Acta Biol. Univ. Daugavp. 22 (2) 2022
ISSN 1407 - 8953

APPLICATION OF LICHEN FUNCTIONAL TRAITS IN IDENTIFICATION OF TEMPERATE OLD-GROWTH BROAD-LEAVED FORESTS

Aleksandra Krugļikova*, Rolands Moisejevs, Māris Nitcis, Anna Mežaka

Krugļikova A., Moisejevs R, Nitcis M., Mežaka A. 2022. Application of lichen functional traits in identification of temperate old-growth broad-leaved forests. *Acta Biol. Univ. Daugavp., 22 (2): 167 – 179.*

Abstract
Woodland key habitats (WKHs) are the main shelter for biodiversity in Latvia which provide shelter not only for widespread forest species, but also for many habitat-specific, rare and unique lichen species. We analyzed epiphytic lichen functional traits in relation to forest stand age in randomly selected thirty broad-leaved forest stands in Latvia. Within the study, in total 92 of epiphytic lichen taxa were found on 150 broad-leaved trees. We found that old-growth broad-leaved forests are more rich in lichen species and functional traits than young and middle-aged forest stands. In determining WKHs, the following groups of functional traits can be indicative: foliose or squamulose thallus, intense yellow and yellow-green thallus color.

Keywords: epiphytic lichens, broad-leaved forests, lichen functional traits, Woodland key habitats.

*Corresponding author: *Aleksandra Krugļikova. Institute of Life Sciences and Technology, Daugavpils University, Parādes Str. 1A, Daugavpils, Latvia, LV5401, E-mail: aleksandra.kruglikova@du.lv*

Aleksandra Krugļikova, Rolands Moisejevs, Māris Nitcis, Anna Mežaka. Institute of Life Sciences and Technology, Daugavpils University, Parādes Str. 1A, Daugavpils, Latvia, LV5401

INTRODUCTION

Forests are the largest and the most important terrestrial ecosystems in a world. Forest habitats have integral role in all life on Earth (Loo 2002). Kuresoo et al. (2020) demonstrated that the last remaining old-growth forests, rich in rare lichen species, are declining.

Forests cover around 52% of the Latvia. Coniferous forests are dominating in Latvia (51% of all forests) while, broad-leaved dominated forests cover less than 2% of all forests (VMD 2022). The current state of Latvian forests has been formed during the last centuries, under the influence of various nature and anthropogenic activities. During the last houndreds of years Latvian forests were used for the needs of society (Strods 1999). In recent decades, the intensity of logging has increased in the territory of Latvia (Anonymous 2019), which has a negative impact on biodiversity throughout the country.

Due to the shrinking of Woodland key habitats (WKHs), epiphytic lichen indicator species play an important role in identifying and preserving

WKHs (Ek et al. 2002). Indicator species are susceptible to unwanted changes in habitats and are demanding to certain microenvironmental conditions, which are specific in WKHs – light conditions, humidity, temperature, deadwood structures (Suško 1998, Johansson & Gustafsson 2001, Auniņš 2013, Mežaka et al. 2015, Moisejevs 2016).

Lichen species richness is an important indicator of habitat quality. However, in many cases, lichen species identification requires also anatomical features (for, example, cortex and medulla structure, spore size and shape), thin-layer chromatography analysis of secondary compounds and even molecular studies (Smith et al. 2009). The high cost of species identification in terms of financial resources and relatively low number of specialists could explain the lack of lichenological research in many parts of the world. The functional traits of lichens and how they reflect environmental conditions are discussed and studied worldwide in recent decades (Díaz & Cabido 2001, Ellis & Coppins 2006a, Giordani et al. 2012, Malíček et al. 2019, Łubek et al. 2021). Previous studies show that lichen functional traits, such as photobiont type, growth form, reproduction type, are dependent and closely related to microclimatic conditions – tree age, crown closure and abiotic climatic factors (Giordani et al. 2012): light conditions Sevgi et al. (2019), temperature and humidity (Ellis & Coppins 2006b, Jüriado & Paal 2018, Pires et al. 2021, Łubek et al. 2021). The present study aims to evaluate lichen taxa richness in young, middle-aged and old-growth broad-leved forests in Latvia, and lichen functional trait potential use for WKH identification in Latvia.

MATERIALS AND METHODS

Study area

Data were collected from 30 randomly selected broad-leaved forest stands throughout of Latvia (Fig. 1). Study sites were divided into three age groups – ten young forest stands (forest age 20–30 years), ten middle-aged forest stands (forest age 50–60 years) and ten old-growth forest stands (EU Habitat code 9020* *Fennoscandian hemiboreal natural old broad-leaved deciduous forests*, forest stand age >100 years) (Tab. 1).

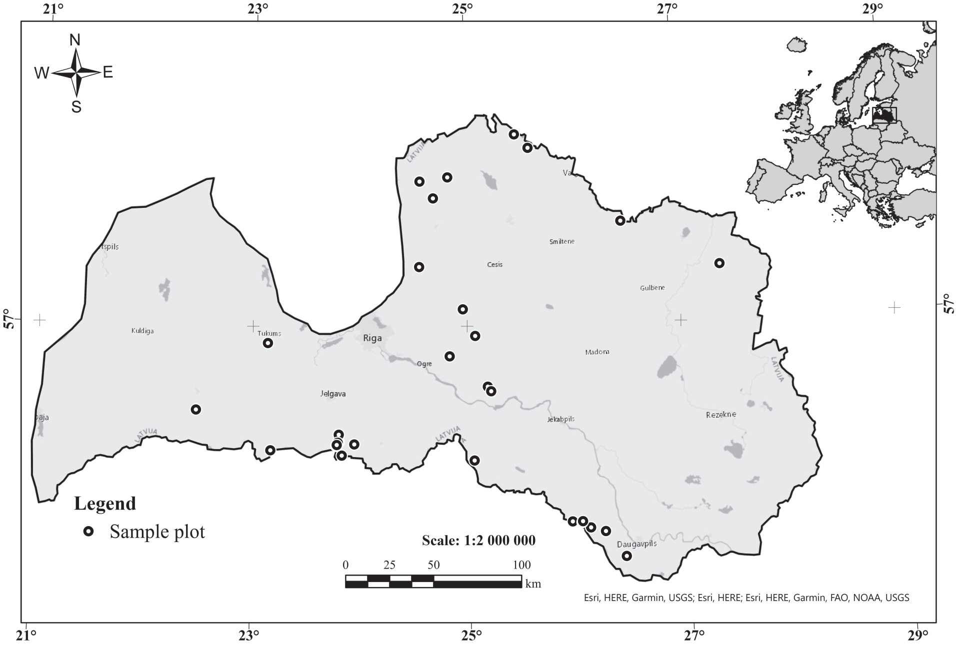

Figure 1. Studied forest stands (noted with dots).

Broad-leaved forests are selected according to the following criteria: 1) little-leaf linden *Tilia cordata* or European ash *Fraxinus excelsior* is dominant in the first floor of the forest stand; 2) *Aegopodiosa* type forests; 3) forest stands that are 100 years old or more and no managerment activities were performed during the last 30 years; 4) selecting forest stands that are 100 years old or more. Their compliance with a protected habitat of EU importance 9020* *Fennoscandian hemiboreal natural old broad-leaved deciduous forests* was vierified by EU habitat experts.

Table 1. Characteristics of studied sample plots. Tree species abbreviations: * Po – *Populus tremula*, Be – *Betula sp.*, Ai – *Alnus incana*, Pic – *Picea abies*, Fra – *Fraxinus excelsior*, Til – *Tilia cordata*, Qr – *Quercus robur*, Ap – *Acer platanoides*, Ul – *Ulmus glabra.*

Sample plot	Coordinates		Forest stand age group	Studied tree species
	X	Y		
1	620830	206977	20 – 30 years	Qr, Ap
2	487753	251917	20 – 30 years	Fra, Po
3	549435	402551	20 – 30 years	Ap, Ul, Be, Pic
4	587296	427007	20 – 30 years	Ul, Fra, Ap
5	406617	270603	20 – 30 years	Fra, Ai
6	447558	308384	20 – 30 years	Po, Ap
7	651491	187338	20 – 30 years	Fra
8	631208	203566	20 – 30 years	Ul, Ap, Qr, Po
9	626319	206621	20 – 30 years	Fra, Ap
10	626623	207119	20 – 30 years	Fra, Ap
11	550834	300804	50 – 60 years	Til, Pic
12	647777	377950	50 – 60 years	Til, Pic
13	565313	312406	50 – 60 years	Ap, Qr, Be
14	489487	244367	50 – 60 years	Fra, Po, Ai
15	448908	247401	50 – 60 years	Be, Pic, Qr
16	487795	256233	50 – 60 years	Po, Qr, Fra
17	572511	283569	50 – 60 years	Til, Po
18	565021	241589	50 – 60 years	Fra, Qr, Ai
19	487216	251692	50 – 60 years	Fra, Ai, Pic, Be
20	486362	249883	50 – 60 years	Fra, Po, Ai
21	639650	201499	≥ 100 years	Fra, Be, Po, Til
22	486636	250400	≥ 100 years	Be, Qr, Fra
23	574429	280969	≥ 100 years	Qr, Pic, Til
24	533467	351576	≥ 100 years	Til, Ul, Fra
25	4966041	250721	≥ 100 years	Fra, Ai
26	558294	327532	≥ 100 years	Fra, Pic, Ul
27	533657	400157	≥ 100 years	Til, Pic
28	704126	353824	≥ 100 years	Pic, Ul, Til
29	595047	419370	≥ 100 years	Fra, Til, Pic, Ul
30	541293	390601	≥ 100 years	Ap, Ai, Fra

Field work

In the spring, summer and autumn seasons of 2021, during field expeditions, data were collected from 150 trees in 30 sample plots. In each study site, one 20x20 m square sample plot (Fig. 2), in which 28 m long transect was established. The 5 living trees with a diameter of at least 10 centimeters, located closest to the transect, were selected within the sample plot, in the direction from south to north, without going outside the boundaries of the sample plot.

In each sample plot, epiphytic lichens were studied on five trees. Lichen occurrences on each selected tree up to a height of 2 m was recorded. Spot-test reactions of thalli were checked with sodium hypochlorite solution (commercial bleach) (C) and/or 10% KOH solution (K) in field. Lichen species which could not be identified in the field, were collected for the identification in a laboratory. Lichen samples collected during field expeditions are stored in the Lichen Herbarium of Daugavpils University (DAU).

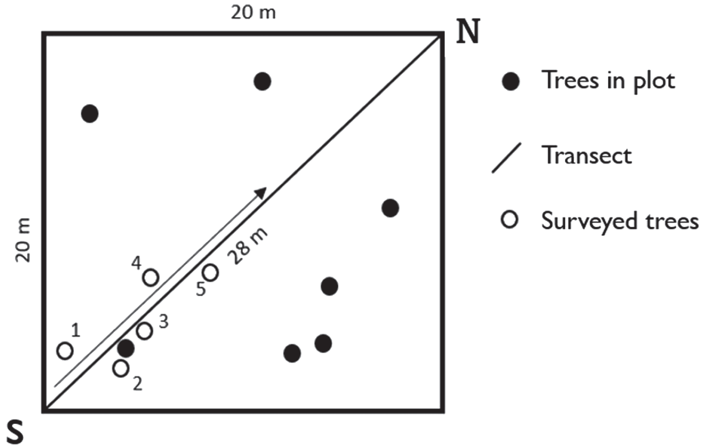

Figure 2. Sample plot. Abbreviations: S – South, N – North. Arrow shows the direction of the sampling in transect. Tree number shows the order of surveyed trees.

Laboratory work

Collected lichen samples were identified in the Daugavpils University Institute of Life Sciences and Technology laboratory using standardized lichenological methods (Smith et al. 2009). Lichen species were identified using microscope Nikon Eclipse E100 and stereomicroscope Nikon SMZ 745T. Morphology of collected lichen specimens was examined under a dissecting microscope, anatomical structures were studied under a light microscope. At the laboratory, ethanol solution of paraphenylenediamine (PD), Lugol solution (I), commercial bleach) (C), 10% KOH solution (K) and 50% HNO3 (N) were employed for additional spot tests and anatomical examinations. Lichen species were identified using microscope Nikon Eclipse E100 and stereomicroscope Nikon SMZ745T. UV light was used for some lichen species identification using CAMAG UV CABINET UV box.

For all lichen species found on the surveyed 150 trees, five functional traits were analysed: growth form (crustose, foliose and squamulose, *Cladonia* type growth form, fruticose, calicioid lichens) photobiont (green algae, cyanobacteria, *Tretntepohlia*), reproduction (sexual, vegetative and mixed), thallus color (grey, green or greenish grey, yellow green, lemon yellow, brownish, colorless) and spore type (simple, septate, spores unknown). Information on the functional traits of each species was obtained from determination literature and key books (McCune & Geiser 1997, Smith et al. 2009, Brodo 2016).

Data analysis

Pearson's Chi-squared test was applied to compare the number of lichen taxa among categories. Indicator species analysis was applied to test the relationship between epiphytic lichen functional traits and forest stand age (environmental variable). Indicator species analysis (ISA) was applied to lichen occurrence data containing at least three records of each lichen species on trees to avoid a random species occurrence. In total 30 forests stands were divided into three age groups – ten young forest stands (20–30 years), ten middle-aged forest stands (50–60 years) and ten old-growht forest stands (≥ 100 years). We analyzed the following epiphytic lichen functional traits: growth form, photobiont, reproductive strategy, thallus color and spore type according to Giordani et al. (2012) and Smith et al. (2010).

Indicator species analysis was performed using the indicspecies package (De Caceres & Legendre 2009). All data analysis were performed using R program version 3.5.1 (Borcard et al. 2018).

Figure 3. One of study sites. Photo: A. Krugļikova.

RESULTS

In total 92 epiphytic lichen taxa were recorded in 30 studied sites (Tab. 2, Fig. 3, Fig. 4). The epiphytic lichens were studied on nine tree species*: Alnus incana*, *Acer platanoides*, *Betula pendula*, *Fraxinus excelsior*, *Picea abies*, *Quercus robur*, *Tillia cordata* and *Ulmus glabratula*. The number of total lichen taxa differed significantly (x^2=32.54, p<0.01) among old-growth, middle-aged and young forest stands. Overall, the highest number of epiphytic lichen taxa was found in old-growth broad-leaved forest stands (79 species, Fig. 5). In middle-aged forest stands we found 42 epiphytic lichen species, but in young forest stands we found only 24 epiphytic lichen taxa. In total, 20 lichen species with conservation concern were recorded. The significant differences (x^2=2.00, p=0.37) in number of WKH indicator species among three forest stand age groups (old-growth, medium-aged, young) was not found. We found significant differences in number of WKH specialist species (x^2=18.00, p<0.01), specially protected species (x^2=18.47, p<0.01) and microreserve species (x^2=18.50, p<0.01) among all three broad-leaved forest stand age groups. Old-growth forests showed also the highest number of WKH lichen specialist species (not found in middle-aged and young forest stands), microreserve species and specially protected species (Fig. 5).

Figure 4. Rare lichen *Thelotrema lepadinum*. Photo: A. Krugļikova.

The lichens found in young, middle-aged and old-growth forest stands were dominated by the lichens of the crustose growth form. The relative abundance of *Cladonia*-type lichens was higher in old-growth broad-leaved stands than in young and middle-aged forest stands. Lichens with calicioid growth form in most cases were found only in old growth broad-leaved stands, only in one case in middle-aged stand (Fig. 6).

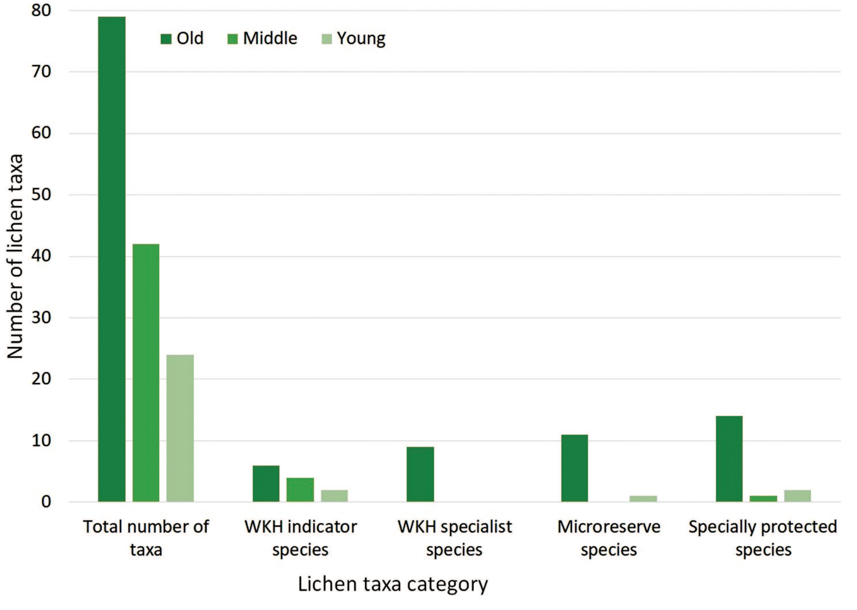

Figure 5. Number of lichen taxa with category of conservation concern in old (old-growth), middle (middle-aged) and young broad-leaved forest stands.

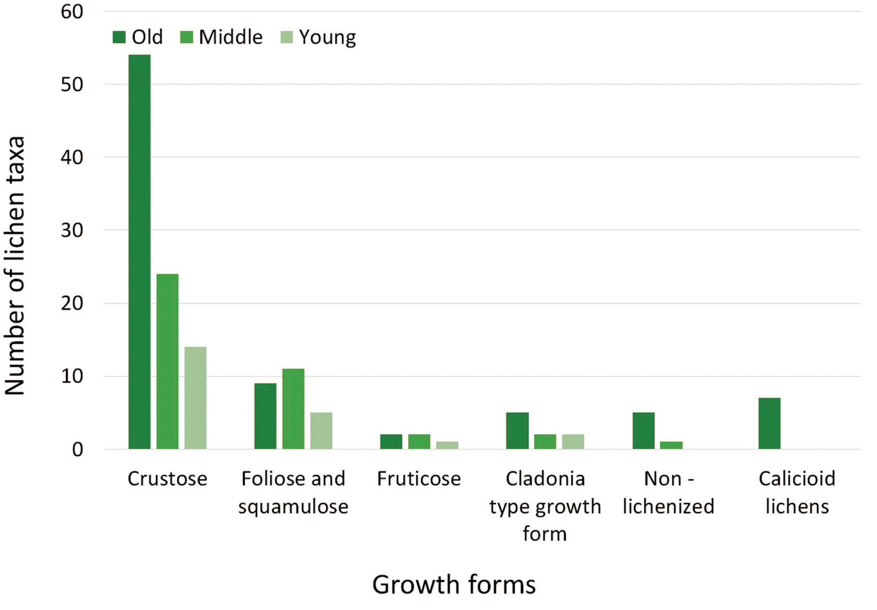

Figure 6. Lichen growth forms in old (old-growth), middle (middle-aged) and young broad-leaved forest stands.

The dominant color of lichens in all age classes was grey (Fig. 7). Lichens with grey, greenish and yellow-green thallus were found in all age classes. Old-growth broad-leaved forest stands represented lichens with all six thallus colors. Lichens with intense yellow thallus were observed only in old growth broad-leaved forests (Fig. 7). Lichen species in all age groups of the forest stand have all three types of reproduction (sexual, vegetative and mixed). In all age groups, sexual reproduction was the main reproduction type (Fig. 8).

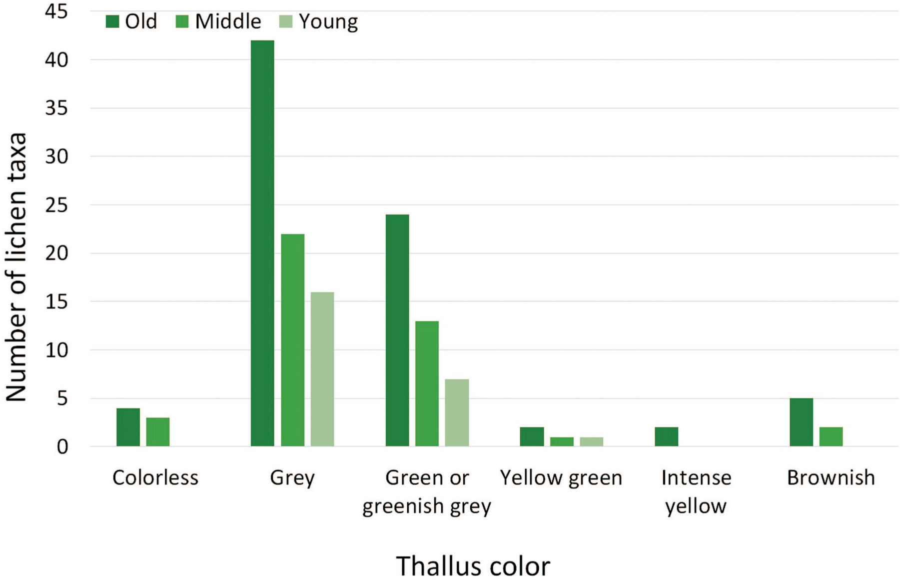

Figure 7. Lichen thallus color in old (old-growth), middle (middle-aged) and young broad-leaved forest stands.

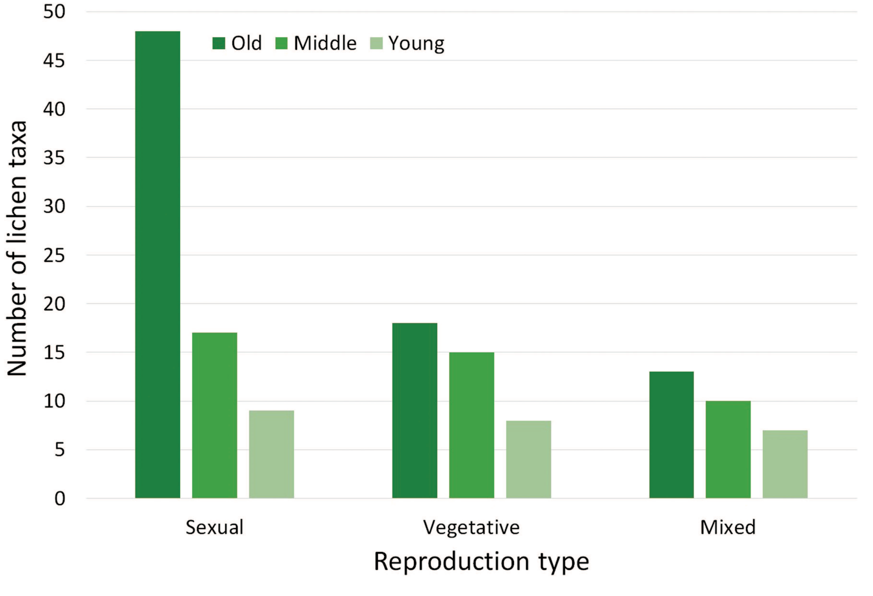

Figure 8. Lichen reproduction type in old (old-growth), middle (middle-aged) and young broad-leaved forest stands.

Green algae and *Trentepohlia* were the most common photobionts in all forest stand age groups (Fig. 9). All reproduction types were found only in old-growth forest stands. Lichens with cyanobacteria photobiont were found only in old-growth forest stands (Fig. 9).

Lichens with septate spores were the most common in old-growth and middle-aged forest stands, while lichens with simple spores were more common in young forest stands (Fig. 10).

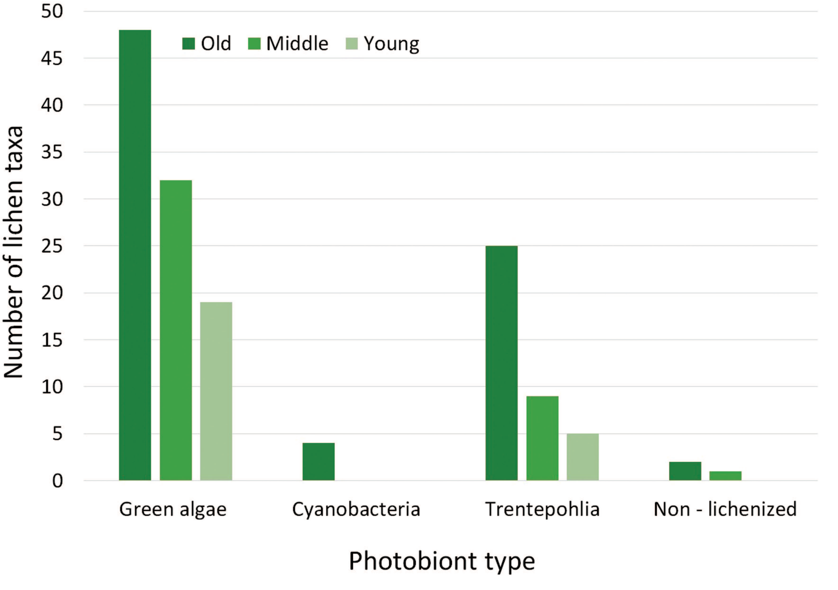

Figure 9. Lichen photobiont type in old (old-growth), middle (middle-aged) and young broad-leaved forest stands.

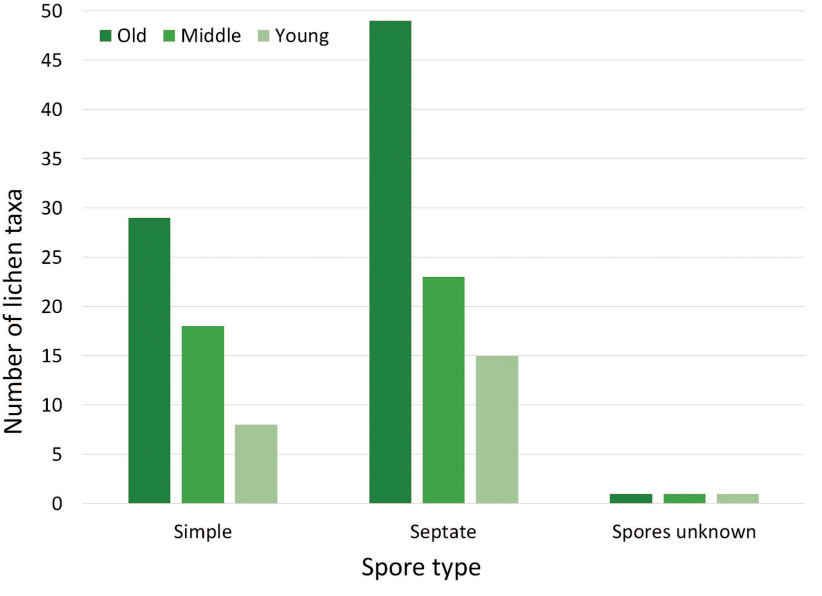

Figure 10. Lichen spore type in old (old-growth), middle (middle-aged) and young broad-leaved forest stands.

Table 2. The list of lichen taxa found in studied forest stands.

No.	Lichen taxa
1	*Acrocordia cavata* (Ach.) R.C. Harris
2	*Alyxoria varia* (Pers.) Ertz & Tehler
3	*Anisomeridium biforme* (Schaer.) R.C. Harris
4	*Arthonia atra* (Pers.) A. Schneid.
5	*Arthonia didyma* Körb
6	*Arthonia mediella* Nyl.
7	*Arthonia radiata* (Pers.) Ach.
8	*Arthonia sp.* Ach.
9	*Arthonia vinosa* Leight.
10	*Bacidia fraxinea* Lönnr.
11	*Bacidia inundata* (Fr.) Vìzda
12	*Bacidia polychroa* (Th. Fr.) Körb.
13	*Bacidia rubella* (Hoffm.) A. Massal.
14	*Bacidina sulphurella* (Samp.) M. Hauck & V. Wirth
15	*Biatoridium monasteriense* J. Lahm ex Körb.
16	*Bilimbia* De Not.
17	*Bilimbia tetramera* De Not.
18	*Buellia griseovirens* (Turner & Borrer ex Sm.) Almb.
19	*Buellia sp.* De Not.
20	*Calicium viride* Pers.
21	*Candelariella sp.* Müll. Arg.
22	*Chaenotheca chrysocephala* (Ach.) Th. Fr.
23	*Chaenotheca ferruginea* (Turner ex Sm.) Mig.
24	*Chaenotheca gracilenta* (Ach.) Mattsson & Middelb.
25	*Chaenotheca stemonea* (Ach.) Müll. Arg.
26	*Chaenotheca trichialis* (Ach.) Hellb.
27	*Cladonia chlorophaea* (Flörke ex Sommerf.) Spreng.
28	*Cladonia coniocraea* (Flörke) Spreng.
29	*Cladonia cornuta* (L.) Baumg.
30	*Cladonia digitata* (L.) Baumg.
31	*Cladonia fimbriata* (L.) Fr.
32	*Cladonia grayi* P. Browne
33	*Cladonia Juv. P. Browne*
34	*Coenogonium pineti* (Ach.) Lücking & Lumbsch
35	*Diarthonis spadicea* (Leight.) Frisch, Ertz, Coppins & P.F. Cannon
36	*Evernia prunastri* (L.) Ach.
37	*Felipes leucopellaeus* (Ach.) Frisch & G. Thor
38	*Graphina anguina* (Mont.) Müll. Arg.
39	*Gyalecta ulmi* (Sw.) Zahlbr.
40	*Hypocenomyce scalaris* (Ach.) M. Choisy
41	*Hypogymnia physodes* (L.) Nyl.
42	*Hypogymnia tubulosa* (Schaer.) Hav.
43	*Inoderma byssaceum* (Weigel) Gray
44	*Lecanactis abietina* (Ehrh. ex Ach.) Körb.
45	*Lecania croatica* (Zahlbr.) Kotlov
46	*Lecanora carpinea Glaucomaria carpinea* (L.) S.Y. Kondr., Lõkös & Farkas
47	*Lecanora chlarotera* Nyl.
48	*Lecanora comp.-exp.* Ach
49	*Lecidea nylanderi* (Anzi) Th. Fr.
50	*Lecidella elaeochroma* (Ach.) M. Choisy
51	*Lecidella euphorea* (Flörke) Kremp.
52	*Lecidella subviridis* Tønsberg
53	*Lepra albescens* (Huds.) Hafellner
54	*Lepra amara* (Ach.) Hafellner
55	*Lepraria sp.* Ach.
56	*Leptorhaphis epidermidis* (Ach.) Th. Fr.
57	*Lobaria pulmonaria* (L.) Hoffm.
58	*Melanelixia glabratula* (Lamy ex Nyl.) Sandler & Arup
59	*Melanohalea exasperatula* (Nyl.) O. Blanco, A. Crespo, Divakar, Essl., D. Hawksw. & Lumbsch
60	*Micarea misella* (Nyl.) Hedl.
61	*Micarea prasina* Fr.
62	*Micarea sp.* Fr.
63	*Nephroma laevigatum* Ach.
64	*Ochrolechia androgyna* (Hoffm.) Arnold
65	*Opegrapha sp.* Ach.
66	*Opegrapha vermicellifera* (J. Kunze) J.R. Laundon
67	*Parmelia sulcata* Taylor
68	*Parmeliella triptophylla*
69	*Parmeliopsis ambigua* (Hoffm.) Nyl.
70	*Peltigera praetextata* (Flörke ex Sommerf.) Zopf
71	*Pertusaria pertusa* (L.) Tuck.
72	*Phlyctis agelaea* (Ach.) Flot.
73	*Phlyctis argena* (Ach.) Flot.
74	*Physcia* (Schreb.) Michx.
75	*Physcia tenella* (Scop.) DC.
76	*Physconia distorta* (With.) J.R. Laundon
77	*Platismatia glauca* (L.) W.L. Culb. & C.F. Culb.
78	*Pseudoschismatomma rufescens* (Pers.) Ertz & Tehler
79	*Pyrenula chlorospila* Arnold
80	*Pyrrhospora quernea* (Dicks.) Körb.
81	*Ramalina farinacea* (L.) Ach.
82	*Reichlingia leopoldii* Diederich & Scheid.
83	*Sarea difformis* (Fr.) Fr.
84	*Sarea resinae* (Fr.) Kuntze
85	*Sclerophora farinacea* (Chevall.) Chevall.
86	*Sclerophora pallida* (Pers.) Y.J. Yao & Spooner
87	*Thelotrema lepadinum* (Ach.) Ach.
88	*Toniniopsis subincompta* (Nyl.) Kistenich, Timdal, Bendiksby & S. Ekman
89	*Varicellaria hemisphaerica* (Flörke) I. Schmitt & Lumbsch
90	*Violella fucata* (Stirt.) T. Sprib.
91	*Zwackhia sorediifera* (P. James) Ertz
92	*Zwackhia viridis* (Ach.) Poetsch & Schied.

The Indicator Species Analysis showed that intense yellow lichen color is indicative to old-growth broad-leaved forest stands ($p<0.05$), while yellow-green color of lichen thallus was indicative to both middle-aged and old-growth broad-leaved forest stands ($p<0.05$). Foliose and squamulose lichens are indicative to middle-aged and old-growth broad-leaved forest stands ($p<0.01$).

DISCUSSION

Effects of stand age on the number of epiphytic lichen taxa

The number of epiphytic lichen taxa found during our study was similar to that obtained by Łubek et al. (2018) in broad-leaved forests in eastern Poland (92 lichen taxa in our study and 107 taxa in Poland). The number of lichen taxa found in this study was relatively high in comparison to similar study conducted by Mežaka et al. (2008), where the authors recorded 57 lichen species. This difference in the number of the recorded species in Latvian studies can be explained by the recent additions to the general knowledge on lichen biota in Latvia (Moisejevs 2015, Motiejunaite et al. 2016, Moisejevs 2017, Moisejevs et al. 2019, Degtjarenko & Moisejevs 2020, Mežaka et al. 2021).

The results of our study showed a significant increase in number of total epiphytic lichen taxa with increasing stand age. Previous studies on the effect of stand age on epiphytic lichen diversity showed a similar trend (Hyvärinen et al. 1992, Sevgi et al. 2019, Miller et al. 2020) in their studies described patterns between the number of epiphytic lichen species and a set of environmental condition characteristic of old-growth forests: light and microclimatic conditions in the forest stand. Our results showed similar patterns as in above mentioned studies. Both, in our study and in studies performed by Sevgi et al. (2019) and Miller et al. (2020) the results showed that old-growth broad-leaved forest stands have a higher number of species than young broad-leaved forest stands.

Lichen functional trait characteristics in broad-leaved forest stands of different ages

Indicator species analysis showed that intense yellow and yellow-green thallus color could be indicative of old-gowth broad-leaved forests (WKHs). It was found that the light forms of the lichens are more represented in habitats with high light intensity in lower forest layers (Robinson et al. 1989). However, we expect that our results are related to relatively low sample size, as species such as *Parmeliopsis ambigua* and *Pyrrhospora quernea* previously were reported as common species in young and midle-aged stands in Baltic forests (Lõhmus 2003, Moisejevs et al. 2016).

We found that foliose and squamulose lichen growth forms are indicative in old-growth forests. Giordani et al. (2012) have not found the significant response of mentioned lichen growth forms for deciduous forests. However, Giordani et al. (2012) studied *Quercus* dominated forests, but in our study we have not studied such stands. As the sample size of our study was relatively not large, we sugest to enlarge the sample size to test the hypothesis.

We have not found lichen species with cyanobacteria photobionts in young and middle-aged forest stands. This type of photobiont is typical for species such as *Lobaria pulmonaria* and *Nephroma laevigatum*. In our study, species with cyanobacteria were found only in several stands. The cyanobacterial photobionts can be considered as indicative for old and natural broad-leaved forests. Gauslaa et al. (2019) concluded that the abundance of cyanobacteria in a forest stand is negatively affected by forest disturbance. Old forests are less disturbed compared to young and middle-aged stands where regular forest management activities take place. The results of this study are similar to a study by Kuusinen (1996) that was carried out in aspen stands in Finland and showed that cyanolichens can be used as bioindicators of old and natural forests. However, as we found only few cyanolichens in several study sites it is difficult to make generalizations.

The mixed lichen reproduction type is represented by proportionally more species in old stands than in young and middle-aged forest stands. A higher proportion of species with vegetative reproduction strategy in managed rather than primary forests was previously observed in the Czech Republic (Malíček et al. 2019). At the same time, results of study performed by Stofer et al. (2006) in key European biogeographical regions (including boreal Finland) and study by Lundström et al. (2013) in Sweden showed the opposite pattern. For this reason, it is difficult to compare the results of this study with other studies done in different geographical regions, and obtained by different study methods.

In addition, the results of our study indicate that the spore types of lichen species growing in broad-leaved forest stands do not change much along the forest stand age. These results are not consistent with a study by Pentecost (1981), who concluded that in young and disturbed stands, the proportion of lichen species reproducing by unicellular spores is higher than species reproducing by dicellular or multicellular spores. However, our study includes only epiphytic lichens in broad-leaved forests, but Pentecost (1981) study included lichens from different substrates and habitats.

Our study showed that hypothesis that old growth broad-leaved forests that comply with the WKHs have lichen functional traits that are absent in young and middle-aged forest stands was confirmed. Old-growth broad-leaved forests represents more lichen taxa and functional traits than young and middle-aged forest stands. The following groups of functional traits may serve as indicative traits for the determination of WKHs: intense yellow and yellow-green lichen thallus color as well as foliose and squamulose lichen growth form. In future studies, for the analysis of functional traits, it is necessary to enlarge the sample size and to carry out research in other geographical regions where broad-leaved forests occur.

ACKNOWLEDGEMENTS

This study was financially supported by the Fundamental and Applied Research project: No. lzp-2020/1-0314 “Successional and spatial models of bryophytes and lichens in deciduous forests”.

REFERENCES

Auniņš A. 2013. Eiropas Savienības aizsargājamie biotopi Latvijā. Noteikšanas rokasgrāmata. 2. precizēts izdevums (European Union protected habitats in Latvia. Identification manual. 2nd edition). Latvijas Dabas fonds, Vides aizsardzības un reģionālās attīstības ministrija, Rīga. 352 pp.

Borcard D., Gillet F., Legendre P. 2018. Numerical Ecology with R Second Edition. Springer International Publishing AG, Cham. 435 pp.

Brodo I.M. 2016. Keys to Lichens of North America: Revised and Expanded., Yale University Press, New Heawen and London. 427 pp.

Brodo I.M., Sharnoff S.D., Sharnoff S. 2001. Lichens of North America. Yale University Press, Yale. 795 pp.

De Caceres M.D., Legendre P. 2009. Associations between species and groups of sites: indices and statistical inference. *Ecology* 90(12): 3566–3574. https://doi.org/10.1890/08-1823.1

Degtjarenko P., Moisejevs R. 2020. Revision of the Genus Cetrelia (Lichenised Ascomycota) in Latvia. *Botanica* 26(1): 88 – 94. https://doi.org/10.2478/botlit-2020-0008

Ek T., Suško U., Auziņš R. 2002. Mežaudžu atslēgas biotopu inventarizācijas metodika (Woodland Key Habitat methodoloy of inventory). Valsts meža dienests, Rīga. 76 pp. (In Latvian).

Ellis C., Coppins B.J. 2006a. Contrasting functional traits maintain lichen epiphyte diversity in response to climate and autogenic succession. *Journal of Biogeography* 33: 1643 – 1656. https://doi.org/10.1111/j.1365-2699.2006. 01522.x

Ellis C.J., Coppins B.J. 2006b. Shifts in lichen species and functional diversity in a primeval forest ecosystem as a response to environmental changes. *Forests* 12(6): 686. https://doi.org/10.3390/f12060686

Gauslaa Y., Bartemucci P., Solhaug K.A. 2019: Forest edge-induced damage of cephalo- and cyanolichens in northern temperate rainforests of British Columbia. *Canadian Journal of Forest Research* 49(5): 434 – 439. https://doi.org/10.1139/cjfr-2018-0187

Giordani P., Brunialti G., Bacaro G., Nascimbene J. 2012. Functional traits of epiphytic lichens as potential indicators of environmental conditions in forest ecosystems. *Ecological Indicators* 18: 413 – 420. https://doi.org/10.1016/j.ecolind.2011.12.006

Hyvärinen M., Halonen P., Kauppi M. 1992. Influence of stand age and structure on the epiphytic lichen vegetation in the middle-boreal forests of Finland. *The Lichenologist* 24(2): 165 – 180. https://doi.org/10.1017/S0024282900500073

Johansson P., Gustafsson L. 2001. Red-listed and indicator lichens in woodland key habitats and production forests in Sweden. *Canadian Journal of Forest Research* 31(9): 1617 – 1628. https://doi.org/10.1139/x01-091

Jüriado I., Paal J. 2018. Epiphytic lichen synusiae and functional trait groups of species in boreo-nemoral deciduous forests are influenced by host tree properties and environmental factors. *Nordic Journal of Botany* 37(1). https://doi.org/10.1111/njb.01939

Kuresoo S., Kuresoo L., Lilleväli U., Kerus V. 2020. Hidden inside a wood pellet. Estonian fund for nature, Estonia. Pp. 4 – 6.

Kuusinen M. 1996. Cyanobacterial macrolichens on *Populus tremula* as indicators of forest continuity in Finland. *Biological Conservation* 75: 43 – 49. https://doi.org/10.1016/0006-3207(95)00039-9

Lõhmus P. 2003. Composition and substrata of forest lichens in Estonia: A meta-analysis. *Folia Cryptogamica Estonica* 40: 19 – 38.

Łubek A., Kukwa M., Jaroszewicz B., Czortek P. 2020. Identifying mechanisms shaping lichen functional diversity in a primeval forest. *Forest Ecology and Management* 475: 118434. https://doi.org/10.1016/j.foreco.2020.118434

Łubek A., Kukwa M., Jaroszewicz B., Czortek P. 2021. Contrasting functional traits maintain lichen epiphyte diversity in response to climate and autogenic succession. *Forests* 12(6): 686. https://doi.org/10.3390/f120 60686

Łubek A., Kukwa M., Jaroszewicz B., Czortek P. 2018. Changes in the epiphytic lichen biota of Białowieża Primeval Forest are not explained by climate warming. *Science of The Total Environment* 643: 468 – 478. https://doi.org/10.1016/j.scitotenv.2018.06.222

Lundström J., Jonsson F., Perhans K., Gustafsson L. 2013. Lichen species richness on retained aspens increases with time since clear-cutting. *Forest Ecology and Management* 293: 49 – 56. https://doi.org/10.1016/j.foreco.2012.12.027

Malíček J., Palice Z., Vondrák J., Kostovčík M., Lenzová V., Hofmeister J. 2019. Lichens in old-growth and managed mountain spruce forests in the Czech Republic: assessment of biodiversity, functional traits and bioindicators. *Biodiversity and Conservation* 28: 3497 – 3528. https://doi.org/10.1007/s10531-019-01834-4

Mežaka A., Brūmelis G., Piterāns A. 2008. The distribution of epiphytic bryophyte and lichen species in relation to phorophyte substrate in Latvian natural old-growth broad leaved forests. *Folia Cryptogamica Estonica* 44: 89 – 99. https://doi.org/10.1007/s10531-019-01834-4

Mežaka A., Moisejevs R., Nitcis M. 2021. The main drivers for the occurrence of six red-listed epiphytic bryophytes and lichens in the boreo-nemoral forest landscape, Latvia. *Folia Cryptogamica Estonica* 58: 229 – 241. https://doi.org/10.12697/fce.2021.58.22

Mežaka A., Putna S., Erta I. 2015. Evaluation and long-term conservation perspectives of woodland key habitat bryophyte and lichen indicators in Latgale. *Environment. Technology. Resources* 2: 197 – 201. https://doi.org/10.17770/etr2015vol2.283

Miller J.E.D., Villella J., Stone D., Hardman A. 2020. Using lichen communities as indicators of forest stand age and conservation value. *Forest Ecology and Management* 475: 0378 – 1127. https://doi.org/10.1016/j.foreco.2020.118436

Moisejevs R. 2015. Some new to Latvia lichens and allied fungi. *Acta Biologica Universitatis Daugavpiliensis* 15(2): 285 – 292.

Moisejevs R. 2016. Ķērpju indikatorsugu rokasgrāmata dabas pētniekiem (Manual of lichen indicator species for nature explorers). Daugavpils Universitāte Dzīvības zinātņu un tehnoloģiju institūts, Daugavpils. 68 pp. (In Latvian).

Moisejevs R. 2017. Lichens and allied fungi new for Latvia. *Folia Cryptogamica Estonica* 54: 9 – 12. https://doi.org/10.12697/fce.2017.54.02

Moisejevs R., Degtjarenko P., Motiejūnaitė J., Piterāns A., Stepanova D. 2019. New records of lichens and lichenicolous fungi from Latvia, with a list of lichenicolous fungi reported from Latvia. *Lindbergia* (1): 1 – 6. https://doi.org/10.25227/linbg.01119

Pentecost A. 1981. Some observations on the size and shape of lichen ascospores in relation toe and taxonomy. *New Phytologist* 89(4): 667 – 678. https://doi.org/10.1111/j.1469-8137.1981.tb02345.x

Sevgi E., Yılmaz O.Y., Çobanoğlu Özyiğitoğlu G., Tecimen HB., Sevgi O. 2019. Factors influencing epiphytic lichen species distribution in a managed Mediterranean *Pinus nigra* Arnold forest. *Biodiversity and Conservation* 11(4): 59. https://doi.org/10.3390/d11040059

Smith C.W., Aptroot A., Coppins B.J., Fletcher A., Gilbert O.L., James P.W., Wolsey P.A. 2009. The Lichens of Great Britain and Ireland. British Lichen Society, London. 1046 pp.

Stofer S., Bergamini A., Aragón G., Carvalho P., Coppins B.J., Davey S., Dietrich M., Farkas E., Kärkkäinen K., Keller C., Lökös L., Lommi S., Máguas C., Mitchell R., Pinho P., Rico V.J., Truscott A.-M., Wolseley P.A., Watt A., Scheidegger C. 2006. Species richness of lichen functional groups in relation to land use intensity. *Lichenologist* 38: 331–353. https://doi.org/10.1017/S0024282906006207

Strods H., Zunde M., Mugurēvičs A., Liepiņa D., Dumpe L. 1999. Latvijas mežu vēsture. WWF – Pasaules Dabas Fonds, Rīga. Pp. 7 – 9. (In Latvian).

Suško U. 1998. Latvijas dabiskie meži. Pētījums par bioloģiskās daudzveidības struktūrām, atkarīgajām sugām un meža vēsturi. WWF – Pasaules Dabas Fonds, Rīga. 186 pp. (In Latvian).

Zemkopības ministrija 2019. Pārskats par koku ciršanu 2019. gadā. URL: 5 https://www.zm.gov.lv/public/ck/files/Parskats%20par%20koku%20cirsanu%202019_gad%C4%81.xlsx [Accessed in 02.01.2023].

Received: 16.11.2022.
Accepted: 05.12.2022.