabinellum	6	18	0.75	0.18	14
	Lecanora norvegica	4	21	1	0.12	12
	Psilolechia clavulifera	4	8	0.67	0.12	8
	Arthonia muscigena	3	13	0.81	0.09	7
	Usnea subfloridana	3	8	0.73	0.09	7
	Micarea hedlundii	2	9	1	0.06	6
	Strangospora moriformis	2	8	0.8	0.06	5
	Calicium pinastri	2	6	0.67	0.06	4
Montane spruce forests	*Lecidea pullata*	23	181	0.82	0.70	57
	Cladonia cenotea	23	154	0.74	0.70	52
	Parmeliopsis hyperopta	23	191	0.69	0.70	48
	Hypogymnia farinacea	19	75	0.71	0.57	41
	Cladonia sulphurina	11	24	0.89	0.33	30
	Cladonia merochlorophaea	13	41	0.72	0.39	28
	Ochrolechia alboflavescens	14	48	0.66	0.42	28
	Lecanora subintricata	8	35	0.92	0.24	22
	Mycoblastus alpinus	10	21	0.72	0.30	22
	Ochrolechia mahluensis	8	26	0.67	0.24	16
	Cladonia deformis	5	13	0.67	0.15	10
	Lecanora sarcopidoides	3	9	0.82	0.09	7
Ash-alder alluvial forests	*Arthonia radiata*	6	16	0.89	0.18	16
	Lecidella subviridis	3	18	0.95	0.09	9
	Phaeophyscia endophoenicea	3	9	0.69	0.09	6
	Opegrapha rufescens	3	13	0.68	0.09	6
	Lecidella elaeochroma	2	10	0.83	0.06	5
	Lecania cyrtella	2	15	0.68	0.06	4
	Arthonia didyma	2	6	0.67	0.06	5

scrubs with *Pinus mugo*) or poorly sampled (ravine forests). Because these forest types are local and rare in the Šumava mountains (Table 1), lichens confined to them must be considered regionally rare too.

The design of this study ensured that the main forest types were sampled extensively, and almost guarantees that all common species were detected. Putting the same conclusion in different words, we can say that any undetected species must

Table 4 Similarities in species compositions between the six types of forest in the Šumava mountains. Measured by number of species in common and by Sørensen's index of similarity

	Beech forests				
Bog and waterlogged forests	100 / 0.637	Bog and waterlogged forests			
Montane spruce forests	91 / 0.625	104 / 0.768	Montane spruce forests		
Ravine forests	62 / 0.528	44 / 0.409	48 / 0.500	Ravine forests	
Ash-alder alluvial forests	69 / 0.533	61 / 0.510	57 / 0.528	45 / 0.562	Ash-alder alluvial forests
Forest habitats formed by human impact	67 / 0.530	69 / 0.592	67 / 0.638	40 / 0.519	61 / 0.685

be regionally rare. The undetected species are numerous, and make a significant contribution to overall biodiversity, but to investigate them will require different methods than those used in this study.

Lichens of montane spruce forests after areal decease of spruce

Large scale mortality of spruce began in the Šumava mountains in the 1990s (Kindlmann et al. 2012) and it continues. According to our observations, only a few spruce forests are still resisting, such as stands at tops of Mt. Boubín and Mt. Smrčina. In affected areas, almost all mature spruce trees died (Cervenka et al. 2016), only exceptionally did a few trees survive, mostly in valleys of brooks or at forest edges. Affected forests turned to fields of snags and logs slowly loosing bark.

Dead trees and snags in all plots with remains of bark share some common characteristics. The southern faces of trunks are almost without lichens, or with unhealthy (burned) thalli of common macrolichens (mainly *Hypogymnia physodes*, *Platismatia, Pseudevernia*). Southern faces of snags without bark are often dominated by *Lecanora subintricata*. Some bark lichens survive on northern faces, without obvious signs of injury, probably because there is little insolation stress. The most common lichen is usually *Cladonia digitata;* other com-

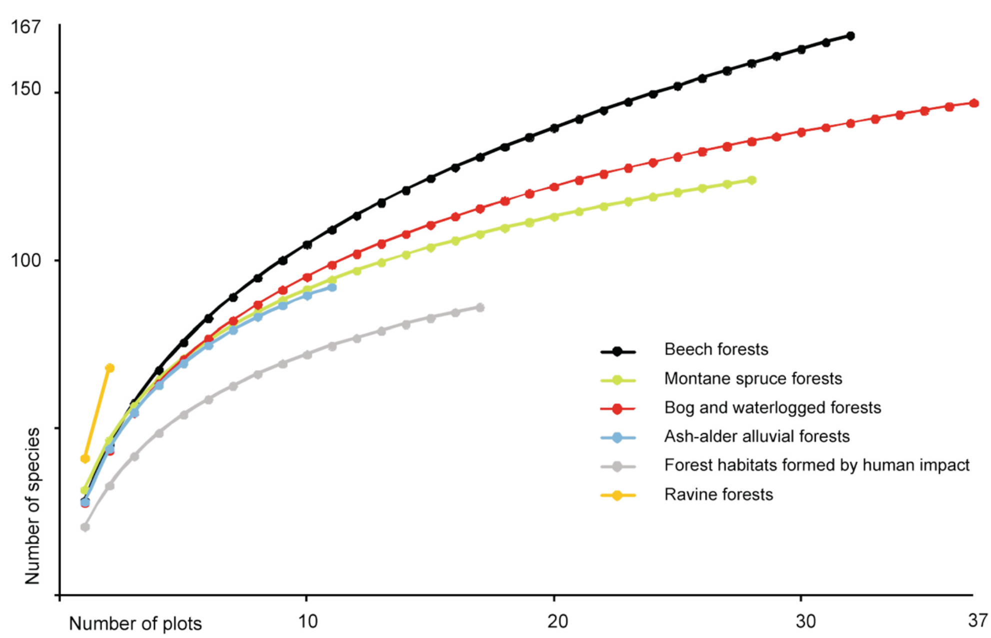

Fig. 3 Accumulation curves of lichen species plotted separately for the six forest categories. Methods described in text; standard deviations not depicted to avoid reduction of clarity

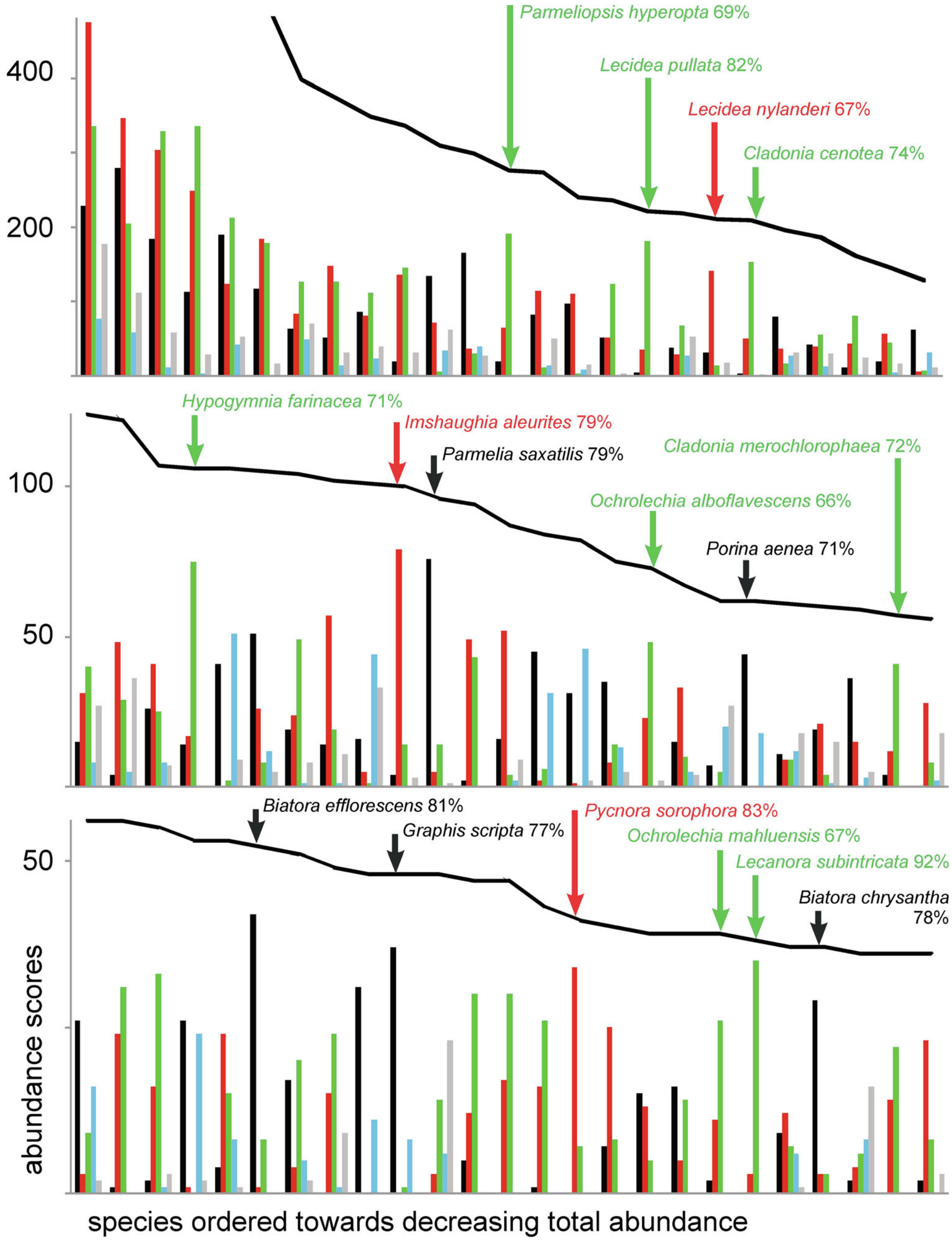

Fig. 4 Total abundance scores (thick black line) and partial abundance scores (colour columns) of frequently recorded species (with total abundance scores 9–1304). Each species is represented by five columns: black – beech forests; red - bog and waterlogged forests; green - montane spruce forests; blue - ash-alder alluvial forests; grey - forest habitats formed by human impact (mostly forest plantations). Species with fidelity to a single forest category above 0.65 (expressed in %) are pointed out in a colour corresponding to particular forest category

mon species are *Cladonia* spp., *Lecidea pullata*, *Mycoblastus* spp. and *Ochrolechia* spp. There is much variability in lichens on decorticated snags, but there is a clear tendency for abundance and diversity to increase with time after loss of bark.

Because of the absence of baseline data from before spruce disease, we cannot prove that the current species composition is poorer, or even different. However, it seems obvious that the massive loss of substrate must have led to a decline in lichen species confined to bark of spruce. There must also have been a decline in species requiring high humidity. Some common species preferring acidic bark of conifers are abundant in bog and waterlogged forests, but they are suspiciously rare in montane spruce forests (Table 5). Highly significant differences are in *Chaenotheca* spp., *Lecanactis abietina*, *Lecidea nylanderi* and *Micarea melaena*, although these species are typical inhabitants of Central European montane spruce forests (Guttová et al. 2012; Palice et al.

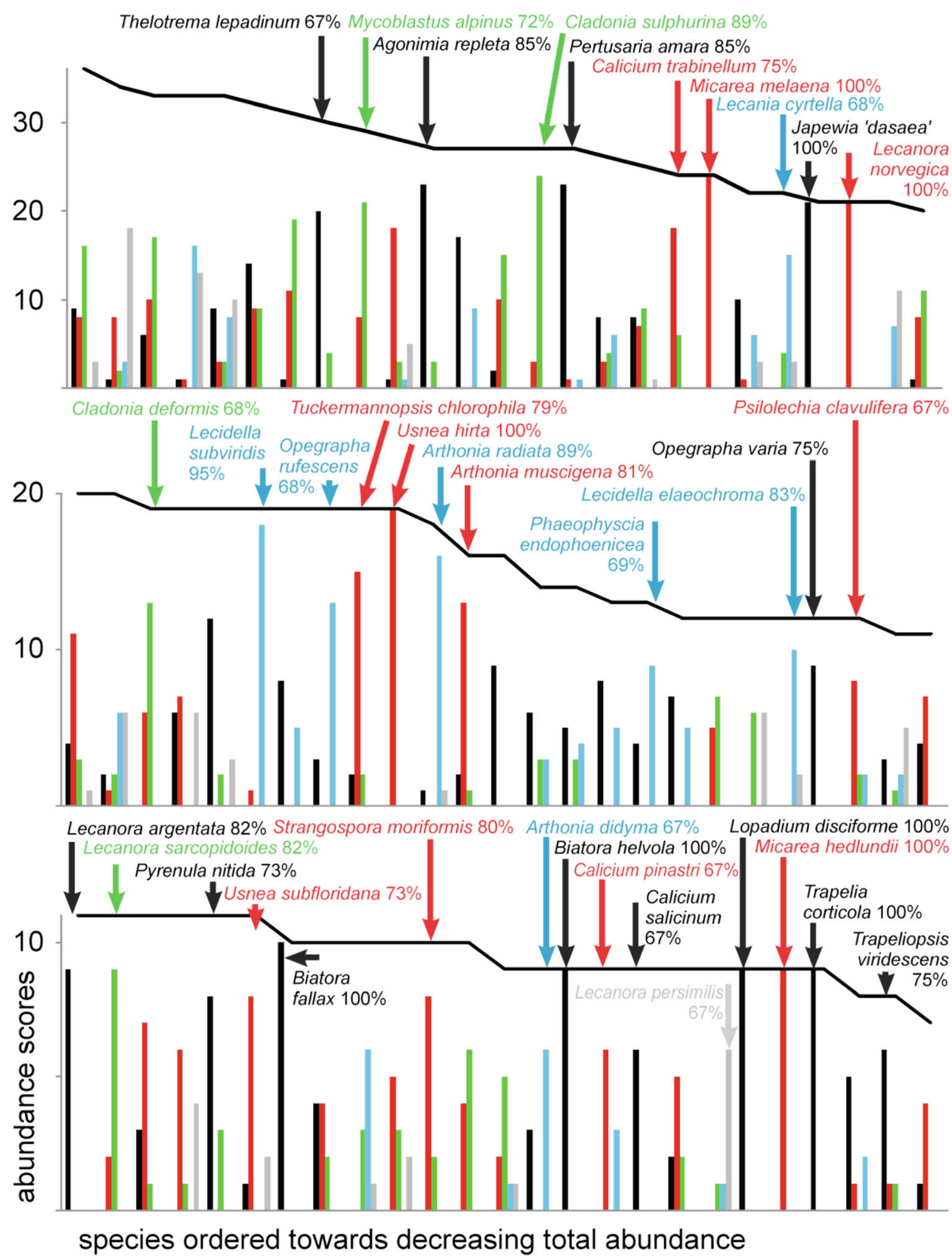

Fig. 4 continued.

unpublished field records and herbarium data) and of boreal spruce forests (Holien 1997; Kuusinen and Siitonen 1998). We also noticed a strong decline in population of *Lepraria jeckey*. This lichen still belongs to predominant species in montane spruce forests, but most thalli are bleached and decaying; typically grey-green thalli are sparse and usually restricted to deep crevices in bark.

The loss of bark has resulted in an increase in exposed wood, and we suggest that some epixylic lichens, especially those that are nitrophilous, are now more abundant than formerly. Young thalli of nitrophilous species on snags are much more frequent in montane spruce plots than in bog and waterlogged forests. Table 5 shows differences in abundances of some epixylic lichens,

Table 5 Species typical of coniferous forests with different abundance scores in bog and waterlogged forests and montane spruce forests. Species are sorted on the basis of supposed declined or increased abundance in montane spruce forests after areal decease of spruce

	Species	Abundance scores	
		Bog and waterlogged forests	Montane spruce forests
Supposed decline in montane spruce forests	*Arthonia leucopelea*	4	0
	Chaenotheca brunneola	7	0
	Chaenotheca ferruginea	110	4
	Chaenotheca chrysocephala	52	4
	Chaenotheca stemonea	15	0
	Cladonia norvegica	7	0
	Jamesiella anastomosans	21	4
	Lecanactis abietina	13	5
	Lecanora norvegica	21	0
	Lecidea nylanderi	142	14
	Loxospora elatina	11	3
	Micarea melaena	24	0
	Micarea micrococca	114	11
Supposed increase in montane spruce forests	*Amandinea punctata*	2	5
	Lecanora saligna	4	20
	Lecanora sarcopidoides	2	9
	Lecanora subintricata	3	35
	Physcia tenella	0	5
	Scoliciosporum sarothamnii	29	68
	Xanthoria polycarpa	3	14
	Xylographa paralella	8	16

including nitrophilous *Amandinea punctata*, *Lecanora saligna*, *Physcia tenella* and *Xanthoria polycarpa*. Some typically epixylic, heliophilous lichens (e.g. *Lecanora subintricata*) are now common in montane spruce forests, and we predict that some epixylic species that at present have low abundance (*Calicium* spp., *Lecanora cadubriae*, *L. sarcopidoides, Lecidea turgidula*) will become more common.

Importance of this study for adjusting the Czech red list

Numerous publications refer to dynamic patterns in distribution of lichens. Some lichen species are recently spreading whereas others are diminishing, which may be caused by climate changes and increasing or reducing of air pollution (e.g. Ellis et al. 2014; Hultengren et al. 2004; Skye and Hallberg 1969). Changes in lichen abundances are also documented for the Czech Republic (e.g. Liška 2012; Liška et al. 1998, 2006; Vondrák and Liška 2010), but only very obvious changes are likely to be documented reliably, because of scarcity of literature data. It is clear that numerous epiphytic macrolichens have declined, especially species with cyanobacterial photobionts (Vězda and Liška 1999), but our knowledge about dynamics in distribution of the hundreds of microlichen species is scanty. Accordingly, the Red List categories for the Czech Republic (Liška and Palice 2010) are vaguely designated for many species.

Our research provides extensive floristic data for 240 species of epiphytic lichens from a large area (about 2% of the area of the Czech Republic). Although the researched territory, the Šumava mountains, is unique in the Czech Republic in having the best preserved epiphytic lichen biota (Liška et al. 2006), our frequency/abundance data suggest some adjustments in the national Red List. We propose a higher category of threat for 14 species, a lower category for 3 species and a transfer from "data deficient" to some of the red list categories for 15 species (Table 6).

Table 6 Suggested changes in current Red List classification of lichens for the Czech Republic

Species	Frequency in Šumava (by data presented here from 128 plots)	Total abundance score in Šumava (by data presented here)	Current Red List category (Liška and Palice 2010)	Suggested change in Red List classification
Agonimia repleta	11	27	DD	NT/VU
Arthonia incarnata	3	4	DD	EN
Calicium montanum	1	1	DD	CR
Cladonia merochlorophaea	21	57	DD	LC/NT
Dictyocatenulata alba	2	3	DD	EN
Fellhanera bouteillei	41	122	CR	LC
Fellhanera viridisorediata	22	56	DD	LC/NT
Graphis scripta	22	48	VU	NT
Hypogymnia tubulosa	46	124	NT	LC
Jamesiella anastomosans	32	60	DD	LC/NT
Japewia subaurifera	9	20	NT	VU
Lecania cyrtellina	1	3	DD	EN
Lecanora conizaeoides	35	107	LC	NT
Lecanora filamentosa	18	43	VU	NT
Lecanora norvegica	4	21	DD	EN
Lecanora phaeostigma	22	55	DD	LC/NT
Lecidea leprarioides	18	31	EN	VU
Lecidea nylanderi	48	211	VU	LC
Lecidea pullata	33	221	NT	LC
Lepraria jackii	122	1019	NT	LC
Micarea adnata	3	6	CR	EN
Micarea globulosella	4	7	DD	VU/EN
Mycoblastus affinis	14	36	CR	VU/EN
Mycoblastus sanguinarius	18	47	EN	VU
Ochrolechia alboflavescens	24	73	EN	NT/VU
Ochrolechia mahluensis	14	39	DD	VU
Opegrapha niveoatra	6	19	NT	VU
Parmeliopsis hyperopta	47	276	NT	LC
Phaeophyscia endophoenicea	5	13	EN	VU
Platysmatia glauca	86	503	NT	LC
Pseudevernia furfuracea	72	337	NT	LC
Rhaphidicyrtis trichosporella	2	4	DD	EN

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Compliance with ethical standards

Conflict of interest All authors declare that they have no conflict of interest.

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