

Does age matter? How tree age affects lichen diversity on beech trunks in a temperate forest

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Figure 1. L. Komposch during collection of environmental variables at Brucksattel forest (tree no 10). Photo: © H. Komposch

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Zusammenfassung 500 Zeichen Deutsch

Es wurden epiphytische Flechten an Buchenstämmen unterschiedlicher Dicke zweier hochmontaner Wälder erhoben. Von den 113 bestimmten Arten waren 31% Rote Liste Arten. Die Artenvielfalt erhöhte sich signifikant mit dem BHD. Die Indikatorartenanalyse erbrachte 11 Altbaum-Indikatoren, darunter *Lobaria pulmonaria* und *Loxospora cristinae*. Die Eigenständigkeit der Flechtengarnitur alter Bäume wurde durch NMS bestätigt. Zur Förderung dieser wurden Handlungsempfehlungen an die Forstwirtschaft formuliert.

Zusammenfassung 500 Zeichen Englisch

Epiphytic lichens were recorded on beech trunks of different thicknesses at two high montane forest sites. Of 113 species recorded, 31% were Red List species. Species richness increased significantly with DBH. The indicator species analysis yielded 11 old tree indicators, including *Lobaria pulmonaria* and *Loxospora cristinae*. NMS confirmed the intrinsic nature of the lichens on old trees. Recommendations for action were formulated for forestry to promote these species.

Anlagen ☒ Anhänge und Daten vollständig in diesem Dokument enthalten	digital ☐ Kartenprodukte ☐ Datenbank ☐ Biodiversitätsdaten für BioOffice ☐ Räumliche Daten (GIS-files) ☐ Fotos, Videos ☒ Rohdaten (gescannt, Tabellenform)	analog ☐ Kartenprodukte ☐ Fotos, Videos ☐ Rohdaten (Aufnahmeblätter, Geländeprotokolle etc.)
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Inhalt

Abstract	4
Introduction	4
Methods	5
Lichen sampling	5
Tree variables.....	5
Data storage and analyses	6
Area of investigation	6
Results	8
Species diversity.....	8
Indicator species	11
Sampled trees in the species space	12
Discussion	13
Conclusions.....	15
Acknowledgements	16
Literature	16
Tables and additional data.....	20
List of tree parameters and lichen responses.....	20
List of lichen species	22
Additional figures and data.....	25

Abstract

Apart from the progressive changes in the tree-dwelling lichen world due to global warming, there has been a strong decline in biodiversity for many decades due to the almost comprehensive intensive forestry use of Central European forests. The exhaustive development of even remote forest areas through the construction of forest roads contributes significantly to this. In addition to focusing on economically interesting tree species, emphasis is placed on achieving the highest possible yields. For this reason, trees are usually harvested at or before their optimum phase and are no longer available for epiphytes. The current study uses indicator species analysis and non-metric multidimensional scaling to find out whether old trees harbor specially adapted lichens that are not or very rarely found on younger trees. Two suitable old-growth forests were selected in the Gesäuse National Park and 54 beech trunks were examined for their lichen cover. Of the 113 identified lichen species, 31% are red-listed species, including two lichens threatened with extinction. This study showed that species diversity increases with increasing trunk diameters and decreases slightly after a maximum. The evaluation of the age of the trees yielded similar results. However, the planned calculation of the tree ages from their diameters was associated with very high uncertainties. NMS ordination showed that old or thick trees differed greatly in their lichen composition from young or thin trees. The indicator species analysis yielded a list of 11 species indicative of very old trees, including *Lobaria pulmonaria* and *Loxospora cristinae*, a sterile lichen species recently described from an old-growth forest in Poland. Management measures to promote the endangered forest lichens are provided and politicians are called upon to offer adequate compensation payments.

Introduction

It all began in the summer of 1745, just as Austria was embroiled in the wars of succession, when the oldest common beeches in the Höllboden forest developed their cotyledons and began to grow. Since 2002, these old mixed beech forests have been protected by the Gesäuse National Park and are no longer in use. This protection made it possible to carry out the current study, that crucial depends on the presence of very old trees.

Austria's living forest trees are endowed with a rich lichen flora of around 880 species (HAFELLNER & TÜRK 2016). However, every second species is red listed, which is largely due to the creation of monocultures, clear cutting, the felling of old forests and old trees, especially deciduous species, and the shortening of rotation times (TÜRK & HAFELLNER 1999). It can be concluded that forest trees rarely reach an advanced age due to the above-mentioned threats. Today, 25 years after the publication of the Red List of endangered lichens in Austria, the shortest possible rotation cycles of approx. 90-120 years or after reaching a DBH of 60 cm are recommended for the production of high-quality timber but also for fuelwood (GOTSMY & BAUMGARTNER 2008, NEUMANN & RÖSSLER 2006, RUHM et al. 2016, SCHUSTER 2023, ZWETTLER 2019). This in turn affects the diversity and composition of epiphytic lichens, as there is a pronounced succession of epiphytic lichens from young to old trees (BARKMAN 1958, JOHANNSON et al. 2007). The lack of old and very old trees, as well as forestry activities associated with extensive thinning, currently mean that tree-dwelling lichens with a wider ecological amplitude and a preference for younger trees predominate in large parts of Central Europe, while specialists of the forest interior, old-growth forests, and old trees further decline (compare ARAGÓN et al. 2010, HEDENÅS & ERICSON 2003, NASCIMBENE et al. 2007, PYKÄLÄ 2004, WIRTH et al. 2009). 29 years ago, HANNAH et al. (1995) reported that only 0.2% of temperate broad-leaf forests in Central Europe could be described as undisturbed. As we know, these forests of high continuity and unaltered forest interior environments maintain the highest epiphyte biodiversity (BERGER et al. 2018, CZEREPKO et al. 2021, DYMYTROVA et al. 2013, HAFELLNER & KOMPOSCH 2007, MALÍČEK & PALICE 2013, MALÍČEK et al. 2018,

MALÍČEK et al. 2019, MARMOR et al. 2011, NASCIMBENE et al. 2010, VONDRÁK et al. 2015). Therefore, it is not surprising that about 9% of all epiphytic lichens in Austria are critically endangered (38 species) or already extinct (38 species), since most of them are forest-bound species (HAFELLNER & TÜRK 2016, WIRTH et al. 2009).

The aim of the study was to determine what contribution the different tree age classes have to lichen diversity and whether there are species that only occur in the oldest tree class, which is the most vulnerable due to present forest practices.

Methods

Lichen sampling

Data collection was carried out between August and October 2023, in two forest stands exclusively on common beech (*Fagus sylvatica*). These are located in the Northern Limestone Alps in Austria. For the study Spruce-(fir-)beech forests with the highest possible overall age and homogeneous climatic conditions were selected. The trees to be examined were selected at a minimum distance of 20 meters from each other and so that a comparable area could be sampled per DBH class. For this purpose, completely accessible, vital-looking trees were chosen, that had a more or less straight trunk, an rich lichen cover and no immediately adjacent neighboring trees. The recording area included the lower two meters of each tree. Within this area, all lichen species identified as different were noted and their cover was estimated. Lichenicolous and saprobic fungi were not identified. In order to be able to derive additional ecological statements about species occurrences, the examined trunk area was divided into four 50 cm wide height zones (zone 1...0 - 50 cm from the ground, etc.) and species occurrences were assigned to these zones. For identification purposes about 800 specimens were collected. They are held in the herbarium of the author. Microscopic characters were studied with a Leica MZ6 stereo-microscope (up to $\times 40$ magnification) as well as with a Zeiss Axioscope (up to $\times 1000$ magnification). High performance thin layer chromatography was carried out on 140 specimens, according to the protocol of SCHUMM & ELIX (2015), secondary compound identifications were primarily carried out by comparing the chromatograms of SCHUMM (2016), SCHUMM & ELIX (2015) and ORANGE et al. (2001). Lichen identification was carried out mainly with the identification keys of Wirth (2013b, a), SMITH et al. (2009), and TØNSBERG (1992). Taxa names follow HAFELLNER & TÜRK (2016), NIMIS et al. (2018), and KISTENICH et al. (2018). The Red List status of each species was taken from TÜRK & HAFELLNER (1999).

Tree variables

For each trunk the following parameters were measured, estimated or collected in the field: geolocation (± 8 m), altitude above sea level, species, DBH by perimeter, inclination to direction, percent cover of bryophytes, percent cover of lichens (based on the examined area of 0 – 2 m), and two canopy photos were taken, one on the south and one on the north side with minimal overlap at the zenith (angle of aperture, approximately $63^\circ \times 49^\circ$ (4:3)) for a rough estimation of canopy openness during summer. The contrast between sky and canopy respectively topography was enhanced by applying the ‘blue pane’, the brightness was reduced by 40%, before it was converted into a black and white image by applying a threshold value (126). From these binary images the benchmark ‘% canopy openness’, i.e., percentage of white pixels, was calculated using a Python routine. The values of both photos were averaged (100% means no shading, 0% complete shading).

For the determination of tree ages, a 2-threads Hagl f Increment Borer was used to extract cores from 22 randomly selected trees of all DBH classes. The cores were glued to a wooden plate and finely sanded, so that the annual rings could be counted. Counting was carried out using a stereo microscope.

Data storage and analyses

Data were collected with QField and stored in MS Access; descriptive and basic statistics were done with Statistica 10. Correlations between species diversity and tree parameters were calculated using Pearson Product Moment Correlation. Group formation was tested using Spearman Rank Order Correlations.

Nonmetric multidimensional scaling (NMS) and indicator species analysis (ISA) were performed using PC-ORD 7.10 (KRUSKAL 1964, MCCUNE & MEFFORD 2018), yielding information about the lichen community and its responses to the environment. For NMS analysis, the distance measure was set to S rensen (Bray-Curtis) and the autopilot mode was used.

For Indicator species analysis, species abundance data were used, therefore the concept based on DUFR NE & LEGENDRE (1997) was applied, the indicator values were tested for statistical significance using a Monte Carlo randomization with 4999 permutations (MCCUNE & GRACE 2002). For NMS and indicator species analyses, species with fewer than three occurrences were omitted.

Table 1. List and description of variables

Variable	Scale	Description
Independent variables at trunk level		
Altitude	continuous	in meters above sea level
DBH	continuous	Trunk diameter in breast height in centimeters
Age	continuous	Tree age in years (counted resp. projected where the heartwoods were rotten or missing (hollows trees) rep. calculated for missing data according to the polynomial function (age = 68.3952+2.8501*DBH-0.0111*DBH^2)
Inclination	continuous	Inclination of trunk in the lowest two meters in degrees
Canopy openness	continuous	Canopy gap area in percent (see methods)
Dependent variables, lichen / bryophyte responses		
Species richness	continuous	No of species per tree trunk
No of red-listed species	continuous	Number of species listed in T�RK & HAFELLNER (1999) for the Alps region
Total lichen cover	continuous	Estimated total cover of lichens within the sampled area in percent
Total bryophyte cover	continuous	Estimated total cover of bryophytes within the sampled area in percent

Area of investigation

The study area is located in the ‘Ennstaler Alpen’, a mountain group that is part of the Northern Limestone Alps within the Eastern Alps. The two selected forests, Brucksattel and H llboden, are in the Ges use National Park area (Figure 1). The Brucksattel forest is a near-natural, north-northwest exposed beech (fir) spruce forest with a great dominance of beech, few sycamores and a rich supply of dead wood, especially on the flat slopes or at the base of the 30 - 45  inclined slope. Old spruce trees were largely removed, as can be seen from the dead wood stumps. The investigated part extends from 920 to 1085 meters above sea level and is bordered in the north by the valley Bruckgraben and in the south by a sharp ridge. The H llboden forest lies on a flattening of the upper Hartelsgraben, a north facing valley between the mountains Zin dl and Lugauer. The study area extends from 990 to 1040 meters above sea level and is characterized by near-natural beech (fir) spruce forests, mostly on

rubble or coarse block material. Although beech is dominant there too, there is significantly more spruce and rarely fir mixed in. Both forests belong to the vegetation type *Adenostylo glabrae*-Fagetum (WILLNER & GRABHERR 2007) and the biotope type 'Karbonatschutt Fichten-Tannen-Buchenwald' according to ESSL et al. (2002) and are characterized by a more or less closed canopy structure.

The following climate parameters were taken from the digital climate atlas of Austria for the two forest locations Brucksattel and Höllboden (AUER et al. 2001): 5.55°C / 4.89°C mean annual temperature in degrees Celsius, 136 / 174 days of snow cover per year when snow height exceeds 1 cm, 81 h / 70 h absolute sunshine time in hours in January when values exceed 120 W/m², 7.5 hPa / 6.6 hPa mean annual vapor pressure, 1715 l/m² / 1973 l/m² corrected annual precipitation in liters per square meter.

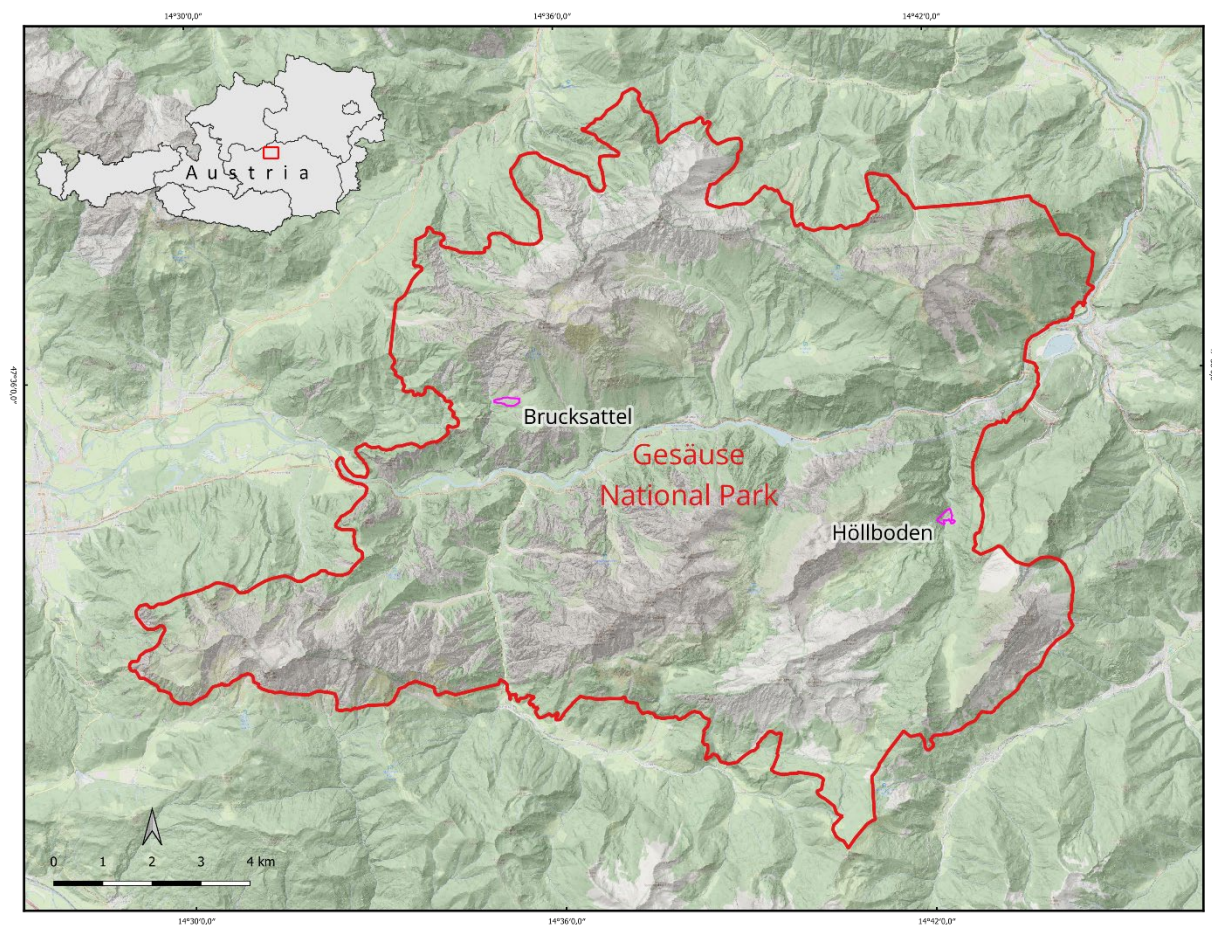


Figure 2. Area of investigation within the Gesäuse National Park, Ennstaler Alpen, Northern Limestone Alps, Austria.

Results

Species diversity

In total 54 trunks of *Fagus sylvatica* were sampled, 35 in the Brucksattel forest and 19 in the Höllboden forest. The altitude of the trees examined was between 930 and 1085 m above sea level (average 1006 m). Tree trunks were mainly vertical, ranging from 0 to 9° (mean 1°). The total sample area was 240 m², ranging from 0.9 to 10.9 m². The mean sample area was 4.4 m². Most tree trunks were shaded by a dense canopy, which was reflected in the canopy openness values ranging from 2.2 to 14.3% (mean 6.8%). Tree trunk diameters ranged between 7 and 87 cm with a mean of 35.4 cm. Tree age ranged from 85 to 278 years (mean 150 years). The original plan was that the tree age of a few trees would be checked using drill cores and would be extrapolated for the others according to the DBH. However, the first evaluated drill cores already showed that the thickness of a tree could not reliably estimate its age; e.g., tree no 31, a small understory tree measuring 19 cm DBH, revealed a cored age of 250 years. For this reason, a total of 22 cores were extracted. Overall, a significant age range was found, particularly in the larger tree diameters (see Figure 2). The annual ring increment in total was very low but varied greatly between 0.4 and 2.5 mm (mean 1.3 mm $\pm$ 0.5 Std. Dev.). Since age was not determined for all trees, trunk diameter at breast height was used as the primarily parameter to form groups that included all trees. The 54 trees surveyed were divided into four groups according to their DBH, in order to analyze species richness (see Table 2).

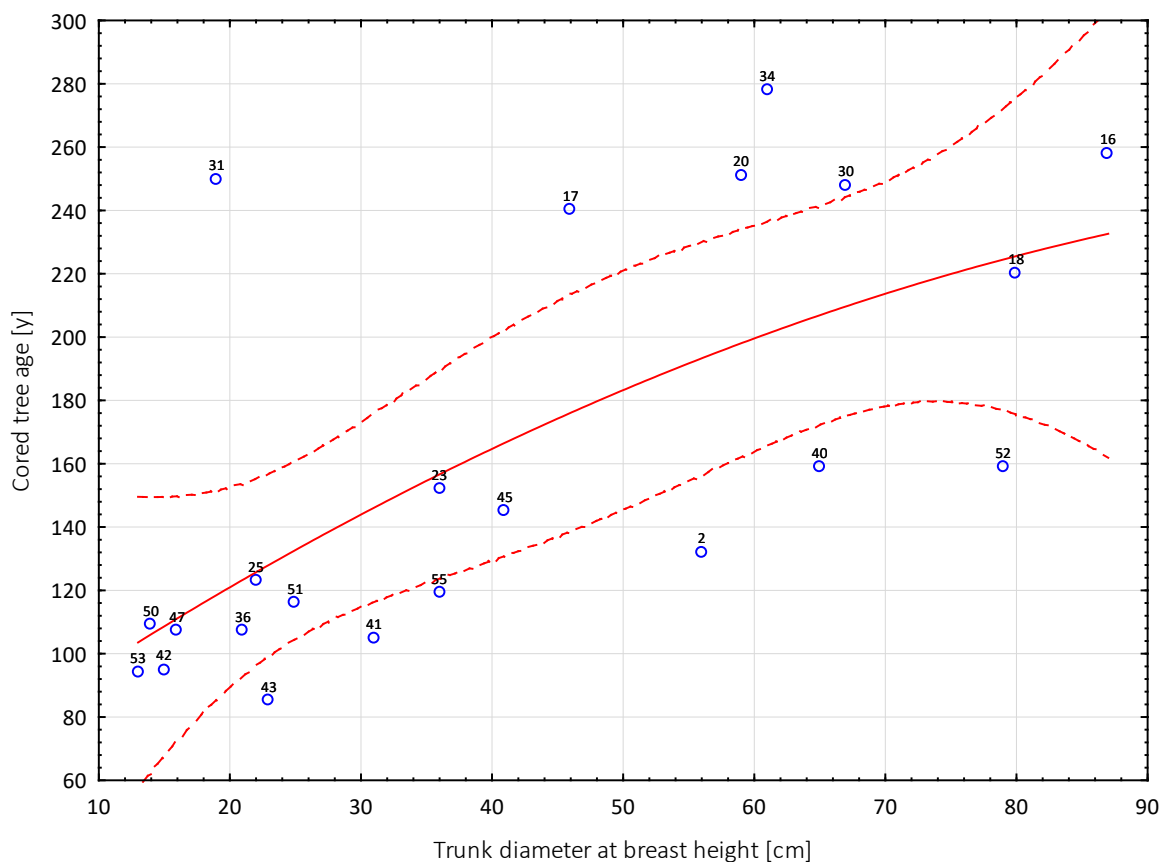


Figure 3. Relationship between trunk diameter and cored tree age, polynomial fit and 95% confidence interval. Point labels are tree numbers.

113 lichen species were identified to species level, the following three identifications of sorediate and sterile crusts remain uncertain: *Lecanora* cf. *expallens*, *Lecidella* cf. *scabra* and *Lepraria* cf. *obtusatica*. The secondary substances detected in *Lecanora* cf. *expallens* differ somehow from the original description, and those of *Lecidella* cf. *scabra* remained unclear after HPTLC. *Lepraria* cf. *obtusatica* showed an additional anthraquinone, that it should not. The distinction between *Pertusaria leioplaca* and *Pertusaria alpina* was rather unsatisfactory, because the separation between 4- and 8-spore asci mentioned in the identification keys was by no means comprehensible in nature. Instead, asci with varying numbers of ascospores were usually found in the hymenia; e.g., 3 - 4, 4 - 6, 4 - 8, 6 - 8 but also other combinations, so that all combinations with 7 or 8 spore asci were referred to as *Pertusaria alpina*. In each location, Brucksattel and Höllboden, 89 lichen species were detected.

The most frequently observed lichens were *Phlyctis argena* (91%), *Strigula stigmatella* (81%), and *Graphis scripta* (76%), followed by *Pyrenula nitida*, and *Zwackhia viridis* with 65% each. Other very common species were *Lecanora argentata* (59%), *Arthonia didyma* (57%), *Peltigera praetextata* (50%), and *Lepraria finkii* (46%). A bulk of 33 species could only be found once (see Table 4).



Figure 4. Height zone 3 of a medium-sized beech in the Höllboden forest, which is completely covered with crustose lichens in this area (Tree no 21, 31 cm DBH, calculated age 146 years). Photo: © H. Komposch

35 lichen species (31%) were red-listed and show varying degrees of endangerment within the Alps. Two of them, *Agonimia allobata* and *Sticta fuliginosa* are critically endangered. 25 species are endangered, namely *Bacidia circumspecta*, *Biatora ocelliformis*, *Catinaria atropurpurea*, *Gyalecta derivata*, *Lecanora expallens*, *Lecidella* cf. *scabra*, *Lepra ophthalmiza*, *Lobaria pulmonaria*, *Lopadium*

disciforme, *Mycobilimbia carneoalbida*, *Mycobilimbia epixanthoides*, *Mycoblastus sanguinarius*, *Nephroma parile*, *Nephroma resupinatum*, *Pannaria conoplea*, *Parmeliella triptophylla*, *Parmelina pastillifera*, *Peltigera collina*, *Pertusaria alpina*, *Pertusaria pertusa* var. *pertusa*, *Pyrenula laevigata*, *Pyrrhospora quernea*, *Rinodina albana*, *Sticta sylvatica*, *Strigula stigmatella* var. *stigmatella*. Eight are vulnerable: *Bacidia viridifarinoso*, *Biatora globulosa*, *Fuscidea pusilla*, *Lecanora horiza*, *Naetrocymbe fraxini*, *Ochrolechia androgyna*, *Ropalospora viridis*, and *Toniniopsis subincompta*.

Table 2. Basic statistics for trees grouped by DBH class (all lichens included). Mean values are given with Standard Deviation ($\pm$ Std. Dev.). Asterisks mark significant differences between means (T-Test for independent samples). Annotation 1: Grouping by tree age resulted in rather different subsamples of trees, because DBH and age did not correspond well.

DBH class	1	2	3	4
Min. – max. DBH [cm]	7 – 27	> 27 – 47	> 47 – 67	> 67 – 87
Mean DBH [cm]	18.1 $\pm$ 5.7	* 36.3 $\pm$ 5.2	* 59 $\pm$ 5.3	* 79.5 $\pm$ 4.8
Mean age [y] ¹⁾	117 $\pm$ 31	154 $\pm$ 31	205 $\pm$ 50	217 $\pm$ 32
No of trees	27	13	8	6
Total sampled area [m ²]	61.4	59.3	59.3	59.9
Mean inclination [°]	0.9 $\pm$ 2.0	0.8 $\pm$ 2.0	1.8 $\pm$ 3.4	1.2 $\pm$ 2.9
Mean altitude [m]	999 $\pm$ 32	1019 $\pm$ 30	1003 $\pm$ 47	1017 $\pm$ 26
Mean canopy openness [%]	5.9 $\pm$ 2.0	7.2 $\pm$ 2.0	7.2 $\pm$ 3.1	9.7 $\pm$ 3.4
Mean total lichen cover [%]	67.8 $\pm$ 25.8	61.2 $\pm$ 18.6	66.4 $\pm$ 24.6	50.8 $\pm$ 16.3
Mean total bryophyte cover [%]	18.3 $\pm$ 19.5	25.1 $\pm$ 21.4	23.3 $\pm$ 20.1	35.8 $\pm$ 11.1
Mean no of taxa	12.3 $\pm$ 3.6	* 18.2 $\pm$ 5.0	21.0 $\pm$ 8.7	20.8 $\pm$ 5.7
Mean no of red listed taxa	2.5 $\pm$ 1.3	* 4.6 $\pm$ 2.4	4.6 $\pm$ 1.6	4.0 $\pm$ 2.1

Table 3. Pearson correlation coefficients among all trees for independent and dependent variables: species richness, number of red listed species, total bryophyte, and total lichen cover. Marked correlations are significant at $p < .05$, $N = 54$. Further significant correlations were seen between altitude and canopy openness ($r = 0.44$), and total bryophyte and total lichen cover ($r = -0.619$).

Variable	Species richness	No of red listed taxa	total bryophyte cover	total lichen cover
Altitude	0,125533	0,061505	0,191084	-0,281933*
DBH	0,561390*	0,384296*	0,350165*	-0,185499
Age	0,281062*	0,343879*	0,167562	-0,031788
Trunk inclination	0,142944	-0,144003	0,346146*	-0,149960
Canopy openness	0,133166	0,096185	0,247312	-0,284912*

Lichen species richness showed the strongest positive correlation with trunk diameter, although the polynomial fit revealed a weak decrease at trunk diameters larger than 60 cm. This slight decrease could not be detected when comparing tree age and lichen diversity (compare Figure 4). However, it is most likely due to the increasing moss cover on larger trees, which is positively correlated with DBH and restricts the space for lichens (see Table 3). A significant positive correlation was also found between the occurrence of Red List species and the trunk diameter; here, the curve flattened at approximately 50 cm DBH and decreased slightly in the area of higher trunk diameters (see Figure 3). Regarding DBH classes, a significant increase in species richness was found between classes 1 and 2, which was independent of the bark area investigated, as this was more or less the same for all classes. Species diversity increased further between classes 2 and 3 and remained similarly high in class 4. For Red List species the increase was pronounced between classes 1 and 2, then stayed at the same level in class 3 and slightly decreased in DBH class 4 (see Table 2).

Total bryophyte cover increased not only with increasing DBH but with stem inclination. On the other hand, total lichen cover decreased with increasing bryophyte coverage and showed a small decrease

with increasing altitude and canopy openness, which could not be explained. Species richness was independent from total lichen cover (see Table 3).

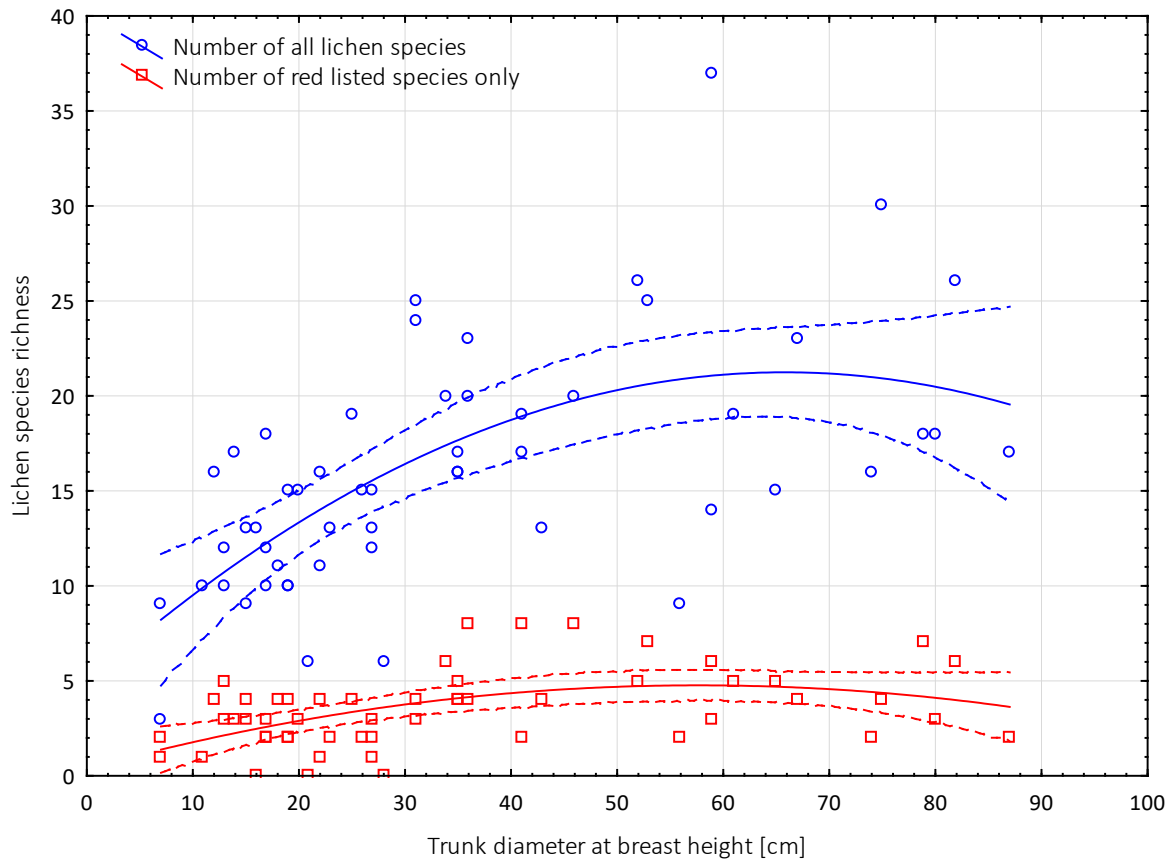


Figure 5. Lichen species richness of all or only the red listed species versus trunk diameter at breast height. Polynomial fit according to the equations: species richness = $4.9289 + 0.4959 \cdot \text{DBH} - 0.0038 \cdot \text{DBH}^2$, red listed species = $0.382 + 0.1519 \cdot \text{DBH} - 0.0013 \cdot \text{DBH}^2$; 95% confidence intervals shown.

Indicator species

The analysis of indicator species for **DBH classes** 1 – 4 revealed 11 significant indicator values in total. For DBH class 1 (7–27 cm) *Naetrocymbe fraxini* was the only calculated indicator species with the highest indicator value. In DBH class 2 (> 27–47 cm) the only indicator species was *Loxospora elatina*. Most indicator species were found for DBH class 3 (> 47–67 cm), viz. *Parmelia sulcata*, *Platismatia glauca*, *Varicellaria hemisphaerica*, *Parmelia saxatilis*, *Parmelina pastillifera*. For DBH class 4 (> 67–87 cm) four indicator species could be extracted: *Opegrapha vulgata*, *Lecanora* cf. *compallens*, *Lecanora horiza*, and *Loxospora cristinae*.

A second ISA was performed using the DBH-derived and the cored **age** for grouping. Both groupings, DBH and age classes, were therefore correlated with each other (Spearman $R = 0.4$ redo, $p < 0.05$). Group 1 and 2 were established to correspond to forestry recommendations and group 3 to grasp the detected outliers. This group was excluded from ISA. The groups were defined as follows; age class 1: 85 – 120 y and $\text{DBH} < 60$ cm (21 trees), age class 2: > 120 – 278 y and $\text{DBH} \geq 60$ cm (9 trees), age class 3 for trees, that did not fall into either the first or the second group: > 120 y but $\text{DBH} < 60$ cm (24 trees) or < 120 y but $\text{DBH} > 60$ cm (0 trees). This grouping resulted again in 11 indicator species reaching a significance level of $p < 0.03$. Two indicator species were found in age class 1: *Pseudosagedia aenea* and *Naetrocymbe fraxini*, and nine in age class 2: *Lecanora* cf. *compallens*, *Lecanora horiza*, *Cetrelia monachorum*, *Pertusaria coronata*, *Peltigera praetextata*, *Pyrenula nitida*,

Lobaria pulmonaria, *Melanelixia glabratula*, and *Varicellaria hemisphaerica* (for complete list see Table 8).

A third ISA was carried out to statistically prove the **height zonation** within the lower two stem meters, which was obvious in the field. In total, 13 lichen species were indicative for certain height zones. Most indicator species were found for the lowest height zone 1 (0 – 50 cm), namely *Strigula affinis*, *Pyrenula nitida*, *Peltigera praetextata*, *Lepraria finkii*, *Cladonia pyxidata*, *Peltigera degenii*, *Coenogonium pineti*, *Cladonia coniocraea*, and *Toniniopsis subincompta*, ranked by decreasing significance. Height zone 2 (> 0.5 m – 1 m) revealed no indicator species. For height zone 3 (> 1 – 1.5 m), *Lecanora argentata*, *Arthonia radiata*, and *Ramalina farinacea* were indicative. *Parmelia saxatilis* was weakly indicative for height zone 4 (> 1.5 – 2 m).

With 67 (20 red-listed) species recorded, height zone 1 was the area with the lowest total number of species. Species richness increased to 79 species (24 red-listed) in height zone 2, was slightly higher in height zone 3 with 82 species (23 red-listed), and finally decreased to 76 species (20 red-listed) in the uppermost height zone 4 (see Table 6).

Sampled trees in the species space

NMS was used to show patterns in species distributions and thus similarities in the sampled trees, that were not detected by basic statistics. The distance-based coefficient of determination in the 79-dimensional species space (54 trees x 79 species) represented a total of 67% variation of the original data (axis 1 $r^2 = 35.4\%$, axis 2 $r^2 = 18.6\%$, axis 3 $r^2 = 13.1\%$). The two-dimensional ordination graph presented in Figure 4 shows 54 beech trees in the species space. From an overview perspective, small DBH classes cluster on the left side and lower parts, whereas high DBH are found in the upper right area. Species richness was strongly correlated to axis 1, which means that small trees normally have lower, large trees have higher species diversity. Along with species richness, the total bryophyte cover vector points in the same direction, which shows that moss cover increases as trees get larger. Tree age and tree diameter are correlated with the first two axes, they both point to the upper right, but their directions differ slightly. The graph shows some trees of DBH class 3 (tree no 11, 30, 20) and of DBH class 2 (tree no 19, 45) right and above those of DBH class 4, indicating some hidden variance either in the way of DBH grouping or in the overlaying age. Tree 31 stands out due to its high age and low DBH, same might be true for trees 19 and 46.

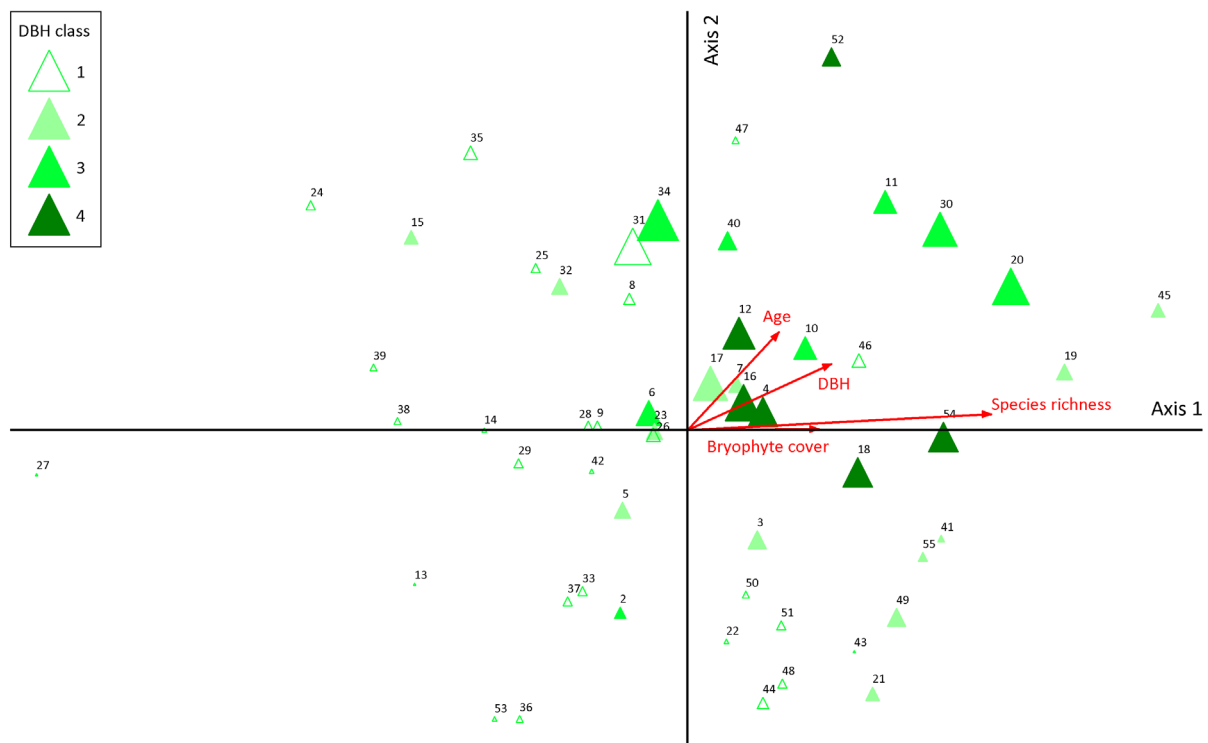


Figure 6. NMS joint plot of sampled trees (tree numbers 2-55) in the species abundance space ($n = 79$ species) grouped by DBH classes (color) and overlaid by tree age (size of triangles). Displayed vectors are variables, that are correlated with ordination scores. Axis 1 and 2 represent 54% of the total variance in species composition.

Discussion

This study adds empirical data demonstrating that lichen species diversity on beech trunks increases with tree age, which had to be approximated by the tree diameter at breast height. Similar results had been reported by, e.g., DMYTROVA et al. (2013), ELLIS & ELLIS (1997), FRIEDEL et al. (2006), JOHANNSON et al. (2007), LIE et al. (2009), MATTEUCCI et al. (2012), MEŽAKA et al. (2012), NASCIMBENE et al. (2012), NIRHAMO et al. (2023), SCHEI et al. (2012). This is particularly true for red-listed species. One reason for this change in species richness and composition with the age of a tree is linked to the change in water capacity of the bark (BARKMAN 1958, ELLIS & EATON 2021). The changes in water interception capacity were in turn lined by ILEK & KUCZA (2014) to changes in bark texture, which they examined in various tree species. For common beech, however, the smallest change was observed.

It could be shown that the increase of species richness was not only due to the larger sampling area for thick trees, at least for the first two DBH classes (see Table 2). Based on species composition alone, a grouping of large trees was also evident using NMS (see Figure 4). Indicator species analysis revealed that thick and old beech trees (> 120 years or > 60 cm) have a unique set of lichens that are not or very rarely found on thinner or younger trees. The reasons for this are attributed to the increasingly rough and cracked bark texture on old trees, which could not be fully measured and assessed in the field because large parts of the bark were hidden under a dense cover of moss or lichen. Other bark parameters such as water capacity and pH could also be involved, but were not collected in this instance (compare BARKMAN 1958).

The distribution of lichens within the two stem meters surveyed was not uniform, but showed a pronounced height zonation. This was confirmed by ISA, particularly for the lowest 50 cm, where most of the indicator species were found. The reasons for this probably lie in the uniqueness of this area: the base of the trunk or the roots are usually much wider, i.e., not vertical, but characterized by

sloping surfaces, and the otherwise smooth beech bark soon cracks here due to secondary thickness growth, even in younger trees. The zone is close to the ground and therefore more humid than those above, and it receives the nutrient-enriched stem runoff from the entire trunk above. It is the oldest part of the tree and often shows sabre growth in sloping terrain, creating overhanging microhabitats on the slope side and very flattened microhabitats on the uphill side. In older trees, cavities often form between the roots, which in turn have a very specific microclimate, and the lowest altitude zone is most frequently damaged by falling rocks or animal activity (see Figure 6). Height zone 1 has the densest moss cover (not surveyed), which is why some moss-dwelling lichens, such as *Peltigera*, *Cladonia* species, and *Strigula stigmatella*, occur here with a particularly high level of consistency. *Pyrenula nitida* is also a very constant indicator species in the lowest height zone; it grows on moss-free bark. NMS showed a high overlap of species, especially in the upper three altitudinal zones (see Figure 6). The fact that a large portion of the lichen diversity can survive on the tree stumps after a clear cutting, as HÄMÄLÄINEN et al. (2015) have stated for Scots pine forests in Finland, would not apply to the studied beech forests. 41% of the lichen diversity would be immediately lost through clear cutting. The survival of the species remaining on the stump is by no means guaranteed by the drastic habitat change. For these reasons, the forestry practice of clear cutting is not considered effective in terms of preserving the biodiversity of lichens in mixed beech forests.



Figure 7. The lower and moss-covered trunk of a large *Fagus sylvatica* in the Brucksattel forest (Tree no 4, 74 cm DBH, calculated age 219 years). The sloping root runs form a wide variety of small habitats, such as cavities, sloping and vertical surfaces with different exposures. The bark alternates between smooth and cracked and has additional structures in the area of injuries. Photo © H. Komposch

The analysis of the tree cores yielded surprising results. The assumption that tree age within a stand or similar stands could be derived as a linear function of tree diameter proved to be incorrect. Although the fitting function was nearly linear, half of the 22 cored tree ages were outside the 95% regression bands (see Figure 2). Competition and locally and temporarily changing growth conditions appear to have a very large influence on thickness growth and were thought to account for the high variance. Due to this high variability, age differences between DBH classes were not significant (see Table 2) and the indicator species analysis detected only four species in the highest DBH class. However, since the aim of the study was to be able to make statements about age classes and their lichen diversity, these were formed for another indicator species analysis. A reduced set of trees was used to create two age classes corresponding to those mentioned in the forestry recommendations. Nine species were found to indicate the highest class, including *Lobaria pulmonaria*, the flagship species of the Lobarion pulmonariae OCHSNER 1927, the alliance of oceanic and ancient broadleaved forests. Two of them, *Lecanora* cf. *expallens* and *Lecanora horiza*, were also recognized as indicators of the largest trunk diameters (DBH class 4), *Loxospora cristinae*, and *Opegrapha vulgata* are also included in the set of old tree indicators. *Loxospora cristinae* was first described in 2018 and reported for Austria from the Rothwald primeval forest (Lower Austria) in the same year; therefore, there is no Red List entry for this sorediate species (BERGER et al. 2018, GUZOW-KRZEMIŃKA et al. 2018). The records of this species in the Gesäuse National Park are the first for the province of Styria. The species is considered rare, but this could also be due to its late first description and purely chemical distinctiveness.

Together with *Lobaria pulmonaria*, a considerable list of endangered lichen species belonging to the Lobarion alliance occur, such as *Catinaria atropurpurea*, *Nephroma parile*, *Nephroma resupinatum*, *Parmeliella triptophylla*, *Peltigera collina*, *Pertusaria pertusa* var. *pertusa*. Although they were not statistically significant as indicators for old trees, probably due to the low number of occurrences and the low numbers of old trees sampled, they are also at risk from short rotations, even by single-stem removal.

Conclusions

This study of epiphytic lichens on common beech in montane spruce (fir) beech forests adds to the body of data showing that species richness and composition change with tree age, and that old trees have a set of specific lichen species that is not present on young trees. The increase in epiphytic lichens is also reflected in an increase in endangered species.

From these findings, the following recommendations for measures to promote the biodiversity of epiphytic lichens in managed forests can be derived: 1) Retention of some old trees per hectare as part of the preferred forestry practice of selective logging. Similar management recommendations are given by AUDE & POULSEN (2000), FRIEDEL et al. (2006), HEDENÅS & ERICSON (2003), NASCIBENE et al. (2007), and RUDOLPHI et al. (2014) and are summarized in NASCIBENE et al. (2013). 2) Retention of patches of old-growth and large trees in forest practices that involve larger clearings, e.g., clear cutting, shelterwood cutting, hem felling (LIE et al. 2009, RUDOLPHI et al. 2014). 3) The extension of rotation times in clear cutting forestry practices, which is strongly opposed. Thinning the canopy by as little as 50% can affect the growth of sensitive forest species such as *Collema furfuraceum* (see HEDENÅS & ERICSON 2003).

A call is made to society to shape the funding environment in such a way that the urgently needed measures to meet biodiversity targets are also economically feasible for forest companies. In any case, the success of these measures should also be scientifically verified.

The scientific community is called upon to provide the basis for such monitoring, for example by compiling an up-to-date and continuously updated Red List of endangered lichens, which can be accessed online.

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Tables and additional data

List of tree parameters and lichen responses

Table 4. List of tree parameters collected in the field or derived. Abbreviations mean: DBH...Diameter at breast height, Age calc. ...calculated age (polynomial function), threat. ...threatened (red-listed), Alt. ...Altitude above sea level, Bry. cov. ...total bryophyte cover, Lich. cov. ...total lichen cover, Incl. ...Inclination in degrees.

Tree no	DBH [cm]	DBH class	Age cored [y]	Age calc. [y]	Age class	No of Taxa	No of threat. Taxa	Alt. [m]	Bry. cov. [%]	Lich. cov. [%]	Incl. [°]	Date	Collectors	Canopy openness [%]	Longitude [decimal degrees, E]	Latitude [decimal degrees, N]	Location
2	56	3	132	132	3	9	2	1080	40	25	0	17.08.2023	HK & LK	9,39	14,58732771	47,59496343	Brucksattel
3	43	2		170	3	13	4	1085	50	50	0	17.08.2023	HK & LK	8,21	14,58734749	47,59483726	Brucksattel
4	74	4		219	2	16	2	1060	45	30	7	17.08.2023	HK & LK	9,93	14,58697599	47,59511954	Brucksattel
5	35	2		155	3	16	4	1050	5	75	0	17.08.2023	HK & LK	11,76	14,58727751	47,59533389	Brucksattel
6	59	3		198	3	14	3	1050	10	70	0	17.08.2023	HK & LK	8,77	14,58674646	47,59534669	Brucksattel
7	35	2		155	3	17	4	1050	18	80	0	17.08.2023	HK & LK	8,08	14,58649387	47,59521798	Brucksattel
8	26	1		135	3	15	2	1060	25	75	8	17.08.2023	HK & LK	10,95	14,58605468	47,59503774	Brucksattel
9	17	1		114	1	12	3	1000	50	45	0	17.08.2023	HK & LK	6,09	14,58456819	47,59545159	Brucksattel
10	53	3		188	3	25	7	985	46	46	5	17.08.2023	HK & LK	11,4	14,58496822	47,59556585	Brucksattel
11	52	3		187	3	26	5	1020	10	80	0	05.09.2023	HK	10,17	14,588362	47,59610626	Brucksattel
12	82	4		227	2	26	6	1025	40	35	0	05.09.2023	HK	12,75	14,58814709	47,59585434	Brucksattel
13	7	1		88	1	9	2	1000	3	15	0	05.09.2023	HK	6,24	14,58762368	47,59621998	Brucksattel
14	11	1		98	1	10	1	1000	2	10	0	05.09.2023	HK	8,38	14,58739932	47,59602194	Brucksattel
15	28	2		139	3	6	0	1010	10	80	0	05.09.2023	HK	7,13	14,58670318	47,59582988	Brucksattel
16	87	4	258	258	2	17	2	1010	45	55	0	05.09.2023	HK	8,95	14,58612039	47,59556738	Brucksattel
17	46	2	240	240	3	20	8	1005	10	40	0	05.09.2023	HK	4,45	14,58585157	47,59561067	Brucksattel
18	80	4	220	220	2	18	3	980	35	55	0	05.09.2023	HK	14,29	14,58533153	47,59590993	Brucksattel
19	34	2		152	3	20	6	1000	30	50	0	06.09.2023	HK	6,49	14,70534526	47,57300246	Höllboden
20	59	3	251	251	3	37	6	1005	10	90	0	06.09.2023	HK	3,85	14,70343243	47,57223926	Höllboden
21	31	2		146	3	24	4	1010	5	40	0	06.09.2023	HK	4,86	14,70358904	47,57208355	Höllboden
22	12	1		101	1	16	4	1010	8	55	0	06.09.2023	HK	9,43	14,70353669	47,57193803	Höllboden
23	36	2	152	152	3	23	8	1030	5	70	0	15.09.2023	HK	5,31	14,58869022	47,59593089	Brucksattel
24	18	1		116	1	11	4	1040	15	80	0	15.09.2023	HK	5,22	14,58845448	47,59576908	Brucksattel
25	22	1	123	123	3	16	4	1060	10	80	0	15.09.2023	HK	7,78	14,5880577	47,59547005	Brucksattel
26	27	1		137	3	12	2	990	70	20	0	15.09.2023	HK	6,19	14,58629985	47,59590326	Brucksattel
27	7	1		88	1	3	1	995	2	80	0	15.09.2023	HK	4,56	14,58661001	47,59605334	Brucksattel
28	20	1		121	3	15	3	985	30	60	0	15.09.2023	HK	2,18	14,58659086	47,59625911	Brucksattel
29	17	1		114	1	10	2	985	15	80	0	15.09.2023	HK	3,94	14,58628392	47,5962436	Brucksattel
30	67	3	248	248	2	23	4	983	55	45	9	15.09.2023	HK	3,79	14,58602168	47,59628167	Brucksattel
31	19	1	250	250	3	10	4	980	40	55	3	25.09.2023	HK & AF	2,93	14,58562772	47,59622566	Brucksattel
32	35	2		155	3	16	5	975	8	90	0	25.09.2023	HK & AF	5,73	14,58546381	47,5962268	Brucksattel

Tree no	DBH [cm]	DBH class	Age cored [y]	Age calc. [y]	Age class	No of Taxa	No of threat. Taxa	Alt. [m]	Bry. cov. [%]	Lich. cov. [%]	Incl. [°]	Date	Collectors	Canopy openness [%]	Longitude [decimal degrees, E]	Latitude [decimal degrees, N]	Location
33	19	1		119	1	15	2	970	7	90	0	25.09.2023	HK & AF	3,98	14,58527152	47,59607255	Brucksattel
34	61	3	278	278	2	19	5	970	5	85	0	25.09.2023	HK & AF	4,72	14,58445686	47,59579425	Brucksattel
35	27	1		137	3	13	3	980	10	85	0	25.09.2023	HK & AF	4,37	14,58428396	47,59557207	Brucksattel
36	21	1	107	107	1	6	0	940	5	85	0	25.09.2023	HK & AF	5,4	14,58342155	47,59589942	Brucksattel
37	19	1		119	1	10	2	950	3	90	0	25.09.2023	HK & AF	4,72	14,58346834	47,59567001	Brucksattel
38	13	1		104	1	10	3	955	5	95	0	25.09.2023	HK & AF	3,56	14,58302334	47,59569834	Brucksattel
39	15	1		109	1	9	3	940	5	95	0	25.09.2023	HK & AF	5,39	14,58299334	47,59581001	Brucksattel
40	65	3	159	159	2	15	5	930	10	90	0	25.09.2023	HK & AF	5,56	14,58269834	47,59580501	Brucksattel
41	31	2	105	105	1	25	3	1034	20	75	3	28.09.2023	HK	5,24	14,70572001	47,57215167	Höllboden
42	15	1	95	95	1	13	4	1033	5	80	0	28.09.2023	HK	7,94	14,70585168	47,57223167	Höllboden
43	23	1	85	85	1	13	2	1040	65	20	0	28.09.2023	HK	6,53	14,7059102	47,57235743	Höllboden
44	22	1		126	3	11	1	1033	8	90	0	28.09.2023	HK	8,59	14,70611834	47,57223834	Höllboden
45	41	2	145	145	3	19	8	1000	60	60	0	28.09.2023	HK	9,71	14,70513203	47,57324872	Höllboden
46	27	1		137	3	15	1	1000	35	55	5	28.09.2023	HK	5,06	14,70538334	47,57367334	Höllboden
47	16	1	107	107	1	13	0	990	7	90	4	28.09.2023	HK	5,27	14,70553501	47,57385501	Höllboden
48	17	1		114	1	18	2	1000	5	90	0	28.09.2023	HK	6,95	14,7059358	47,57352398	Höllboden
49	41	2		167	3	17	2	1005	45	55	7	02.10.2023	HK	6,54	14,70488743	47,57374723	Höllboden
50	14	1	109	109	1	17	3	1005	20	70	0	02.10.2023	HK	7,24	14,70494314	47,57393097	Höllboden
51	25	1	116	116	1	19	4	1010	38	60	3	02.10.2023	HK	4,8	14,70377888	47,57292619	Höllboden
52	79	4	159	159	2	18	7	1015	35	55	0	02.10.2023	HK	6,91	14,70406332	47,57312278	Höllboden
53	13	1	94	94	1	12	5	1020	5	80	0	02.10.2023	HK	6,62	14,70377334	47,57354501	Höllboden
54	75	4		220	2	30	4	1010	15	75	0	02.10.2023	HK	5,15	14,7038344	47,57314702	Höllboden
55	36	2	119	119	1	20	4	995	60	30	0	02.10.2023	HK	9,89	14,70481334	47,57439167	Höllboden

List of lichen species

Table 5. List of lichen species with corresponding abundances in percent on sampled trees.

[illegible]

Additional figures and data

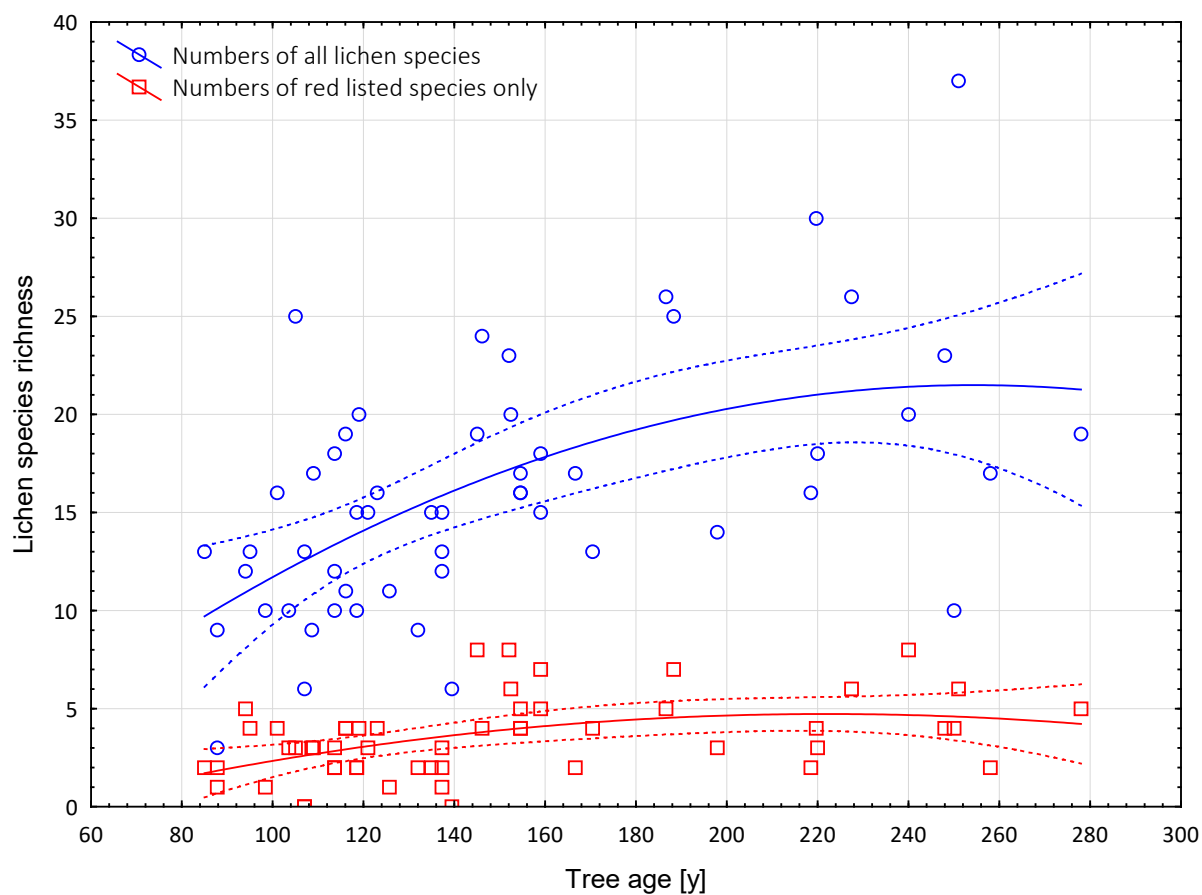


Figure 8. Lichen species richness of all or only the red listed species versus tree age. Polynomial fit according to the equations: species richness = $-5.0777 + 0.2089 \cdot \text{age} - 0.0004 \cdot \text{age}^2$, red listed species = $-3.1976 + 0.0714 \cdot \text{age} - 0.0002 \cdot \text{age}^2$; 95% confidence intervals shown.

Lichen species	No of observ.	Lichen species	No of observ.
Lepraria vouauxii (Hue) R.C.Harris	8	Pertusaria coccodes (Ach.) Nyl. var.	2
Pyrrhospora quereana (Dicks.) Körb.	8	Platismatia glauca (L.) W.L.Culb. &	2
Lepra amara (Ach.) Hafellner	7	Scytinium lichenoides (L.) Otálora,	2
Melanelixia subaurifera (Nyl.)	7	Sticta fuliginosa (Hoffm.) Ach.	2
Peltigera degenii Gyeln.	7	Violella fucata (Stirt.) T.Sprib.	2
Biatorea efflorescens (Hedl.) Räsänen	6	Agonimia globulifera M.Brand &	1
Lepraria elobata Třnsberg	6	Alyxoria varia (Pers.) Ertz & Tehler	1
Menegazzia terebrata (Hoffm.)	6	Amandinea punctata (Hoffm.)	1
Ramalina farinacea (L.) Ach.	6	Arthonia punctiformis Ach.	1
Acrocordia gemmata (Ach.)	5	Bacidia circumspecta (Nyl.) Malme	1
Cladonia coniocraea (Flörke) Spreng.	5	Bacidia rubella (Hoffm.) A.Massal.	1
Coenogonium pineti (Schrad.)	5	Bacidia viridifarinoso Coppins &	1
Gyalecta derivata (Nyl.) H.Olivier	5	Biatorea globulosa (Flörke) Fr.	1
Lopadium disciforme (Flot.) Kullh.	5	Biatorea helvola Körb.	1
Ochrolechia androgyna (Hoffm.)	5	Bilimbia sabuletorum (Schreb.)	1
Agonimia tristicula (Nyl.) Zahlbr.	4	Bryobilimbia hypnorum (Lib.)	1
Bacidina sulphurella (Samp.)	4	Catillaria nigroclavata (Nyl.) J.Steiner	1
Biatorea ocelliformis (Nyl.) Arnold	4	Catinaria atropurpurea (Schaer.)	1
Buellia disciformis (Fr.) Mudd. var.	4	Flavoparmelia caperata (L.) Hale	1
Candelariella reflexa (Nyl.) Lettau	4	Lecanora chlarotera Nyl.	1
Cetrelia cetrarioides (Delise)	4	Lecanora expallens Ach.	1
Lecanora carpinea (L.) Vain.	4	Lecanora impudens Degel.	1
Lecanora horiza (Ach.) Linds.	4	Lecanora thysanophora R.C.Harris	1
Loxospora cristinae Guzew-Krzem.,	4	Lepra ophthalmiza (Nyl.) Hafellner	1
Mycobilimbia epixanthoides (Nyl.)	4	Leptogium saturninum (Dicks.) Nyl.	1
Chaenotheca furfuracea (L.) Tibell	3	Micarea micrococca (Körb.) Gams	1
Collema flaccidum (Ach.) Ach.	3	Mycobilimbia carneoalbida	1
Evernia prunastri (L.) Ach.	3	Mycoblastus sanguinarius (L.)	1
Fuscidea pusilla Třnsberg	3	Nephroma resupinatum (L.) Ach.	1
Lecania croatica (Zahlbr.) Kotlov	3	Parmeliopsis ambigua (Hoffm.) Nyl.	1
Lecanora albella (Pers.) Ach.	3	Parmeliopsis hyperopta (Ach.) Arnold	1
Micarea peliocarpa (Anzi) Coppins	3	Pertusaria pertusa (L.) Tuck. var.	1
Parmelia sulcata Taylor	3	Phaeophyscia endophoenicea	1
Parmelina pastillifera (Harm.) Hale	3	Pyrenula laevigata (Pers.) Arnold	1
Peltigera collina (Ach.) Schrad.	3	Rinodina albana (A.Massal.)	1
Peltigera horizontalis (Huds.) Baumg.	3	Ropalospora viridis (Třnsberg)	1
Agonimia allobata (Stizenb.) P.James	2	Sticta sylvatica (Huds.) Ach.	1
Arthonia spadicea Leight. var.	2	Thelotrema lepadinum (Ach.) Ach.	1
Nephroma parile (Ach.) Ach.	2		
Pannaria conoplea (Ach.) Bory	2		
Parmeliella triptophylla (Ach.)	2		

Table 7. Monte Carlo test of significance of observed maximum indicator value for species according to DBH classes (see Table 4). Indicator species are marked for a significance value (p) of $p < 0.05$. Ordered according to age class and significance level. IV...indicator value.

Lichen species abbreviated	DBH class	IV observed	IV mean randomized	Std. Dev.	p
Art-didy	1	21.9	32.8	9.91	0.8944
Lep-voua	1	7.0	13.6	7.05	0.8824
Art-radi	1	15.6	20.4	7.50	0.6777
Art-spad	1	7.4	8.8	5.08	0.6141
Lec-croa	1	11.1	9.9	5.62	0.3875
Acr-gemm	1	18.5	11.4	6.72	0.1662
Pse-aene	1	37.3	23.1	8.20	0.0676
Pse-rufe	1	26.9	14.4	7.04	0.0628
Nae-frax	1	61.3	24.2	8.74	0.0026
Lec-albe	2	4.4	9.9	5.40	0.9228

Lichen species abbreviated	DBH class	IV observed	IV mean randomized	Std. Dev.	p
Ago-allo	2	5.0	9.0	5.03	0.8728
Lec-elae	2	11.7	17.2	7.23	0.7752
Mic-peli	2	7.1	9.9	5.48	0.6845
Bac-sulp	2	7.8	10.7	6.04	0.6759
Lec-scabra	2	8.7	12.1	6.73	0.5959
Pel-coll	2	8.9	9.9	5.37	0.5147
Lep-ebur	2	14.6	15.3	7.17	0.4361
Phl-arge	2	31.3	31.0	4.26	0.4209
Ram-fari	2	12.9	11.9	6.82	0.3787
Nor-pulc	2	20.7	17.8	7.18	0.2468
Lec-arge	2	30.0	26.3	6.85	0.2378
Lec-intu	2	20.4	16.5	7.43	0.2348
Sti-fuli	2	15.4	9.0	5.40	0.1914
Lop-disc	2	17.0	12.1	6.81	0.1850
Ton-subi	2	21.1	15.6	7.36	0.1724
Vio-fuca	2	15.4	8.9	5.05	0.1424
Bue-gris	2	26.1	17.5	7.47	0.1208
Nep-pari	2	15.4	9.3	4.42	0.0876
Lep-amar	2	25.3	13.5	7.11	0.0720
Lox-elat	2	39.7	18.4	7.44	0.0186
Bue-disc	3	5.0	10.6	6.02	0.9458
Lep-albe-al	3	10.1	16.0	7.51	0.7870
Coe-pine	3	6.5	11.2	6.39	0.7467
Col-flac	3	6.3	9.9	5.58	0.7367
Zwa-viri	3	24.3	29.3	7.41	0.7299
Fus-pusi	3	7.3	10.0	5.62	0.6413
Eve-prun	3	7.7	9.8	5.60	0.6045
Par-trip	3	7.7	9.2	4.64	0.5011
Mel-subaur	3	11.7	12.7	6.97	0.4597
Lep-elob	3	11.3	11.7	6.55	0.4375
Och-andr	3	14.3	11.3	6.65	0.2551
Cla-coni	3	14.2	10.9	6.09	0.2438
Per-alpi	3	26.0	21.2	7.98	0.2302
Pel-prae	3	28.6	23.3	6.57	0.1778
Cla-pyxi	3	25.0	19.5	6.69	0.1750
Bia-effl	3	18.5	12.6	6.93	0.1660
Bia-ocel	3	17.2	10.5	6.06	0.1526
Gra-scri	3	35.5	29.5	5.74	0.1488
Str-stig	3	34.3	29.0	4.51	0.1308
Pyr-nitida	3	34.8	27.1	6.12	0.1144
Mel-glabratu	3	34.9	19.9	8.67	0.0632
Men-tere	3	25.3	12.3	6.89	0.0530
Cet-mona	3	28.1	13.7	7.34	0.0530
Par-past	3	23.6	9.9	5.48	0.0386
Par-saxa	3	33.4	15.3	7.52	0.0352
Var-hemi	3	31.3	14.8	7.10	0.0340
Pla-glau	3	25.0	9.3	4.45	0.0296
Par-sulc	3	37.5	9.8	5.44	0.0024
Pyr-quer	4	7.4	13.8	7.19	0.8608
Per-leio	4	11.8	19.1	8.08	0.8486
Lec-carp	4	6.8	10.6	6.15	0.7620
Can-refl	4	6.8	10.4	5.92	0.6751
Ago-tris	4	6.8	10.4	5.90	0.6651
Gya-deri	4	8.6	11.2	6.35	0.5655
Cha-furf	4	8.8	9.8	5.63	0.5465
Pel-dege	4	11.1	12.5	6.74	0.4947
Cet-cetr	4	10.6	10.9	6.10	0.3557
Myc-epix	4	12.1	10.8	6.41	0.3341

Lichen species abbreviated	DBH class	IV observed	IV mean randomized	Std. Dev.	p
Pan-cono	4	11.4	9.4	4.58	0.2613
Pel-hori	4	12.7	9.7	5.34	0.2054
Scy-lich	4	13.6	9.3	4.61	0.1992
Per-cocc-co	4	12.1	9.2	4.77	0.1858
Per-coro	4	20.0	14.3	7.33	0.1648
Lob-pulm	4	26.3	19.6	7.42	0.1528
Lep-fink	4	35.8	23.0	6.94	0.0556
Lox-cris	4	24.1	10.6	6.10	0.0456
Lec-hori	4	25.5	11.0	6.39	0.0412
Lec-comp	4	31.1	11.4	6.24	0.0186
Ope-vulg	4	40.4	17.7	7.89	0.0168

Table 8. Monte Carlo test of significance of observed maximum indicator value for species according to age classes (see Table 4). Indicator species are marked for a significance value (p) of $p < 0.05$. Ordered according to age class and significance level. IV...indicator value.

Lichen species abbreviated	DBH class	IV observed	IV mean randomized	Std. Dev.	p
Fus-pusi	1	4.8	6.7	2.94	1.0000
Lec-albe	1	4.8	6.7	2.93	1.0000
Lec-elae	1	10.7	18.5	7.53	0.9214
Bue-disc	1	9.0	14.5	6.44	0.9050
Lep-ebur	1	13.4	20.5	7.60	0.9014
Lep-voua	1	8.0	14.3	6.28	0.8934
Lox-elat	1	12.4	20.9	7.93	0.8932
Lep-amar	1	9.5	9.7	4.49	0.7866
Bac-sulp	1	9.5	9.6	4.31	0.7846
Art-spad	1	9.5	9.4	4.60	0.7760
Mel-subaur	1	10.7	14.3	6.11	0.7317
Lec-carp	1	10.5	14.1	6.54	0.7281
Ton-subi	1	17.5	20.7	7.77	0.6705
Zwa-viri	1	41.7	47.1	9.11	0.6615
Art-radi	1	26.5	28.7	8.64	0.6257
Acr-gemm	1	9.5	9.9	3.95	0.5687
Lep-elob	1	9.5	9.8	3.90	0.5557
Lec-croa	1	14.3	11.9	5.53	0.5251
Art-didy	1	50.7	43.7	9.50	0.2515
Pse-rufe	1	23.8	17.0	7.09	0.2338
Phl-arge	1	58.2	52.8	6.05	0.1878
Bue-gris	1	33.3	20.4	7.55	0.1086
Pse-aene	1	63.5	38.2	9.54	0.0190
Nae-frax	1	61.9	33.1	9.42	0.0082
Bia-ocel	2	6.0	11.7	6.02	1.0000
Cha-furf	2	7.8	9.8	3.81	1.0000
Cla-coni	2	6.0	11.7	5.86	1.0000
Men-tere	2	7.8	9.8	3.82	1.0000
Och-andr	2	7.8	9.9	3.93	1.0000
Ram-fari	2	7.8	9.8	3.85	1.0000
Gya-deri	2	6.8	11.9	5.89	0.8422
Cla-pyxi	2	15.6	22.3	7.52	0.7898
Cet-cetr	2	8.4	9.8	3.86	0.7820
Mic-peli	2	9.5	9.7	4.19	0.7796
Str-stig	2	42.9	47.4	7.24	0.7007
Coe-pine	2	7.8	11.6	5.93	0.6851
Lec-arge	2	36.9	40.1	8.17	0.5825
Per-alpi	2	19.9	22.7	8.00	0.5411
Lox-cris	2	15.6	14.1	6.52	0.5281
Lep-albe-al	2	16.7	16.6	6.97	0.4093

Lichen species abbreviated	DBH class	IV observed	IV mean randomized	Std. Dev.	p
Per-leio	2	22.4	22.5	7.67	0.3913
Gra-scri	2	47.0	44.3	8.87	0.3365
Par-trip	2	11.1	6.7	2.94	0.3093
Lop-disc	2	11.1	6.7	2.93	0.3055
Par-sulc	2	11.1	6.7	2.93	0.3055
Pel-hori	2	11.1	6.7	2.92	0.3029
Bia-effl	2	11.1	6.7	2.91	0.3003
Myc-epix	2	11.1	6.7	2.91	0.3003
Pel-coll	2	11.1	6.7	2.91	0.3003
Per-cocc-co	2	11.1	6.7	2.91	0.3003
Scy-lich	2	11.1	6.7	2.91	0.2985
Par-past	2	11.1	6.6	2.90	0.2971
Ago-tris	2	11.1	6.6	2.90	0.2961
Can-refl	2	11.1	6.6	2.90	0.2961
Col-flac	2	11.1	6.6	2.90	0.2961
Pan-cono	2	11.1	6.6	2.90	0.2961
Lep-fink	2	39.1	35.5	8.60	0.2885
Pyr-quer	2	23.3	18.7	7.17	0.2873
Nor-pulc	2	23.3	16.4	6.42	0.2833
Lec-intu	2	30.4	21.3	7.70	0.1370
Ope-vulg	2	39.9	26.8	8.65	0.1066
Lec-scabra	2	22.2	9.4	4.33	0.0792
Pel-dege	2	25.2	14.3	6.31	0.0708
Par-saxa	2	30.1	19.0	7.32	0.0644
Lec-comp	2	33.3	12.3	5.39	0.0242
Lec-hori	2	33.3	12.1	5.69	0.0240
Cet-mona	2	33.3	12.0	5.58	0.0186
Per-coro	2	46.5	18.6	7.18	0.0044
Pel-prae	2	61.5	29.4	7.89	0.0038
Pyr-nitida	2	70.9	40.4	8.42	0.0026
Lob-pulm	2	61.1	22.5	7.96	0.0022
Mel-glabratu	2	64.9	23.7	8.20	0.0006
Var-hemi	2	66.7	18.3	7.17	0.0002

Table 9. Alphabetic list of lichen species and their summed occurrences in the different height zones 1 – 4 (hz), independent of DBH and age, thus much biased by the high number of young/small trees.

Lichen species	hz 1	hz 2	hz 3	hz 4
Acrocordia gemmata (Ach.) A.Massal. var. gemmata	1	2	1	3
Agonimia allobata (Stizenb.) P.James	2	0	0	0
Agonimia globulifera M.Brand & Diederich	1	0	0	0
Agonimia tristicula (Nyl.) Zahlbr.	2	1	2	1
Alyxoria varia (Pers.) Ertz & Tehler	0	1	1	0
Amandinea punctata (Hoffm.) Coppins & Scheid.	0	0	0	1
Arthonia didyma Körb.	11	22	22	17
Arthonia punctiformis Ach.	0	0	0	1
Arthonia radiata (Pers.) Ach.	0	7	15	11
Arthonia spadicea Leight. var. spadicea	1	1	1	0
Bacidia circumspecta (Nyl.) Malme	1	1	0	0
Bacidia rubella (Hoffm.) A.Massal.	1	0	1	0
Bacidia viridifarinoso Coppins & P.James	0	0	1	1
Bacidina sulphurella (Samp.) M.Hauck & V.Wirth	1	2	4	3
Biatora efflorescens (Hedl.) Räsänen	3	3	3	1
Biatora globulosa (Flörke) Fr.	0	1	0	0
Biatora helvola Körb.	1	0	0	0
Biatora ocelliformis (Nyl.) Arnold	2	1	1	0
Bilimbia sabuletorum (Schreb.) Arnold var. sabuletorum	1	0	0	0
Bryobilimbia hypnorum (Lib.) Fryday, Printzen & S.Ekman	1	0	0	0

Lichen species	hz 1	hz 2	hz 3	hz 4
Buellia disciformis (Fr.) Mudd. var. disciformis	0	0	3	3
Buellia griseovirens (Turner & Borrer) Almb.	1	11	12	10
Candelariella reflexa (Nyl.) Lettau	0	2	3	2
Catillaria nigroclavata (Nyl.) J.Steiner	0	1	1	1
Catinaria atropurpurea (Schaer.) Vězda & Poelt	1	0	0	0
Cetrelia cetrarioides (Delise) W.L.Culb. & C.F.Culb.	0	2	4	4
Cetrelia monachorum (Zahlbr.) W.L.Culb. & C.F.Culb.	0	3	8	7
Chaenotheca furfuracea (L.) Tibell	3	0	0	0
Cladonia coniocraea (Flörke) Spreng.	5	2	0	0
Cladonia pyxidata (L.) Hoffm.	17	7	1	1
Coenogonium pineti (Schrad.) Lücking & Lumbsch	5	0	0	0
Collema flaccidum (Ach.) Ach.	3	0	0	0
Evernia prunastri (L.) Ach.	0	0	3	3
Flavoparmelia caperata (L.) Hale	0	0	0	1
Fuscidea pusilla Tønsberg	0	0	0	2
Fuscidea pusilla Tønsberg	0	1	3	0
Graphis scripta (L.) Ach. s.lat.	16	28	28	28
Gyalecta derivata (Nyl.) H.Olivier	4	2	0	0
Lecania croatica (Zahlbr.) Kotlov	2	2	2	1
Lecanora albella (Pers.) Ach.	1	2	2	1
Lecanora argentata (Ach.) Malm	1	16	27	16
Lecanora carpinea (L.) Vain.	0	1	3	3
Lecanora cf. compallens Herk & Aptroot	2	1	3	2
Lecanora chlarotera Nyl.	0	0	0	1
Lecanora expallens Ach.	0	0	1	1
Lecanora horiza (Ach.) Linds.	0	1	3	3
Lecanora impudens Degel.	0	0	1	1
Lecanora intumescens (Rebent.) Rabenh.	0	6	9	9
Lecanora sp.	0	3	3	3
Lecanora thysanophora R.C.Harris	0	1	1	0
Lecidella cf. scabra (Taylor) Hertel & Leuckert	0	5	5	4
Lecidella elaeochroma (Ach.) M.Choisy forma elaeochroma	0	4	10	8
Lepra albescens (Huds.) Hafellner var. albescens	1	7	9	8
Lepra amara (Ach.) Hafellner	1	6	6	4
Lepra ophthalmiza (Nyl.) Hafellner	1	0	0	1
Lepraria cf. obtusata Tønsberg	1	0	0	0
Lepraria eburnea J.R.Laundon	9	7	4	2
Lepraria elobata Tønsberg	4	2	1	0
Lepraria finkii (B. de Lesd.) R.C.Harris	23	12	8	6
Lepraria vouauxii (Hue) R.C.Harris	7	5	3	1
Leptogium saturninum (Dicks.) Nyl.	0	0	1	0
Lobaria pulmonaria (L.) Hoffm.	9	5	8	7
Lopadium disciforme (Flot.) Kullh.	1	1	4	3
Loxospora cristinae Guzow-Krzem., Łubek, Kubiak & Kukwa	0	1	3	0
Loxospora elatina (Ach.) A.Massal.	4	7	9	10
Melanelixia glabratula (Lamy) Sandler & Arup	0	4	12	10
Melanelixia subaurifera (Nyl.) O.Blanco, A.Crespo, Divakar, Essl., D.Hawksw. & Lumbsch	0	1	4	5
Menegazzia terebrata (Hoffm.) A.Massal.	0	1	5	6
Micarea micrococca (Körb.) Gams	0	0	0	1
Micarea peliocarpa (Anzi) Coppins & R.Sant.	2	2	1	1
Mycobilimbia carneoalbida (Müll.Arg.) S.Ekman & Printzen	1	1	1	0
Mycobilimbia epixanthoides (Nyl.) Vitik., Ahti, Kuusinen, Lommi & T.Ulvinen	3	0	0	0
Mycoblastus sanguinarius (L.) Norman	0	1	0	0
Naetrocymbe fraxini (A.Massal.) R.C.Harris	5	15	19	18
Nephroma parile (Ach.) Ach.	2	2	2	1
Nephroma resupinatum (L.) Ach.	0	0	1	0
Normandina pulchella (Borrer) Nyl.	2	9	11	7
Ochrolechia androgyna (Hoffm.) Arnold	0	1	4	4
Opegrapha vulgata Ach.	7	8	8	8

Lichen species	hz 1	hz 2	hz 3	hz 4
Pannaria conoplea (Ach.) Bory	1	1	1	0
Parmelia saxatilis (L.) Ach.	0	2	7	9
Parmelia sulcata Taylor	0	0	2	3
Parmeliella triptophylla (Ach.) Müll.Arg.	2	0	0	0
Parmelina pastillifera (Harm.) Hale	0	0	2	3
Parmeliopsis ambigua (Hoffm.) Nyl.	0	1	0	0
Parmeliopsis hyperopta (Ach.) Arnold	0	1	0	0
Peltigera collina (Ach.) Schrad.	1	2	2	1
Peltigera degenii Gyeln.	7	0	0	0
Peltigera horizontalis (Huds.) Baumg.	3	0	0	0
Peltigera praetextata (Flörke) Zopf	27	1	0	0
Pertusaria alpina Hepp	6	15	15	7
Pertusaria coccodes (Ach.) Nyl. var. coccodes	1	1	1	1
Pertusaria coronata (Ach.) Th.Fr.	2	5	5	2
Pertusaria leioplaca DC.	2	9	12	10
Pertusaria pertusa (L.) Tuck. var. pertusa	0	1	0	0
Phaeophyscia endophaenicea (Harm.) Moberg	0	0	1	0
Phlyctis argena (Spreng.) Flot.	30	46	44	39
Platismatia glauca (L.) W.L.Culb. & C.F.Culb.	0	0	1	2
Pseudosagedia aenea (Wallr.) Hafellner & Kalb	14	14	16	14
Pseudoschismatomma rufescens (Pers.) Ertz & Tehler	4	8	7	7
Pyrenula laevigata (Pers.) Arnold	0	1	0	0
Pyrenula nitida (Weigel) Ach.	30	21	11	4
Pyrrhospora quercea (Dicks.) Körb.	4	5	3	2
Ramalina farinacea (L.) Ach.	0	2	6	3
Rinodina albana (A.Massal.) A.Massal.	0	1	1	0
Scytinium lichenoides (L.) Otálora, P.M.Jørg. & Wedin var. lichenoides	2	0	0	1
Sticta fuliginosa (Hoffm.) Ach.	1	1	2	1
Sticta sylvatica (Huds.) Ach.	0	0	1	1
Strigula stigmatella (Ach.) R.C.Harris var. stigmatella	43	3	3	1
Thelotrema lepadinum (Ach.) Ach.	0	1	1	1
Toniniopsis subincompta (Nyl.) Kistenich, Timdal, Bendiksbj & S.Ekman	8	4	2	1
Varicellaria hemisphaerica (Flörke) Schmitt & Lumbsch	2	7	6	5
Violella fucata (Stirt.) T.Sprib.	1	1	1	1
Zwackhia viridis (Pers.) Poetsch & Schied.	21	32	29	17
Total no of species 114	67	79	82	76