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ORIGINAL PAPER

Topographic and forest-stand variables determining epiphytic lichen diversity in the primeval beech forest in the Ukrainian Carpathians

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Abstract The Uholka-Shyrokyi Luh area of the Carpathian Biosphere Reserve is considered the largest and the most valuable primeval beech forest in Europe for biodiversity conservation. To study the impact of different topographic and forest-stand variables on epiphytic lichen diversity a total of 294 systematically distributed sampling plots were surveyed and 198 epiphytic lichen species recorded in this forest landscape, which has an uneven-aged structure. The obtained data were analysed using a non-metric multidimensional ordination and a generalized linear model. The epiphytic lichen species density at the plot level was mainly influenced by altitude and forest-stand variables. These variables are related to both the light availability i.e. canopy closure, and the habitat diversity, i.e. the developmental stage of the forest stands and the mean stem diameter. We found that lichen species density on plots with a relatively open canopy was significantly higher than on plots with a fairly loose or closed canopy structure. The late developmental stage of forest stands, which is characterized by a large number of old trees with rough and creviced bark, had a strong positive effect on lichen species density. In the Uholka-Shyrokyi Luh primeval forest the mean stem diameter of beech trees significantly correlated with lichen species density per plot. Similar trends in the species diversity of nationally red-listed lichens were revealed. Epiphytic lichens with a high conservation value nationally and

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internationally were found to be rather abundant in the Uholka-Shyrokyi Luh area, which shows its international importance for the conservation of forest-bound lichens.

Keywords Lichenized fungi · Primeval forest · *Fagus sylvatica* · Topographic and forest-stand factors · Carpathian Biosphere Reserve · Ukraine

Introduction

European beech forests have been the subject of continuing ecological, paleoecological and genetic research in recent decades due to their wide distribution and high economic importance (Magri et al. 2006). The remnant primeval beech forests are particularly interesting objects for forest research as they provide excellent and necessary conditions for studying and understanding ecosystem processes in forests where no human intervention has occurred for a long time. The Carpathians are a kind of *locus classicus* for virgin beech forest studies in Europe (Commarmot et al. 2013).

The largest primeval beech forest in Europe is the Uholka-Shyrokyi Luh (over 10,000 ha) in the Ukrainian Carpathians which was added to UNESCO'S World Heritage list in 2007 (Commarmot et al. 2013). Due to the absence of navigable rivers, steep slopes and their remoteness, the beech forests in the area have remained unaffected by logging, but they were used for other human activities, especially hunting and gathering (Brändli and Dowhanytsch 2003). These unique forests have been preserved by assigning them a conservation status. The first forest reserve was founded in the Shyrokyi Luh area («Lužanský prales») in 1936 by the Czechoslovakian Republic. In 1958 the government of the Ukrainian Soviet Republic created the Uholka forest reserve. In 1970 and 1980s both areas were included in the newly founded Carpathian Reserve (Hamor and Berkela 2011).

The primeval forest of Uholka-Shyrokyi Luh has an outstanding importance for biodiversity conservation and is now strictly protected. The spatio-temporal forest connectivity on the landscape scale is intact and includes a small mosaic of forest developmental stages with patches ranging from young to old. It is characterised by collapsing stands, a small-scale uneven-aged and multilayered stand structure with a wide range of tree diameter (up to 150 cm DBH) and a large amount of deadwood and veteran trees (up to 500 years old) (Trotsiuk et al. 2012; Commarmot et al. 2013; Hobi 2013).

Old-growth beech forests harbour a specific lichen biota which includes many red-listed species and indicators of woodland key habitats (Sillet et al. 2000; Coppins and Coppins 2002; Printzen et al. 2002; Kondratyuk and Coppins 2000). Since such beech forests have a high conservation status in Europe (Brändli and Dowhanytsch 2003; Fritz et al. 2008b), lichen diversity and its determining environmental factors have been investigated intensively (Pirintsos et al. 1995; Aude and Poulsen 2000; Nascimbene et al. 2007; Fritz et al. 2008b; Fritz 2009; Moning and Müller 2009 etc.). Researches on lichen biota in the primeval beech forests of the Ukrainian Carpathians have, however, hitherto been limited to floristic studies (Navrotska 1984; Kondratyuk and Coppins 2000; Kondratyuk et al. 2003; Vondrák et al. 2010; Dymytrova et al. 2013 etc.).

Thus, the aim of our research was to evaluate the relative influences of environmental variables on species richness, density and composition of epiphytic lichens in the primeval beech forest of the Ukrainian Carpathians. Specifically, the following research questions were addressed: (1) How do topographic and forest-stand variables affect lichen species density at the plot level in the primeval beech forest? (2) What are the most important factors determining the distribution of red-listed lichens in the study area?

Materials and methods

Study area

The Uholsko-Shyrokoluzhanskyi massif is situated in the south-western part of Ukraine (48°18′22″N, 23°41′46″E) and belongs to the Eastern Carpathian Mountains (Fig. 1). It is located on the southern and eastern slopes of the Menchul Mountain (1,501 m) and on the southern slopes of Krasna ridge (400–1,400 m). The almost pure beech forest includes two contiguous areas: Uholka and Shyrokyi Luh, which are protected within the Carpathian Biosphere Reserve. The massif is located between 400 and 1,400 m a.s.l. and consists mainly of flysch layers with Jurassic limestone, calcareous conglomerates, marls and sandstone (Commarmot et al. 2013). The slopes are rather steep with a mean inclination of 27–58 % (rarely up to 84 %) (Hnatiuk and Zinko 1997). The Shyrokyi Luh area is dominated by north- and east-exposed slopes, while in the Uholka area less steep and mainly south-exposed slopes are frequent (Commarmot et al. 2013). The climate is temperate and characterized by an annual average temperature of +7.7 °C. The mean temperature in July is +17.9 °C and in January −2.7 °C, measured at the meteorological station of the Carpathian Biosphere Reserve in Uholka at 430 m altitude (Commarmot et al. 2013). In Shyrokyi Luh the annual temperatures are slightly lower than in Uholka (Bursak 1997). The annual average precipitation at the same meteorological station in Uholka was 1,134 mm (from 1980 to 2010) (Commarmot et al. 2013). The average air humidity is very high (approx. 85 %) (Bursak 1997).

Virgin beech forests make up 88 % of the total forest area of the Uholsko-Shyrokoluzhanskyi massif. The timberline is at 1,140 m a.s.l., which is 100–200 m lower than the natural timberline because of human activity in the form of intense livestock pasturing on the mountain meadows (Commarmot et al. 2013). These forest stands are characterized by an uneven-aged and multilayered structure, a high canopy closure and little floristic variety (Sheliag-Sosonko et al. 1997; Commarmot et al. 2005). The median tree age of randomly cored beech trees is 211 in the Uholka and 187 years in the Shyrokyi Luh area and the oldest reliably dated beech tree had an age of 451 years (Trotsiuk et al. 2012; Hobi 2013).

Field methods

The lichens were sampled during July and August 2010, as part of the forest inventory carried out in the primeval beech forest of the Uholsko-Shyrokoluzhanskyi massif within the framework of a cooperation project of the Swiss Federal Institute for Forest, Snow and Landscape Research WSL, the Ukrainian National Forestry University UNFU and the Carpathian Biosphere Reserve (Commarmot et al. 2013). The sampling design of the inventory was a non-stratified systematic cluster sampling (Mandallaz 2008). Each cluster consisted of two sample plots (500 m^2; horizontal radius of 12.62 m) 100 m apart. The clusters were arranged on a 445 × 1,235 m rectangular grid with a randomly chosen starting point. This resulted in a total of 294 plots in the study area. At the sampling plots mainly *Fagus sylvatica* L., *Carpinus betulus* L., *Acer pseudoplatanus* L., *Acer platanoides* L. and *Abies alba* Mill. were present. Key advantages of this design compared to a regular grid of single plots are the lower inventory costs including shorter walking distances and the operational advantage in case of emergency that two survey teams could work within alarm distance of each other (Lanz et al. 2013). The spatial autocorrelation within clusters was tested for stem density and tree volume by comparing the empirical variance of the

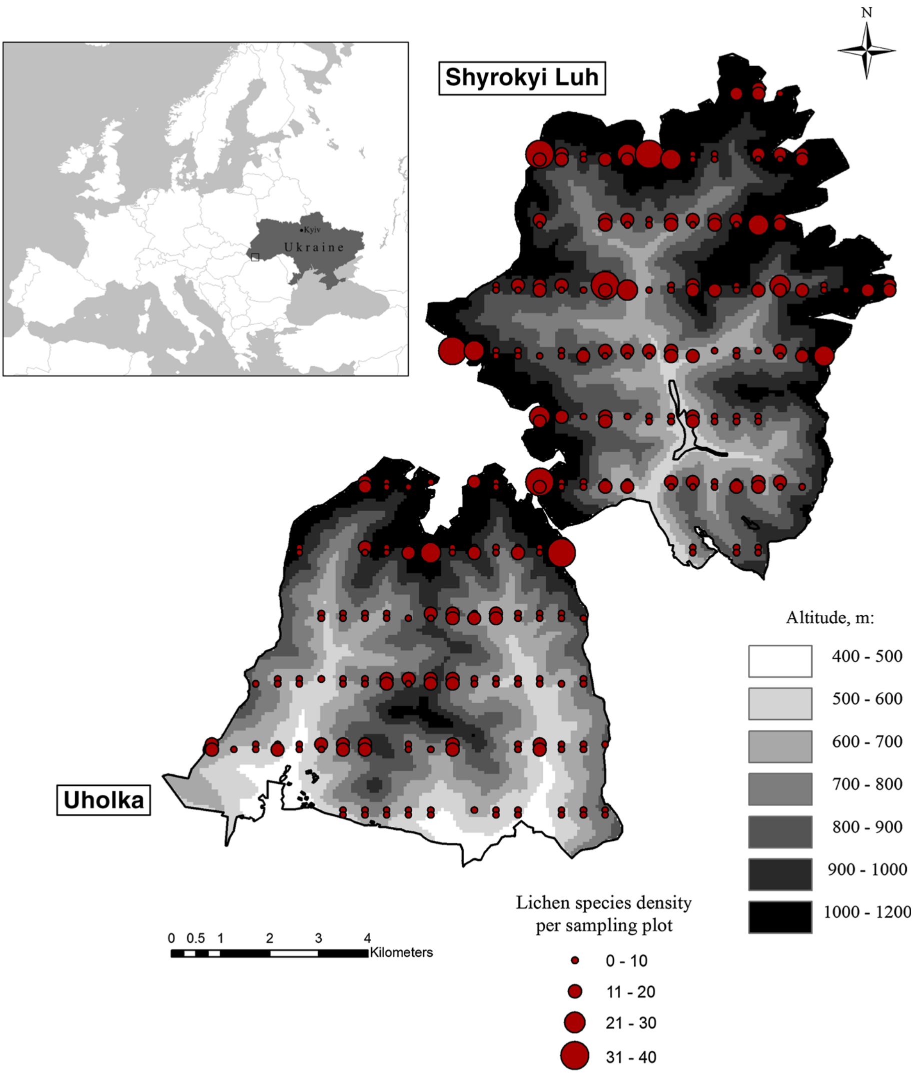

Fig. 1 Lichen species density on 294 sampling plots in the primeval beech forests Uholka-Shyrokyi Luh of the Carpathian Biosphere Reserve

estimates under an estimator ignoring the clustered distribution of sampling plots and an estimator taking the cluster structure into account (Mandallaz 2008). There was only a very small difference between the two variance estimates, and we conclude that the spatial autocorrelation within clusters is very small (Lanz 2011).

On each of the 294 plots (Fig. 1) 5–10 trees with lichen occurrence and DBH >6 cm were randomly selected and the epiphytic lichen diversity was assessed. The bark of living and dead-standing trees all around the trunk, from the base up to 2 m, was carefully observed. If possible, the lichens were identified in the field. If they were morphologically very similar and could not be distinguished in the field, they were listed as species aggregates (see Table 4 in Appendix 1). For example, *Candelariella xanthostigma* aggr.

includes *Candelariella xanthostigma*, *Candelariella reflexa*, *Candelariella efflorescens*, and *Candelariella faginea*. Unidentified specimens were collected and later determined under a microscope and by chemical spot tests using different identification keys. All sterile specimens, as well as *Cetrelia*, *Lecanora strobilina, Lecanora polytropa, Ochrolechia pallescens* and *Parmotrema arnoldii,* were determined or checked by thin layer chromatography with solvent system A, B, C (White and James 1985). Nomenclature generally follows "The third checklist of lichen-forming and allied fungi of Ukraine" (Kondratyuk et al. 2010).

The topographic and forest-stand variables (Table 1) were assessed by the survey teams of the forest inventory on each sampling plot, as described in Commarmot et al. (2010, 2013). To describe the forest structure, canopy openness parameters, which reflect the frequency and size of canopy gaps in the upper forest layer, were used. Forest stands characterized by a canopy structure with gaps smaller than one tree crown, were classified as '*closed*', and areas with several gaps large enough to fit more than one tree '*scattered*'. '*Loose*' forest stands were regarded as an intermediate stage with few gaps the size of a canopy tree (Commarmot et al. 2013). In addition, we visually classified the forest stand into three different developmental stages according to the predominant age of the trees on each sampling plot: (1) *'young'* if the plot is dominated by densely growing young trees with smooth bark; (2) *'mature'* if mostly mature trees with rough bark are present on the plot, and (3) '*overmature*' stands if the plots contain very old trees with creviced bark, often covered by mosses and/or damaged by pathogens or natural disturbances such as lightening or strong wind. The different developmental stages of forest stands cover a wide diversity of microhabitats for epiphytic lichens, including those with patchy light availability, diverse bark structures, and enough stability for lichen species to develop and reproduce over several decades, i.e. over several lichen generations.

Statistical analyses

Statistical analyses were carried out with R version 2.13.1 (The R Foundation for Statistical Computing, 2011). Maps were drawn using ArcMap 8 (ESRI).

Two datasets were statistically analysed at the plot level. The first set consisted of data on lichen species composition (presence/absence data) collected on 294 sampling plots (294 plots $\times$ 171 species), and the second of two response variables and 11 environmental variables, divided into two groups: (1) topographic (four variables) and (2) forest-stand parameters (seven variables) (Table 1). Some variables, e.g. tree species were omitted from analysis due to their low variability. Correlations between the environmental variables and the lichen species density were calculated with Spearman correlation coefficient.

Non-metric multidimensional analysis (NMDS) was performed to describe the lichen species composition on beech trunks within sampling plots using the R package *vegan* (Oksanen et al. 2012). This ordination method is very suitable for analysing the relationships among objects in large datasets, as well as for effectively describing non-linear species responses on different ecological gradients (Borcard et al. 2011; Oksanen 2011). Only lichen species with more than five observations were included in this analysis because rare species usually have an unduly high influence on the ordination results (Oksanen et al. 2012). The Bray-Curtis distance measured with 50 runs with 200 iterations was used. Correlations between the environmental variables and the ordination axes were calculated with the Pearson correlation coefficient. The NMDS ordination of lichen species composition was interpreted with statistically significant environmental variables ($p < 0.05$).

Table 1 Description of the environmental variables and the responses used in the analyses

Variables	Scale	Description
Topographic parameters at plot level (4)		
Altitude	Continuous	Elevation above sea level at the sampling plot in m
Aspect	Continuous	Exposition at the sampling plot in gon
Slope	Continuous	Mean inclination of the slope at the sampling plot in %
Relief	Ordinal	Position of the sampling plot on the slope: 1 bottom; 2 lower; 3 middle; 4 upper; 5 ridge
Forest-stand parameters at plot level (7)		
Canopy cover	Continuous	Estimated total canopy cover on the sampling plot in %
Mean DBH	Continuous	Mean diameter at breast height (1.3 m) of the measured trees on the sampling plot in cm
Forest stage	Ordinal	The developmental stage of forest stands on sampling plots: 1 young; 2 mature; 3 overmature
Lying deadwood	Continuous	Total volume of lying deadwood sampled with a line intersect method in m^3/ha
Canopy closure	Ordinal	Aggregation of tree crowns in the upper canopy layer on the sampling plot: 1 closed; 2 loose; 3 scattered
Tree number	Continuous	Number of living trees ≥6 cm DBH per sampling plot
Tree species	Nominal	Tree species growing on sampling plots: 1 *Fagus sylvatica*; 2 *F. sylvatica* and *Acer pseudoplatanus;* 3 *F. sylvatica* and *Abies alba;* 4 *A. alba;* 5 *F. sylvatica* and *Acer platanoide*
Responses (2)		
Lichen_SD	Continuous	Lichen species density on the sampling plot
Redlisted_SD	Continuous	Red-listed lichen species density on the sampling plot

To assess the effect of environmental variables on the lichen species density, generalized linear models (GLM) were created on the basis of the second dataset using standard R functions. Total lichen species density was analyzed by Poisson distribution with log-linear regression. The density of red-listed lichen species was transformed into presence/absence values and then a binomial distribution with logistic regression was applied. At first all variables were added to the model by the forward stepwise procedure using the Akaike Information Criterion (AIC) as the selection parameter. Then statistically insignificant variables ($p > 0.05$), e.g. lying deadwood, slope, aspect and relief, were manually removed. Additionally the percentage of variation explained by each GLM model was calculated.

Tukey's HSD test for uneven groups was applied to test for significant differences in the mean lichen species density between groups of the developmental stages and the canopy closure of forest stands. Indicator values for each lichen species for different forest stage classes were calculated (Roberts 2011). All species with a total number of records < 3 were omitted from this analysis.

Environmental variables at plot level

Nearly 70 % of the sampling plots were situated between 600 and 1,000 m a.s.l. The lowest plot was at 458 m in the Uholka area and the highest at 1,269 m in the Shyrokyi Luh area. More than 80 % of the 294 sampling plots studied were located in the middle

(122) or upper parts of slopes (97), while 13 plots were on mountain ridges, 49 on the lower parts of slopes and only 13 plots at the bottom of valleys. The mean inclination of slopes was 50 % and varied from 4 to 90 %. Nearly 80 % of the plots were shaded habitats with a total canopy cover of 70–100 % and only 13 plots had a total canopy cover below 50 %.

Lichens were recorded on plots with different stand densities: closed (88 plots), loose (153) and scattered (52). Most of the plots (200) were situated in mature forest stands, while 85 plots were located in young and only nine plots in overmature forest stands. The mean DBH of beech trees per sampling plot was 35 ± 10.8 cm. The maximum DBH was 113.7 cm, while 92.5 % of the plots had a mean DBH of up to 50 cm. Only one plot with a mean DBH over 70 cm was analyzed. DBH revealed a strong negative correlation with stem density and the number of trees per sampling plot (Table 2).

Results

Lichen species density at plot level

A total of 198 epiphytic lichen species were recorded; 160 in Uholka and 166 in Shyrokyi Luh (See Table 4 in Appendix. 1, Fig. 1). The mean number of lichen species per sampling plot was 10.2. According to Tukey's HSD test, the lichen species density at the plot level was significantly higher on plots with a scattered forest canopy (mean density 14.1 per plot) than on plots with a closed (8.7 per plot, $p < 0.01$) or loose canopy (10.1 per plot, $p < 0.01$). The lichen species density on closed and fairly loose plots was not significantly different (Fig. 2b). Similarly, the lichen species density was significantly higher in overmature ($p = 0.01$) and mature forest stands ($p = 0.01$) than in young forest stands, but not significantly different in mature and overmature forests, with mean lichen species densities (8.6, 10.9 and 14.7) in young, mature and overmature forest stands, respectively (Fig. 2a).

Lichen species density increased steadily along the altitudinal gradient (r = 0.39, $p < 0.05$), and was also strongly affected by the forest-stand variables that reflect the light conditions at the plots, e.g. canopy closure (r = 0.23, $p < 0.05$) and canopy cover (r = −0.22, $p < 0.05$) (Table 2; Fig. 3). The highest lichen species density per sampling plot (36–40 species per plot) was recorded on beech trees growing near the timberline (over 1,200 m a.s.l.) in relatively open forest with scattered canopy. Nearly all plots (99 %) with a closed forest canopy had a low lichen species density (below 20 species per plot) and were evenly spread over the entire altitudinal gradient. The lichen species density >20 was mostly found on plots with scattered or loose canopy above 800 m a.s.l. and only once recorded on a plot with closed forest canopy (Figs. 1, 3).

Lichen species density negatively correlated with the number of trees per sampling plots (r = −0.19, $p < 0.05$), while topographic parameters, e.g. aspect, slope and relief, had no effect on this response variable (Table 2). The amount of lying deadwood on the plots did not significantly affect the species density of epiphytic lichens on the trunks of living and dead-standing trees in studied forest. Our analysis revealed that mean DBH of trees significantly affected the lichen species density per plot (r = 0.18, $p < 0.05$) (Fig. 4; Table 2). The results of GLM analysis confirmed that altitude, mean DBH and a late developmental stage of forest stands (i.e. overmature) were the most important factors influencing the lichen species density on sampling plots (Fig. 5).

Table 2 Spearman correlation coefficients between environmental variables and responses

	Relief	Forest stage	Altitude	Slope	Aspect	Canopy cover	Canopy closure	Lying deadwood	Mean DBH	Tree number	Redlisted_SD
Environmental variables											
Altitude	0.29***	0.15*									
Slope	−0.13**		0.22***								
Canopy cover		−0.17*									
Canopy closure		0.36***	0.17**			−0.45***					
Lying deadwood					−0.17**	−0.20***	0.26***				
Mean DBH		0.21***	0.17**								
Tree number			−0.13*			0.24***	−0.18**	−0.16***	−0.70***		
Responses											
Redlisted_SD		0.12*	0.35***				0.15**		0.19**		
Lichen_SD		0.21***	0.39***			−0.22***	0.23***		0.18**	−0.19**	0.51***

Only significant correlations are presented

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$

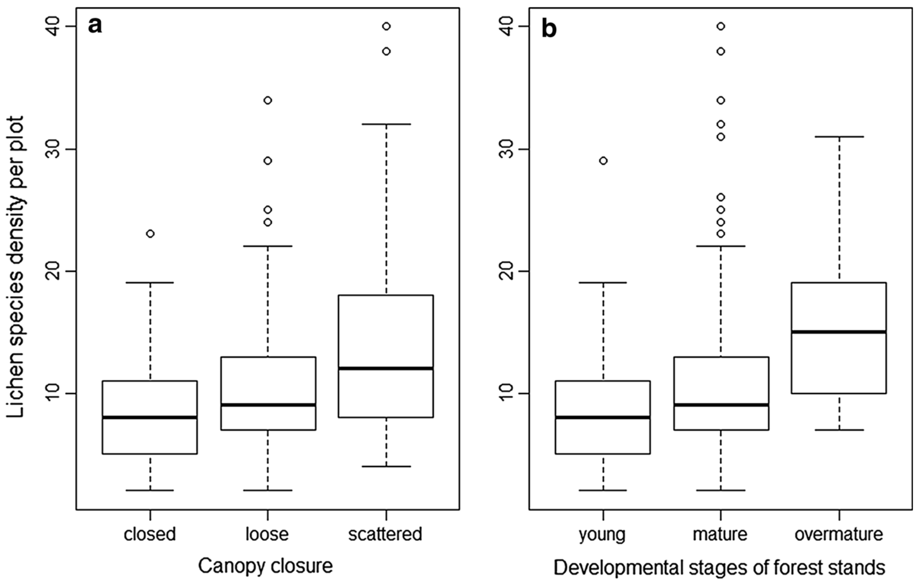

Fig. 2 **a** Lichen species density at plots with closed ($n = 88$), loose ($n = 153$) and scattered canopy ($n = 52$), $r = 0.23$, $p < 0.05$. **b** Lichen species density at plots with young ($n = 85$), mature ($n = 200$) and overmature forest stands ($n = 9$), $r = 0.21$, $p < 0.05$

Lichen species composition at plot level

The most frequent lichens in both areas were crustose species, e.g. *Phlyctis argena* (98 % of plots), *Pyrenula nitida* (88 %), *Graphis scripta* (87 %), *Lepraria lobificans* aggr. (46 %) and *Lecanora argentata* (43 %). Approximately 50 % of the total number of species (e.g. 104 lichen species) had low frequencies and were found on less than five sampling plots (See Table 4 in Appendix 1). Forty-three species were recorded only once, 39 were found only in Shyrokyi Luh and 33 only in Uholka. Some species, e.g. *Biatora vernalis, Collema flaccidum, Dictyocatenulata alba, Leptogium lichenoides, L. cyanescens, Thelotrema lepadinum* and *Peltigera praetextata,* occurred more frequently in the Shyrokyi Luh area.

The NMDS analysis of the lichen species composition on the sampling plots resulted in a two-dimensional solution with final stress 0.25, accounting for 47 % of the total variance (Figs. 6, 7). The most important gradient (NMDS axis 2, $r^2 = 0.27$) was mainly related to the topographic parameters: aspect and slope, but their effects were very slight. The second gradient (NMDS axis 1, $r^2 = 0.20$) was highly correlated with altitude, mean DBH as well as the parameters reflecting light availability (e.g. canopy cover) (Table 3). Thus, all these variables influenced the lichen species composition at the plot level. The most important factor, however, was the altitudinal gradient ($r = 0.94$ to NMDS axis 1, $r^2 = 0.21$, $p = 0.001$).

On the NMDS ordination plot, three groups of lichens were distinguished (Fig. 6). The first was situated on the right of the NMDS ordination and combined lichens growing in open habitats, e.g. *Amandinea punctata, Buellia disciformis, Flavoparmelia caperata, Lecanora leptyrodes, Lecidella elaeochroma, Parmelia submontana, Parmelia sulcata, Platismatia glauca* and *Ramalina fastigiata*. The second was on the left of the NMDS ordination and was occupied by lichen species that occur mostly in shaded and rather

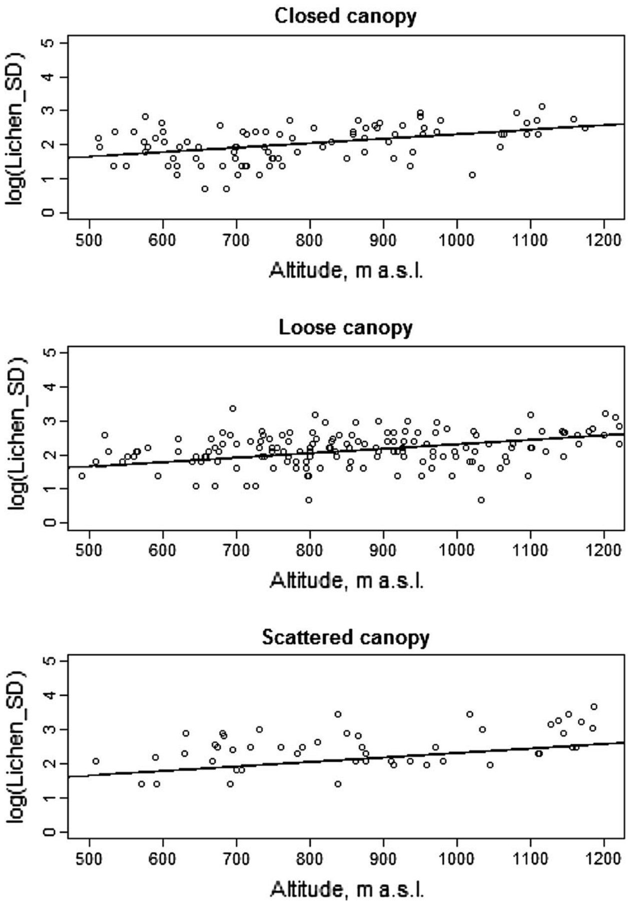

Fig. 3 Lichen species density along the altitudinal gradient on sampling plots with closed ($r = 0.39$, $p < 0.001$), loose ($r = 0.27$, $p < 0.001$) and scattered ($r = 0.52$, $p < 0.001$) canopy fitted by a linear regression

humid habitats, including *Acrocordia gemmata, Belonia herculina, Collema flaccidum, Gyalecta truncigena, Leptogium cyanescens, Leptogium lichenoides, Thelotrema lepadinum* and many others. For example, *Parmelia submontana* (from the first ordination group) was found in rather open habitats with a canopy cover of 40–75 %, while *Gyalecta truncigena* (from the second ordination group) preferred shaded habitats with a canopy cover of 50–95 %. The third group (at the centre of NMDS ordination) included very common beech-forest lichens, such as *Graphis scripta, Phlyctis argena* and *Pyrenula nitida,* which had a rather wide ecological amplitude.

The developmental stages of the beech forests weakly correlated with the lichen species composition ($r^2 = 0.04$, $p = 0.001$). However, several species, e.g. *Belonia herculina, Biatora epixanthoides, B. vernalis, Collema flaccidum, Nephroma parile, Opegrapha varia* and *Parmelina pastillifera* clearly preferred overmature forests as the relative frequency of these species in overmature forest was much higher than in mature or young forests. The indicator values of these species in overmature forest stands were highly significant (See Table 4 in Appendix 1). Other species, such as *Graphis scripta, Lepraria lobificans* aggr.,

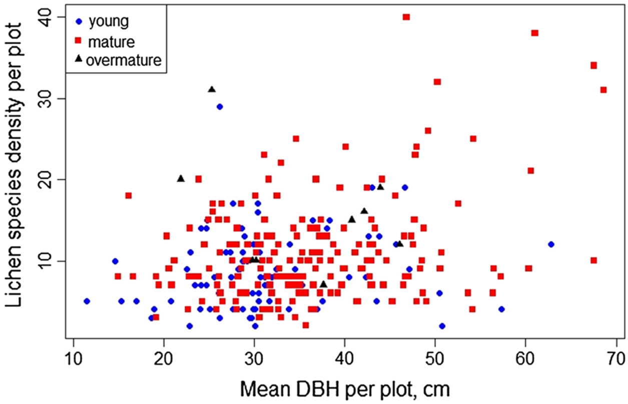

Fig. 4 Relationship between lichen species density and mean DBH of the studied trees ($r = 0.56$, $p < 0.05$) at the sampling plots grouped by the different developmental stages of the forest stands

Phlyctis argena and *Pyrenula nitida*, had similar relative frequencies in all classes of forest stage and thus their indicator values for stand stages were correspondingly insignificant.

Occurrence of rare and red-listed lichen species

Red-listed species were found on 99, i.e. one third, of the studied plots. The maximum number of red-listed species per sampling plot was four, recorded only once, and the mean number was 0.5. At the plot level, the red-listed species density correlated highly with the total lichen species density ($r = 0.51$, $p < 0.05$). Most topographic variables, in particular, the relief, aspect and slope, had no effect on the occurrence of red-listed lichens. According to the GLM analysis, at the plot level the most important factor influencing the density of the red-listed lichen species was altitude (Fig. 8).

Discussion

Altitude influences lichen species density and composition

Altitude was the most important factor explaining lichen species composition and density at the plot level (Table 3; Figs. 3, 5, 8). Altitude is an indirect climatic variable connected with temperature and precipitation, and is thus widely used as a surrogate for climate (Will-Wolf et al. 2006; Moning et al. 2009). Because many lichens are aero-hygrophytic (Pirintsos et al. 1995; Scheidegger et al. 1995; Nascimbene et al. 2007), the high humidity due to fog and low-lying clouds at high altitudes favours the occurrence of lichen species, including many cyanolichens. Our results confirm previous findings that the high humidity is associated with more diverse lichen communities (Heylen et al. 2005; Pirintsos et al. 1995; Ozturk et al. 2010; Werth et al. 2005). The various microclimatic and light parameters related to the interaction of the altitudinal gradient and forest-structure factors are likely to simultaneously affect lichen species density.

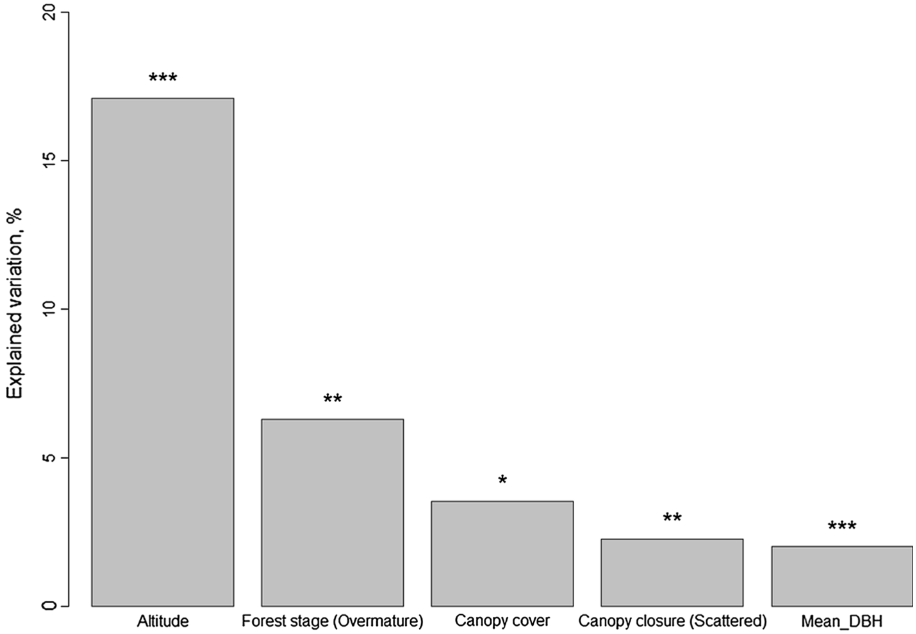

Fig. 5 The variation in lichen species density explained by environmental variables according to GLM analysis. The final model explains 35.1% of total variation. Significance levels: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$

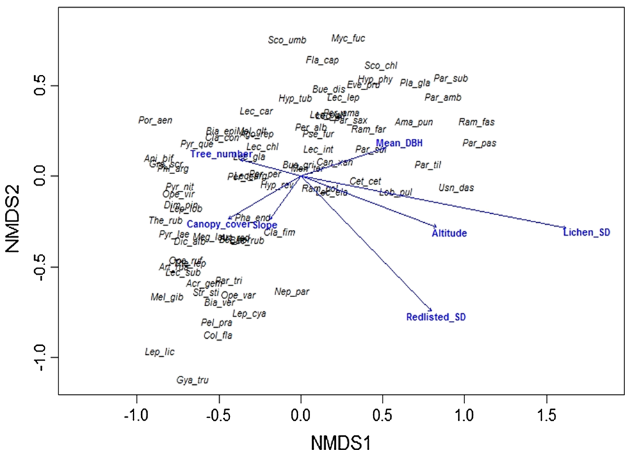

Fig. 6 Non-metric multidimensional scaling (NMDS) ordination of species based on lichen species composition at the plot level. Bray-Curtis distance was used. Correlations with statistically significant environmental variables and responses ($p < 0.05$) are shown. Only lichen species with frequency >5 are shown. See Table 4 in Appendix 1 for species abbreviations and Table 1 for an explanation of the variables

Lichen species density may, however, also increase at higher altitudes due to human impact, especially in the form of traditional livestock pasturing on mountain meadows. At 1,100 m a.s.l. and above, beech trees grow in the ecotone belt, where each summer sheep and goat grazing is rather intensive. The proximity of sheep flocks to the forest might lead

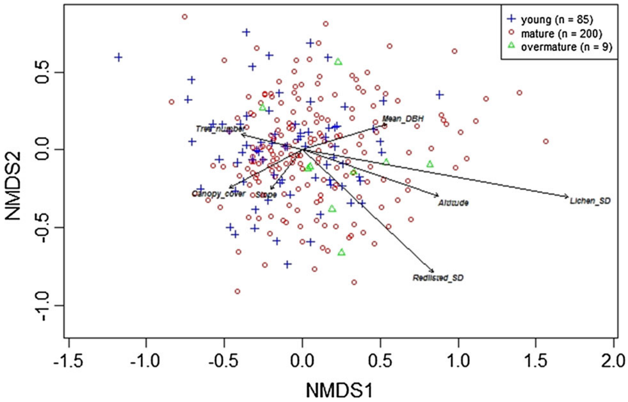

Fig. 7 Non-metric multidimensional scaling (NMDS) ordination of the sampling plots. Bray-Curtis distance was used. The biplot shows the three developmental stages of forest stands: young, mature and overmature. Correlations with statistically significant environmental variables and responses ($p < 0.05$) are shown. See Table 1 for an explanation of the variables

Table 3 Pearson correlation coefficients, coefficients of determination (r^2) and *p*-value of the MNDS ordination axes with environmental variables and responses

Variables	Axis 1	Axis 2	r^2	*P*	
Responses					
Lichen_SD	0.98	−0.17	0.75	0.001	***
Redlisted_SD	0.73	−0.68	0.33	0.001	***
Environmental variables					
Altitude	0.94	−0.32	0.21	0.001	***
Mean_DBH	0.96	0.29	0.08	0.001	***
Canopy_cover	−0.88	−0.47	0.07	0.001	***
Tree_number	−0.97	0.24	0.04	0.003	**
Slope	−0.63	−0.78	0.03	0.019	*
Aspect	−0.63	−0.78	0.01	0.619	
Lying deadwood	−0.07	0.99	0.01	0.922	
Canopy closure	–	–	0.05	0.001	***
Forest stage	–	–	0.04	0.001	***
Relief	–	–	0.05	0.002	**

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$

to nutrient-rich deposits, which may promote the development of nitrophilous epiphytic lichens on *Fagus* trunks nearby the meadows. These lichens include: *Amandinea punctata, Candelariella xanthostigma, Lecanora polytropa, Phaeophyscia orbicularis, Physcia adscendens, Xanthoria fulva, Xanthoria parietina, Xanthoria ulophyllodes* and *Caloplaca* spp. (Barkman 1958; Wirth 1995), which are otherwise rare in beech forests. However, their occurrence may also be explained by the activity of wood-decaying fungi. Fritz and Heilmann-Clausen (2010) showed that the surface of beech bark is often enriched by nutrients from mould in holes with rot. Indeed, the bark of old beech trees growing near the

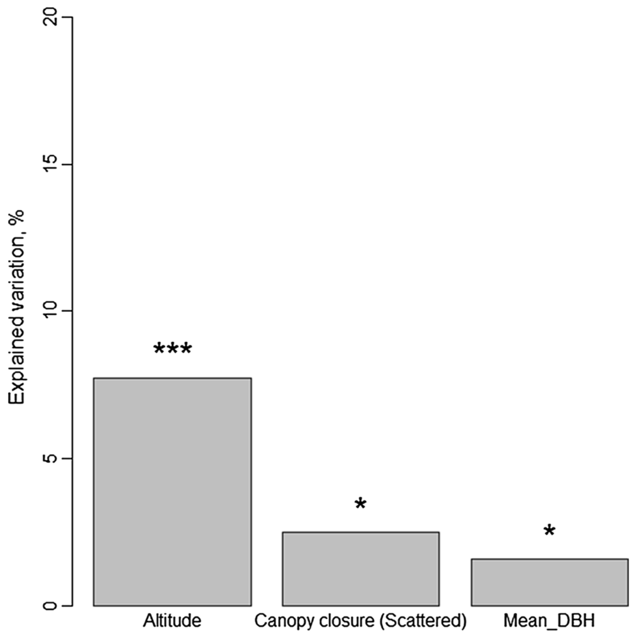

Fig. 8 The variation in species density of red-listed lichens explained by environmental variables according to GLM analysis. The final model explains 17.5 % of total variation. Significance levels: ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$

meadows in Uholka-Shyrokyi Luh area is often damaged by lightning or wood-decaying fungi that favour the formation of cankers and holes with a nutrient-enriched bark surface.

Forest stand structure affects lichen species density

We found a strong relationship between lichen species density and forest-stand variables that reflect the light conditions on the trunks, e.g. canopy closure and canopy cover. This correlation confirms trends found in managed forest stands (Barkman 1958; Löbel et al. 2006; Moning et al. 2009) and some old-growth coniferous forests (Marmor et al. 2011a). A low canopy closure had a positive effect on lichen species density. We showed that the density of lichen species was significantly higher on plots with a relatively open canopy than on plots with fairly loose or very dense canopy structure (Fig. 2b). Since lichen diversity in pure beech forests is known to be low due to limited light (Watson 1936), our results correspond with those of other studies that emphasize the importance of sufficient solar radiation for a high lichen species density.

Canopy closure is a key forest parameter, which reflects not only the developmental stage of forest stands, but also the vertical and horizontal forest structure, including natural disturbances such as wind or snowstorms. Canopy closure is also indirectly related to air humidity and light availability at sampling plots (Commarmot et al. 2013). Forest stands with a scattered canopy transmit more light, but their average air humidity trends to be lower in stands with loose or closed canopy. The availability of more light positively affects the growth of most foliose and fruticose lichens (Barkman 1958; Moning et al. 2009). Thus stands with a scattered canopy favour the occurrence of light-demanding lichens, such as *Flavoparmelia caperata, Lecanora argentata, Parmelia sulcata* and

Parmelina tiliacea, while stands with a dense canopy harbour more shade-tolerant lichens, e.g. *Belonia herculina, Gyalecta truncigena, Parmeliella triptophylla, Strigula stigmatella*. On the other hand, previous studies indicated that logging suddenly increases the solar radiation on any remaining trees, which may lead to light intensities that are lethal for several old-growth forest lichens (Gauslaa and Solhaug 2000). Many lichens associated with old-growth forests reproduce by thallus fragmentation, readily detached lobules or soredia and their dispersal is limited (Sillet et al. 2000; Scheidegger and Werth 2009). The natural death of old beech trees, which may result in scattered forest stands, can also lead to a decrease in many indicator and red-listed lichens, as they often have a low dispersal ability. Canopy closure is thus a complex forest-stand parameter, which is interrelated to several other interdependent variables, including solar radiation, humidity and forest age, and has a strong effect on the pattern of lichen occurrence in beech forests.

Mean stem diameter influences lichen species density

We showed that the mean DBH is one of the most important factors determining the lichen species density and composition on the sampling plots (Tables 2, 3; Figs. 4, 5, 8). Our results confirm findings of previous studies, which revealed a strong positive correlation between mean DBH and lichen species richness (Aude and Poulsen 2000; Fritz et al. 2008a, b; Mikhailova et al. 2005; Löbel et al. 2006; Mežaka et al. 2008, 2012).

Friedel et al. (2006) pointed out that the diameter of trees at breast height provides an indication of the microhabitat diversity required for tree colonization by epiphytic lichens, which includes bark pH and the presence of crevices. Commarmot et al. (2013) showed that, most types of microhabitats, such as bark damage, cracks, holes and cavities, were related to tree age and occur mainly in old trees with a mean DBH of 35–44 cm in Uholka-Shyrokyi Luh. Our study showed that species richness of epiphytic lichens was highest (>30 species per tree) on old and overmature beech trunks growing at higher altitudes where they had a very uneven and often damaged bark structure with cracks and cavities. Thus we can conclude that DBH and bark structure, which correlate with tree age, influence lichen species diversity at the plot level substantially.

In our study we tested the developmental stage of forest stands to approximately assess the age and bark features of beech trees. We found that the late developmental stage of forest stands, which is characterized by a large number of old trees with rough and creviced bark, had a significant positive effect on lichen species density (Table 2; Fig. 5). The composition of lichen species at the plot level was, however, only weakly correlated with a stand's developmental stage (Table 3; Fig. 7) because the forests we studied generally have an uneven-aged stand structure (Trotsiuk et al. 2012; Hobi 2013). This means that, on each plot, trees of different age classes are mixed, which is beneficial for lichen diversity as they vary greatly in their preferences for age classes and bark structure properties. The presence of even just one old tree on a sampling plot with mainly young beeches, which harbours many old-growth lichen species and indicators of woodland key habitat, is very likely to considerably promote lichen species density. In most managed forest landscapes, in contrast, old-growth forest lichens are often restricted to protected stands with old-growth characteristics but not to isolated old trees in otherwise young forests (Frey 1958).

Importance of Uholka-Shyrokyi Luh for the conservation of forest-bound lichens

Among the total epiphytic lichens recorded, 13 nationally red-listed species were found in Uholka-Shyrokyi Luh (See Table 4 in Appendix 1). These make up 25 % of all the lichen species included in the Ukrainian Red Data Book (Didukh 2009). Furthermore, 35 lichen species are known as indicators of ecological forest continuity (Coppins and Coppins 2002; Kondratyuk 2008) or woodland key habitats (Norén et al. 2002; Ek et al. 2002), e.g. *Agonimia allobata, Arthonia vinosa, Bacidia subincompta, Biatora epixanthoides, Leptogium cyanescens, L. lichenoides, Megalaria laureri, Menegazzia terebrata, P. crinitum, Peltigera collina, Piccolia ochrophora, Porina hibernica, P. leptalea, Pyrenula nitida, Thelopsis rubella, Thelotrema lepadinum, Usnea ceratina* and *Wadeana dendrographa* (See Table 4 in Appendix 1). Among them, the most frequent lichens on the plots studied are: *Belonia herculina* (found on 61 sampling plots), *Lobaria pulmonaria* (on 45 plots), *Parmeliella triptophylla* (on 16 plots), *Gyalecta truncigena* (on 11 plots) and *Nephroma parile* (on 10 plots). In Uholka-Shyrokyi Luh, the species with a high national and international conservation value, are *Belonia herculina, Biatoridium monasteriense, Gyalecta flotowii, Lecanora intumescens, Lobaria amplissima, Megalaria laureri, Melaspilea gibberulosa, Parmeliella triptophylla, Parmotrema arnoldii, Peltigera collina, Ramonia luteola, Strigula stigmatella, Thelopsis rubella, T. flaveola* and *Thelotrema lepadinum.* These are mostly restricted to old beech trees. Many of these species are also red-listed in other European countries (Cieśliński et al. 2003; Liška et al. 2008; Scheidegger et al. 2002 etc.).

Conclusion

The epiphytic lichen species density at the plot level in the primeval beech forest of Uholka-Shyrokyi Luh, with its uneven-aged structure, was mainly influenced by altitude and forest-stand variables. These factors are mostly related to light availability (i.e. canopy closure) or habitat diversity (the developmental stages of the forest stands and the mean stem diameter). Thus our results confirm previous studies that found climatic and forest-stand variables to be highly relevant for lichen communities (Werth et al. 2005; Giordani 2006; Will-Wolf et al. 2006; Ellis and Coppins 2006; Fritz 2009; Moning et al. 2009; Mežaka et al. 2012). DBH and bark structure both influence lichen species diversity in studied beech forest but are interdependent. Both are important for the maintaining of high lichen species richness, including rare and threatened species. The abundance of epiphytic lichens with national and international conservation value in the Uholka-Shyrokyi Luh primeval forest underlines the international importance of the studied area for the conservation of forest-bound lichens.

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Appendix

See Table 4.

Table 4 The total number of records, total frequency and relative frequency in each class of forest stage and indicator value (Ind.Val.) of epiphytic lichen species found in Uholka ($n = 160$) and Shyrokyi Luh ($n = 166$) of the Carpathian Biosphere Reserve

Species	Abbreviations	Total number	Frequency, %	Young	Mature	Over-mature	Ind. Val.	*p* value
Acrocordia gemmata	Acr_gem	61	17.3	0.15	0.19	***0.22***	0.09	0.61
Agonimia allobata	Ago_all	2	0.6	–	–	–	–	–
Agonimia repleta	Ago_rep	12	3.4	0.02	***0.05***	–	0.03	0.68
Agonimia tristicula	Ago_tri	3	0.9	–	–	–	–	–
Amandinea punctata	Ama_pun	12	3.4	–	0.04	***0.11***	0.08	**0.03**
Anaptychia ciliaris	Ana_cil	11	3.1	–	***0.02***	–	0.02	0.60
Anisomeridium biforme	Ani_bif	16	4.5	0.05	0.05	***0.11***	0.06	0.29
Arthonia didyma	Art_did	3	0.9	–	–	–	–	–
Arthonia dispersa	Art_dis	1	0.3	–	–	–	–	–
Arthonia radiata	Art_rad	19	5.4	0.02	0.07	***0.11***	0.06	0.18
Arthonia vinosa	Art_vin	21	6.0	0.01	***0.02***	–	0.01	1.00
Arthopyrenia analepta	Art_ana	1	0.3	–	–	–	–	–
Arthopyrenia punctiformis	Art_pun	1	0.3	–	–	–	–	–
Arthopyrenia rhyponta	Art_rhy	1	0.3	–	–	–	–	–
Arthothelium ruanum	Art_rua	14	4.0	0.05	0.04	***0.11***	0.06	0.29
Bacidia circumspecta	Bac_cir	4	1.1	–	0.02	***0.11***	0.10	**0.05**
Bacidia incompta	Bac_inc	2	0.6	–	–	–	–	–
Bacidia phacodes	Bac_pha	5	1.4	0.01	0.01	***0.11***	0.10	0.09
Bacidia rosella	Bac_ros	4	1.1	–	***0.02***	–	0.02	0.61
Bacidia rubella	Bac_rub	12	3.4	0.01	0.03	***0.11***	0.08	0.10
Bacidia subincompta	Bac_sub	5	1.4	0.01	***0.02***	–	0.01	1.00
Belonia herculina	Bel_her	69	19.6	0.22	0.19	***0.78***	0.51	**0.00**
Biatora carneoalbida	Myc_car	1	0.3	–	–	–	–	–
Biatora chrysantha	Bia_chr	6	1.7	0.01	***0.02***	–	0.01	1.00

Table 4 continued

Species	Abbreviations	Total number	Frequency, %	Young	Mature	Over-mature	Ind. Val.	*p* value
Biatora efflorescens	Bia_eff	5	1.4	–	***0.02***	–	0.02	0.40
Biatora epixanthoides	Bia_epi	114	32.4	0.33	0.35	***0.78***	0.42	**0.01**
Biatora sphaeroides	Myc_pil	1	0.3	–	–	–	–	–
Biatora tetramera	Myc_tet	1	0.3	–	–	–	–	–
Biatora vernalis	Bia_ver	54	15.3	0.13	0.15	***0.56***	0.37	**0.00**
Biatoridium monasteriense	Bia_mon	5	1.4	***0.02***	0.01	–	0.02	0.62
Bilimbia sabuletorum	Myc_sab	2	0.6	–	–	–	–	–
Bryoria fuscescens	Bry_fus	1	0.3	–	–	–	–	–
Buellia chloroleuca	Bue_chl	1	0.3	–	–	–	–	–
Buellia disciformis	Bue_dis	27	7.7	0.06	***0.10***	–	0.06	0.34
Buellia griseovirens	Bue_gri	28	8.0	0.05	0.08	***0.11***	0.05	0.40
Buellia insignis	Bue_ins	2	0.6	–	–	–	–	–
Buellia schaereri	Bue_sch	1	0.3	–	–	–	–	–
Caloplaca cerina var. *cerina*	Cal_cer	3	0.9	–	–	–	–	–
Caloplaca cerina var. *chloroleuca*	Cal_chl	1	0.3	–	–	–	–	–
Caloplaca monacensis	Cal_mon	1	0.3	–	–	–	–	–
Candelaria concolor	Can_con	2	0.6	–	–	–	–	–
Candelariella xanthostigma	Can_xan	29	8.2	0.02	***0.07***	–	0.05	0.55
Cetrelia cetrarioides	Cet_cet	44	12.5	0.07	0.10	***0.22***	0.13	0.10
Cetrelia olivetorum	Cet_oli	3	0.9	–	–	–	–	–
Chaenotheca furfuracea	Cha_fur	2	0.6	–	–	–	–	–
Chaenotheca phaeocephala	Cha_pha	1	0.3	–	–	–	–	–
Chaenotheca trichiales	Cha_tri	1	0.3	–	–	–	–	–
Cladonia chlorophaea	Cla_chl	2	0.6	–	–	–	–	–
Cladonia coniocraea	Cla_con	89	25.3	0.20	***0.27***	0.22	0.10	0.80

Table 4 continued

Species	Abbreviations	Total number	Frequency, %	Young	Mature	Over-mature	Ind. Val.	*p* value
Cladonia fimbriata	Cla_fim	69	19.6	0.14	0.20	***0.56***	0.35	**0.01**
Cladonia ochrochlora	Cla_och	1	0.3	–	–	–	–	–
Cladonia pyxidata	Cla_pyx	4	1.1	***0.01***	0.01	–	0.01	1.00
Collema flaccidum	Col_fla	26	7.4	0.04	0.07	***0.22***	0.15	**0.03**
Collema subflaccidum	Col_sub	1	0.3	–	–	–	–	–
Dictyocatenulata alba	Dic_alb	13	3.7	***0.05***	0.04	–	0.03	0.84
Dimerella lutea	Dim_lut	1	0.3	–	–	–	–	–
Dimerella pineti	Dim_pin	21	6.0	0.05	0.06	***0.11***	0.06	0.36
Evernia prunastri	Eve_pru	23	6.5	0.05	***0.06***	–	0.03	0.85
Flavoparmelia caperata	Fla_cap	11	3.1	0.01	***0.03***	–	0.02	0.75
Graphis scripta	Gra_scr	307	87.2	0.93	0.91	***1.00***	0.35	0.38
Gyalecta flotowii	Gya_flo	2	0.6	–	–	–	–	–
Gyalecta truncigena	Gya_tru	13	3.7	0.04	0.04	***0.11***	0.07	0.21
Gyalecta ulmi	Gya_ulm	1	0.3	–	–	–	–	–
Haematomma ochroleucum	Hae_och	5	1.4	***0.04***	0.01	–	0.03	0.26
Heterodermia speciosa	Het_spe	13	3.7	***0.02***	0.01	–	0.02	0.61
Hypogymnia physodes .	Hyp_phy	50	14.2	0.05	***0.15***	0.11	0.07	0.47
Hypogymnia tubulosa	Hyp_tub	26	7.4	0.02	0.10	***0.22***	0.14	**0.03**
Hypogymnia vitatta	Hyp_vit	1	0.3	–	–	–	–	–
Hypotrachyna revoluta	Hyp_rev	10	2.8	***0.04***	0.02	–	0.02	0.54
Lecanora allophana	Lec_all	28	8.0	0.04	***0.07***	–	0.05	0.67
Lecanora argentata	Lec_arg	150	42.6	0.34	0.47	***0.67***	0.30	**0.04**
Lecanora carpinea	Lec_car	15	4.3	0.04	***0.04***	–	0.02	1.00
Lecanora chlarotera	Lec_chl	32	9.1	***0.13***	0.08	0.11	0.05	0.60
Lecanora glabrata	Lec_gla	44	12.5	0.09	***0.16***	0.11	0.07	0.77

Table 4 continued

Species	Abbreviations	Total number	Frequency, %	Young	Mature	Over-mature	Ind. Val.	*p* value
Lecanora impudens	Lec_imp	3	0.9	–	–	–	–	–
Lecanora intumescens	Lec_int	12	3.4	0.02	***0.04***	–	0.02	0.80
Lecanora leptyrodes	Lec_lep	12	3.4	0.02	***0.05***	–	0.03	0.64
Lecanora polytropa	Lec_pol	14	4.0	–	0.02	***0.11***	0.09	**0.03**
Lecanora pulicaris	Lec_pul	27	7.7	0.04	0.10	***0.11***	0.05	0.49
Lecanora rugosella	Lec_rug	3	0.9	–	–	–	–	–
Lecanora sambuci	Lec_sam	3	0.9	–	–	–	–	–
Lecanora strobilina	Lec_str	1	0.3	–	–	–	–	–
Lecanora subrugosa	Lec_sub	16	4.5	0.04	0.04	***0.11***	0.07	0.20
Lecanora symmicta	Lec_sym	1	0.3	–	–	–	–	–
Lecidea pullata	Lec_put	2	0.6	–	–	–	–	–
Lecidella elaeochroma	Lec_ela	52	14.8	0.08	0.11	***0.11***	0.04	0.87
Lepraria elobata	Lep_elo	2	0.6	–	–	–	–	–
Lepraria lobificans	Lep_lob	160	45.5	0.75	0.78	***0.78***	0.26	0.91
Leptogium cyanescens	Lep_cya	12	3.4	0.02	0.04	***0.11***	0.07	0.12
Leptogium gelatinosum	Lep_gel	3	0.9	–	–	–	–	–
Leptogium lichenoides	Lep_lic	28	8.0	***0.09***	0.09	–	0.05	0.66
Leptogium saturninum	Lep_sat	12	3.4	***0.01***	0.01	–	0.01	1.00
Lobaria amplissima	Lob_amp	3	0.9	–	–	–	–	–
Lobaria pulmonaria	Lob_pul	47	13.4	0.02	***0.10***	–	0.08	0.19
Lopadium disciforme	Lop_dis	1	0.3	–	–	–	–	–
Loxospora elatina	Lox_ela	2	0.6	–	–	–	–	–
Megalaria laureri	Meg_lau	8	2.3	0.02	0.02	***0.11***	0.08	0.15
Melanelia subargentifera	Mel_sbg	43	12.2					
Melanelia subaurifera	Mel_sub	9	2.6	–	***0.01***	–	0.01	1.00

Table 4 continued

Species	Abbreviations	Total number	Frequency, %	Young	Mature	Over-mature	Ind. Val.	*p* value
Melanelixia glabratula	Mel_glt	139	39.5	0.34	0.42	***0.56***	0.23	0.13
Melanohalea elegantula	Mel_ele	8	2.3	***0.01***	0.01	–	0.01	1.00
Melanohalea exasperatula	Mel_exa	3	0.9	–	–	–	–	–
Melaspilea gibberulosa	Mel_gib	22	6.3	***0.09***	0.07	–	0.06	0.34
Menegazzia terebrata	Men_ter	17	4.8	0.02	0.06	***0.11***	0.07	0.15
Micarea peliocarpa	Mic_pel	2	0.6	–	–	–	–	–
Micarea prasina	Mic_pra	3	0.9	–	–	–	–	–
Mycoblastus fucatus	Myc_fuc	6	1.7	***0.02***	0.02	–	0.01	1.00
Nephroma parile	Nep_par	20	5.7	–	0.05	***0.11***	0.08	**0.05**
Nephroma resupinatum	Nep_res	6	1.7	–	***0.02***	–	0.02	0.61
Normandina pulchella	Nor_pul	5	1.4	–	***0.02***	–	0.02	0.59
Ochrolechia androgyna	Och_and	5	1.4	–	***0.01***	–	0.01	0.62
Ochrolechia pallescens	Och_pal	3	0.9	–	–	–	–	–
Opegrapha herbarum	Ope_her	1	0.3	–	–	–	–	–
Opegrapha rufescens	Ope_ruf	8	2.3	***0.04***	0.02	–	0.02	0.52
Opegrapha varia	Ope_var	15	4.3	0.04	0.04	***0.22***	0.17	**0.03**
Opegrapha vermicellifera	Ope_ver	1	0.3	–	–	–	–	–
Opegrapha viridis	Ope_vir	23	6.5	0.05	***0.09***	–	0.06	0.33
Opegrapha vulgata	Ope_vul	1	0.3	–	–	–	–	–
Pannaria conoplea	Pan_con	1	0.3	–	–	–	–	–
Parmelia glabra	Mel_gla	10	2.8	–	***0.02***	–	0.02	0.61
Parmelia saxatilis	Par_sax	57	16.2	0.07	0.16	***0.22***	0.11	0.15
Parmelia submontana	Par_sub	19	5.4	0.01	***0.05***	–	0.04	0.47
Parmelia sulcata	Par_sul	53	15.1	0.08	***0.14***	–	0.09	0.42
Parmeliella triptophylla	Par_tri	22	6.3	0.05	***0.07***	–	0.04	0.90

Table 4 continued

Species	Abbreviations	Total number	Frequency, %	Young	Mature	Over-mature	Ind. Val.	*p* value
Parmelina pastilifera	Par_pas	16	4.5	–	0.03	***0.11***	0.09	**0.04**
Parmelina tiliacea	Par_til	18	5.1	0.01	***0.03***	–	0.02	0.73
Parmeliopsis ambigua	Par_amb	12	3.4	0.02	***0.03***	–	0.02	1.00
Parmeliopsis hyperopta	Par_hyp	3	0.9	–	–	–	–	–
Parmotrema arnoldii	Par_arn	1	0.3	–	–	–	–	–
Parmotrema crinitum	Par_cri	6	1.7	–	***0.02***	–	0.02	0.59
Parmotrema perlatum	Par_per	2	0.6	–	–	–	–	–
Peltigera collina	Pel_col	1	0.3	–	–	–	–	–
Peltigera degenii	Pel_deg	2	0.6	–	–	–	–	–
Peltigera horizontalis	Pel_hor	4	1.1	0.01	0.01	***0.11***	0.10	0.09
Peltigera polydactylon	Pel_pol	1	0.3	–	–	–	–	–
Peltigera praetextata	Pel_pra	45	12.8	0.09	0.12	***0.33***	0.20	**0.05**
Pertusaria albescens	Per_alb	15	4.3	0.07	***0.18***	0.11	0.09	0.53
Pertusaria amara	Per_ama	41	11.6	0.05	0.11	***0.11***	0.05	0.69
Pertusaria coccodes	Per_coc	1	0.3	–	–	–	–	–
Pertusaria constricta	Per_con	3	0.9	–	–	–	–	–
Pertusaria coronata	Per_cor	8	2.3	–	***0.02***	–	0.02	0.40
Pertusaria hemisphaerica	Per_hem	1	0.3	–	–	–	–	–
Pertusaria leioplaca	Per_lei	13	3.7	0.04	0.04	***0.11***	0.07	0.20
Pertusaria pertusa	Per_per	46	13.1	0.15	0.14	***0.22***	0.10	0.41
Pertusaria pustulata	Per_pus	2	0.6	–	–	–	–	–
Phaeophyscia endophoenicea	Pha_end	10	2.8	***0.02***	0.02	–	0.01	1.00
Phaeophyscia orbicularis	Pha_orb	4	1.1	–	***0.02***	–	0.02	0.60
Phlyctis argena	Phl_arg	346	98.3	0.99	0.95	***1.00***	0.34	0.78
Physcia adscendens	Phy_ads	3	0.9	–	–	–	–	–

Table 4 continued

Species	Abbreviations	Total number	Frequency, %	Young	Mature	Over-mature	Ind. Val.	*p* value
Physconia detersa	Phy_det	10	2.8	–	***0.01***	–	0.01	0.62
Physconia distorta	Phy_dis	4	1.1	–	***0.01***	–	0.01	0.63
Physconia enteroxantha	Phy_ent	6	1.7	–	***0.01***	–	0.01	0.60
Physconia perisidiosa	Phy_per	4	1.1	–	***0.01***	–	0.01	0.64
Piccolia ochrophora	Pic_och	2	0.6	–	–	–	–	–
Platismatia glauca	Pla_gla	46	13.1	0.04	0.11	***0.11***	0.05	0.58
Porina aenea	Por_aen	11	3.1	***0.05***	0.03	–	0.03	0.58
Porina hibernica	Por_hib	3	0.9	–	–	–	–	–
Porina leptalea	Por_lep	4	1.1	0.01	***0.02***	–	0.01	1.00
Pseudevernia furfuracea	Pse_fur	66	18.8	0.04	***0.14***	–	0.11	0.25
Pyrenula coryli	Pyr_cor	1	0.3	–	–	–	–	–
Pyrenula laevigata	Pyr_lae	9	2.6	–	***0.04***	–	0.04	0.38
Pyrenula nitida	Pyr_nit	309	87.8	0.85	0.91	***1.00***	0.36	**0.05**
Pyrrhospora quernea	Pyr_que	6	1.7	***0.02***	0.02	–	0.01	1.00
Ramalina farinacea	Ram_far	36	10.2	0.04	0.05	***0.22***	0.16	**0.03**
Ramalina fastigiata	Ram_fas	18	5.1	0.02	0.04	***0.11***	0.07	0.16
Ramalina fraxinea	Ram_fra	3	0.9	–	–	–	–	–
Ramalina pollinaria	Ram_pol	83	23.6	0.11	0.20	***0.33***	0.17	0.07
Ramonia luteola	Ram_lut	7	2.0	–	***0.01***	–	0.01	1.00
Reichlingia leopoldii	Rei_leo	1	0.3	–	–	–	–	–
Rinodina capensis	Rin_cap	1	0.3	–	–	–	–	–
Rinodina conradi	Rin_con	1	0.3	–	–	–	–	–
Rinodina pyrina	Rin_pyr	5	1.4	–	***0.01***	–	0.01	1.00
Rinodina sophodes	Rin_sop	2	0.6	–	–	–	–	–
Ropalospora viridis	Rop_vir	4	1.1	0.01	0.01	***0.11***	0.09	0.09

Table 4 continued

Species	Abbreviations	Total number	Frequency, %	Young	Mature	Over-mature	Ind. Val.	*p* value
Sclerophora pallida	Scl_pal	2	0.6	–	–	–	–	–
Scoliciosporum chlorococcum	Sco_chl	13	3.7	0.01	0.04	***0.11***	0.08	0.09
Scoliciosporum umbrinum	Sco_umb	12	3.4	0.04	0.06	***0.11***	0.06	0.22
Stenocybe pullatula	Ste_pul	1	0.3	–	–	–	–	–
Sticta fuliginosa	Sti_ful	3	0.9	–	–	–	–	–
Strigula stigmatella	Str_sti	21	6.0	0.04	0.06	***0.11***	0.06	0.25
Thelocarpon laureri	The_lau	1	0.3	–	–	–	–	–
Thelopsis flaveola	The_fla	1	0.3	–	–	–	–	–
Thelopsis rubella	The_rub	8	2.3	***0.04***	0.02	–	0.02	0.52
Thelotrema lepadinum	The_lep	40	11.4	0.09	0.10	***0.11***	0.04	0.93
Trapeliopsis flexuosa	Tra_fle	4	1.1	0.01	***0.02***	–	0.01	1.00
Tuckermannopsis chlorophylla	Tuc_chl	2	0.6	–	–	–	–	–
Usnea ceratina	Usn_cer	1	0.3	–	–	–	–	–
Usnea dasypoga	Usn_das	7	2.0	–	0.03	***0.11***	0.09	**0.04**
Usnea lapponica	Usn_lap	2	0.6	–	–	–	–	–
Usnea subfloridana	Usn_sbf	7	2.0	0.01	***0.02***	–	0.01	1.00
Usnea substerilis	Usn_sbs	2	0.6	–	–	–	–	–
Usnea wasmuthii	Usn_was	1	0.3	–	–	–	–	–
Verrucaria viridigrana	Ver_vir	1	0.3	–	–	–	–	–
Vulpicida pinastri	Vul_pin	16	4.5	–	0.02	***0.11***	0.10	**0.04**
Wadeana dendrographa	Wad_den	2	0.6	–	–	–	–	–
Xanthoria fulva	Xan_ful	1	0.3	–	–	–	–	–
Xanthoria parietina	Xan_par	7	2.0	–	***0.01***	–	0.01	1.00

Table 4 continued

Species	Abbreviations	Total number	Frequency, %	Young	Mature	Over-mature	Ind. Val.	*p* value
Xanthoria ulophyllodes	Xan_ull	1	0.3	–	–	–	–	–

Red-listed species are underlined. The relative frequency of each lichen species in the forest stage class where the species has its maximum indicator value (Ind.Val.) are marked in bold italics. Only lichen species with records >3 are shown

$p < 0.05$ is marked in bold

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