

Distribution of Epiphytic Lichens along a Tree's Trunk

E. E. Muchnik^{a, *, **} and E. Yu. Blagoveschenskaya^b

^a Institute of Forest Science, Russian Academy of Sciences, Uspenskoye, Moscow oblast, 143030 Russia

^b Moscow State University, Moscow, 119991 Russia

*e-mail: emuchnik@outlook.com

**e-mail: eu.muchnik@yandex.ru

Received March 17, 2022; revised April 27, 2022; accepted May 25, 2022

Abstract—A study of the trunks of spruce and birch trees after a windblow on the territory of the Zvenigorod Biological Station of Moscow State University and the Sima Quarry Nature Reserve (Moscow oblast) was carried out. The diversity of epiphytic lichens depending on height of the trunk was studied. It is shown that the position on the tree trunk significantly affects the number of identified lichen species, which increases monotonously with height. Both spruce and birch trees are characterized by a high non-matching diversity of lichen biota in the lower and upper parts of the trunk (and especially in the crown). The complex of the dominant lichen species was changing throughout trunks examined. It is noted that the finds of *Bryoria* and *Usnea* spp. protected in the Moscow oblast are concentrated in the upper part of the trunks.

Keywords: lichen biota, biodiversity, height gradient, coniferous-deciduous forests, spruce, birch, protected species, Moscow oblast

DOI: 10.1134/S106741362206011X

Most studies of epiphytic lichens are based on collections carried out from a height of up to 2–2.5 m along a tree trunk. Thus, a significant part of the information on the biological diversity of lichens remains inaccessible. According to estimates by various authors [1–3], from half to two thirds of the total species richness of lichen biota is not taken into account. Meanwhile this can be of great importance for assessing the overall biodiversity of forest communities, for detecting rare species, and for conducting bioindicative studies.

Despite the fact that the heterogeneous vertical distribution of lichens along the phorophyte trunk has been repeatedly noted [4–11], there are still very few detailed studies of the lichen diversity along the height gradient. However, it was shown that in the coniferous forests of America, a change in the prevailing formations up the trunk from mosses to lichens is shown [12–14]. In addition, it was noted that in old-growth forests, the dominant species of the genera *Hypogymnia* and *Platismatia* grow in the upper part of the crowns only [12]. Moreover, rare and protected lichen species are also often confined to crowns [3, 12, 13], and it has been shown [2] that the composition of lichen biota in the upper crowns of spruce and pine forests is more informative for assessing dust content. The paucity of detailed studies of epiphytic lichens diversity at different tree trunk heights [6] is associated with objective methodological difficulties: inspecting trees along the entire height requires either special

expensive equipment and relevant specialists, or cutting down the trees under study, which will cause significant harm to the forest community, especially when providing a sample sufficient for statistical processing.

Therefore, windblows are the best option for such a study, when quite a few recently fallen trees of different species and age are available for collecting epiphytic lichen biota at all heights. The purpose of this work is to identify patterns in the distribution of epiphytic lichens along the height of the trunk using the example of recently fallen trees in the territory of the Zvenigorod Biological Station of Moscow State University and the Sima Quarry (ZBS MSU). Working hypothesis: species diversity and occurrence of epiphytic lichens at different heights of the same phorophyte differ significantly; there are general trends in the distribution of the diversity of epiphytic lichens along the trunks of phorophytes of different species.

MATERIAL AND METHODS

Research Area

The Zvenigorod Biological Station of Moscow State University and the Sima Quarry with an area of 1116.3 ha is located in the west of the Moscow oblast on the right bank of the Moskva river (Fig. 1). Land use restriction is closest to strict reserve [15]. The climate is temperate continental, the average monthly temperature ranges from -10.6°C in January to

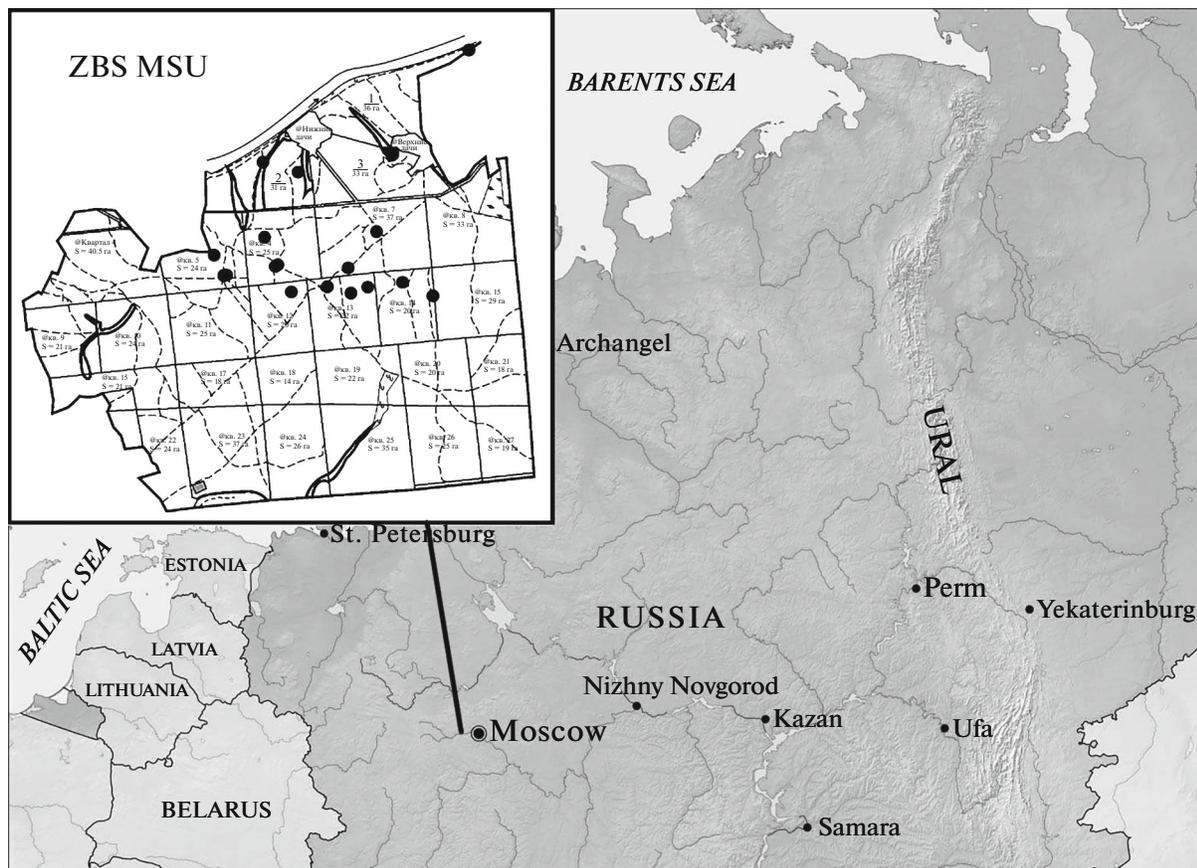


Fig. 1. Geographic location of the survey area and lichen collection points.

+17.2°C in July, the amount of precipitation per year exceeds 700 mm. Climate conditions are typical for Moscow oblast. The territory belongs to the coniferous-broadleaved subzone. The vegetation cover is very diverse and includes coniferous pine and spruce forests, oak-linden forests, alder forests, swamps and meadows. The main forest-forming species is european spruce (*Picea abies* (L.) H. Karst.). In recent years, its strong loss due to the activity of the bark beetle typographer (*Ips typographus* L.) has been observed. In addition, in 2016 and 2017 strong windfalls damaged the forests of the reserve.

Material Collection and Processing

During two field seasons (2016–2017), epiphytic lichens were collected from freshly felled trees in a subnemoral spruce forest on the territory of ZBS MSU. A total of 10 fallen spruce trunks (*Picea abies*) and 13 birch trunks (*Betula pendula* Roth) were examined in several quarters of the reserve (Fig. 1, inset).

The collection of lichens was carried out at the base of the trunks, at a level of 5 m high, and then with a step of 5 m. For birch, the collection was carried out before the beginning of trunk branching, then crown

lichens (both main branches and small branches) were taken into account separately. For spruce, the collection was carried out similarly, with the correction that the main spruce trunk does not branch, therefore, the totality of tree branches was taken as the crown [16]. The collected material (289 samples) was identified using standard lichenological methods [17]. The nomenclature of the mentioned lichen species corresponds to Santesson's checklist of fennoscandian lichen-forming and lichenicolous fungi [18].

Data Analysis

To compare the species composition of lichen biota on spruce and birch, the Sørensen coefficient (K_S) was used [19]. Since it turned out that the composition of lichens on spruce and birch is noticeably different, further analyzes for these species were carried out separately. To test the influence of the position factor on the trunk on the number of lichen species, a one-way analysis of variance (one-way ANOVA) was carried out for both spruce and birch. The similarity between the species compositions of lichen biota at different heights was also determined by Sørensen coefficient. A distance matrix based on this coefficient was com-

piled, where the value $1 - K_S$ was used as the distance, and a complete-linkage clustering was carried out (farthest neighbour clustering).

To assess biodiversity, an indirect indicator of abundance was introduced, which was calculated as follows. The presence of a species at a certain height of a particular tree was taken as a “finding”. Thus, a certain number of “findings” could be assigned to each lichen species on a particular tree species, from 1 in the case of a single discovery to the total number of all analyzed heights for all trees of a given species (75 for birch and 48 for spruce). This number was considered as an indicator of the absolute abundance of the species. Abundance (p_i) was defined as the number of “findings” of a particular lichen species divided by the sum of “findings” of all lichen species for a given tree species (181 for birch and 89 for spruce). Thus, the sum of all abundances is 1. Based on the obtained data, graphs of the species abundance distribution were built. Using a similar method for individual heights of trees of a certain species, the Shannon index (H) and the Simpson index (D) [19] were calculated for each height.

The analysis was carried out in Microsoft Excel 2010 and Statistica 8.0.

RESULTS

In total, 37 species of epiphytic lichens were found on birch, and 23 species were found on spruce. The coefficient of similarity between tree species was 51%. The dominant lichen species on birch were *Hypogymnia physodes*, *Parmelia sulcata*, *Cladonia coniocraea*, *Melanohalea olivacea*. Dominants on spruce were *H. physodes*, *P. sulcata*, *Cladonia digitata*, *H. tubulosa* (Fig. 2).

The influence of the position on the tree trunk on the number of detected species turned out to be significant for both birch ($F = 65.6$; $df = 6$; $p < 0.01$) and spruce ($F = 25.6$; $df = 6$; $p < 0.01$). Thus, lichen biota at different levels of the trunk is characterized by different species richness. In total, the largest number of species is found in the crown (16 species for birch and 10 for spruce). The data for other heights are quite heterogeneous, although it can be said that the first 10 m of the trunk give similar values of the total number of species (8–10 for birch and 5–7 for spruce). A more illustrative picture was shown by the analysis of the number of species found on average on one tree: the average number of species monotonically increases in the direction from the base to the crown, especially for birch (Fig. 3).

The lichen biodiversity also differs depending on height (Table 1, Figs. 4, 5), and when moving from the base up the trunk, the dominant species are changing. The latter can be clearly shown if we take lichen species that are found at a specific height on more than half of the trees studied (Fig. 6). For spruce, *Cladonia*

Table 1. Shannon (H) and Simpson (D) indices for epiphytic lichenobiota at different trunk heights

Index	Tree	Height level					
		base	5 m	10 m	15 m	20 m	crown
H	Birch	2.90	2.25	2.39	1.44	3.21	3.33
	Spruce	2.50	1.51	2.09	1.63		2.87
D	Birch	0.18	0.32	0.31	0.42	0.15	0.14
	Spruce	0.22	0.50	0.35	0.38		0.18

is more common at the base of the trunk, and *Parmelia sulcata* is among the dominants in the upper part. The main species for the base of the birch trunk is *C. coniocraea*, which is found twice as rare already at a height of 5 m and was recorded only once at a height of 10 m. *Hypogymnia physodes* occurs along the entire height of the trunk, reaching 100% occurrence at the level of 15 m and slightly reducing its presence further. *Parmelia sulcata* was noted only from 10 m, but then it occurs at all heights of the surveyed birches. *Melanohalea olivacea* was found only from a height of 20 m, but it dominates in the branches of the crown. The following species were found exclusively in the crown part of the birch: *Cetraria sepincola*, *Evernia prunastri*, *Lecanora circumborealis*, *L. pulcaris*, *L. symmicta*, *Naevia punctiformis*, *Usnea dasypoga*, *Vulpicida pinastris*.

For spruce, data are given on the height at which the species is found, and what lighting preferences for this species are known (Table 2).

DISCUSSION

The difference in the lichen biota of birch and spruce is most likely caused by differences in the properties of the bark of these trees, which corresponds to the data of some authors [21]. Since both phorophytes belong to the group of trees with “acidic” bark ($\text{pH} < 4.7$) [22], it is assumed that the main role is played by such factors as surface structure and bark durability [4], as well as the microclimate in the crowns and beneath crowns [23].

Despite the fact that the average number of species is lower in the lower part of the tree (Fig. 3), the species composition varies significantly from tree to tree, which gives relatively high values of the total species richness of lichen biota at the base of the trunk. Thus, the species composition of lichens at the lower part of the trunk varies more than in the crown. On the birch, the lowest diversity of lichens ($H = 1.44$, $D = 0.42$) was noted on the height of 15 m, that is, the lichen biota at this level is represented mainly by the most common lichens. On the whole, the diversity of lichen biota is higher for birch, which is basically due to the greater number of species found on this phorophyte. Both tree

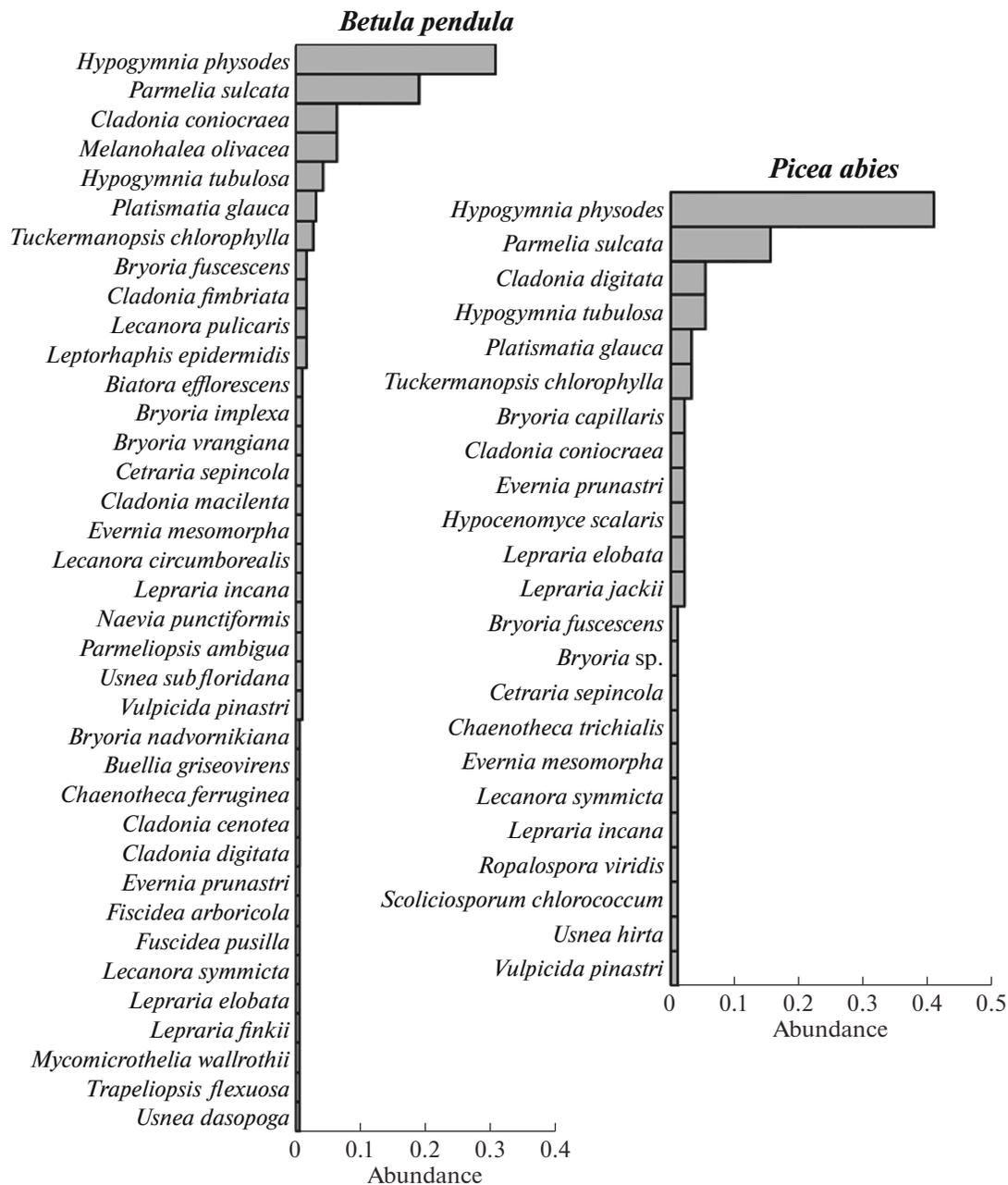


Fig. 2. Lichen abundance on *Betula pendula* and *Picea abies*.

species are characterized by a high diversity of lichens in the lower and upper parts of the trunk (especially in the crown) and some “fall” in the middle part. This is especially clearly illustrated by the number of lichen species found only at a particular height (Fig. 4).

The observed vertical zonation of the lichen distribution along the tree trunk is stipulated by differences in microclimatic conditions, among them are humidity, light conditions, chemical and physical properties of the bark [4, 21–24]. If we consider the trunks of birch and spruce, then the most important factor is

probably just the illumination, although the microclimate of the very base of the trunk also has significant features associated with proximity to the ground. Clustering shows that the upper part of the trunk is joined with the crown (Fig. 5), while in the lower part of the trunks of spruce and birch we observe some differences. For spruce, the level of the base of the trunk forms a separate clade, which is due to the growth of species of the genus *Cladonia* only at the base of the trunk. On the contrary, the features of the birch bark, combined with the fact that the trunk may not have

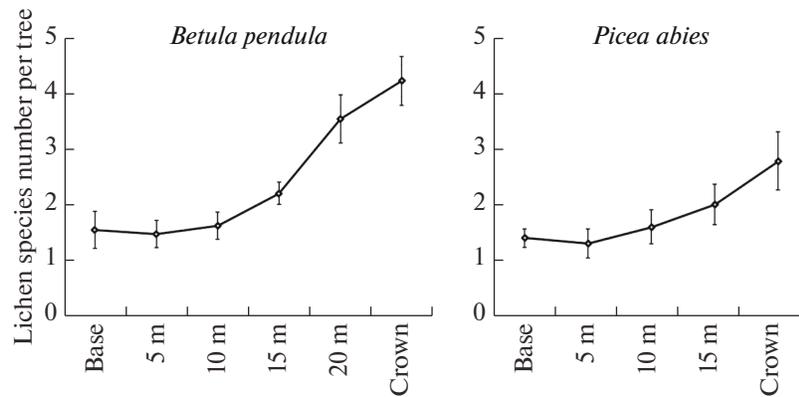


Fig. 3. Average number of lichen species per tree for *Betula pendula* and *Picea abies* (bars indicate standart errors).

originally been strictly vertical, allows *Cladonia* species on birch to occur quite high up the trunk, providing a combination of base and height positions of 5 m.

The fact that *Parmelia sulcata* tends to the upper part of trees (Fig. 6) was also noted by other authors [4, 6, 7], and in some cases it is indeed noted as a dominant [4, 7]. The dominating of *Hypogymnia physodes* are widely known as well [4, 7, etc.]. It should be noted that this species in our zone is certainly more tolerant to illumination, its intervals for this factor should not be 3–4 (as in the Mediterranean, according to [20]), but 2–4 (5) points. This interval is also wider for *H. tubulosa* (in the direction of increase), amounting not to 3 points, but to 3–4(5). High demands on light caused this species to be seldom encountered during route lichenological studies, therefore, for a long time it was considered rare in the Moscow oblast and was even listed as protected [25]. However, from a height of 15 m on spruce (Table 2) and from a height of 10 m on a birch, this species is one of the most common (Fig. 2). Thus, the illumination optima of some lichens obviously vary depending on the climatic zone.

At the base of both spruce and birch, comparatively shade-tolerant species of the genus *Cladonia* predominate. Their ratio to light is 2–4 points [20], and for *C. digitata* in the conditions of the Moscow oblast, where it prefers shaded and very shaded conditions, an estimate of 1–3 points is more fair. It is characteristic that a more shade-tolerant species of the genus *Cladonia* was noted for spruce, which has less crown transparency, which leads to a noticeable decrease in illumination at the base of the trunk.

It should be mentioned that the lichen species that are protected in the Moscow oblast [26] (*Bryoria capillaris*, *B. fuscescens*, *B. implexa*, *B. nadvornikiana*, *B. vrangiana*, *Usnea dasyypoga*, *U. hirta*, *U. subfloridana*) are noted mainly starting from a height of 20 m (*Bryoria fuscescens* is found from 10 m). This corresponds to the data of other authors [3, 13, 27] that rare

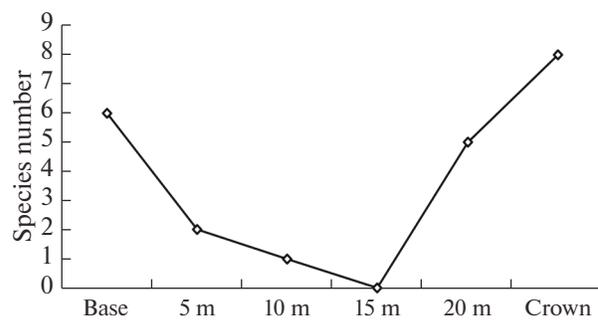


Fig. 4. Number of lichen species found on *Betula pendula* only at a certain height level.

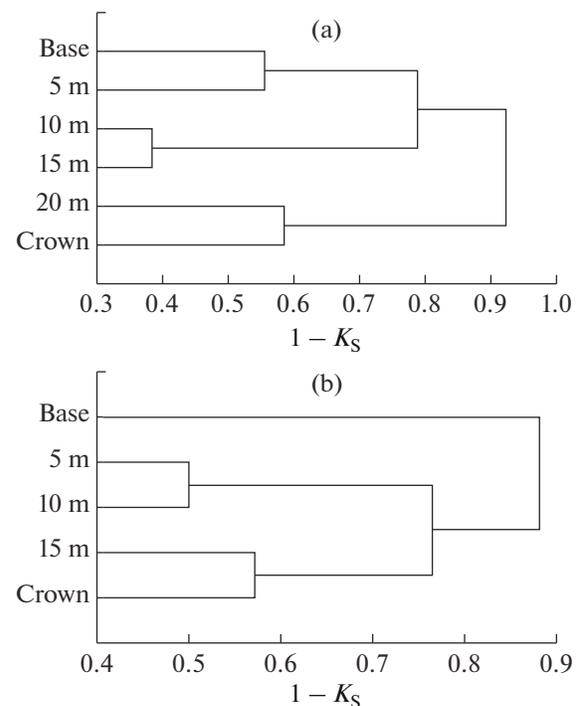


Fig. 5. Dendrogram output for hierarchical clustering of lichen species of different height level. (a) *Betula pendula*, (b) *Picea abies*.

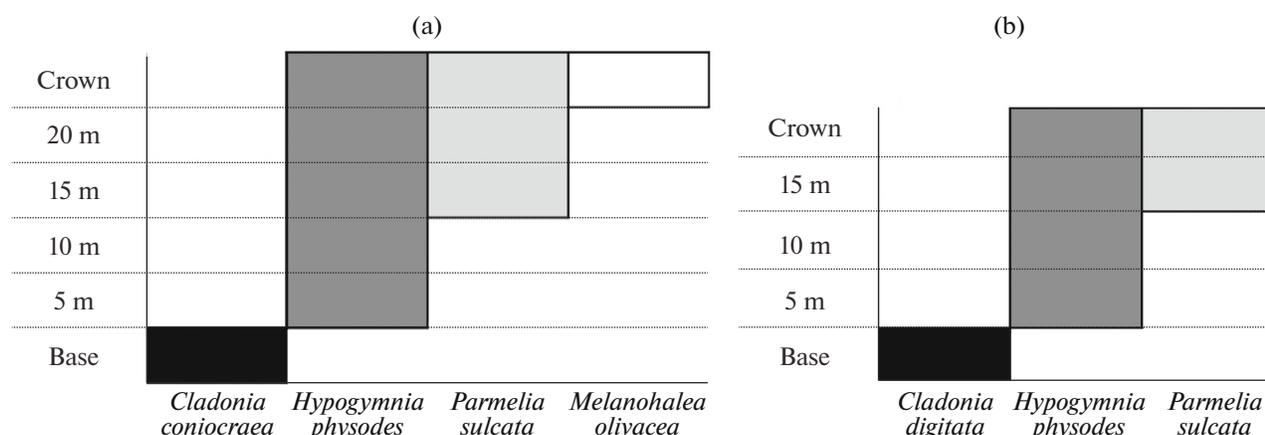


Fig. 6. Diagram of dominant lichens at different height level. (a) *Betula pendula*, (b) *Picea abies*.

and protected lichen species are concentrated mainly in the crown of trees.

CONCLUSIONS

The survey revealed some regularities in the vertical distribution of epiphytic lichens on birch and spruce trunks. Despite a small degree of similarity in the spe-

cies composition of epiphytes of these trees, some general trends are observed in the distribution of species richness of epiphytic lichens along the height of the trunks of both phorophytes.

The hypothesis of a significant difference in species diversity and occurrence of epiphytic lichens at different heights of the same phorophyte was confirmed. Both birch and spruce are characterized by a high

Table 2. Vertical distribution of some lichens along the trunks of spruce trees (the species are arranged in order of increasing requirements for light, the range is given on a 5-point scale [20])

Species	Optimal insolation level	Height level			
		Base	5–10 m	15 m	Crown
<i>Chaenotheca trichialis</i>	1–3	+			
<i>Lepraria jackii</i>	2–3	+			
<i>Scoliciosporum chlorococcum</i>	2–3		+		
<i>Lepraria elobata</i>	2–4	+	+		
<i>Lepraria incana</i>	2–4	+			
<i>Hypogymnia tubulosa</i>	3			+	+
<i>Hypogymnia physodes</i>	3–4	+	+	+	+
<i>Cladonia coniocraea</i>	3–4	+			
<i>Cladonia digitata</i>	3–4	+			
<i>Ropalospora viridis</i>	3–4		+		
<i>Lecanora symmicta</i>	3–4		+		
<i>Tuckermanopsis chlorophylla</i>	3–4			+	+
<i>Parmelia sulcata</i>	3–5		+	+	+
<i>Platismatia glauca</i>	3–5		+		+
<i>Vulpicida pinastri</i>	3–5		+		
<i>Hypocenomyce scalaris</i>	3–5		+		
<i>Bryoria capillaris</i>	3–5			+	+
<i>Evernia prunastri</i>	3–5			+	+
<i>Bryoria fuscescens</i>	3–5				+
<i>Usnea hirta</i>	4–5				+
<i>Cetraria sepincola</i>	4–5				+
<i>Evernia mesomorpha</i>	4–5				+

diversity of lichen biota in the lower and upper parts of the trunk (and especially in the crown), and relatively low diversity in the middle part. It should be noted that there are fewer lichen species in the lower part of each particular trunk than in the upper one, but the species composition varies greatly from tree to tree, which gives relatively high values of the total species richness of the base of the trunk.

From the base up the trunk, there is a change in the dominant species. For birch: *Cladonia coniocraea* (base)/*Hypogymnia physodes* (5–10 m)/*H. physodes*, *Parmelia sulcata* (10–20 m)/*H. physodes*, *P. sulcata*, *Melanohalea olivacea* (crown). For spruce: *Cladonia digitata* (base)/*Hypogymnia physodes* (5–10 m)/*H. physodes*, *Parmelia sulcata* (15 m, crown). Light conditions apparently have the greatest influence on the change of dominants; this dependence is better seen in the height distribution on spruce, which has an evergreen crown. The fact that *H. tubulosa* can only be found on the upper part of the spruce indicates that this species prefers higher insolation in our zone (temperate continental climate of the coniferous-broadleaved sub-zone) than when growing in the Mediterranean.

It is very important for conservation activities that the finds of species of the genera *Bryoria* and *Usnea* protected in this area are concentrated in the crowns and in the upper part of the trunks. This must be taken into account when studying their actual distribution and the size of their populations in the Moscow oblast.

ACKNOWLEDGMENTS

The authors are sincerely grateful to PhD I.D. Insarova for valuable comments and recommendations in preparing the article.

FUNDING

The research was carried out as part of the state assignment of the Institute of the Forest Science RAS no. AAAA-A19-119053090074-7 “Structure, Dynamics and Productivity of Natural and Artificial Forest Communities in the Center of the Russian Plain” and the State Order of the Government of Russian Federation to Lomonosov Moscow State University no. 121032300081-7.

CONFLICT OF INTEREST

The authors declare that they have no conflicts of interest.

COMPLIANCE WITH ETHICAL STANDARDS

This article does not contain studies involving humans or animals as research subjects.

REFERENCES

- Boch, S., Müller, J., Prati, D., et al., Up in the tree – the overlooked richness of bryophytes and lichens in tree crowns, *PLoS One*, 2013, vol. 8, no. 12, p. e84913. <https://doi.org/10.1371/journal.pone.0084913>
- Marmor, L., Tõrra, T., Saag, L., et al., Lichens on *Picea abies* and *Pinus sylvestris* – from tree bottom to the top, *Lichenologist*, 2013, vol. 45, no. 1, pp. 51–63. <https://doi.org/10.1017/S0024282912000564>
- Kiebacher, T., Keller, C., Scheidegger, C., and Bergamini, A., Hidden crown jewels: the role of tree crowns for bryophyte and lichen species richness in sycamore maple wooded pastures, *Biodiversity Conserv.*, 2016, vol. 25, pp. 1605–1624. <https://doi.org/10.1007/s10531-016-1144-4>
- Hale, M.E., Vertical distribution of cryptogams in a red maple swamp in Connecticut, *Bryologist*, 1965, vol. 68, no. 2, pp. 193–197.
- Holien, H., The lichen flora on *Picea abies* in a suboceanic spruce forest area in Central Norway with emphasis on the relationship to site and stand parameters, *Nordic J. Bot.*, 1997, vol. 17, no. 1, pp. 55–76.
- Caruso, A. and Thor, G., Importance of different tree fractions for epiphytic lichen diversity on *Picea abies* and *Populus tremula* in mature managed boreonemoral Swedish forests, *Scand. J. For. Res.*, 2007, vol. 22, no. 3, pp. 219–230. <https://doi.org/10.1080/02827580701346031>
- Fritz, Ö., Vertical distribution of epiphytic bryophytes and lichens emphasizes the importance of old beeches in conservation, *Biodiversity Conserv.*, 2009, vol. 18, no. 2, pp. 289–304. <https://doi.org/10.1007/s10531-008-9483-4>
- Teplykh, A.A., Patial and age-vitality population structure in the lichen *Pseudevernia furfuracea* (L.) Zopf at the conditions of a raised bog, in *Nauchnye Trudy Gosudarstvennogo Prirodnogo Zapovednika “Bolshaia Kokshaga”* (Scientific Works of the State Nature Reserve “Bolshaya Kokshaga”), 2008, no. 3., pp. 143–158.
- Lie, M.H., Arup, U., Grytnes, J.-A., and Ohlson, M., The importance of host tree age, size and growth rate as determinants of epiphytic lichen diversity in boreal spruce forests, *Biodiversity Conserv.*, 2009, vol. 18, no. 13, pp. 3579–3596. <https://doi.org/10.1007/s10531-009-9661-z>
- Yatsyna, A.P., Structure of epiphytic lichen communities on *Pinus sylvestris* L. in Belarus, *Vestn. Vitsebsk. Dzierzhavnaga Univ.*, 2013, no. 1, pp. 45–49.
- Nadyeina, O., Dymytrova, L., Naumovych, A., et al., Distribution and dispersal ecology of *Lobaria pulmonaria* in the largest primeval beech forest of Europe, *Biodiversity Conserv.*, 2014, vol. 23, no. 13, pp. 3241–3262. <https://doi.org/10.1007/s10531-014-0778-3>
- McCune, B., Gradients in epiphyte biomass in three *Pseudotsuga-Tsuga* forests of different ages in Western Oregon and Washington, *Bryologist*, 1993, vol. 96, no. 3, pp. 405–411.
- Rosso, A.L., McCune, B., and Rambo, T.R., Ecology and conservation of a rare, old-growth associated canopy lichen in a silvicultural landscape, *Bryologist*, 2000, vol. 103, no. 1, pp. 117–127.
- Ellyson, W.J.T. and Sillet, S.C., Epiphyte communities on Sitka spruce in an old-growth redwood forest, *Bryologist*, 2003, vol. 106, no. 2, pp. 197–211.

- [https://doi.org/10.1639/0007-2745\(2003\)106\[0197:ECOS-SI\]2.0.CO;2](https://doi.org/10.1639/0007-2745(2003)106[0197:ECOS-SI]2.0.CO;2)
15. *Sbornik materialov X rabochego soveshchaniya komissii po izucheniyu makromitsetov i VI mikologicheskoy shkoly-konferentsii "Mitselialnyi obraz zhizni i ekologo-troficheskiye gruppy gribov"* (Proc. X Meeting of Commission on Macromycete study and VI Mycological Conference "Mycelial Mode of Life and Ecological Groups of Fungi"), Dyakov, M.Yu, Popov, E.S., and Voronina, E.Yu, Eds., Moscow, 2014.
 16. Anuchin, N.P., *Lesnaia taksatsiia* (Forest Taxation), Moscow: Lesn. Prom-st., 1982.
 17. Stepanchikova, I.S., Gagarina, L.V., Collecting, identification, and storage of lichenological collections, *Flora lishainikov Rossii. Biologiya, ekologiya, raznoobraziye, rasprostraneniye i metody izucheniya lishainikov* (The Lichen Flora of Russia. Lichen Biology, Ecology, Diversity, Distribution and Methods to Study Lichens), Moscow: KMK, 2014, pp. 204–219.
 18. Westberg, M., Moberg, R., Myrdal, M., et al., *Santesson's Checklist of Fennoscandian Lichen-Forming and Lichenicolous Fungi*, Uppsala University: Mus. Evol., 2021.
 19. Mirkin, B.M., Rozenberg, G.S., and Naumova, L.G., *Slovar poniatii i terminov sovremennoi fitotsenologii* (Glossary of Concepts and Terms of Modern Phytocenology), Moscow: Nauka, 1989.
 20. Nimis, P.L., Martellos, S., *ITALIC – The Information System on Italian Lichens. Version 6.0*, University of Trieste, 2021. <http://dryades.units.it/italic>. Cited December 12, 2021.
 21. Peciar, V., Epiphytische Moosgesellschaften der Slowakei, *Acta Fac. Rer. Nat. Univ. Comeniae, Bot.*, 1965, vol. 9, no. 12, pp. 371–470.
 22. Du Rietz, G.E., Om fattigbark – och rikbarsamhällen, *Sven. Bot. Tidskr.*, 1945, vol. 39, no. 1, pp. 147–150.
 23. Campbell, J. and Coxson, D.S., Canopy microclimate and arboreal lichen loading in subalpine spruce-fir forest, *Can. J. Bot.*, 2001, vol. 79, no. 5, pp. 537–555. <https://doi.org/10.1139/cjb-79-5-537>
 24. Korchikov, E.S., *Lishayniki Samarskoy Luki i Krasnosamarskogo lesnogo massiva* (Lichens of Samarskaya Luka and Krasnosamarskiy Forest Massif), Samara: Samar. Univ., 2011.
 25. *Krasnaya kniga Moskovskoi oblasti* (Red List of Moscow Oblast), Moscow: KMK, 2008.
 26. *Krasnaya kniga Moskovskoi oblasti* (Red List of Moscow Oblast), Moscow Oblast: Verkhov'e, 2018.
 27. McCune, B., Rosentreter, R., Ponzetti, J.M., and Shaw, D.C., Epiphyte habitats in an old conifer forest in Western Washington, U.S.A., *Bryologist*, 2000, vol. 103, no. 3, pp. 417–427. [https://doi.org/10.1639/0007-2745\(2000\)103\[0417:EHIA-OC\]2.0.CO;2](https://doi.org/10.1639/0007-2745(2000)103[0417:EHIA-OC]2.0.CO;2)