

Vertical distribution of epiphytic bryophytes depends on phorophyte type; a case study from windthrows in Kampinoski National Park (Central Poland)

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Abstract: The vertical distribution of epiphytic bryophytes in European forests are still relatively poorly understood. The aim of the study was to analyse the diversity and vertical zonation of epiphytic mosses and liverworts on selected tree types (*Quercus petraea*, *Betula pendula* and *Pinus sylvestris*) within windthrow areas in the Kampinoski National Park (Central Poland). The investigations were performed in five parts of the trees: the tree base, lower trunk, upper trunk, lower crown, and upper crown. Deciduous trees have more species than pine trees (13 on *Quercus* and *Betula*, 8 on *Pinus*). The type of phorophyte was crucial for the differences in the species composition from the tree base to the upper crown that was observed. The highest richness of bryophytes was recorded on the tree bases, while the lowest was recorded in the upper parts of the crowns. The variability of the habitat conditions in the vertical gradient on the trunk that affected the patterns of the occurrence of species with different ecological preferences was determined using the Ellenberg indicator values. An increase in the value of the light and acidity indicators from the base of the trunk upwards and decreasing tendency in the case of moisture indicator was noted.

Keywords: mosses, liverworts, phorophyte, vertical gradient, height zones, Ellenberg indicator values

INTRODUCTION

Epiphytes belong to organisms that are particularly specialised in terms of habitat (Smith, 1982; Vanderpoorten & Goffinet, 2009). Their occurrence is conditioned by a number of factors, which are associated with the type of phorophyte they inhabit, as well as with the general environmental conditions (e.g. climate, forest type, air pollution) (Barkman, 1958; Smith, 1982; Acebey et al., 2003; Frego, 2007; Sporn et al., 2010).

The species of tree species is one of the most important factors that explain epiphytic species diversity and distribution (Cornelissen & ter Steege, 1989; Putna & Mežaka, 2014). This is primarily due to differences in the bark structure and chemistry, especially pH (Gustafsson & Eriksson, 1995; Mežaka et al., 2008). These features change over time, therefore the age and diameter of a phorophyte are also of great importance (Gustafsson & Eriksson, 1995; Márialigeti et al., 2009; Strazdiņa, 2010). The more cracked, sometimes in places decayed bark of older trees is characterised by a larger resources of microhabitats convenient for colonization (McGee & Kimmerer, 2002; Vuidot et al., 2011).

The location along the vertical gradient within the trunk and crown of a tree is also important for epiphytes (Mazimpaka & Lara, 1995; Boch et al., 2013; Oliveira & Oliveira, 2016; Mellado-Mansilla et al., 2017; Campos et al., 2019). The vertical distribution is mainly determined by the microclimatic factors such as humidity and light availability (Hosokawa & Odani, 1957; Sillet & Rambo, 2000; Sporn et al., 2010).

Due to the limited access to the higher parts of trees, research on epiphytic biotas are most often limited to the lower parts of the trunk, usually to a height of 2 m above the ground (e.g. Fritz et al., 2008; Friedel et al., 2006; Marmor et al., 2012). A study of the epiphytes around the whole tree requires the use of climbing techniques (Diaz et al. 2010; Boch et al., 2013; Campos et al., 2015) or felling trees (Marmor et al., 2013). A relatively rarely used opportunity to analyse epiphytes in the full height gradient are naturally formed windthrows.

In 2017, in several locations of the Kampinoski National Park (Central Poland), the wind felled

fragments of stands, which were used to the study epiphytic bryoflora within entire trees. The aim of the study was to analyse the diversity and vertical zonation of epiphytic mosses and liverworts on selected types of trees: *Quercus*, *Betula* and *Pinus*. Our main questions were: 1) are there differences in vertical zonation of epiphytic bryophytes between the analyzed types of phorophytes? 2) what factors determine the vertical distribution of epiphytes?

MATERIALS AND METHODS

Study area

The study was conducted in the forests in the Kampinoski National Park (Central Poland) on two areas with windthrows: 1) a range named “Rózin” – a mixed forest with the character of acidic oak forest about 104 years old, the stand is dominated by *Quercus petraea* (Matt.) Liebl. and *Betula pendula* Roth (forest allotment 258 a, b; 52.273319°N, 20.634140°E) and 2) a range named “Grabina” – mixed forest with the character of a fresh mixed coniferous forest about 84 years old, which is dominated by *Pinus sylvestris* L. (forest allotment 125 a, c; 52.306723°N, 20.570321°E). The field study was carried out in September 2018.

Sampling

Fallen trees of *Quercus petraea*, *Betula pendula* and *Pinus sylvestris* were selected for the study – ten oaks and ten birches on the “Rózin” floor and ten pines on the “Grabina” floor. All the trees were healthy and had no visible signs of damage. Their diameter at breast height was: *Quercus* – 42–68 cm, *Betula* – 36–50 cm and *Pinus* – 33–53 cm.

There were five vertical zones distinguished on every tree: tree base (TB) – the trunk base up to a height of 1 m; the lower trunk (LT) – the lower half of the trunk (trunk = between the base and the first main branch of the crown); the upper trunk (UT) – the upper half of the trunk; the lower crown (LC) – the lower half of the crown (crown = between the first crown branch and the crown top) and the upper crown (UC) – the upper half of the crown. The species composition of the bryophytes growing on each section of a tree was determined. Additionally, the cover of species patches on each section of

a tree was also estimated using the categories of coverage (cover index), which depend on the size of the area covered by species patches, that was proposed by the authors: 1 – up to 10 cm² (estimated to 3×3 cm), 2 – 10 to 100 cm² (estimated from 3×3 cm to 10×10 cm), 3 – 100 to 1 000 cm² (estimated from 10×10 cm to 30×30 cm), 4 – more than 1 000 cm² (estimated more than 30×30 cm). Frequency of recorded species was defined as the number of inhabited trees (in total and for individual vertical zones).

Although most species were identified in the field, in some cases it was necessary to collect small samples of herbarium material for their determination in laboratory conditions (e.g. *Uloa* and *Orthotrichum* species).

The sampling effort for totally 30 randomly trees (each 10 of three species) expressed as accumulation species curve of epiphytic bryophytes is presented in Supplement. Based on species cover of epiphytic flora of bryophytes as proxies of habitat requirements of species Ellenberg indicator values (EIVs) for light (EIV-L), temperature (EIV-T), moisture (EIV-F) and substratum (soil) reaction (EIV-R) were computed (Ellenberg & Leuschner, 2010). EIVs were calculated as cover-weighted values.

Statistical analysis

All statistical tests were performed by means of R language and environment (R Core Team 2019). Significance of difference in species richness and cumulative cover per tree among species of host tree was compared using Kruskal-Wallis test followed by post-hoc Conover test (package *agricolae*). In order to identify factors influencing colonization by bryophytes (coded as 1-colonized tree vs 0 non-colonized tree) generalized linear model GLM with binomial distribution (logistic regression) was applied using package *stats* and function *glm()*. The species identity of tree (i.e. birch, oak, pine) and type of vertical zones (TB, LT, UT, LC, UC) were regarded as explanatory variables. G-test was used to show significance of differences in frequency in case of categorical variables (package *DescTools*). The conditional plot that show probability of colonization due to distance of vertical zone from ground was created. In turn, total cover of bryophytes and species richness and habitat requirements of species expressed by cover-weighted Ellenberg

values as responses to the same environmental factors were tested in Linear Mixed Effect Model (LMM) model with Gaussian distribution by means of package *lme4*. Due to the fact that several vertical zones colonized by bryophytes could be located at the same tree individual tree was regarded as random effect. The significance of the final model with presentation of Wald chi-square statistics and p-values of each covariates were done by means of *car* package. The *post-hoc* procedure using Tukey test after LMM was done using packages *lsmeans* and *multcomp*.

To show how environmental factors: species identity of tree, type of vertical zones, DBH, biodiversity indices and EIVs explain species diversity Principal Components Analysis (PCA) with Hellinger transformation due to a lot of absence in data set was performed (package *vegan*). Passive projection of explanatory variables into ordination with permutation test (999 iterations) was conducted and value of pseudo-

F and p-value was calculated. PERMANOVA analysis was conducted to examine significance of differences in species composition among tree species, type of vertical zone and their interaction using Adonis function (*vegan* package). The indicator value (fidelity) of species to particular species of tree was calculated. The significance of fidelity was performed using 999 permutations (package *labdsv*).

Nomenclature

Nomenclature for liverworts is given according to Söderström et al. (2016), and for mosses follows to Hill et al. (2006).

RESULTS

A total of 22 species of bryophytes (20 mosses and 2 liverworts), which occurred in a varied frequency and abundance, were found on the 30 fallen trees that were tested (Table 1). There

Table 1. Frequency and (/) average values of the cover index (only for colonized trees) on distinguished vertical tree zones: TB – tree base, LT – lower trunk, UT – upper trunk, LC – lower crown, UC – upper crown. O – oak, B – birch, P – pine; *, -p<0.05, *-p<0.01, ***-p<0.001.

	Oak					Birch					Pine					IndVal
	TB	LT	UT	LC	UC	TB	LT	UT	LC	UC	TB	LT	UT	LC	UC	
<i>Aulacomnium androgynum</i>	-	-	-	-	-	-	-	-	-	-	1/2	-	-	-	-	
<i>Dicranoweisia cirrata</i>	-	5/1.8	6/2.7	7/3	4/1.25	1/4	3/2.7	3/2.7	1/1	-	-	-	-	-	-	0.31***O
<i>Dicranum flagellare</i>	-	-	-	-	-	-	-	-	-	-	1/1	-	-	-	-	
<i>Dicranum montanum</i>	3/1.7	7/2.3	6/2.8	4/2	-	10/2.9	9/2.5	5/1.6	1/1	-	3/1	1/1	-	-	-	0.27**B
<i>Dicranum scoparium</i>	1/1	-	5/1	4/1.3	-	7/2.7	4/2	1/1	-	-	-	-	-	-	-	0.17*B
<i>Dicranum tauricum</i>	-	-	-	-	-	-	1/2	-	-	-	-	-	-	-	-	
<i>Hypnum cupressiforme</i>	10/4	10/3.8	10/3.9	10/4	10/2.3	8/2.6	8/1.9	7/2.9	7/1.9	-	-	-	-	-	-	0.72***O
<i>Hypnum pallescens</i>	-	2/2	2/2.5	7/2.1	-	-	-	-	1/1	-	-	-	-	-	-	0.21**O
<i>Lophocolea heterophylla</i>	-	-	-	-	-	1/1	-	-	-	-	7/2	-	-	-	-	0.13**P
<i>Orthotrichum affine</i>	-	-	1/2	3/2	3/1.3	-	-	-	1/1	-	-	-	-	-	-	0.12**O
<i>Orthotrichum anomalum</i>	-	-	-	1/1	-	-	-	-	-	-	-	-	-	-	-	
<i>Orthotrichum speciosum</i>	-	-	1/2	5/1.8	4/1	-	-	-	-	-	-	-	-	-	-	0.20**O
<i>Plagiomnium affine</i>	-	-	-	-	-	1/2	-	-	-	-	-	-	-	-	-	
<i>Plagiothecium curvifolium</i>	-	-	-	-	-	-	-	-	-	-	1/2	-	-	-	-	
<i>Platygyrium repens</i>	-	6/2.7	8/3	9/3.1	9/1.8	-	2/1.5	2/2	-	-	-	-	-	-	-	0.59**O
<i>Pleurozium schreberi</i>	-	-	-	-	-	-	-	1/2	-	-	-	-	-	-	-	
<i>Poblia nutans</i>	-	-	-	-	-	1/2	-	-	-	-	2/1.5	-	-	-	-	
<i>Ptilidium pulcherrimum</i>	-	3/2.3	3/2	3/1.7	-	3/3	2/2.5	-	-	-	-	-	-	-	-	0.10*O
<i>Sciuro-hypnum oedipodium</i>	1/3	-	-	-	-	-	-	-	-	-	1/1	-	-	-	-	
<i>Terraphis pellucida</i>	-	-	-	-	-	-	-	-	-	-	1/2	-	-	-	-	
<i>Ulotia bruchii</i>	-	-	-	3/1.7	-	-	-	-	-	-	-	-	-	-	-	
<i>Ulotia crispa</i>	-	-	-	2/1.5	1/1	-	-	-	-	-	-	-	-	-	-	
<i>Number of species:</i>	4	6	9	12	6	8	7	6	5	0	8	1	0	0	0	

were 13 species of bryophytes on both the oaks and birches, but only 8 on the pine. Ten species significantly are associated with particular species of tree including, seven for oak, two for birch and only one species for pine (Table 1). The highest mean number of species per tree and total cover was observed in oaks followed by birch and pine (Fig. 1).

There was a high level of species diversity between the examined parts of the trees. Generally, the greatest number of species was found on the tree bases (13 species) and the fewest in the upper parts of the crowns (6 species) (Fig. 2, Table 1). *Hypnum cupressiforme* Hedw. (on oak and birch), *Dicranum montanum* Hedw., *D. scoparium* Hedw. (mainly on birch) and *Lophocolea heterophylla* (Schrad.) Dumort. (mainly on pine) were the most frequent and abundant in the tree bases. Eight species, which mainly occurred on the oak and birch, were found on the lower parts of the trunks (*Hypnum cupressiforme* and *Dicranum montanum* were most abundant). Bryophytes were found in the upper parts of trunks only on the oak and birch, a total of 10 species (mainly *Hypnum cupressiforme*, *Dicranum montanum* and *Platygyrium repens* (Brid.) Schimp.). In the lower parts of the crowns, bryophytes were mainly found on the oak, where 12 species grew (most often and most abundantly *Hypnum cupressiforme* and *Platygyrium repens*). There were only 5 species

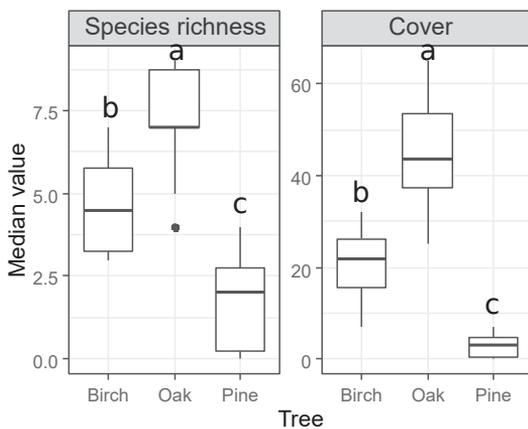


Fig. 1. Median number of species richness and cumulative cover of bryophytes per a tree among species. The different letters denote significance of difference at $p < 0.05$ (Kruskal-Wallis test followed by *post-hoc* Conover test).

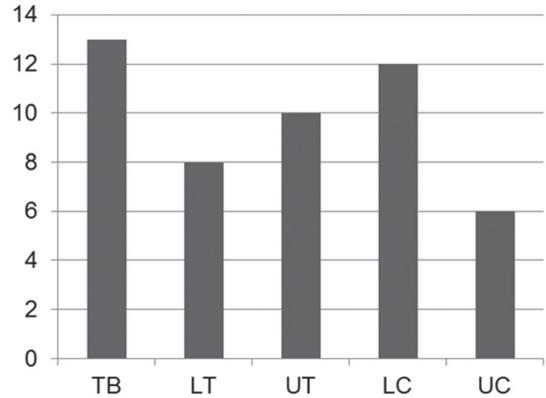


Fig. 2. Total number of species on distinguished vertical tree zones. TB – tree base, LT – lower trunk, UT – upper trunk, LC – lower crown, UC – upper crown.

on the birch (most often *Hypnum cupressiforme*) and none on the pine. In the upper parts of the crowns bryophytes were found only on the oak, where six species were observed, mainly *Hypnum cupressiforme* and *Platygyrium repens*.

The distribution of the number of species that was recorded on the individual parts of the analysed trees was characteristic (Fig. 3). In the case of the oaks, this number increased from the base of the tree to the lower part of the crown (they were recorded the most here) but decreased in the upper parts of the crowns. On the birches, the most species were found on the base of the trunks and their number gradually decreased upwards (no bryophytes were found in the upper part of the crowns). On the pine, bryophytes were found almost exclusively on the base of trunks.

The GLM showed that species identity and type of vertical zones, especially its location significantly enhances species colonization (Fig. 4a). In detail, G-test revealed that number of colonized trees differed significantly among tree species (Fig. 4a). This analysis confirms that oaks were colonized in the whole of vertical gradient, whereas majority of pines vertical zones were not colonized. Taking into account all trees probability of colonization decreases with location of vertical zone i.e. its distance from the ground (Fig. 4b). The highest probability was found for lower part of tree: tree base and lower trunk.

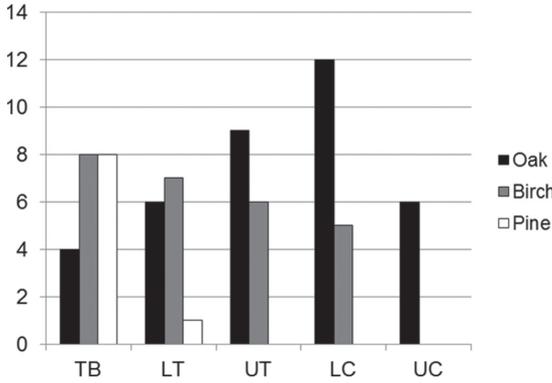


Fig. 3. Variation in the number of species on distinguished vertical tree zones. TB – tree base, LT – lower trunk, UT – upper trunk, LC – lower crown, UC – upper crown.

According to LMMs species richness differed among vertical zones but not among tree species (Table 2). In birch and in pine the highest number of species was found in tree base, whereas in oak in lower crown. In turn, regarding cover of species mean the highest cover per vertical zone was found in oak. The lower crowns and upper trunks had significantly highest cover (Fig. 5).

Table 2. Average values of EIVs for species occurring on distinguished vertical tree zones: TB – tree base, LT – lower trunk, UT – upper trunk, LC – lower crown, UC – upper crown; L – light, T – temperature, F – moisture, R – reaction. The different letters show significance of differences among species (in a column) and among types of tree zones (in a row) at $p < 0.05$.

		TB	LT	UT	LC	UC
		a	a	a	a	a
L	<i>Quercus</i>	4.8	6	6.2	6.01	6.2
	<i>Betula</i>	5.5	5.7	5.8	6.2	-
	<i>Pinus</i>	4.5	6	-	-	-
		ab	a	ab	b	ab
T	<i>Quercus</i>	3.5	4.2	3.9	3.6	4
	<i>Betula</i>	3.8	4	4.3	4.3	-
	<i>Pinus</i>	3.28	3	-	-	-
		a	a	a	a	a
F	<i>Quercus</i>	4.8	4.7	4.6	4.5	4.7
	<i>Betula</i>	4.5	4.4	4.3	4.6	-
	<i>Pinus</i>	4.9	5	-	-	-
		c	c	bc	a	ab
R	<i>Quercus</i>	3.3	3.5	4	4.3	4.8
	<i>Betula</i>	3.4	3.7	3.8	3.8	-
	<i>Pinus</i>	2.3	2	-	-	-

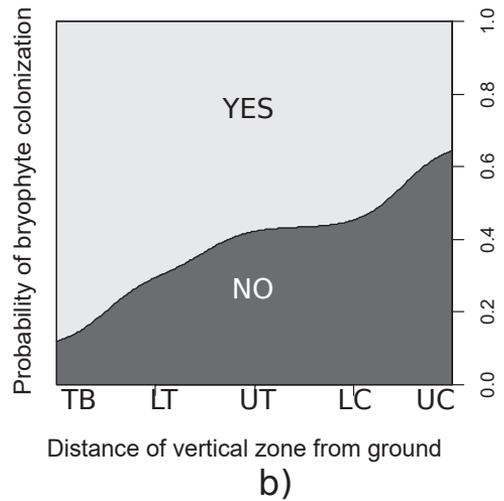
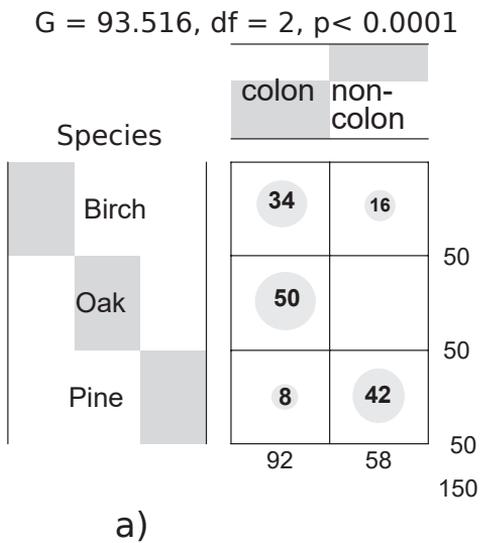


Fig. 4. Differences in frequency of colonized habitats (a) and conditional plot of type of vertical zone on probability of colonization by bryophytes (b).

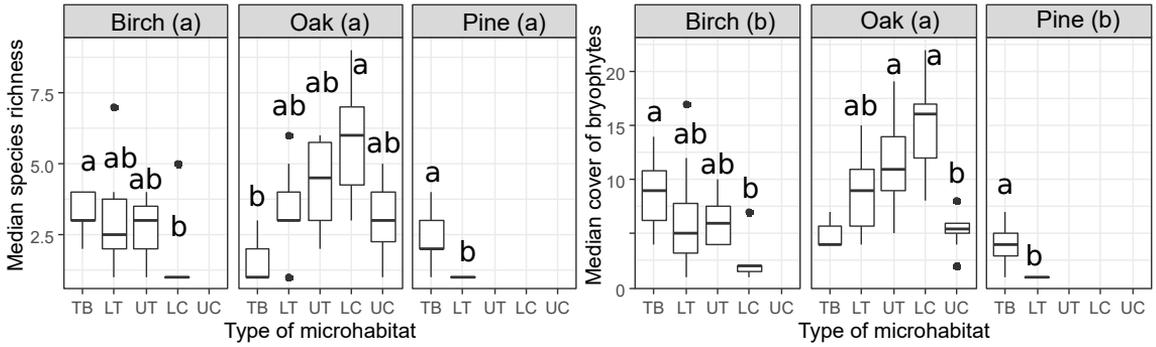


Fig. 5. Comparison of median species richness and median cover in vertical zones: TB – tree base, LT – lower trunk, UT – upper trunk, LC – lower crown, UC – upper crown. The different letters show significance of differences among species (near tree names) and among types of vertical zone (above boxes) at $p < 0.05$.

The values of EIVs differ significantly among tree species and among vertical zones except for light (Table 3). An analysis of the average values of the indicator numbers of the species growing on individual parts of the analysed trees showed that specific relationships existed (Table 3). In the case of the L (light) indicator, there was a clear upward trend from the base of the trunk

upwards, except for the lower part of the oak crowns where these values decreased slightly. A similar trend occurs in the case of the R (acidity) indicator for oak and birch. The average value of the F (moisture) index had a decreasing tendency in the case of the oak and birch, except for the crown where the value of this indicator increased (UC of *Quercus* and LC of *Betula*). The

Table 3. Results of GLM and LMM tests showing significance of type of vertical zone and species identity of tree on probability of colonization, species richness, cover as well as EIVs.

Type of test		Wald X^2	DF	P-value
Generalized Linear Model				
Response: colonization	Type of vertical zone	63.5	4	<0.0001
	Tree Species	133.3	2	<0.0001
Linear Mixed-Effects Models:				
Species richness	Type of vertical zone	11.0363	4	0.02616
	Tree Species	3.9741	2	0.13710 (NS)
Cover	Type of vertical zone	16.094	4	0.0028959
	Tree Species	13.865	2	0.0009755
EIV L	Type of vertical zone	5.6745	4	0.224807 (NS)
	Tree Species	12.0251	2	0.002448
EIV T	Type of vertical zone	15.248	4	0.004214
	Tree Species	57.317	2	<0.0001
EIV F	Type of vertical zone	14.135	4	0.006876
	Tree Species	25.810	2	<0.0001
EIV R	Type of vertical zone	37.576	4	<0.0001
	Tree Species	11.320	2	0.003482

average values of the indicator T (temperature) for the birch and pine increased gradually, while they fluctuated for the oak.

PCA demonstrated that all studied factors were significant. The samples of epiphyte vegetation differentiate along first axis of PCA (Fig. 6) and are transition from oak through birch to pine (this also applies values of EIVs). Both vector fitting of species identity onto ordination and PERMANOVA tests showed significant differences in species composition of bryophytes colonizing different trees. The highest DBH and values of biodiversity were also associated with oaks. Colonization of upper parts of tree was typical for oak (Fig. 6). Some variables as species richness are located across tree species and not along them.

DISCUSSION

The factors that influence the local diversity of epiphytes are different and they interact comprehensively (Barkman, 1958; Smith, 1982). The type of phorophyte is widely considered to be the most important factor (Barkman, 1958; Cleavitt et al., 2009; Putna & Mežaka, 2014).

Generally, the cover and diversity of epiphytic bryophytes is much lower on conifers compared to deciduous tree species (Snäll et al., 2004; Király et al., 2013). This study confirmed this phenomenon. There were more species on the oak and birch and the coverage of epiphytes on these trees was much higher compared to the pine. In addition, half of the species that were recorded on the pine did not occur on the other types of trees. These differences result from the differences of the bark properties. The analyzed trees differ in the features of the bark, such as the degree of cracking, the degree of flaking and pH, and that influence their colonisation by epiphytes. Oaks and birches are trees with a mesotrophic bark, which is relatively durable, more cracked, and less acidic compared to pine trees (Barkman, 1958). Cracked bark retains more moisture (Mežaka & Znotiņa, 2006) and humus accumulates in cracks (Chomba, 2014), which generally creates better conditions for the settlement of epiphytes (settling and germination of spores) (Király & Ódor, 2010). In turn, pine bark is acidic and strongly flaky (Barkman, 1958; Hauck & Javkhlán, 2008), and is also a relatively dry and oligotrophic habitat (Király & Ódor, 2010; Strazdiņa, 2010; Ilek et al., 2017).

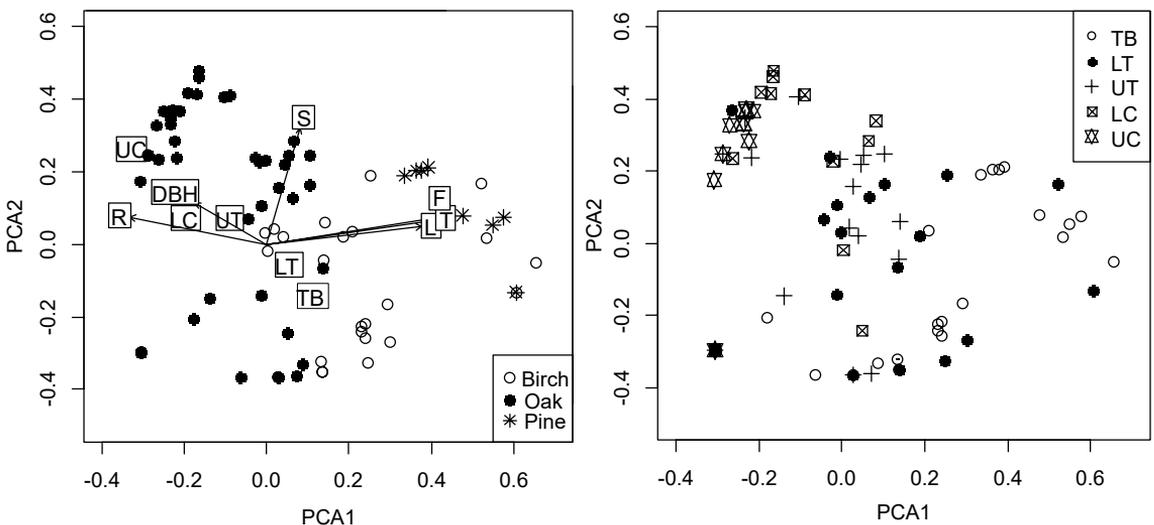


Fig. 6. Biplot of PCA based on cover of epiphyte bryophytes species with passive projection of environmental factors. Factors which were significant ($p < 0.05$) were shown. TB – tree base, LT – lower trunk, UT – upper trunk, LC – lower crown, UC – upper crown; L – light, T – temperature, F – moisture, R – reaction. Species composition differ significantly among trees (pseudo-F=36.03, $p < 0.001$) and vertical zones (pseudo-F=7.36, $p < 0.001$) and their interaction (pseudo-F= 7.41, $p < 0.001$; PERMANOVA).

For this reason, it is usually less colonised by epiphytes (Király & Ódor, 2010; Király et al., 2013). In this study, most of the epiphytes also avoided its colonisation pine except for *Lophocolea heterophylla*, which was recorded on the majority of the colonised pines (7 of the 8 with epiphytes). Similar observations were described by Mežaka & Znotiņa (2006), Ódor et al. (2013) and Pundiak & Grodzki (2017). The species that were recorded only on the pine, *Aulacomnium androgynum* (Hedw.) Schwägr., *Dicranum flagellare* Hedw., *Plagiothecium curvifolium* Schlieph. ex Limpr. and *Tetraphis pellucida* Hedw., are acidophilous species (Ellenberg & Leuschner, 2010).

Some other preferences were observed that were associated with the type of colonized phorphytes. Some species were found only on oak and birch, but avoided pine, e.g. *Dicranoweisia cirrata* (Hedw.) Lindb., *Dicranum scoparium*, *Hypnum cupressiforme*, *H. pallescens* (Hedw.) P.Beauv., *Platygyrium repens* and *Ptilidium pulcherrimum* (Weber) Vain., while *Orthotrichum anomalum* Hedw., *O. speciosum* Nees, *Ulota bruchii* Hornsch. ex Brid. and *U. crispa* (Hedw.) Brid. were only observed on oak.

Generally, the most recorded species were *Dicranum montanum*, *D. scoparium*, *Hypnum cupressiforme* and *Ptilidium pulcherrimum*. In temperate forests, they belong to the most common epiphytes, especially *Hypnum cupressiforme* (Mežaka et al., 2008; Ódor et al., 2013; Putna & Mežaka, 2014). An interesting species is *Dicranum tauricum* Sapjegin, which is an acidophilous epiphyte that was quite rare in Poland in the 1980s, although in recent decades it has spread intensively and is now common locally (Stebel et al., 2012).

On a tree, as the height of the trunk increases, the microclimatic conditions change; the humidity decreases and the intensity of light, wind and evaporation increases (Hosokawa & Odani, 1957; Peck et al., 1995; Sales et al., 2016). This affects species diversity on the examined parts of the trees (Sporn et al., 2010). Generally, the most species were recorded on the bases of the trunks. This is largely due to the transient nature of this habitat as was evidenced by Kenkel & Bradfield (1981) and Mazimpaka & Lara (1995). Soil and decaying organic matter accumulate

in the crevices at the base of the trunks, which makes this microhabitat a somewhat extended ground environment. Therefore, in addition to the typical epiphytes, species that are usually terrestrial enter here (in our case, they were *Plagiomnium affine* (Blandow ex Funck) T.J.Kop., *Pohlia nutans* (Hedw.) Lindb. and *Sciuro-hypnum oedipodium* (Mitt.) Ignatov & Huttunen), which results in a greater diversity of bryoflora (Mazimpaka & Lara 1995; Mežaka & Znotiņa, 2006; Márialigeti et al., 2009). *Lophocolea heterophylla* was found most often on the pine trunk bases; Pundiak & Grodzki (2017) and Fojcik et al. (2019) also mention such a preference of this liverwort on epiphytic habitats. The occurrence of bryophytes on the trunk bases is also an advantage due to the higher humidity compared to the higher parts of a tree (Mazimpaka & Lara 1995; Pundiak & Grodzki, 2017), as well as a higher degree of bark cracking (Ranius et al., 2008). For these reasons bryoflora is relatively rich here, which has been confirmed by our G-test analysis indicating that the probability of colonization decreases with height of vertical zone. The main factor limiting the occurrence of epiphytes on the trunk bases is reduced light access (Sporn et al., 2010; Ódor et al., 2013; Sales et al., 2016).

In this study, differences were observed in colonisation of individual parts of trees by the bryoepiphytes. The tendency to decrease the coverage and abundance of bryophytes along the vertical gradient that was described by some authors (Jarman & Kantvilas, 1995; Coote et al., 2008) was only confirmed for the birch. The situation was opposite on the oak where the total number of species increased in the higher parts of the trees and reached a maximum in the lower parts of the crowns, while on the pine trees the bryophytes grew almost exclusively on the bases of the trunks (sporadically on the lower part of the trunk). It should be noted that in the upper parts of the crowns bryophytes only occurred on the oaks, which can be explained by the unfavorable features of the bark in the crowns of birches and pines (it is relatively smooth and flaky here). Species of the genera *Orthotrichum* and *Ulota* had a preference for only the upper parts of the trees, especially in the crowns, which is similar to the studies of other authors (Trynoski & Glime, 1982; Mellado-Mansilla et al., 2017). Such species, occurring mainly in the

upper zones of the trees, are referred to as sun epiphytes (Richards, 1984). They are photophilous, desiccation-resistant bryophytes adapted to the more xerothermic conditions in higher canopy strata (Barkman, 1958; Cornelissen & ter Steege, 1989). They show several morphological adaptations to drought, as compact life forms, small thick-walled cells and papillose leaf surfaces (León-Vargas et al., 2006 albo Uniyal et al 2007; Stanton & Reeb, 2016; Mellado-Mansilla et al., 2017). It must be also mentioned that the occurrence of crown species can be particularly underestimated if epiphytic studies investigate only the lower parts of trees (Boch et al., 2013).

It can be assumed that the differences in vertical colonisation may also result from differences in the age of the individual parts of a tree – their age decreases as their height increases and because the structure and properties of the bark change with age, the colonisation time is also longer (Mazimpaka & Lara, 1995; Sillett & Antoine, 2004; Lobel et al., 2006; Fritz et al., 2008). The bark on the older parts of trees like that on old trees is more cracked and can be rotten in places, and therefore there is a greater diversity of microhabitats. A bark's pH also increases with age. All these factors promote the colonisation by bryophytes (Gustafsson & Eriksson, 1995; Snäll et al., 2004; Ranius et al., 2008; Fritz & Heilmann-Clausen, 2010). It should also be remembered that within the same part of a tree, there may be very diverse microhabitats including more shady and humid ones, which are more often inhabited by epiphytic bryophytes, e.g. fragments of trunks and thick branches sheltered from the light, bark cracks and rotten places (Kenkel & Bradfield, 1981; Gustafsson & Eriksson, 1995; Ranius et al., 2008).

Differences in the species composition from the tree base to the crown are related to microclimatic gradients within the vertical profile (Bates, 1992; Mazimpaka & Lara, 1995; Mellado-Mansilla et al., 2017). In this study, the variability of vertical gradient conditions was not only reflected in the diversity of the bryophyte species, but also in the trends that were observed in the variability of the average of indicator values. Specifically, the clear upward trend of the average L (light) indicator was in line with the reports of other authors about an increase in the degree of lighting in the vertical gradient on

the trunk of a tree (Hosokawa & Odani, 1957; Trynoski & Glime, 1982; Sales et al., 2016). Another important factor that determines the vertical distribution of epiphytes is humidity because the humidity level is usually the highest at the base of the trunk and gradually decreases with the increasing height of the trunk (Ódor et al., 2013; Sporn et al., 2010; Ranius et al., 2008). Within the higher parts of trees, the water capacity of the bark also decreases (Levia & Wubbena, 2006; Everhart et al., 2008). In the case of the analysed F (moisture) indicator, the average values for the oak and birch decreased on the trunk and then increased slightly in the highest crowns (for the oak, it was the upper part of the crown, for the birch – the lower part of the crown). This indicates differences in the degree of the xerophytism of the habitats in the crowns of these trees. In the case of the pine trees, the variability of the mean F indicator was insignificant.

Many authors emphasize that the bark properties (texture and chemistry) are probably the main factors determining epiphyte preferences for host trees (e.g. Mezaka & Znotina, 2006; Márialigeti et al., 2009; Király et al., 2013; Chomba, 2014). The bark reaction is also an important factor that influences the diversity of epiphytic communities (Barkman, 1958; Putna & Mežaka, 2014; Batista & Santos, 2016). The recorded average R (acidity) indicator increased with increasing height on the oak and birch trunks. This is in line with reports from various authors that the higher parts of trees are usually characterised by higher pH values (Kermit & Gauslaa, 2001; Marmor et al., 2010).

The presented studies showed a significant diversity of bryoflora in relation to both the different types of phorophytes and in the aspect of vertical differentiation. The results, despite the limited number of attempts, are relatively clear and would confirm the thesis of Gradstein et al. (1996) that in homogeneous stands, the number of trees that are examined does not have to be large in order to properly reflect the diversity of the epiphytic bryoflora (according to these authors, it is sufficient to thoroughly study 4-5 trees to show the trends for more than 75% of species). It was also confirmed that the main factors determining the vertical distribution of epiphytes are connected with microclimatic

gradient (light and humidity), bark properties may also be relevant (texture and chemistry).

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Supplement. The species accumulation curves for site 1 – a, site 2 – b, birch – c, oak – d and pine – e.

