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ORIGINAL PAPER

Lichens in old-growth and managed mountain spruce forests in the Czech Republic: assessment of biodiversity, functional traits and bioindicators

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Abstract

Natural spruce forests are restricted to the highest mountain ranges in the Czech Republic. Spruce is also the commonest tree species in managed forests. Owing to a massive decline of spruce forests in Central Europe, caused by recent climatic fluctuations and disturbances, the lichen diversity and species composition was compared between ten representative natural mountain old-growth forests in the Czech Republic and their counterparts in mature managed forests. The old-growth forests are characterized by a higher species richness, abundance, number of Red-listed species, functional, taxonomic and phylogenetic diversities. Plots with the highest species richness are situated in the Šumava Mountains, an area with a relatively low sulphur deposition in the past. Bioindication analysis searching for lichen indicators supported several species (e.g. *Xylographa vitiligo*, *Chaenotheca sphaerocephala*) and genera (e.g. *Calicium*, *Xylographa*) with a strong preference for old-growth forests. Analysis of lichen functional traits revealed a higher abundance of species with a vegetative reproduction in managed forests that may be explained by a higher efficiency in colonization by young successional stages. Lichens with stalked apothecia, pigmented ascospores and large ascospores are more frequent in old-growth forests. Our results are briefly discussed in terms of nature conservation, focusing on national refugees of old-growth forest species, biodiversity hot-spots, practical use of indicator species and representative measures for an evaluation of forest quality.

Keywords Functional diversity · Functional traits · Phylogenetic diversity · Species richness · Substrate specialists · Taxonomic diversity

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Introduction

Forest ecosystems in Europe belong to a dominant vegetation type, harbouring a major part of the biodiversity (Bengtsson et al. 2000; Loo 2009). Their species composition, area and distribution have been considerably changed by direct human activities. Current forest communities throughout Europe are greatly endangered by global climate change (e.g. Spathelf et al. 2014; Dyderski et al. 2017). Changing environment and local climatic conditions strongly influence all woodland organisms as well as human society, for which forests serve numerous important ecosystem functions (Krieger 2001; Thom and Seidl 2016). In comparison to managed forests, primeval and old-growth forests provide specific services, such as habitats for specialized flora and fauna (Brockerhoff et al. 2017), and differ in many attributes, such as a spatial heterogeneity, time of development and stability (Spies 2004). They also provide other services, e.g. pure water, carbon storage, regeneration of nutrients, maintenance of soils, and micro- and macro-climate control (Zahner 1996).

In Central Europe, most of the native forests have been destroyed by forest management and replaced by spruce monocultures. The exploitation of last extensive primeval forests started during the colonization of mountain areas, which peaked in the thirteenth and fourteenth centuries, when some stands were clearcut and replaced by agricultural land, while the remaining ones were used for selective timber logging and livestock grazing (Nožička 1957). The spread of modern forestry practices in the first half of the nineteenth century resulted in clear-cutting and establishment of extensive even-aged spruce plantations (Chytrý 2017).

An effective protection of forests is impossible without a thorough knowledge of their biodiversity, ecology and degree of naturalness. Thus, an assessment of forest quality, such as its continuity, human impact or number of endangered species, is a key requirement in conservation of forests. Bioindicators are effective and useful tools used in the nature conservation for an assessment of forest stands degree of naturalness (e.g. Kotwal et al. 2008). Lichens, known to be suitable bioindicators (e.g. Conti and Cecchetti 2001; Thormann 2006; Kuldeep and Prodyut 2015), are highly effective for diagnosing many aspects of forest quality since they are regarded as substrate or habitat specialists (Resl et al. 2018). For example, some lichens are characterized by their strong preference to old woodland stands (Marmor et al. 2011; Zemanová et al. 2017; Williams and Ellis 2018), being associated with over-mature senescent trees (Nascimbene et al. 2009) and large trees (Kruys et al. 1999), i.e. substrates that are poorly represented in managed forests.

Epiphytic and epixylic lichens, as a selected model group, have been studied in one of the most endangered forest habitat in Central Europe, namely natural montane spruce forests, dominated by *Picea abies*. In the Czech Republic, natural spruce forests are distributed in several mountain ranges in the upper-montane (supramontane) belt at elevations of 1000–1370 m a.s.l. (Chytrý 2017), with mean annual temperatures of 2–4 °C and precipitations of 1100–1600 mm (Jirásek 1996). Only a few remnants of old-growth spruce stands are maintained in the highest ranges, such as the Krkonoše, Hrubý Jeseník, Králický Sněžník, Šumava and Beskydy Mountains. Spruce also occurs regularly in mixed stands with beech and silver fir in the montane and submontane belt in boggy and water-logged sites. Archive sources indicate that spruce was rather common from the upper-colline belt to higher elevations in the sixteenth to eighteenth centuries (Mráz 1959; Nožička 1972; Szabó et al. 2017).

Natural spruce forests in the Czech Republic have undergone numerous serious disturbances in the last half century. Large areas died in the 1980s, especially in the Krušné and Jizerské hory Mts, and also, to a notable extent, in the Krkonoše and Moravskoslezské Beskydy Mts, as a result of atmospheric emissions of sulphur dioxide (Kubíková 1991). Sulphur emissions were greatly reduced in the 1990s (Vestreng et al. 2007), but spruce decline has continued in both managed and natural spruce forests. A recent decline has mainly been caused by outbreaks of bark beetle, *Ips typographus* (Čada et al. 2016), as part of the natural dynamics of spruce forests (e.g. Chytrý 2017). Outbreaks culminate in seasons with hot summers followed after wind storms (Müller et al. 2008), such as Kyrill in 2007. Šumava was the most affected mountain range after the Kyrill event. Today, most of the Czech forests are affected by the bark beetle. Additionally, spruce is very sensitive to more frequent drought events and tends to respond to climate change (increasing temperature, decreasing precipitation) by shifting its optimum to higher elevations (Ponocná et al. 2016).

In this study, various aspects of the lichen biota in the most important natural mountain spruce forests in the Czech Republic were compared with those in surrounding managed forests as follows:

1. Which old-growth spruce forests are the most valuable and have the highest nature protection potential, using the lichen species richness, composition and number of Red-listed taxa as the main criteria?
2. Which lichens could be used as the most suitable indicators of old-growth spruce forests in terms of nature conservation aims?
3. Do the species, taxonomic, phylogenetic and functional diversity differ between old-growth and managed forests?
4. Do any functional traits predominate in a particular forest type?

Materials and methods

Study sites

Based on our previous field experiences, consultations with forest ecologists and our own studies, ten sites with old-growth spruce mountain forests in the highest Czech mountains: Beskydy, Hrubý Jeseník, Králický Sněžník, Krkonoše and Šumava were selected (Fig. 1). Our aim was to explore old woodlands with minimal recent and historical management practices and rich lichen communities. These sites (Table 1) were situated in forests with naturally dominated by *Picea abies*, above 1100 m a.s.l. The only exception, at 930 m a.s.l., was an old spruce forest in a wet valley of a brook, forming a core part of the Boubín primeval forest reserve protected since 1858. Some of the most important, natural old-growth forest sites in the Šumava Mts (Mt Trojmezná, Prameny Vltavy, Mt Jezerní hora and Mokrůvka) were excluded due to the recent bark beetle outbreak.

Each of the ten plots in old-growth spruce forests had a counterpart plot in a nearby managed forest according to the twin-plot design of Stape et al. (2006) and Bazalová et al. (2018). All managed plots were up to 1 km distance from the old-growth forest plot and usually at a similar elevation and exposition. Managed forests (> 50 years old) were indicated by numerous stumps after felling, similar tree size (and age) and often poorly developed herb layer due to shady conditions.

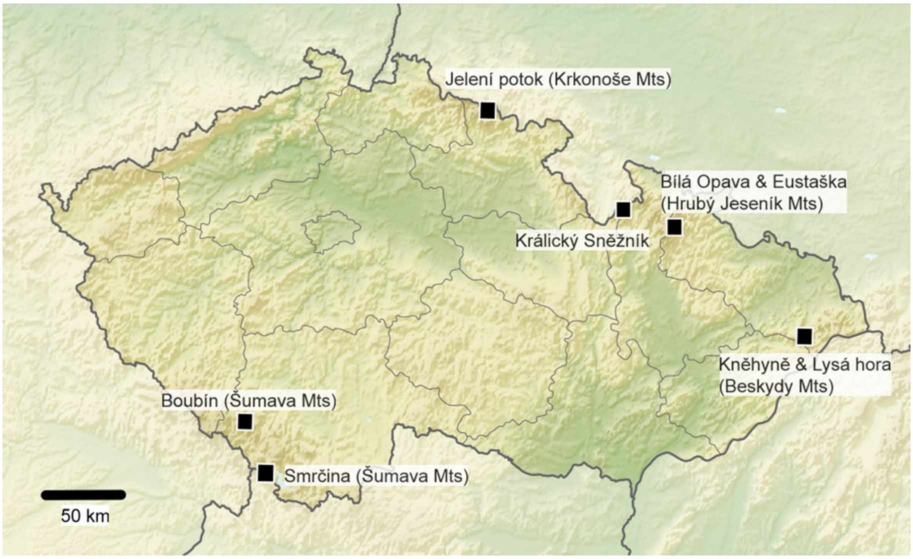


Fig. 1 Study sites in the Czech Republic. (*Source* Wikipedia Commons)

Sampling methods

In every old forests patch, a 1-ha plot in an assumed biodiversity hot-spot was selected according to the criteria of Vondrák et al. (2018). Although this method can cause bias in statistical analyses (e.g. due to an absence of hot-spots at small localities), subjectively selected plots are more representative of the locality than the randomly selected ones, which are often situated in species-poor and very uniform sites. Although biodiversity is generally unevenly distributed within a locality, which is a complication for research design, all studied sites were homogenous in terms of geomorphology and vegetation. Therefore, important influences of extreme conditions, such as a specific microclimate, light conditions or tree species composition which are typical for deep humid valleys or rocky ridges, were not expected. Plots were selected primarily (and optimally) on the basis of the presence of a wide substrate spectrum and light conditions in a dense and well-lit forest patch. The complexity of data is another advantage of the method employed; the species lists are usually close to the total diversity at a locality (i.e. a forest stand up to ca. 30 ha) according to our previous experiences. The selected method is always a trade-off between objectivity of independent statistical analyses, quality of data and research goals. Methods by Vondrák et al. (2018) were selected since they appear to be very effective for studies on lichen diversity in European forests and very appropriate for nature conservation aims. Since managed forests proved to be very homogenous and hot-spots were unidentified, plots close to the old-growth plot within a managed forest interior to eliminate a border effect were preferentially selected.

All plots were explored by three lichenologists (first three authors), who were exhaustively searching for new species until no additional lichen was recorded within at least 15 min. Old-growth forest localities were surveyed for 5–7 h, managed sites for 2.5–4 h. Epiphytic and epixylic lichens were recorded on all available organic substrates, such as living and dead trees including roots, trunks, twigs, needles, epiphytic bryophytes and

Table 1 List of studied localities and environmental variables

Localities	Mts	Visited	Latitude	Longitude	Altitude (m)	Exposition	Slope (%)	Forest type	Trees
Bílá Opava 1	Hrubý Jeseník	24-06-2015	50.07051	17.24841	1290	N	10	Old	PA, SA
Bílá Opava 2	Hrubý Jeseník	26-06-2015	50.07681	17.26545	1160	N	12	Man	PA
Bílá Opava 3	Hrubý Jeseník	25-06-2015	50.07723	17.25190	1190	SE	18	Old	PA, (FA, SAM)
Bílá Opava 4	Hrubý Jeseník	26-06-2015	50.08051	17.26586	1080	S	41	Man	PA
Eustaška 1	Hrubý Jeseník	21-08-2015	50.06039	17.25289	1230	NE	12	Old	PA
Eustaška 2	Hrubý Jeseník	20-08-2015	50.05971	17.25387	1210	NE	8	Man	PA, (SA)
Králický Sněžník 1	Králický Sněžník	23-08-2015	50.20028	16.85627	1190	SE	19	Old	PA, (SA)
Králický Sněžník 2	Králický Sněžník	22-08-2015	50.20148	16.85793	1210	S	15	Man	PA, (SA)
Smrčina/Hochficht 1	Šumava	04-10-2015	48.73992	13.92085	1320	N	4	Old	PA, (SA)
Smrčina/Hochficht 2	Šumava (Austria)	05-10-2015	48.73844	13.91997	1310	W	14	Man	PA, SA
Boubín top 1	Šumava	06-10-2015	48.99242	13.82148	1250	NE	23	Old	PA
Boubín top 2	Šumava	15-07-2015	48.99505	13.81825	1270	E	14	Man	PA
Boubín low 1	Šumava	23-10-2015	48.97439	13.81814	930	E	7	Old	PA, (AA, FA, SA, SAM)
Boubín low 2	Šumava	09-10-2015	48.97084	13.82203	900	E	5	Man	PA, (BP, FA)
Jelení potok 1	Krkonoše	06-11-2015	50.73773	15.75878	1225	NE (SE)	18	Old	PA, (SA)
Jelení potok 2	Krkonoše	07-11-2015	50.73554	15.76280	1145	SE	25	Man	PA, (SA, SAM)
Lysá hora—Mazák 1	Beskydy	30-08-2016	49.54467	18.44514	1185	SW	37	Old	PA, (AP, FA, SA)
Lysá hora—Mazák 2	Beskydy	29-08-2016	49.54783	18.43525	1090	W	18	Man	PA, (young AA, FA, SA)
Kněhyně 1	Beskydy	31-08-2016	49.49667	18.31558	1190	E	16	Old	PA, (AP, FA)
Kněhyně 2	Beskydy	01-09-2016	49.49730	18.31851	1110	E	23	Man	PA (FA)

Localities	Max. tree diameter	Logs	Snags	Temperature (°C)	Precipitation (mm)	S 1950–1999 (kg)	S 2000–2010 (kg)	N 1950–1999 (kg)	N 2000–2010 (kg)
Bílá Opava 1	100	+	+	3.151	1171	25.6	10.8	20.3	13.7
Bílá Opava 2	40	±	−	3.830	1138	24.8	10.7	19.8	13.6
Bílá Opava 3	80	+	+	3.641	1138	24.7	10.6	19.7	13.5
Bílá Opava 4	50	+	+	4.124	1089	24.0	10.5	19.2	13.3

Table 1 (continued)

Localities	Max. tree diameter	Logs	Snags	Temperature (°C)	Precipitation (mm)	S 1950–1999 (kg)	S 2000–2010 (kg)	N 1950–1999 (kg)	N 2000–2010 (kg)
Eustaška 1	80	+	+	3.344	1170	24.7	10.6	19.7	13.5
Eustaška 2	40	+	+	3.579	1143	24.6	10.6	19.7	13.5
Králický Sněžník 1	80	+	+	3.091	1217	24.9	10.5	19.9	13.6
Králický Sněžník 2	40	+	+	3.308	1258	24.9	10.5	19.9	13.6
Smrčina/Hochficht 1	100	+	+	3.122	1007	8.7	4.0	13.7	9.6
Smrčina/Hochficht 2	40	+	+	3.122	984	8.7	4.0	13.7	9.6
Boubín top 1	80	+	+	3.507	1015	10.1	4.3	13.8	9.5
Boubín top 2	60	−	−	3.426	999	10.1	4.3	13.7	9.4
Boubín low 1	100	+	+	5.121	831	8.3	4.1	12.6	9.2
Boubín low 2	60	±	−	5.285	836	8.0	4.0	12.3	9.1
Jelení potok 1	80	+	+	2.727	1365	29.3	11.5	22.5	15.2
Jelení potok 2	40	±	+	3.060	1318	28.3	11.3	21.8	14.9
Lysá hora—Mazák 1	70	+	+	3.875	1333	22.4	9.8	18.0	12.4
Lysá hora—Mazák 2	40	±	±	4.589	1204	21.0	9.5	17.0	12.0
Kněhyně 1	60	+	+	3.750	1338	21.3	9.4	17.5	12.1
Kněhyně 2	40	±	−	4.107	1231	21.3	9.4	17.5	12.1

Forest type: *man* managed, *old* old-growth; trees (minor trees in brackets): AA, *Abies alba*; AP, *Acer pseudoplatanus*; BP, *Betula pendula*; FA, *Fagus sylvatica*; PA, *Picea abies*; SA, *Sorbus aucuparia*; SAM, *Sambucus* sp.; logs, snags: present (+), rarely present (±) and absent (−). Annual mean temperature, precipitation (both from years 1961–2010), mean historical (1950–1999) and recent (2000–2010) sulphur and nitrogen deposition in kg on 1 ha were extrapolated for studied plots from a climatic model. GPS coordinates according to WGS84 datum polypores, shrubs, lying wood, snags, stumps and woody debris. Following Vondrák et al. (2015), the lichen abundance was determined according to the three abundance categories: 1 = rare (≤ 3 records), 2 = scattered (4–10 records) and 3 = abundant (> 10 records). Terricolous and saxicolous lichens were omitted due to their uneven and sparse distribution in spruce forests. Species were identified in the field and ambiguous samples were collected for identification in the laboratory.

Identifications of lichens, nomenclature and vouchers

Specimens (see Table 6 in Electronic Appendix; column Vouchers) were identified using routine methods, including TLC analyses (Orange et al. 2010) and UV light. DNA barcoding (nrITS and mtSSU regions) was used for identifications of two samples: *Biatora vacciniicola* (MH174254 and MH174255) and *Pertusaria pupillaris* (MK756039). Collected vouchers are deposited in the herbarium PRA and the private herbarium of J. Malíček (JM). The nomenclature and Red-list categories follow Liška and Palice (2010), Malíček et al. (2018) and Kocourková (2000). Species absent from these publications are provided by author abbreviations.

The final dataset contains several questionable taxa: (1) species identified with a high degree of uncertainty, usually due to poorly developed thalli (*Agonimia flabelliformis*, *Arthonia excipienda*, *Bacidia circumspecta*, *Bacidina* sp., *Bacidina caligans*, *Mycoblastus* sp., *Porina lectissima*, *Usnea* sp.), (2) taxa with doubtful species delimitation (*Bryoria* spp.) and (3) distinct but undescribed species provided by provisional names (*Japewia 'dasaea'*, *Micarea 'substipitata'*, *Strigula 'inconspicua'*). Two taxonomically problematic species, not distinguished by us, are united with their phenotypic twins (*Cladonia ochrochlora* with *C. coniocraea*, *Parmelia ernstiae* with *P. saxatilis*).

Species richness and composition

Differences between old-growth and managed forests (see Fig. 2) were tested in R. 3.3.3. (R Core Team 2018) using the application R Commander. The normality of data was verified by the Shapiro–Wilk test (Shapiro and Wilk 1965). Paired *t* test and non-parametric paired-samples Wilcoxon test (used only for caliciod lichens and fungi) were used for testing of null hypotheses of normally distributed data and data with rejected normal distribution, respectively. Correlations of species richness with functional, taxonomic and phylogenetic diversity were tested using the Linear regression model. Species accumulation curves were built for a determination of total lichen species pools associated with either managed or old-growth forest stands. Exact accumulation curves with 1000 permutations and unconditioned standard deviation and extrapolated incidence-based estimations of species richness accounting for undetected species using function 'specaccum' in the package 'Vegan' were computed (Oksanen et al. 2018).

Similarity of species composition among sites has been displayed by Principal Component Analysis (PCA) in Canoco 5 (Šmilauer and Lepš 2014). The PCA analysis was based on 232 species and 18 plots since species composition of two Boubín lowland plots differed significantly (see Electronic Appendix, Fig. 3). These two outliers were identified via differences in Sørensen β-diversity using function 'scores' in the package 'outliers' (Komsta 2015) and removed from the final analysis. Data standardization in PCA was carried out by centring by species and had a gradient of 1.7 SD units long. Explained variabilities in diagrams with and without ourliers were slightly better in that without outliers. General

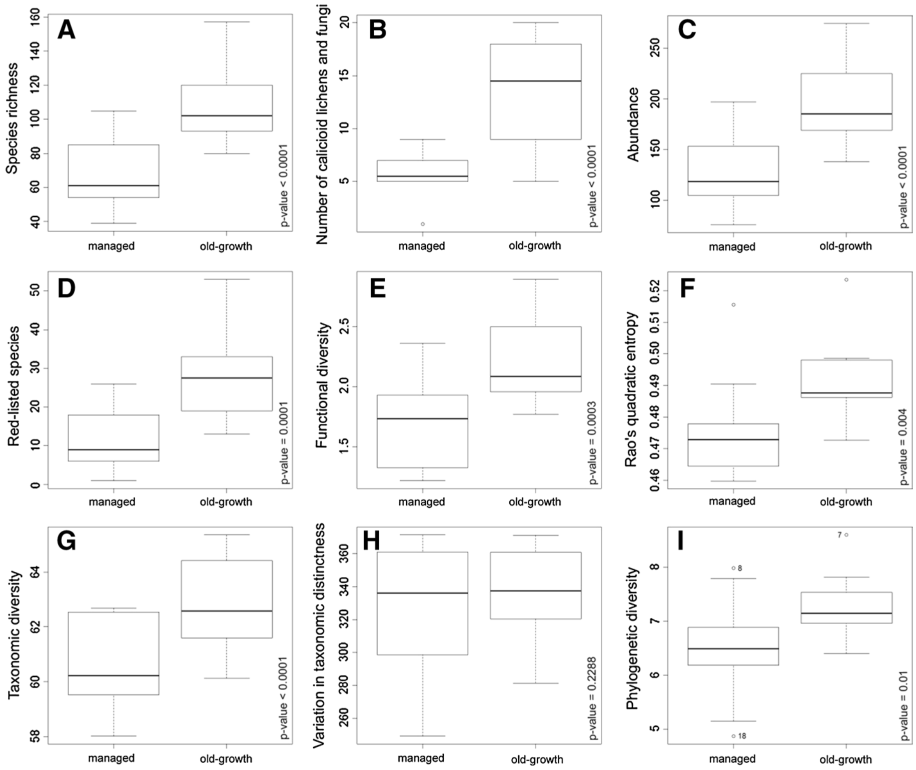


Fig. 2 Comparison between managed and old-growth forests, including p values (paired t-test, paired-samples Wilcoxon test): **a** species richness; **b** number of calicioid lichens and fungi; **c** species richness and abundance; **d** number of Red-listed species (Liška and Palice 2010); **e** functional diversity (Petchey and Gaston 2002); **f** Rao's quadratic entropy (Botta-Dukát 2005); **g** taxonomic diversity, distinctness and average taxonomic distinctness (Warwick and Clarke 1995; Clarke and Warwick 1998); **h** variation in taxonomic distinctness (Clarke and Warwick 2001); and **i** phylogenetic diversity (Faith 1992)

distribution of sites in the diagram did not differ considerably (see Figs. 3 and 5 in Electronic Appendix).

Drivers shaping species richness and composition of lichens

The effects of environmental variables (see Table 1) on lichen diversity were tested using the Generalized least squares fit by REML in R software. Mean annual precipitations and temperatures between years 1961 and 2010 were interpolated from so-called technical series (TS) for the Czech Republic provided by the Czech Hydrometeorological Institute for this period. TS represent qualitatively checked, homogenized data for each location, e.g. station (Štěpánek et al. 2013). Data for particular data points were then generated using linear regression of daily climatic parameter and elevation and the Inverse Distance Weighting interpolation of all parameters of regression (Štěpánek et al. 2011). Total annual means of sulphur and nitrogen deposition in kg/ha from years 1950 to 1999, provided by the Czech Hydrometeorological Institute, were interpolated for our plots according to a model. Maximum tree diameter, measured in the field, served as an approximate proxy of tree age, which was unavailable for our localities. Categories for tree species composition were as follows: 1 = only spruce present, 2 = spruce and one other tree species present, and 3 = spruce and two or more trees present. At all plots, spruce predominates and other trees were rarely intermixed (maximum of a few trees only). Strong positive correlations among precipitations, temperatures, N and S depositions were observed (see Electronic Appendix, Table 1; counted by Pearson's correlation matrix in R). Due to a limited number of variables, which could be included into a model, insignificant variables were first excluded before creating a set of models by sequentially adding mutually correlated variables. The Akaike information criterion (AIC) of these models was compared with that of the initial model.

Indicator species

The affinity of lichen species to either old-growth or managed forests using indicator species analysis was tested (De Cácerés and Jansen 2015). The analysis combines values of positive predictive value (specifity) and sensitivity (fidelity) of each particular lichen species to the old and managed forests. The indicator value was computed for each lichen species occurring in more than 5 plots. The statistical significance of indicator values was assessed by 9999 permutations at $p < 0.05$ using function 'multipatt' in the package 'indicspecies' in R software (De Cácerés and Jansen 2015).

Functional diversity and traits

Ten functional traits (listed below) for 247 species were used for an analysis of functional diversity according to Petchey and Gaston (2002). The trait "fruit-body type" and species with missing data on ascomata and ascospores were excluded due to the analysis limitations. The trait "macrolichen" was excluded from all functional diversity analyses since this character is included in the trait "thallus". Eleven traits for 263 species were used for an analysis of functional diversity measured by Rao's quadratic entropy. Values of this index positively correlate with diversity of functional traits. Introduction of new species into the community increase the species-abundance diversity, but it may decrease the average dissimilarity among species (Botta-Dukát 2005) which leads to a lower RaoQ value. Other indexes of functional diversity (e.g. Villéger et al. 2008; Laliberté and Legendre 2010) were also considered, but our data does not comply with analysis requirements, for example a low species richness and high number of traits that are out of exponential relationship (see Villéger et al. 2008). Functional diversity was evaluated via a method for a calculation of Faith's Phylogenetic Diversity using the R package 'Picante' (Kembel et al. 2014). Rao's quadratic entropy was calculated using function 'rao.diversity' in the package 'SYNCSA' (Debastini 2018).

Functional traits of lichen species, inspired by Bässler et al. (2016), have been mostly extracted from a common bibliography (Smith et al. 2009; Wirth et al. 2013 and the *Nordic Lichen Flora* I–VI); in a few cases, monographs or own data have been used. All the selected traits belong to easily observed and well studied characters. Differences in proportions or mean values of individual traits in old-growth and managed forests were tested in R. 3.3.3. (R Core Team 2018) using the application R Commander. Non-parametric paired-samples Wilcoxon test was used for testing of null hypotheses. In total, we tested eleven morphological, anatomical and chemical traits (see Electronic Appendix, Table 2):

(1) *Thallus* (crustose/foliose/fruticose). More detailed classification was not used due to many intermediate forms. Leprose types were included under the crustose thallus (present only in a few species) and a placodioid type was absent in the dataset. In the paired-samples test, only a category "macrolichen" was used, including foliose and fruticose types. The thallus form is closely connected with basic ecological strategies (Rogers 1990). Individual types differ in their sensitivity to environmental changes (Ellis and Coppins 2006; Johansson et al. 2007) and are used as indicators (e.g., Giordani et al. 2012).

(2) *Photobiont* (trebouxioid/trentepohlioid/absent). No species with cyanobacteria are present in the dataset, but some taxa without photobionts (e.g. *Chaenothecopsis*) were included. In the paired-samples test, the photobiont type was separated on trebouxioid and trentepohlioid. Trebouxioid photobionts are the commonest type in lichens (Friedl and Büdel 2008) and their proportion increases with intensification of land use (Stofer et al. 2006). Trentepohlioid photobionts tend to occur in areas with higher temperature (Aptroot and van Herk 2006; Marini et al. 2011), such as tropical regions (Friedl and Büdel 2008).

(3) *Metabolites* (present/absent). Only secondary lichen metabolites detectable by thin-layer chromatography (TLC), the traditional method used in lichenology, were considered. Lichen compounds may help to protect thalli against herbivores, competitors, UV radiation and increase a pollution tolerance (Molnár and Farkas 2010).

(4) *Vegetative reproduction* (present/absent). Isidia, blastidia, thlasidia, squamules, cortical plates, soredia, microsquamules, goniocysts and thallus fragments are included in the vegetative type of reproduction. For the analysis of functional diversity, vegetative reproduction was divided to three categories: soredia, isidia and an absence of these and similar propagules. Ecological importance of the vegetative reproduction is described in Discussion.

(5) *Conidia* (presence/absence). Although many species produce conidia, their presence is poorly documented, but this trait is thought to be worthy of inclusion in the dataset. Ecological importance of distribution by conidia remains poorly known. This type of reproduction seems to be cost-effective, as it is an investment into a large number of very small propagules, which are able to spread for long distances.

(6) *Fruit body type* (basidiomata/perithecioid/elongated apothecia/stalked apothecia/rounded apothecia/unknown). Perithecioid ascomata include all types of closed fruit bodies; elongated apothecia are present, e.g. in *Graphis*, *Opegrapha*, *Xylographa*; stalked apothecia were used exclusively for calicioid lichens and fungi, and remaining types are regarded as rounded apothecia. Ascomata are unknown in some lichens (*Dictyocatenulata alba*, *Japewia dasaea*, *Lepraria* spp., *Pycnora leucococca*). The fruit body type seems to be more connected with phylogeny than ecology. The paired-samples test included only stalked and others fruit bodies since the basidiomata, perithecia and elongated apothecia were rarely present in the dataset. Stalked apothecia are typical for calicioid lichens and fungi that do not form a monophyletic group (Prieto et al. 2013), but share a strong affinity to old trees and snags (Holien 1996).

(7) *Fruit body area* For rounded, perithecioid, stalked apothecia and basidiomata, the diameter was measured and the area counted separately for rounded and elongated types: $\pi \times r^2$ and $\pi \times a \times b$. This trait is connected for example with a number of produced ascospores.

(8) *Spore septation* (simple/septate/muriform). Spores with two or more cells have an increased chance for a germination (Pentecost 1981).

(9) *Spore pigmentation* (colourless/pigmented). Pigmentation generally increases a resistance to UV radiation (Durrell 1964) or high and low temperatures (Rehnstrom and Free 1996), which can help spreading on longer distances.

(10) *Spore shape*—mean length/width. Ecological aspects of this trait are poorly known among lichens; it probably influences spreading of spores.

(11) *Spore volume*—mean width and length: $\sqrt{(4/3\pi \times \mathrm{width}^2 \times \mathrm{length})}$. The spore volume is closely connected with their dispersion and establishment, such as an increased colonization rate of small ascospores (Johansson et al. 2012) and a higher content of nutrients of bigger ascospores (Sanders and Lücking 2002).

Taxonomic and phylogenetic diversity

A taxonomic diversity index, empirically related to Shannon species diversity, was used; this represents an average path length through the taxonomic tree between every pair of individuals (Warwick and Clarke 1995). Similar taxonomic indexes reaching the same values were also tested: taxonomic distinctness (Warwick and Clarke 1995) and average taxonomic distinctness (Clarke and Warwick 1998), based on the same principle, but both employing species instead of individuals. Another tool of taxonomic diversity used, the variation in taxonomic distinctness (Clarke and Warwick 2001), reflects the variance of the pairwise path lengths in the taxonomic tree. Presence/absence of species at localities and taxonomic data, i.e. species, genus, family, order, class and phylum, for 260 species were analysed; the genera *Microcalicium* and *Puttea* with an uncertain taxonomic position were excluded from the dataset. Taxonomic distances were calculated using the function ‘taxondive’ in R package ‘Vegan’ (Oksanen et al. 2018).

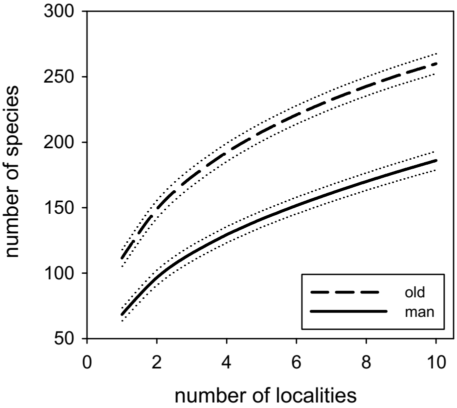
Phylogenetic diversity, defined as the minimum total length of all the phylogenetic branches required to span a given set of taxa on the phylogenetic tree (Faith 1992), has been counted for single sites. Based on nrITS phylogeny, managed and old-growth forests were compared. Sequences were downloaded from the GenBank database and supplemented by three of our unpublished sequences (*Japewia dasaea*, *Lecanora cadubriae*, *Steinia geophana*). After excluding a few doubtful samples, nrITS was available for 201 species, i.e. 76% of all recorded taxa. Sequences were aligned by the on-line application MAFFT version 7 (Katoh and Standley 2013) with FFT-NS-i method (Katoh et al. 2002). Ambiguous positions were excluded using Gblocks 0.91b (Castresana 2000). The final alignment contained 345 positions. PD was calculated using function ‘pd’ in the R package ‘Picante’ (Kembel et al. 2014) for each site using 50 randomly selected species with 9 repetitions.

Results

Comparison of old-growth and managed forests

Old-growth forests are characterized by the higher species richness, abundance of lichens, number of Red-listed species, functional, phylogenetic and taxonomic diversities (Figs. 2, 3), but no significant differences in the variation of taxonomic distinctness were found (Fig. 2h).

Fig. 3 Accumulation species curves (± s.d.) of lichens including calicioid fungi in spruce old-growth (old) and managed (man) forests



Species richness and floristic composition

In total, we recorded 254 lichenized fungi, 10 non-lichenized calicioid fungi and 15 other lichen-allied and lichenicolous fungi, traditionally studied by lichenologists (see Table 6 in Electronic Appendix). Some of them were recorded for the first time from the Czech Republic and have been published separately (Malíček et al. 2017a, b, 2018; Palice et al. 2018). According to the Czech Red-list (Liška and Palice 2010), two species were regarded as regionally extinct (*Calicium lenticulare* and *Ramboldia cinnabarina*), 16 species critically endangered, 22 species endangered, and 51 species vulnerable. Localities with the highest species richness are situated in the Šumava Mts; species diversity per a 1-ha plot reached 156 species in a primeval forest and 105 in the richest managed forest. Localities with the lowest richness are situated in the Beskydy and Králický Sněžník Mts (Table 2).

Rare boreal lichens typical for spruce forests were recorded mainly in the Šumava Mts, Hrubý Jeseník Mts and Krkonoše Mts. *Chaenotheca hygrophila*, *Micarea anterior*, *Ochrolechia mahluensis*, *Ramboldia cinnabarina* and *Xylographa soralifera* occurred exclusively in the Šumava Mts; *Anzina carneonivea*, *Biatora vacciniicola* and *Chaenotheca laevigata* in the Hrubý Jeseník Mts; *Chaenotheca gracillima*, *Hypogymnia bitteri* and *Lichenomphalia hudsoniana* in the Krkonoše Mts. New localities for rare macrolichens, such as *Alectoria sarmentosa*, *Evernia divaricata* and *Hypogymnia vittata*, recently known mostly from the Šumava Mts, have been recorded at new sites in the Krkonoše Mts and the Hrubý Jeseník Mts.

Several rare species have been exclusively found on intermingled trees of *Sorbus aucuparia*, e.g. *Bryoria bicolor*, *Caloplaca herbidella*, *Lecanora exspersa* and *Sphaerophorus globosus* in the Hrubý Jeseník Mts, and *Bacidia incompta*, *Lecanora subsaligna* and *Pycnora leucococca* in the Šumava Mts. This substrate also supported several nitrophilous species, such as *Candelariella efflorescens* agg., *Catillaria nigroclavata*, *Halecania viridescens*, *Lecania naegelii*, *Lecanora persimilis*, *Physcia adscendens*, *P. stellaris*, *P. tenella*, *Xanthoria parietina* and *X. polycarpa*.

Species composition at several sites was influenced by the presence of additional trees with a higher bark pH—*Acer pseudoplatanus* and *Fagus sylvatica*, especially the two lower Boubín's plots in the valley of a brook where the species composition of several beeches differs significantly from the other plots (see Electronic Appendix, Fig. 3). *Biatora fallax*, *B. helvola*, *Dictyocatenulata alba*, *Fellhaneropsis vezdae*, *Lopadium*

Table 2 An overview of species richness, abundance (i.e. sum of all species abundances), Red-listed species, functional diversity, Rao's quadratic entropy (RaoQ), taxonomic diversity, variation in the taxonomic distinctness (VarTD) and phylogenetic diversity for individual localities

Locality	Forest type	Lichens	Calicioid lichens and fungi	Lichens and calicioid fungi	Species abundance	Red-listed species	Critically endangered	Endangered
Bílá Opava 1	Old	98	15	100	181	33	8	6
Bílá Opava 2	Man	58	5	58	111	10		
Bílá Opava 3	Old	95	15	98	189	26	3	6
Bílá Opava 4	Man	53	6	54	105	6		
Boubín low 1	Old	**151**	18	**156**	**274**	**52**	**8**	**16**
Boubín low 2	Man	87	6	88	147	22	2	3
Boubín top 1	Old	123	**20**	129	233	39	4	11
Boubín top 2	Man	79	9	80	172	15	1	6
Eustaška 1	Old	98	18	104	175	27	4	7
Eustaška 2	Man	64	5	64	125	7		1
Jelení potok 1	Old	107	13	111	206	28	4	7
Jelení potok 2	Man	82	9	85	153	18	1	1
Kněhyně 1	Old	93	5	93	169	19	1	2
Kněhyně 2	Man	**39**	**1**	**39**	**76**	2		
Králický Sněžník 1	Old	80	8	80	138	17	1	2
Králický Sněžník 2	Man	56	5	56	112	8		
Lysá hora 1	Old	86	9	88	160	13	1	2
Lysá hora 2	Man	44	**1**	45	86	**1**		
Smrčina 1	Old	116	14	120	225	30	4	7
Smrčina 2	Man	103	7	105	197	26	1	6

Locality	Forest type	Vulnerable	Functional diversity	RaoQ	Taxonomic diversity	VarTD	Phylogenetic diversity
Bílá Opava 1	Old	19	2.053807	0.478452	63.018	328.733	7.442
Bílá Opava 2	Man	10	1.320507	0.467224	60.055	325.609	6.189

Table 2 (continued)

Locality	Forest type	Vulnerable	Functional diversity	RaoQ	Taxonomic diversity	VarTD	Phylo-genetic diversity
Bílá Opava 3	Old	17	1.958948	0.488579	64.244	360.69	7.533
Bílá Opava 4	Man	6	1.811526	0.47781	62.675	342.197	6.448
Boubín low 1	Old	**28**	**2.890983**	**0.523411**	**65.351**	339.431	7.011
Boubín low 2	Man	17	2.305677	0.515483	62.688	340.418	6.886
Boubín top 1	Old	24	2.738433	0.49867	64.487	355.244	**8.600**
Boubín top 2	Man	8	1.930855	0.468983	62.542	361.002	7.985
Eustaška 1	Old	16	2.113014	0.498077	64.421	371.208	6.962
Eustaška 2	Man	6	1.55654	0.460549	61.432	**371.332**	6.887
Jelení potok 1	Old	17	2.172468	0.486718	61.592	365.618	7.149
Jelení potok 2	Man	16	1.817299	0.477701	60.395	364.33	7.793
Kněhyně 1	Old	16	1.772511	0.486208	61.568	281.391	7.819
Kněhyně 2	Man	2	1.326445	0.476625	**58.017**	297.435	6.222
Králický Sněžník 1	Old	14	1.867121	0.472588	60.125	335.223	6.401
Králický Sněžník 2	Man	8	1.659932	**0.459785**	59.523	331.625	5.147
Lysá hora 1	Old	10	2.05772	0.489059	62.131	320.391	6.728
Lysá hora 2	Man	**1**	**1.220194**	0.464497	59.518	298.589	**4.873**
Smrčina 1	Old	19	2.49916	0.486522	61.944	299.951	7.142
Smrčina 2	Man	19	2.360896	0.490426	59.645	**249.226**	6.534

Maximum and minimum values in bold

disciforme, *Opegrapha niveoatra*, *O. rufescens*, *O. varia*, *Pyrenula nitida*, *Rinodina efflorescens* and *Thelotrema lepadinum* are examples of species recorded exclusively on these plots, and mostly on beech.

Indicator species

Indication analysis did not find any species that specifically prefer managed forests, since they are mainly inhabited by widespread and non-specialized lichens. Based on p-values of both specificity and fidelity (Table 3), 11 indicator species were recognized for old-growth forests. *Xylographa vitiligo*, *Chaenotheca sphaerocephala* and *Parmelia saxatilis* agg. were selected as the most suitable indicators of old-growth spruce stands.

The genera *Arthonia*, *Calicium*, *Chaenothecopsis*, *Mycoblastus*, *Ochrolechia*, *Pycnora* and *Xylographa* showed an affinity to old-growth forests, while the genus *Thelocarpon* to managed forests (Fig. 4). However, statistically significant p-values (<0.05) in the indication analysis were only observed for the genera *Parmelia*, *Calicium* and *Xylographa* (Electronic Appendix Tables 3, 4). A distinctly higher diversity of calicioid lichens and fungi (*Calicium*, *Chaenotheca*, *Chaenothecopsis*, *Cyphelium*, *Microcalicium*, *Mycocalicium*) was observed in old-growth forest sites (Fig. 2b).

Table 3 Indication analysis for old-growth forests

Species	Abundance	Specifity	Fidelity	Both	p value
Xylographa vitiligo	10	**0.9**	0.9	0.9	0.0012**
Chaenotheca sphaerocephala	9	**0.8889**	0.8	0.843	0.0046**
Parmelia saxatilis agg.	14	0.7143	1	0.845	0.0098**
Chaenotheca trichialis	14	0.7143	1	0.845	0.0105*
Lecanora subintricata	8	**0.875**	0.7	0.783	0.0178*
Mycoblastus sanguinarius	10	**0.8**	0.8	0.8	0.0226*
Mycoblastus affinis	8	**0.875**	0.7	0.783	0.0229*
Calicium glaucellum	15	0.6667	1	0.816	0.032*
Chaenothecopsis pusilla	5	**1**	0.5	0.707	0.0337*
Lepraria rigidula	15	0.6667	1	0.816	0.0341*
Calicium viride	5	**1**	0.5	0.707	0.0349*
Ochrolechia alboflavescens	7	**0.8571**	0.6	0.717	0.0524
Chaenothecopsis viridireagens	7	**0.8571**	0.6	0.717	0.0534
Fellhanera subtilis	13	0.6923	0.9	0.789	0.055
Ochrolechia microstictoides	13	0.6923	0.9	0.789	0.0555
Lecidea leprarioides	13	0.6923	0.9	0.789	0.0572
Bryoria capillaris/nadvornikiana	7	**0.8571**	0.6	0.717	0.0597
Micarea globulosella	7	**0.8571**	0.6	0.717	0.0604
Chaenotheca brunneola	11	0.7273	0.8	0.763	0.0688

Only 20 species with the highest p-values are displayed. Abundance represents a number of occurrences at studied plots. Numbers in bold indicate specifity >0.80

p-values: $** < 0.01$, $* < 0.05$

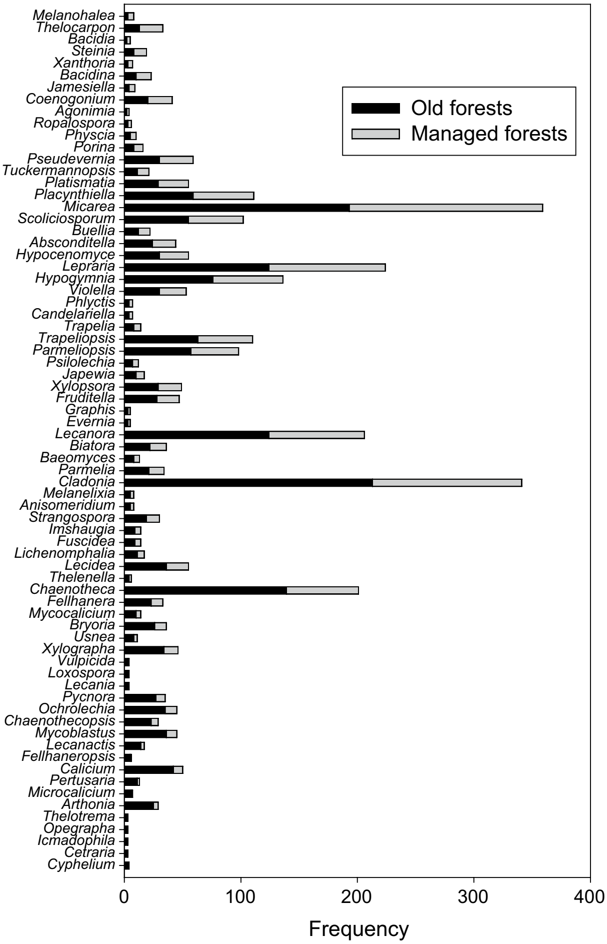


Fig. 4 Numbers of records for lichen genera in old-growth and managed forests according to their proportion in old-growth forests. Genera with at least three records are displayed

Taxonomic and phylogenetic diversity

Taxonomic diversity generally increases with the species richness ($p < 0.001$), but a few localities do not follow this trend (see Electronic Appendix, Fig. 2). The results are influenced by the presence/absence of species on long taxonomic branches; for example, the basidiolichens (*Lichenomphalia*, *Multiclavula*) are completely absent from both Smrčina plots with a relatively low index of taxonomic diversity (Table 2).

Due to the character of our data (i.e. presence/absence data, no abundances included in taxonomic and phylogenetic analyses), the same values were obtained for taxonomic diversity as well as for the taxonomic distinctness and average taxonomic distinctness. The variation in taxonomic distinctness does not correspond to the species richness ($p = 0.63$), but indexes for individual pairs of localities (old-growth *vs* managed) are close to each other.

Values for taxonomic and phylogenetic diversities correlate to each other ($p = 0.005$). Phylogenetic diversity increases with the species richness ($p = 0.004$), but several localities do not comply (Electronic appendix, Fig. 2). The influence of long phylogenetic branches on the tree (see Electronic Appendix, Fig. 1), represented e.g. by basidiolichens and the genus *Absconditella*, seems to be evident, but not very strong.

Functional diversity and traits

Functional diversity and Rao's quadratic entropy are distinctly higher in old-growth forests (Fig. 2e, f) and both correlate with the species richness ($p < 0.0001$). Values for individual localities are arranged in a similar order in both the Rao's quadratic entropy and functional diversity (Table 2).

Ascospores are distinctly bigger in old-growth forests (mean standardized volume of 127 vs. 73; $p = 0.006$). Stalked apothecia are more frequent in old-growth forests (12.5% vs. 8%; $p = 0.002$) as well as pigmented ascospores (7% vs. 3.5%; $p = 0.01$). Vegetative reproduction slightly predominates in managed forests (62% of species in managed vs. 58% in old-growth forests; $p = 0.048$). Seven other tested traits, such as the trentepohlioid photobiont, fruit body area and ascospores shape (see "Materials and methods"), do not differ significantly between old-growth and managed forests (Electronic Appendix, Table 5).

Main drivers of species richness and composition

The PCA diagram (Fig. 5) demonstrates similarities in the species composition among forest types and geographical position. Species-rich managed stands in the Šumava Mts are close to most of old-growth forest plots, but species-poor old-growth forests in the Beskydy and Králický Sněžník Mts are closer to managed forests. Model with the lowest AIC value (Table 4) contained the forest type (managed *vs* old-growth), tree species composition, amount of dead wood, maximal tree diameter and recent sulphur deposition. The effect of other types of pollution was significant in models without precipitation that strongly positively correlates with N and S depositions (see Electronic Appendix, Table 1).

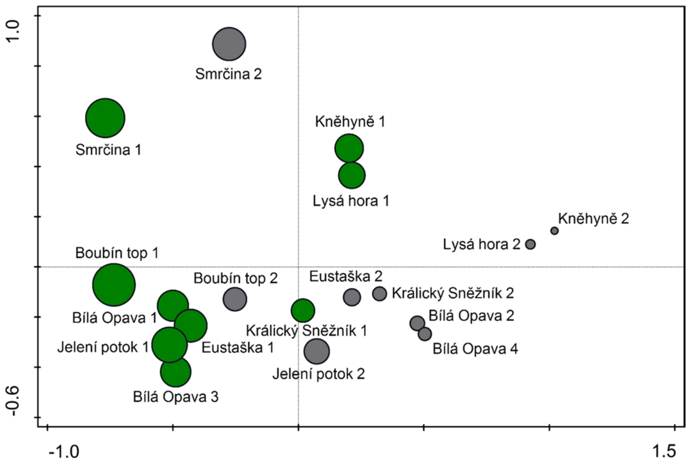


Fig. 5 Similarities in lichen composition among plots. PCA diagram showing 18 plots, 9 in managed (grey) and 9 in old-growth (green) forest stands. The first two axes are shown, explaining 26.8% and 12.1% of the variability. The size of circles corresponds to species richness. (Color figure online)

Table 4 Generalized least square models predicting species richness, demonstrating differences in the AIC (ΔAIC) compared with the intial model

Model	Explanation variables	AIC	ΔAIC
1.	**FT** + TS + DW + **MD** + **AP**	137.72	
2.	**FT** + TS + **MD** + **AP**		+ 23.54
3.	**FT** + DW + **MD** + **AP**		+ 8.98
4.	**FT** + MD + **AP**		+ 31.70
1.1.	**FT** + TS + DW + **MD** + **AP** + Npast		− 2.10
1.2.	**FT** + TS + DW + **MD** + **AP** + Nrecent		− 2.99
1.3.	**FT** + TS + DW + **MD** + **AP** + Spast		− 1.37
1.4.	**FT** + TS + DW + **MD** + **AP** + Srecent		− 3.99
1.5.	**FT** + TS + DW + **MD** + **Npast**		− 5.56
1.6.	**FT** + TS + DW + **MD** + **Nrecent**		− 6.38
1.7.	**FT** + TS + DW + **MD** + **Spast**		− 5.82
1.8.	**FT** + TS + DW + **MD** + **Srecent**		− 8.71

Variables with significant effect ($p < 0.05$) in bold

Variables abbreviated as follows: forest type (FT), tree species (TS), deadwood (DW), maximum tree diameter (MD), annual precipitation (AP), sulphur deposition from 1950 to 1999 (Spast), sulphur deposition from 2000 to 2010 (Srecent), nitrogen deposition from 1950 to 1999 (Npast) and nitrogen deposition from 2000 to 2010 (Nrecent)

Substrate preferences

Substrate diversity in montane spruce forests is generally low, consisting of a few tree species, decaying wood (usually from spruce only) and several other specialized substrates, such as roots of wind-blown trees, polypores and *Vaccinium* stems. Spruce is the predominating tree; broad-leaved trees are rare, usually present as single trees, or even completely absent. The highest number of species (171) occurred on dead wood that is usually very scarce in managed forests. Spruce bark and needles harboured 159 species, followed by *Sorbus aucuparia* (82) and *Fagus sylvatica* (69); see Table 5. Substrate specialists, i.e. species recorded exclusively on a single type of substrate, were associated mostly with dead wood (45 species), followed by *Picea abies* (23), *Sorbus aucuparia* (19) and *Fagus sylvatica* (10). Lichens exclusively recorded on dead wood included numerous *Micarea* and *Xylographa* species, and on spruce various *Chaenotheca* species.

Discussion

Species richness

The lichen diversity on 1-ha plots in montane spruce forests in the Czech Republic seems to be higher than in boreal forests of southern Finland, where Kuusinen and Siitonen (1998) recorded 76–94 species on 1-ha old-growth forest plots. This number is comparable to species-rich managed stands and species poor old-growth stands influenced by acid rain in the Czech Republic. However, Kuusinen and Siitonen (1998) used a different method

Table 5 Substrate preferences

Substrate	No.	Specialists	Specialists examples
Dead wood	171	45	**Commonest** *Micarea denigrata*, *M. misella*, *Steinia geophana*, *Thelocarpon lichenicola*, *Xylographa parallela*; **Rare** *Anzina carneonivea*, *Biatora ligni-mollis*, *Chaenotheca hygrophila*, *Micarea anterior*, *M. contexta*, *M. deminuta*, *Xylographa soralifera*, *X. trunciseda*
Picea abies	159	23	**Commonest** *Chaenotheca stemonea*, *Hypogymnia vittata*, *Scoliciosporum curvatum*; **Rare** *Arthonia incarnata*, *Calicium lenticulare*, *Chaenotheca gracillima*, *C. laevigata*, *Evernia divaricata*, *Fellhaneropsis myrtillicola*, *Hypogymnia bitteri*, *Ramboldia cinnabarina*
Sorbus aucuparia	82	19	**Rare** *Bryoria bicolor*, *Caloplaca herbidella*, *Lecanora exspersa*, *Pycnora leucococca*, *Sphaerophorus globosus*, *Vezdaea stipitata*
Fagus sylvatica	69	10	*Biatora fallax*, *Dictyocatenulata alba*, *Opegrapha varia*, *Pyrenula nitida*, *Rinodina efflorescens*
Acer pseudoplatanus	35	2	*Biatora globulosa*, *Rinodina degeliana*
Roots	20	3	*Cryptodiscus gloeocapsa*, *Micarea lithinella*, *Microcalicium arenarium*
Sambucus nigra	19	4	*Arthonia ruana*, *Lecania cyrtella*, *Macentina abscondita*, *Ramonia interjecta*

Total numbers of species, numbers of species exclusively recorded on a single substrate type, and examples of the commonest and rare, usually Red-listed, species of the field research (lower sampling effort, plot selection with different criteria) which may be responsible for the lower numbers. Diversity on plots in the Šumava Mts is similar to plots of the same area in a flood-plain forest in south Moravia with 112 species (Vondrák et al. 2016), the Austrian Neuwald beech-silver fir forest with 126 species (Hafellner and Komposch 2007) and a lowland scree and oak forest in the Czech Republic with 153 species (Malíček et al. 2017a). Species richness in the Carpathian primeval beech forest Uholka (181–228 species; Vondrák et al. 2018) and Caucasian virgin forests (233–358 species; Vondrák et al. 2019) achieved considerably higher numbers.

According to generalized least square models, the forest type, maximal tree diameter, annual precipitation, and sulphur and nitrogen deposition are the main factors influencing species richness. These results correspond well with our predictions and previous ecological studies (e.g. Holien 1997; Hofmeister et al. 2015; Bässler et al. 2016). The forest type, which is usually connected with tree diameter and age, is one of the most important factors influencing the lichen diversity, as well as annual precipitations that are related to elevation at least at a regional scale (see below). In Central Europe, air pollution in terms of sulphur and nitrogen deposition, is one of the main drivers of species richness and composition in epiphytic lichen biota (e.g. Svoboda et al. 2010; Guttová et al. 2017; Łubek et al. 2018).

Comparison of old-growth and managed forests

Forest management plays a very important role for bryophytes, fungi and lichens. Compared with old-growth forests, managed forests generally have lower species richness caused by: (a) low structural heterogeneity (Nascimbene et al. 2010; Strengbom et al. 2011), (b) lower light intensity of even-aged monocultures with dense canopies, and (c) short rotation times and low availability of coarse woody debris (Strengbom et al. 2011). Logging and removal of timber obviously decreases the cover and species richness in all epixylic species groups (Rabinowitsch-Jokinen et al. 2012). Diversity also decreases with forest fragmentation (Hilmo and Holien 2002).

Concerning the species richness, our results are not exceptional in context of other studies focused on a comparison of managed, unmanaged and old-growth forest with *Picea abies*. The studies emphasize higher species richness of lichens in unmanaged stands that is conditioned mainly by forest age (Holien 1996; Hilmo et al. 2009; Lie et al. 2009; Marmor et al. 2011; Dittrich et al. 2013; Zemanová et al. 2017), light availability (Gauslaa et al. 2008; Marmor et al. 2012) and dispersal limitations of some old-growth forest species (Sillett et al. 2000; Hilmo and Såstad 2001). Species richness is also positively correlated with elevation (Holien 1996; Nascimbene and Marini 2015; Bässler et al. 2016), admixture of other tree species (Kuusinen and Siitonen 1998) and microclimatic factors like a higher humidity in swamp forests (Kuusinen 1996). A stand age of 200 years seems to be the lower limit for species-rich communities, for species with limited dispersal abilities and niche specialists (Dittrich et al. 2013; Zemanová et al. 2017). Intensity of forest management has a strong negative impact on the number of Red-listed lichens and substrate specialists (Boch et al. 2013; Ardelean et al. 2015).

Four managed plots in the Šumava and Krkonoše Mts are species rich (80–105 species). These stands are characterized by their position in humid valleys, admixture of other trees such as *Fagus sylvatica* and *Sorbus aucuparia* and/or a presence of typical old-growth forest structures such as snags and logs. Paired old-growth plots were situated in very similar conditions with comparable substrates.

Comparison of taxonomic, phylogenetic and functional diversity demonstrated a distinct difference between managed and old-growth stands. In contrast to our results, functional diversity in terms of Rao's quadratic entropy did not increase with the forest stand age in a Brazilian tropical rain forest and was highest in intermediate successional stages (Koch et al. 2013). Reference studies dealing with these diversity measures and aimed at managed *vs* old-growth forests are lacking.

Indicators species

A selection of suitable bioindicators and their use on a spatial and time scale is accompanied by some restrictions. Firstly, although lichens have large distributional ranges, bioindicators are usually used at a regional level (e.g. Sætersdal et al. 2005; Whittet and Ellis 2013). Secondly, for forest types, an ideal indicator is confined to a single selected habitat (Liira et al. 2007), being present at all sites and completely absent from other habitats. Thirdly, a suitable indicator should be a well-recognizable and conspicuous species, optimally, in the case of lichenized fungi, a macrolichen. However, very few species fulfill all these criteria in Central European forests.

In old-growth montane spruce forests in the Czech Republic, potentially suitable indicators, such as conspicuous foliose and fruticose lichens restricted to old forest stands, are either absent or restricted to one or a few sites only. This is a case of the traditional indicators of well-preserved coniferous woodlands in Europe and Canada, such as *Alectoria sarmentosa*, *Sphaerophorus globosus* and *Usnea longissima* (Esseen et al. 1996; Nilsson et al. 2001; Esseen 2006; Cameron and Bondrup-Nielsen 2012) and of other macrolichens scarcely recorded in our old-growth stands, e.g. *Bryoria capillaris/nadvornikiana*, *Cladonia norvegica* and *Hypogymnia vittata* (Fig. 6).

In contrast to most published studies, Tibell (1992) created a list of 20 exclusively crustose lichens considered as indicators of boreal coniferous forests with a long continuity in Sweden. Similarly Marmor et al. (2011) supposed *Arthonia leucopellaea*, *Chrysothrix candelaris*, *C. flavovirens* and *Lecanactis abietina* as suitable indicators of old coniferous forests with a long continuity in Estonia.

Our results revealed following microlichens as indicators with the highest specifity and fidelity values to old-growth spruce stands: *Xylographa vitiligo*, *Chaenotheca sphaerocephala*, *Parmelia saxatilis* agg., *Chaenotheca trichialis* and *Lecanora subintricata*. This emphasizes regional differences for suitable bioindicators since all of them are absent from studies focused on this topic in other regions (e.g. Marmor et al. 2011; Tibell 1992). *Mycoblastus sanguinarius*, *M. affinis*, *Micarea globulosella* and *Bryoria* spp. are other taxa with a tendency to occur mostly in old-growth stands and considered as indicators of old-growth spruce forests (Tibell 1992; Bradtka et al. 2010; Marmor et al. 2011; Zemanová et al. 2017). *Lecanactis abietina*, a lichen with a distinct preference for old-growth spruce stands (Bradtka et al. 2010; Marmor et al. 2011; Zemanová et al. 2017), also occurred in our two managed stands, but its indication value was not so high as expected. However, all managed plots were close or even adjacent to old-growth stands that favour a dispersal of old-growth forest species to suitable microhabitats in selected plots of managed forests (Williams and Ellis 2018).

Xylographa vitiligo is an obligatory lignicolous species (Spribille et al. 2009) and prefers large coarse woody debris (Svensson et al. 2013) in well-lit places that are sometimes present also in gaps in managed forests. In contrast, *Chaenotheca sphaerocephala* usually occurs in deep shady hollows at bases of large *Picea abies* trees. *Parmelia saxatilis* agg.

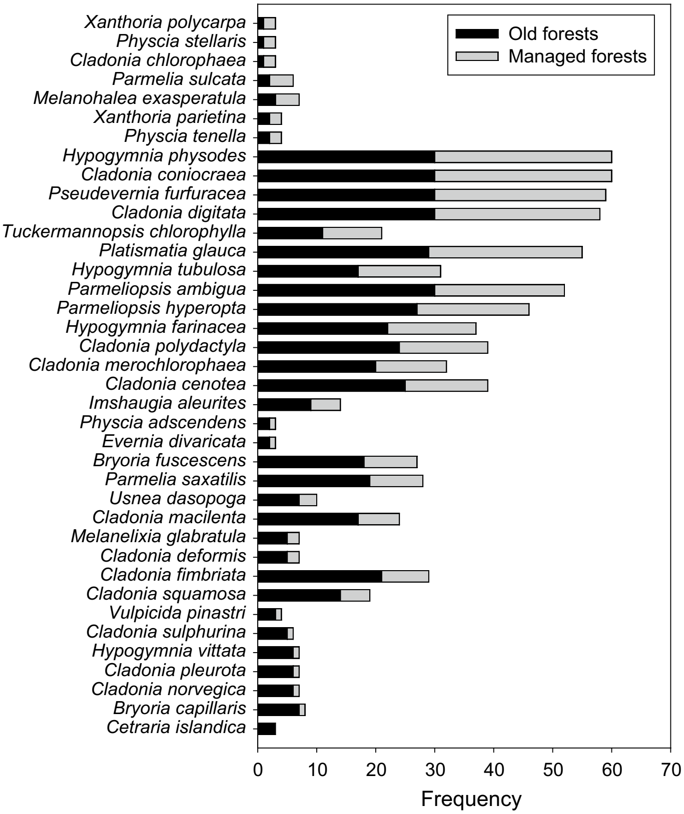


Fig. 6 Frequencies of macrolichen species (based on abundance data, see Table 6 in Electronic Appendix) in old-growth and managed forests according to their proportion in old-growth forests. Species with at least three records are displayed

occurs mostly on broad-leaved trees and in case of coniferous forests mostly in well-lit places such as tree crowns; therefore, our results can be distorted by overlooking of this species in managed forests, where upper parts of trunks and branches are usually inaccessible. *Lecanora subintricata* prefers sun-exposed snags that are usually missing in managed forests; however, it also occurs on worked timber, such as poles and fences. *Chaenotheca trichialis* is also not restricted to coniferous forests, being widely distributed from lowland to montane forests across Central Europe; it was recorded in all studied old-growth spruce stands, usually in high frequencies, and as a rare species in four of 10 managed stands. Both *Mycoblastus* species occur on tree trunks of various sizes, but with a distinct preference for old forests.

After an assessment of ecological preferences and distribution of species with the highest indication values, *Xylographa vitiligo*, *Chaenotheca sphaerocephala*, *Mycoblastus sanguinarius* and *M. affinis* were judged to be the best indicators of old-growth spruce stands in the Czech Republic, where all these more or less well recognizable species occur predominantly in old-growth spruce forests, but are absent or rare in other forest types.

Dictinct affinities of calicioid lichens and fungi to old-growth forests were demonstrated at the species (Table 3), genus (Fig. 4) and diversity level (Fig. 2b). Seven calicioid lichens

(*Calicium* and *Chaenotheca*) and fungi (*Chaenothecopsis*) were placed among twenty species with highest specificity and fidelity values. Earlier studies in Fennoscandia and North America demonstrated that these well known indicators are confined to old stands of boreal coniferous forests with a long continuity (Halonen et al. 1991; Hyvärinen et al. 1992; Tibell 1992; Selva 1994; Holien 1997; Kuusinen and Siitonen 1998).

Functional diversity and traits

Functional diversity is regarded as a key indicator of ecosystem functions such as productivity, resilience and nutrient cycling (e.g. Petchey et al. 2004). Community-mean traits have been repeatedly linked to environmental conditions over large spatial scales, while local factors (e.g. abiotic and biotic heterogeneity) can predict functional trait diversity (Vanneste et al. 2019). Functional diversity could be used as an alternative or supplementary approach to species diversity and composition analysis. Its application also appears to be useful in cases when the species identification is incomplete (Koch et al. 2013).

Functional diversity and traits in lichens have been rarely employed for comparing forest types (Koch et al. 2013; Li et al. 2013; Bässler et al. 2016; Prieto et al. 2017; Benítez et al. 2018; Lelli et al. 2019). For our data, an analysis of the Rao's quadratic entropy (Botta-Dukát 2005) seems to be more appropriate. In contrast to the functional diversity index proposed by Petchey and Gaston (2002), this method accounts for species abundances and the final result is not so strongly influenced by species richness. Nevertheless, plots with high species richness (e.g. two low-altitudinal Boubín plots) showed high values for both functional diversity indexes. This corresponds well to a very heterogeneous species composition, including various functional traits and taxonomic groups. The species composition seems to be connected with microhabitat diversification, which was generally high in old-growth forests as well as species-rich managed forests. Plots rich in various niches for lichens probably support species with various traits, but our sampling is too limited for a verification of this hypothesis. Several other plots reached lower functional diversity (e.g. Kněhyně 1) or higher RaoQ index (e.g. Kněhyně 2, Lysá hora 1) than expected according to their species richness (see Table 2). These demonstrate deviations in the local trait variability within lichen communities.

It is still poorly known which traits could indicate, for example, the forest naturalness and continuity. According to our results, old-growth stands have more species with stalked apothecia and pigmented ascospores. Both traits are characteristic for calicioid genera, often confined to old-growth stands (see above). Pigmented ascospores are also typical of nitrophilous species of the Physciaceae that rarely occur in montane spruce forests where they are usually restricted to twigs of broad-leaved trees.

More interesting results are connected with the proportion of vegetative reproduction and size of ascospores between the forest types. According to our results, vegetative strategies, i.e. the production of soredia, isidia and similar propagules, are more frequent in managed forests. This fact could be connected with the more effective colonization by vegetative diaspores (with both symbiotic partners involved) than via ascospores only (Bowler and Rundel 1975; Bailey 1976; Jahns 1988; Werth et al. 2006). In view of population dynamics, asexual species may be better adapted to local conditions and have a wider ecological amplitude (Buschbom and Mueller 2006; Ertz et al. 2018), which enables their survival in managed forests with a uniform habitat structure; for example, vegetatively dispersed generalists, such as various *Cladonia* and *Lepraria* species or many Parmeliaceae, are abundant in both forests types, but proportionally predominate in managed forests with distinctly lower species richness.

Higher proportions of asexual species in secondary rather than in primary forests in China were also demonstrated by Li et al. (2013). However, other sources note the opposite trend, with, for example, sexually reproducing lichens predominating on young substrates in fragmented and intensively managed landscapes (Stofer et al. 2006; Ellis and Coppins 2007; Lundström et al. 2013), and species reproducing by vegetative diaspores seem to be more common in old-growth forests in Europe (Stofer et al. 2006). Dispersion by vegetative propagules may be highly efficient at a local scale for epiphytic cryptogams (Hedenås et al. 2003), but it is limited in the long-distance dispersal due to the large propagule size (Hedenås and Ericson 2000; Löbel et al. 2006; Johansson et al. 2012). Modes of reproduction can be affected by various factors, such as the community and habitat structure, disturbance frequency, ratio of vegetative versus generative reproduction in individual species (including conidia), intensity of diaspore production and sizes of diaspores. Generally, the difference between sexual and asexual strategies may represent an ecological trade-off between long-distance colonization and successful local establishment (Ellis 2012).

Our data indicated a distinctly larger volume of ascospores in old-growth forests. Similar trend is also apparent in Stofer et al. (2006, Fig. 1d) who compared an ascospore length between managed and old-growth forests. Also Johansson et al. (2007) pointed out that lichens most frequently occurring on old ash trees in Sweden had larger spores comparing to young ones. Larger ascospores may cause a higher rate of dispersal limitation; this is also in agreement with metapopulation dynamics theory (Hanski 1999), exemplified by Johansson et al. (2012) who demonstrated a higher colonization rate for lichen generalists with smaller propagules than for specialists with larger propagules on old oak trees.

Differences between proportions of species with trentepohlioid photobiont, which decrease with higher management or disturbances intensity (Stofer et al. 2006; Benítez et al. 2018), were not observed in our studies; they rarely occur in montane spruce forests and their more or less random occurences do not enable objective comparisons.

Taxonomic and phylogenetic diversity

In current nature conservation, species richness and presence of endangered or endemic species are not the only priorities (Brooks et al. 2006). Implementation of taxonomic and phylogenetic diversities may help to protect not only species rich sites, but also genetically rich or unique populations and areas (e.g. Faith 1992). Compared to species diversity, it may be better to predict general biodiversity patterns in reflecting historical relationships among areas (Faith 1992). Additionally, indexes of taxonomic and phylogenetic diversity do not require comprehensive field surveys (see Harper and Hawksworth 1994) and can provide a reasonable biodiversity estimation.

Our results demonstrate significant correlations between lichen species richness and taxonomic as well as phylogenetic diversity: the number of taxonomically and genetically distant species increase in species-rich sites, in this case old-growth spruce forests. Thus, lichens with a sparse occurrence at plots are frequently not related to ubiquitous taxa. It is concluded that richness may be a representative measure for conservation purposes for lichen communities at a regional/national scale in Central European forests. On the other hand, some deviations from this trend have been observed in our survey, caused at least in some cases by the presence of species groups from distant taxonomic lineages or placed on long phylogenetic branches, such as basidiolichens and *Absconditella* species. For example, both localities with the absence of basidiolichens and *Absconditella* species (Králický Sněžník 2, Smrčina 2) reached a low phylogenetic diversity index (Table 2) despite of the high species richness recorded in Smrčina 2. The locality with the highest phylogenetic diversity, Boubín top 1, was rich in phylogenetically distant taxa.

Furthermore, the results are certainly influenced by a high proportion of species from large families, the Parmeliaceae and Cladoniaceae that include many common forest species. Their high proportion in plots could considerably decrease the total phylogenetic diversity. Unfortunately, our results could be influenced by incomplete molecular data (available only for 76% of species), the single marker (nrITS) used in the phylogenetic analysis, and a limited number of examined plots (n = 20). The variation in taxonomic distinctness demonstrated an interesting trend, where the values for managed and old-growth forests in studied pairs are very similar, probably reflecting similar species composition at the small spatial scale. Species pool in a managed forest, comprising mostly common and widespread lichens, is usually contained in the neighbouring old-growth type. This hypothesis is supported by very different values for the locality Smrčina, where both plots differ significantly in their species composition.

National hot-spots and refugia for rare lichens

Sites with the highest species richness are situated in the Šumava Mts, a region traditionally regarded as the last refuge for rare epiphytic lichens in the Czech Republic (Liška et al. 1996, 1998, 2006). The impact of acid rain there was significantly lower than in other studied sites and the forest area, continuity and the number of old-growth and primeval forest patches unequivocally exceed all other Czech mountains (NATURALFORESTS.CZ 2018).

Despite high acidic deposition, the species richness and proportion of Red-listed taxa are also rather high in the Hrubý Jeseník Mts (Table 2). Our plots were situated in a large complex of natural montane spruce forests, covering more than 10 km^2 on Mt Praděd (NATURALFORESTS.CZ); currently the largest area of such forest type with living mature trees in the Czech Republic. Large forest patches provide a distinctly higher number of microhabitats and substrates serving as micro-refugia for sensitive and specialized species, and enable their local surviving despite of a strong reduction of original populations by acidification in the past. Such species can hardly survive in small old-growth forest fragments, e.g. in the Beskydy and Králický Sněžník Mts, simply due to their smaller overall frequencies and abundances.

Substrate preferences

Our work shows that dead wood is the substrate richest in lichens (171 species) and generally support the following conclusions. Large-diameter snags and logs in an advanced stage of decay, that are characteristic for old-growth forests, harbour more species than smaller fragments in the early stages of decay (Söderström 1988; Dittrich et al. 2014; Svensson et al. 2014, 2016; Hofmeister et al. 2015; Staniaszek-Kik et al. 2019). Coarse woody debris also supports Red-listed species (Kruys et al. 1999), and the presence of older snags promotes species diversity of calicioid lichens (Holien 1996). In the managed forest landscape, stumps may provide important habitats for rare species (Caruso et al. 2008; Svensson et al. 2016).

Total species richness on individual tree species is connected with their proportions. *Picea abies*, as the most abundant tree, hosted the highest number of lichens (159 species), despite the very low pH of its bark (e.g. Barkman 1958), which decreased further by acid rain. *Sorbus aucuparia*, the commonest broad-leaved tree in montane spruce forests but usually rare in plots (only a few individuals present) or even absent, supported only 82 lichen species. The occurrence of *Acer pseudoplatanus* and *Fagus sylvatica* was exceptional, but added to the number of lichen species recorded in the plots.

Conclusions

Old-growth spruce montane forests belong to strongly endangered habitats in Central Europe due to their limited distribution, outbreaks of bark beetle, and global climate change. In the future, a further reduction of their area and biodiversity loss is expected. The most important sites of living tree layer and their lichen biota were studied subjectively using selected hot-spots. This controversial method seems to be very suitable for nature conservation purposes since grid and random sampling often omit hot-spots that mostly have a very limited distribution in forests. However, such places often harbour a major proportion of the total lichen diversity at a locality, as well as many rare and specialized species. Our study revealed significant differences between old-growth and managed spruce forests. Apart from species richness and number of Red-listed species, analyses of functional, taxonomic and phylogenetic diversities were employed. Such a complex analysis has never been used before for a comparison of lichen biota in various forest types. These diversity indexes correspond with species richness, which is an appropriate measure of the site importance in sense of nature protection.

The most valuable plots are situated in the Šumava Mts, an important refugium for rare epiphytic lichens in Central Europe. Although the species richness at other localities is lower, many rare and old-growth forest species also occur in the Krkonoše and Hrubý Jeseník Mts. A few managed forests also have great potential for biological conservation, especially those with an admixture of other tree species, forest gaps and large amounts of dead wood. Such stands should be excluded from management programmes and maintained for decreasing populations of threatened forest organisms. Beside of forest parameters and structure, selected lichen bioindicators will be invaluable in diagnosing important sites. However, all of the supposed “old-growth forests species” belong to microlichens and therefore could not be employed in conservation practices by non-lichenologists. Similar problems arise with functional traits, such as the main differences, for example, of microscopically observed ascospores and ascomata types of microlichens. Despite of all these complications, lichens are excellent bioindicators, being able to indicate even minor differences in forest types.

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