



# Non-forested vs forest environments: The effect of habitat conditions on host tree parameters and the occurrence of associated epiphytic lichens

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## ABSTRACT

The study compares the epiphytic lichen communities of two different ecological systems of northern Poland, a non-forested area and a natural lowland deciduous forest corresponding to the potential vegetation flora of a large part of Central Europe, in relation to the same tree species. The impact of habitat type and tree species on individual tree properties and the association between tree size, bark pH, conductivity, water-holding capacity, bark splitting, light intensity at tree trunks and the composition of lichens were analysed. Three sets of lichens were identified: confined to non-forested areas (40 species), confined to forests (61 species), and non-specific mutual species (53 species). The results indicate that most species demonstrate specificity to habitat type rather than to tree species. Factors related to tree species and bark properties gain in importance at the level of a specific habitat. Bark pH and water-holding capacity are decisive factors for lichen occurrence in both habitat types; additionally, in forests, tree diameter is important. The paper provides potentially useful ecological data for campaigns aimed at lichen conservation and at shaping the environment with concern for biodiversity.

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## 1. Introduction

The continuity of the ecosystem of the forest and the degree of naturalness of the processes occurring in its interior are important factors conditioning the existence of many epiphytic lichens (Rose, 1976; Cieśliński et al., 1996; Nordén et al., 2014), which often represent an important component of biodiversity in forest ecosystems, playing a significant functional role in their interiors (Ellis, 2012). Large-scale climatic gradients and specific soil conditions determine the compositions of trees that create specific forest communities (Walthert and Meier, 2017). In turn, trees modify soil properties (Lodhi, 1977) and microclimatic conditions by affecting light availability, humidity, and temperature (Wang et al., 2015; Sercu et al., 2017). Throughout their life cycle and after death, trees perform numerous ecosystem functions and provide a range of microhabitats (Harmon et al., 1986; Jones et al., 1997; Saxe et al.,

2001; Gutowski et al., 2004; Büttler et al., 2013; Lutz et al., 2013). There have been many studies on the effect of abiotic and biotic factors on the diversity and distribution of epiphytic lichens in different ecosystems, including boreal (e.g. Gauslaa et al., 2007, 2014; Hauck, 2011; Esseen et al., 2016), Mediterranean (e.g. Burgaz et al., 1994; Giordani, 2006; Aragón et al., 2010; Merinero et al., 2014) and temperate (e.g. Svoboda et al., 2010; Kubiak and Osyczka, 2017) forests. Precise information is necessary to prevent current biodiversity losses, especially with regard to the most sensitive species and their habitats (Mihoub et al., 2017). This seems to be an urgent problem in the light of the reports on dramatic losses in the diversity of epiphytic lichens in temperate deciduous forests of Europe over the last century (Hauck et al., 2013).

Historical and contemporary human activity has had a profound impact on the coverage area, distribution, and composition of forests in densely populated Central Europe (Kaplan et al., 2009). Approximately 1000 years ago, forests occupied about 80% of Poland (Plit, 2016). In the mid-twentieth century, forest cover was reduced to 21% (Polish Forests, 2019), the lowest level in history.

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Although forest cover in Poland and many other European countries has been steadily growing since then (Keenan et al., 2015), the level of biodiversity of forest ecosystems is, ominously, falling (Balvanera et al., 2006; Scherer-Lorenzen et al., 2007). This is the result of, *inter alia*, several hundred years of the cultivation of a small group of quick-growing tree species, mainly coniferous, in the majority of natural forest habitats (Bremer and Farley, 2010). Original deciduous and mixed forests, which are the richest and most diverse in species, have been affected to the greatest extent, since, due to their fertile soil, they were readily occupied for purposes of cultivation and breeding (Matuszkiewicz, 2008; Löf et al., 2016).

In parallel, for nearly 500 years in many regions of Central Europe, deciduous trees have been planted in deforested areas, especially in the form of tree avenues. This term (also *tree alley* or *allée*) has slightly different meanings in different parts of the world. In European landscaping, the word 'alley' means a row of trees along a road or lane, crossing cultural landscapes (European Avenues, 2019). Most of the currently preserved avenues were planted about 100 years ago, and since then have become important elements shaping the local landscape. However, in connection with environmental risks resulting from the development of transport, well-preserved old tree avenues are rare, constituting a threatened element of the cultural landscape (Forrest and Konijnendijk, 2005). This is particularly worrisome, given that they play an important role in enhancing the biodiversity of non-forested landscapes (Pradines, 2012; Barrios et al., 2018). In addition, questions have arisen as to what extent such trees can mitigate the effects of fragmentation and isolation of natural forest habitats (Collinge, 1996; Fahring, 2003) and whether they can effectively serve as ecological corridors (Forman and Alexander, 1998).

Due to the poikilohydric nature, specific physiology, and structural variety of lichen thalli, the occurrence of particular epiphytic species depends on the properties of tree species and the climatic conditions where they grow (Barkman, 1958). Factors at the scale of the host-tree appear to be particularly important for epiphytes with narrow ecological amplitude. Physicochemical bark properties, such as thickness and degree of splitting, pH value, water-holding capacity, and eutrophication, regulate the presence, richness, and biodiversity of lichens (Bates and Brown, 1981; Kuusinen, 1996b; Löbel et al., 2006; Mustafa et al., 2009; McDonald et al., 2017). The attributes of a given tree can change as a tree ages and may be modified to a certain extent by natural environmental conditions and anthropogenic influences (Giordani and Malaspina, 2017). External factors related to stand characteristics, i.e. the composition and age structure of tree species, tree density and canopy cover, moisture regime, and light availability, are also crucial for epiphytes (Fritz et al., 2009; Randlane et al., 2017; Štikāne et al., 2017; Westerberg et al., 2017).

The main purpose of this study was to identify and compare epiphytic lichen communities that develop in two different types of habitat: (1) non-forested landscape area in the form of tree avenue; (2) mixed deciduous lowland forest corresponding to the potential natural vegetation of Central Europe. The research encompassed five species of trees, native to Central Europe and common in various natural and anthropogenic environments. On this basis, we wished to determine to what extent these two selected ecosystems are similar and how greatly they differ in terms of lichen diversity and composition. We intended to identify which environmental variable most significantly affects the richness and occurrence of epiphytic lichens. We included primarily the factors following from the autogenous properties of a given tree species, with regard to their phenotypic plasticity and to light intensity as conditioned by the crown of a tree and its immediate surroundings. Additionally, in

reference to these aims, we set the following general hypotheses regarding epiphytes related to deciduous trees: (1) most lichen species demonstrate greater attachment to type of habitat than to specific host-tree species; (2) the number of lichen species confined to forest habitat is greater than the number of species closely related to open area; and (3) the lichen species richness increases with the increase of tree size and bark pH in both habitat types.

## 2. Materials and methods

### 2.1. Study area

The study was conducted in NE Poland within the Olsztyn Lakeland mesoregion (Fig. S1). This area belongs, as does the entire country, to the Continental Biogeographical Region of Europe (EEA, 2019). The landscape of this area was formed as a result of the last glaciation, which ended about 13,500 years ago. The topography is typical of young glacial landscapes and characterised by a variety of terrain forms, with a large number of lakes (more than 4% of the total area) and lowland forests (37%). The area lies at altitudes of 100–200 m a.s.l., with relative elevations of the highest hills about 30 m. The climate is temperate; the annual mean temperature is +7.2 °C, average annual rainfall varies from 550 to 570 mm, and the vegetation period lasts about 195–200 days. The potential natural vegetation is mixed deciduous forest composed mainly of oak, hornbeam, and lime (Leuschner and Ellenberg, 2017), corresponding to the *Tilio cordatae-Carpinetum betuli* association (Matuszkiewicz, 2008).

### 2.2. Host trees

We selected five deciduous tree species: *Acer platanoides* – Ac (Norway maple), *Fraxinus excelsior* – Fr (ash), *Tilia cordata* – Ti (lime), *Quercus robur* – Qu (pedunculate oak), and *Ulmus laevis* – Ul (European white elm); the abbreviations given here are used subsequently in the paper. These trees constitute an important natural component of the eutrophic and mesoeutrophic forest communities in this part of Europe (Matuszkiewicz, 2008) which have high value for biodiversity conservation (Council Directive, 1992). Unfortunately, such forests are currently rare due to land conversion activities (Kubiak et al., 2016). Nevertheless, selected tree species have frequently been planted along roads, especially in the second half of the 19<sup>th</sup> century and in the early 20<sup>th</sup> century (Worobiec and Liżewska, 2009).

Because it is difficult to separate the effect on bark properties of tree age from that of tree size (see Johansson et al., 2007), a minimum diameter of 40 cm at breast height was established as the basic criterion for inclusion of an individual tree in the study. We assumed that this size is sufficient to guarantee the complete development of most periderm properties typical of a given tree species. Moreover, irrespective of the biological life span of an individual tree, it can be assumed that the potential period of colonisation was long enough for the tree trunk to acquire a relatively stable lichen community on its surface. The age of studied trees and the stability (continuity) of their habitats (both natural and anthropogenic) minimizes the possible impact of past, heterogeneous habitat conditions (see also Ellis and Coppins, 2007). Additionally, only individual trees in good health, characterised by a single straight trunk and topped with a typical crown, were included. Such selection was necessary because of the limited occurrence of diseased, dying or irregular trees along roads resulting from elimination of individuals that might fall and pose a threat to road safety. Based on the available field documentation, the age of studied trees is estimated as 100–150 y.

### 2.3. Field data collection

Epiphytic lichens were studied on 100 trees (20 per species) from each habitat type: (1) non-forested area – well-preserved stretches of tree avenues (ca 200 m in length) growing in similar topographical conditions and located at least 200 m from the forest border (Fig. S2A), and (2) forest – best-preserved parts of forest sub-divisions (largely protected within the NATURA 2000 network) with uniform and undisturbed patches of vegetation corresponding to potential for this area, located at least 200 m from the nearest forest border (Fig. S2B). Tree avenues along local roads with negligible traffic and situated at least 200 m from the nearest farm buildings were included in the study. This approach was aimed to minimize the impact of local factors, in particular the potential supply of nitrogen compounds, on lichen composition patterns and to recognize the actual diversity of epiphytic lichens characteristic of non-forest areas in the study area. In the case of forest habitat, a review of available source documents (Forest Data Bank, 2018) was the basis for the designation of localities with appropriate tree stands (based on the species and age of trees) (Table S1). We made efforts to select trees according to the density and local distribution type of particular species in both landscapes.

The diameter at breast height (DBH; 1.3 m from the ground) and depth of periderm cracks (DPC; using callipers at four points corresponding to major geographical coordinates) of each tree were measured. Then, three bark pieces were collected 1.5 m from the ground (the first from a randomly chosen side of the trunk and the next two at an equal distance from each other around the trunk perimeter) for chemical analysis. In addition, to estimate micro-climatic conditions, light intensity (Kipp & Zonen PAR Quantum Sensor) and relative humidity (Testo, Inc. hygrometer) were recorded at breast height close to the tree trunks. Light intensity was measured in four directions with the sensor applied to the tree trunk in a horizontal orientation. The average values of parameters for individual tree specimens were treated as a single observation. Measurements were performed in the middle of clear days with moderate cloud cover towards the end of May. Because the growth rate of thalli during the year may be different for various lichens, and shadow or insolation may inhibit or promote particular lichens, we decided to accept the intermediate state of the annual tree development, i.e. between the leafless period in winter and the period of densest foliage in the summer. Special rounds of all sampling sites were made to accomplish this task.

To reflect the fullest possible biodiversity, lichens were identified over the entire surface of tree trunks at a height of 0–2 m from the ground. The lichen species were classified into five classes according to the cover-abundance scale: (1) < 1% or single individual/individuals; (2) 1–5% or several individuals; (3) 5–25% or over a dozen individuals; (4) 25–50%; (5) > 50%.

### 2.4. Lichen species determination

Lichens were identified in the field, when possible; however, most individuals were collected for detailed morphological and chemical examinations. Chemical properties were analysed using standard thin-layer chromatography (TLC), in accordance with the method summarised by Orange et al. (2001). The nomenclature follows Index Fungorum (2018); the collected material is deposited in the OLTC herbarium (Thiers, 2019).

### 2.5. Chemical analysis of tree bark

The samples were thoroughly cleaned of organic debris prior to analyses. The mean value calculated from the measurements of three separate bark pieces was treated as the final observation.

**Bark pH:** Acidity was measured using an Extech PH100 pH meter with a flat-surface electrode. To enable the rapid solution of hydrogen ions, 0.5 ml of 0.1 M KCl was placed on the bark 1 min before measuring the pH, as done previously in lichenological studies (Marmor et al., 2010).

**Water-holding capacity (WHC):** Bark fragments were air-dried for 2 weeks. Equal sized ( $\varnothing$  10 mm) and 2–3 mm thick discs were cut from the bark samples using a cork borer. The discs were weighed, then completely submerged in deionised water and shaken for 24 h. Next, the discs were drained of excess water and re-weighed. Water-holding capacity was expressed as the percent increase in weight.

**Conductivity:** Bark pieces were cleaned of foreign materials, dried to a constant weight, and milled as composite samples. Samples weighing 2 g were soaked in glass weighing bottles with 20 ml of deionised water and shaken, using a vibration shaker, for 4 h. Conductivity was measured following suspension filtration using a conductivity meter (SevenGo Duo SG23-FK5; Mettler Toledo).

### 2.6. Statistical analyses

Initially, the mixed model ANOVA with tree species and habitat treated as fixed factors and locality as a random factor nested within habitat was performed to test their effect on bark properties (i.e. pH, conductivity, WHC, DPC), diameter (DBH), and light intensity. Since the effect of locality turned out to be insignificant ( $p > 0.05$ ) for each dependent variable (see Osyczka and Kubiak, in print), locality was considered as a negligible factor and consequently two-way analysis of variance (tree species  $\times$  habitat), followed by Tukey's (HSD) test, was performed to verify significant differences in parameters across particular tree species and habitat types. Prior to the analysis, distribution normality was verified using the Kolmogorov-Smirnov test. Levene's test was performed to assess the equality of variances. Data which did not meet the assumptions for normality were Box-Cox-transformed. The correlations (Pearson's coefficient) between bark parameters, tree diameters, and the intensity of light falling on tree trunks were tested for each tree species with respect to habitat type in order to learn whether there were any general significant relationships between these variables.

Multiple regression analysis was used to determine which of the variables related to bark properties were the best predictors of the richness of lichen communities on all examined tree trunks ( $n = 200$ ) in terms of numbers of species and the Shannon index. The stepwise forward variable selection procedure, with a threshold of  $p < 0.05$ , was applied and the variance inflation factors calculated in advance to determine whether any serious multicollinearity ( $VIF > 10$ ) existed. Additionally, a detailed residual analysis was performed in order to verify if any outliers (extreme cases) exist and obtain reliable regression coefficients.

Non-metric multidimensional scaling (NMDS) was used to find the pattern of similarities between examined tree individuals in terms of lichen composition. The analysis was based on a matrix of the abundance of lichen species on particular trees, using the Bray-Curtis coefficient. Simultaneously, two-way non-parametric multivariate analysis of variance (two-way NPMANOVA) and post-hoc pairwise comparison test were performed (Anderson, 2001). Detrended correspondence analysis (DCA) was performed to show the association of particular lichens with host tree species (with regard to habitat type); this analysis based on the mean frequency of lichen species on particular trees. Canonical correspondence analysis (CCA) was used to relate the abundance of particular lichens to habitat variables. Forward selection was used to select the explanatory variable from the set of all variables. A Monte Carlo

permutation test based on 9999 random permutations was performed in order to assess the statistical significance of relationships between species and habitat factors and between species and canonical axes (terBraak and Šmilauer, 2002). The analysis was carried out on the basis of two data matrices drawn from trees from the non-forested area and from the forest. Ordination analyses (except DCA) and multivariate tests were based on ordinal abundance scale. The statistical analyses were performed using following software: CANOCO 5 (CCA); STATISTICA 12 (ANOVA, MRA); PAST 3.25, Hammer et al. (2001) (NMDS, NPMANOVA, DCA).

### 3. Results

#### 3.1. Microhabitat properties

Significant effects ( $p < 0.05$ ) of both tree species and habitat, as well as interaction between these variables, were found for most of the measured bark parameters, i.e. pH, WHC, and DPC. Conductivity was influenced only by tree species; however, significant tree-habitat interaction ( $p < 0.05$ ) was revealed (Table 1). *Ac*, *Fr*, and *Ti* individuals from non-forested and forest habitats were characterised by relatively similar and higher values of bark pH compared to *Qu* and *Ti*. Regardless of the habitat, *Qu* was characterised by the most acidic bark. Similarly to *Qu*, the pH values of *Ti* bark for individuals from the forest were low; however, in a non-forested habitat, this tree developed considerably less acidic bark (Fig. 1A).

Conductivity of the solution obtained from bark varied somewhat between tree species and habitat (Fig. 1B). However, there were no significant intraspecific differences between *Ac*, *Fr*, and *Ti* growing in non-forested and forest habitats. Significant differences ( $p < 0.05$ ) in conductivity in *Qu* and *Ul* growing in different habitat conditions were revealed; however, in this respect, these tree species were opposite in character, as conductivity from a non-forested habitat was lower for *Qu* and higher for *Ul* compared to representatives from the forest.

The bark of *Ti* and *Ul* was characterised by the greatest water-holding capacity (WHC) in comparison to the bark of the remaining tree species. The bark of *Ul* from the forest, in particular,

absorbed large amounts of water, significantly more than the bark of all other trees. The least WHC was recorded for the bark of *Qu* in both habitats as well as for that of *Ac* and *Fr* in open habitats (Fig. 1C).

*Qu* trees, especially those growing in a forest, were characterised by the most deeply cracked bark. Other tree species were found with considerably shallower cracks of the periderm. Nevertheless, in these species, as opposed to *Qu*, slightly deeper DPCs were usually associated with the non-forested habitat (Fig. 1D).

As in the case of most bark properties in question, a significant effect of both tree species and habitat, as well as interaction between the variables ( $p < 0.05$ ), was found for tree diameter (Table 1). In general, tree trunks growing in forest conditions were narrower compared to trunks from the non-forested habitat. In this regard, the differences in DBH for *Qu* and *Ul* were the most pronounced (Fig. 2). It is difficult to identify any important associations between the variables of a general nature. However, some significant relationships ( $p < 0.05$ ) were revealed, for example, positive correlations between DBH and DPC in the cases of *Ac* and *Qu* from the forest, positive correlations between DBH and WHC in the case of *Qu* from the non-forested area, and a negative correlation between DBH and bark pH in the case of *Ul* from the forest (Osyczka and Kubiak, in print).

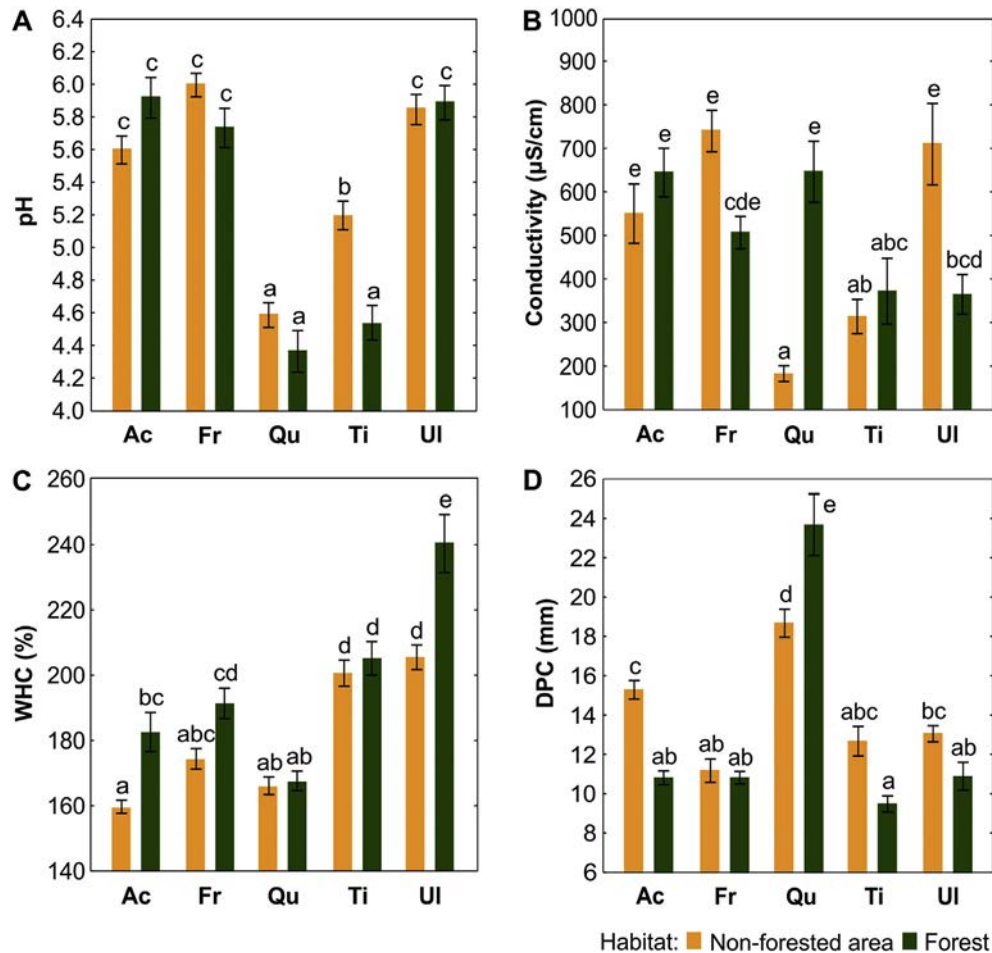
The intensity of light falling on tree trunks in the non-forested habitat was higher than in the forest environment, irrespective of tree species (significant habitat effect, Table 1). All trunks from the non-forested habitat were exposed to a relatively equal degree during measurements (Fig. S3). Inside forests, considerably more light fell on *Qu* and *Fr* trunks than on those of the other trees (significant tree effect, Table 1). The relative humidity was around 10% lower in non-forested habitat than in forest habitat.

#### 3.2. Richness of lichen species

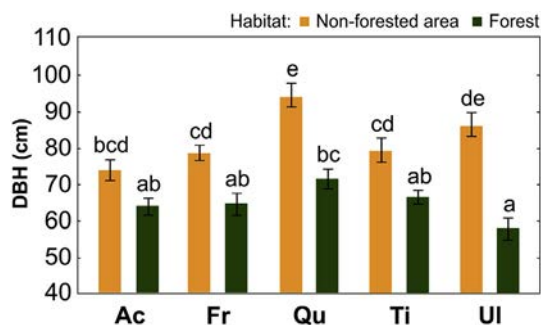
Altogether, 154 epiphytic lichen species were found during the study (Table S2). Three sets of species were identified (Osyczka and Kubiak, in print): (1) lichens exclusive to the non-forested habitat (40 species, 12 of which are endangered); (2) lichens exclusive to

**Table 1**  
Results of two-way of ANOVA for the effects of tree species (TREE) and habitat (HAB) on pH value, conductivity, water-holding capacity (WHC), depth of periderm cracks (DPC) of tree bark, diameter of trees (DBH) and light intensity measured at the breast height of trees.

Source of variation	Factors Interactions	SS (Sum of Squares)	MS (Mean Square)	DF (Degrees of Freedom)	F	p
pH	TREE	72.84	18.21	4	88.35	< 0.001
	HAB	1.46	1.46	1	7.08	< 0.001
	TREE × HAB	6.10	1.53	4	7.40	< 0.001
	Error	39.17	0.21	190		
Conductivity	TREE	2,332,267	583,067	4	16.30	< 0.001
	HAB	2934	2934	1	1.07	0.303
	TREE × HAB	4,028,751	1,007,188	4	20.67	< 0.001
	Error	13,270,370	69,844	190		
WHC	TREE	88,875	22,219	4	48.90	< 0.001
	HAB	13,252	13,252	1	29.17	< 0.001
	TREE × HAB	7573	1893	4	4.17	0.003
	Error	86,332	454	190		
DPC	TREE	3261	815	4	71.24	< 0.001
	HAB	28.28	28.28	1	5.33	0.022
	TREE × HAB	671	168	4	13.26	0.001
	Error	1954	10.28	190		
DBH	TREE	4484	1121	4	7.38	< 0.001
	HAB	15,068	15,068	1	99.23	< 0.001
	TREE × HAB	2327	582	4	3.83	0.005
	Error	28,853	152	190		
Light intensity	TREE	7939	1985	4	3.99	0.004
	HAB	543,090	543,090	1	1092.89	< 0.001
	TREE × HAB	1203	301	4	0.61	0.659
	Error	94,416	497	190		



**Fig. 1.** Parameters of bark for particular trees: (A) pH, (B) conductivity, (C) water holding capacity (WHC) and (D) depth of periderm cracks (DPC). Points indicate mean values, whiskers indicate SE (n = 20); the same letter indicate that the trees are not significantly different at the  $p < 0.05$  level according to Tukey's test. Tree species abbreviations: Ac – *Acer platanoides*, Fr – *Fraxinus excelsior*, Ti – *Tilia cordata*, Qu – *Quercus robur*, Ul – *Ulmus laevis*.



**Fig. 2.** Diameter of trees (DBH); points indicate mean values, whiskers indicate SE (n = 20). Letters denote the results of Tukey's test; different letters above the bars indicate statistically significant differences ( $p < 0.05$ ). Tree species abbreviations as in Fig. 1.

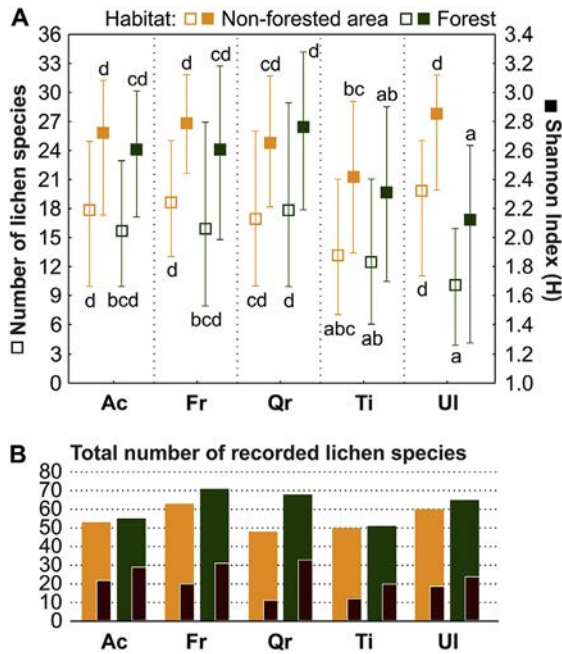
the forest (61 species, including 36 endangered); and (3) non-specific lichens associated to varying degrees with both habitat types (53 species, including 14 endangered). The multiple regression analyses revealed that the number of lichen species on trees was positively related to DBH (standardized B coefficient  $\beta = 0.155$ ,  $p = 0.001$ ), pH of bark ( $\beta = 0.168$ ,  $p = 0.005$ ), the conductivity ( $\beta = 0.176$ ,  $p = 0.009$ ) and negatively related to water-holding capacity ( $\beta = -0.239$ ,  $p < 0.001$ ). As regards the Shannon index, in

general, similar results were obtained ( $\beta = 0.160$ ,  $p < 0.001$ ;  $\beta = 0.179$ ,  $p = 0.002$ ;  $\beta = 0.157$ ,  $p = 0.017$  and  $\beta = -0.289$ ,  $p < 0.001$ ; for DBH, pH, conductivity and WHC, respectively). These regression models were significant ( $F = 9.89$ ,  $p < 0.001$ ;  $F = 12.21$ ,  $p < 0.001$ , respectively) and explained 33.5% and 29.5% of the variability in the number of lichen species and in the Shannon index.

Significant differences in diversity indices between particular trees were revealed (species number  $F = 10.73$ ,  $p < 0.001$ ; the Shannon index  $F = 12.95$ ,  $p < 0.001$ ). The mean number of lichen species and mean Shannon index per single tree trunk were slightly higher for Ac, Fr, and Ti and significantly higher ( $p < 0.05$ ) for Ul from the open habitat. Differences between mean values in relation to habitat type were most evident for Ul. This was not the case for Qu, for which species richness was somewhat greater in the forest. Poorest in quantified lichen communities were the trunks of Ti and Ul from the forest (Fig. 3A). The results are different when the entire pool of all recorded lichen species on trees is considered; in total, greater biodiversity was found in the forest; this also applies to threatened lichens (Fig. 3B).

### 3.3. Lichen species composition

Lichen species composition differed significantly among host tree species and between habitats (two-way NPMANOVA: tree species  $F = 9.13$ ,  $p < 0.05$ ; habitat  $F = 96.66$ ,  $p < 0.05$ ; tree



**Fig. 3.** (A) Richness of lichen communities for particular trees expressed as mean number of lichen species (blank squares) and mean Shannon index (filled squares) per tree. Points indicate mean values, whiskers indicate minimum and maximum values ( $n = 20$ ); different letters indicate significant differences at the  $p < 0.05$  level according to Tukey's test. (B) Total number of lichen species recorded on particular tree species; dark bars inside columns indicate the number of species from the Red List of threatened lichens in Poland. Tree species abbreviations as in Fig. 1.

species  $\times$  habitat  $F = 5.30$ ,  $p < 0.05$ ). Pairwise comparisons revealed significant differences between all tree species (with respect to habitat type), with the exception of the pairs Ac–Fr from the non-forested habitat and Ac–Fr from the forest complexes. Lichen communities from forest and non-forested habitats were much less similar than those from different tree species within a certain habitat type (Fig. 4). Ti trunks from the non-forested habitat are placed closest to forest trunks on the NMDS diagram.

DCA determined the direction and range of variability of lichen

vegetation with respect to the examined trees (Fig. 5). The eigenvalues of axes 1 and 2 were 0.542 and 0.131, respectively. The ordination diagram clearly separated all trees from the non-forested habitat, placing them on the left side and placing all trees from the forest on the right side. The scattering of lichen species may be divided into three main groups. Epiphytic lichens concentrated on the left side of the diagram are associated mainly with non-forested habitats; species associated with the forest are generally grouped along the second axis on the right side. Several epiphytes that demonstrated no special preferences as to habitat type are located in the central part of the diagram. Generally, the DCA diagram shows a stronger association of lichens with habitat type than with particular tree species.

#### 3.4. Effect of habitat factors on epiphytic lichens occurrence

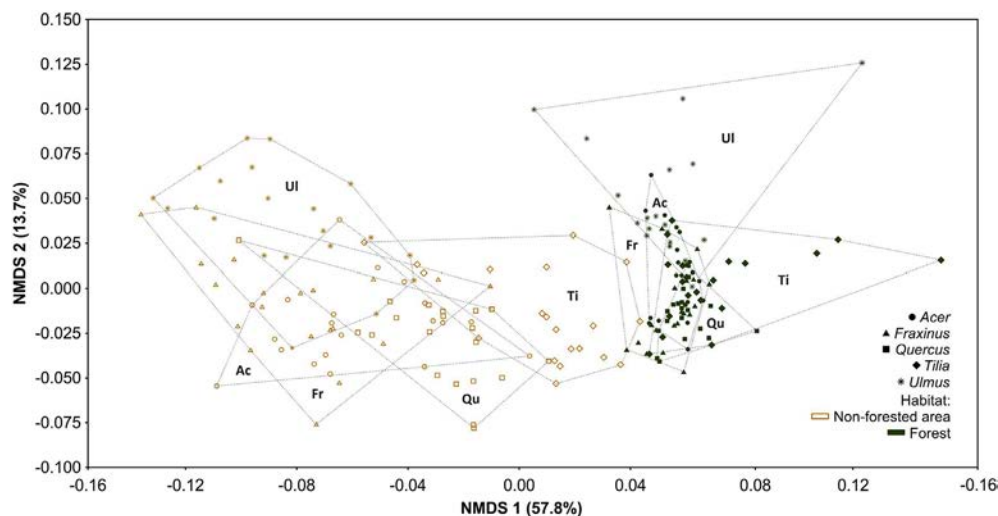
Since differences in species composition of the communities referring to non-forested and forest habitats were pronounced, we performed CCA separately for both habitat types (Figs. 6 and 7). As regards non-forested habitat, the forward selection procedure identified pH of bark and WHC as significant explanatory variables ( $F = 3.6$ ,  $p < 0.001$ ;  $F = 2.1$ ,  $p < 0.001$ , respectively). The eigenvalues of axes were as follows: 0.122 for axis 1 and 0.069 for axis 2. The species richness increases with the increase of bark pH.

As regards forest habitat, three factors, i.e. pH, WHC and DBH, were indicated as significant explanatory variables by the forward selection procedure ( $F = 2.9$ ,  $p < 0.001$ ;  $F = 1.9$ ,  $p = 0.004$ ; and  $F = 1.6$ ,  $p = 0.021$ , respectively). The eigenvalues of axes 1 and 2 were 0.169 and 0.110, respectively. General species richness increases with increasing diameter of trees and decreases when the value of WHC variable increases.

## 4. Discussion

### 4.1. Main factors responsible for the composition of epiphytic lichens

Three distinctive sets of epiphytic lichens can be distinguished (Osyczka and Kubiak, in print). The largest includes species recorded only on tree trunks forming stands of natural oak-linden-hornbeam forest. More than half of these species are threatened to varying degrees by extinction in Poland (Cieśliński et al., 2006).



**Fig. 4.** Non-metric multidimensional scaling (NMDS) ordination diagram showing the distribution of studied trees in terms of lichen species composition. Convex hulls encompass tree individuals from the same species and habitat type, percentage of variance accounted by the axis 1 and axis 2 is provided.

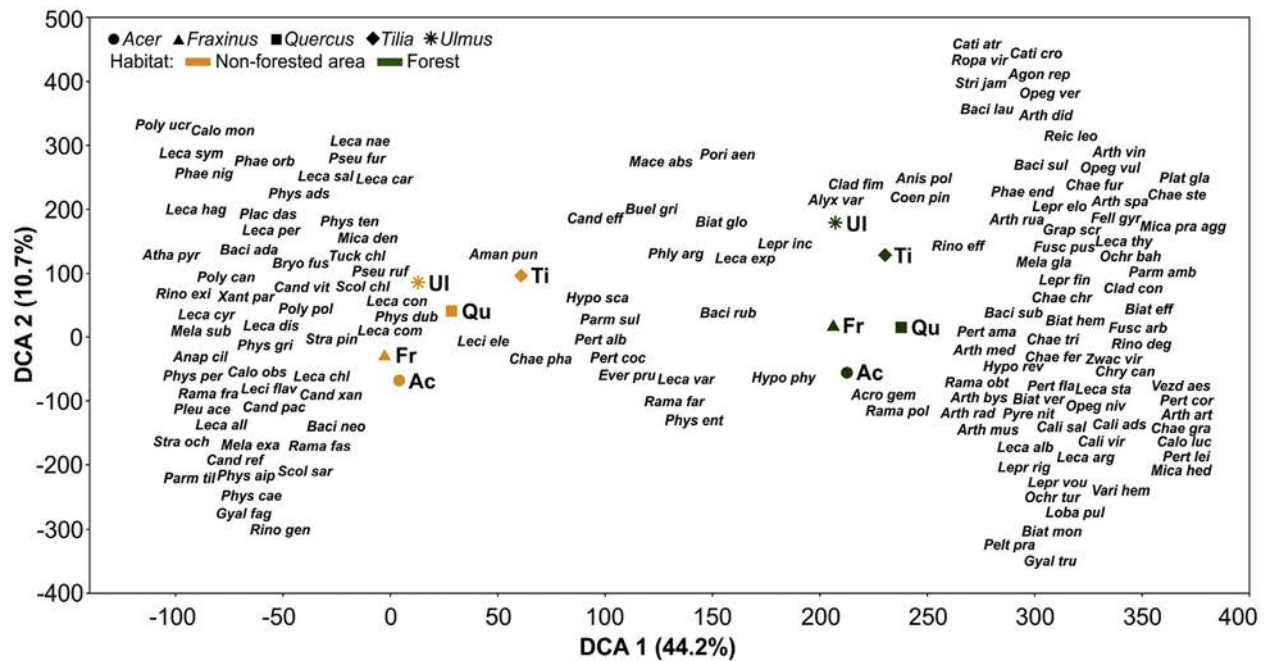


Fig. 5. Detrended correspondence analysis (DCA) ordination diagram of the studied trees and associated lichens, percentage of variance explained by first two axes is provided; for lichen species abbreviations see Table S2.

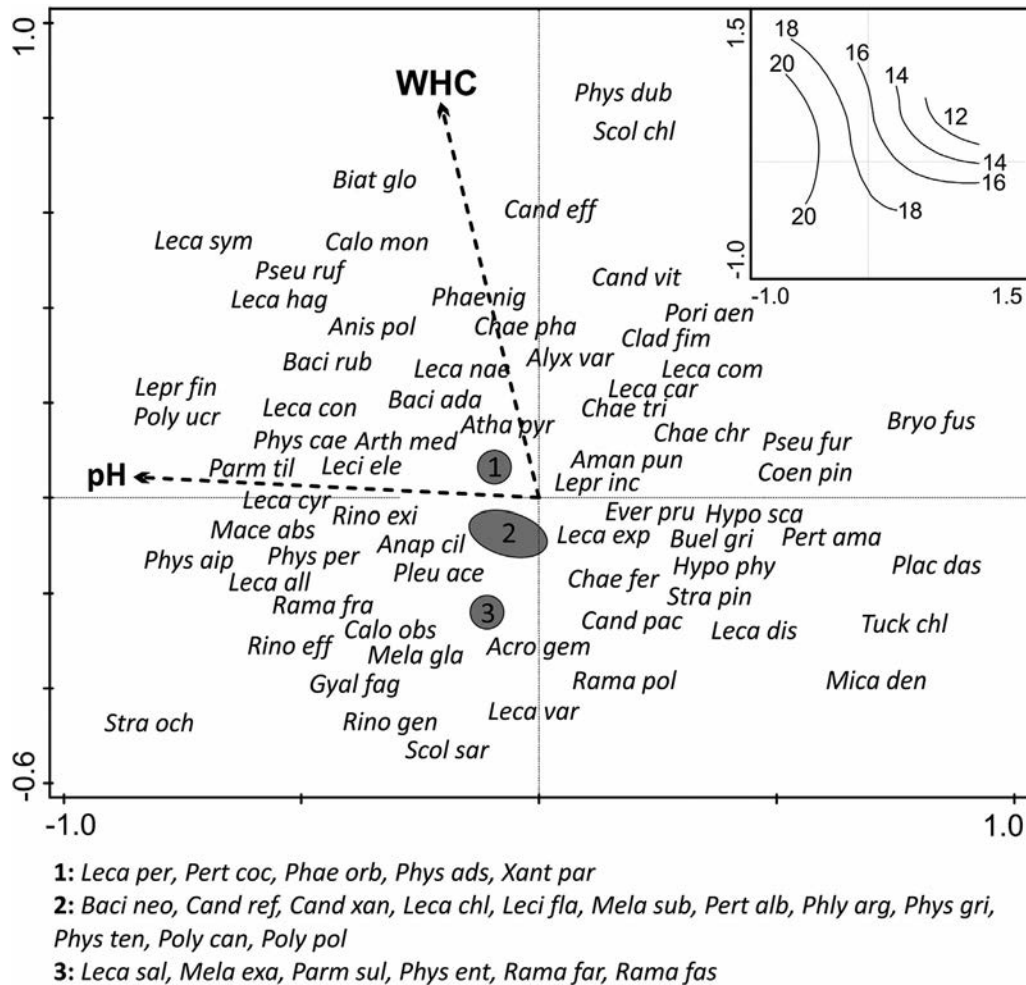
The second set consists of non-specific and usually ubiquitous species that can occur in both habitat types. Relatively few lichens are confined exclusively to trees from open non-forested areas. The shrinking and increasingly fragmented areas of primeval lowland deciduous forest have become the last refuges of many lichen species. For these species, such forests provide a natural and virtually irreplaceable habitat (see Cieśliński et al., 1996; Motiejūnaitė et al., 2004). Identification of the actual requirements of lichen species for habitat and host trees appears to be of great importance in the context of the decline in diversity within forests (Hauck et al., 2013).

Physicochemical properties of bark may be a severely limiting factor for many lichens confined to a specific substrate (Brodo, 1973; Kuusinen, 1996a; Hauck et al., 2006; Thor et al., 2010). The bark properties are characteristic for each tree species (Kuusinen, 1996b; Löbel et al., 2006; Bäcklund et al., 2016) but habitat conditions can change them to some extent in different directions (Fig. 1, Table 1). The bark pH of *Ti* (Fig. 1A), the conductivity of *Qu* and *Ul* (Fig. 1B), the WHC of *Ac* and *Ul* (Fig. 1C), and the DPC of *Ac* and *Qu* (Fig. 1D) all exhibit a high level of intraspecific variability in this respect. Nevertheless, even if there are no significant differences in tree bark parameters between the two habitat types, in the case of *Fr*, for example, the lichen compositions on tree trunks from the open habitat and on those from the forest are completely different. On the other hand, parameters of *Qu* bark usually differ significantly from those of other tree species in both habitat types; nevertheless, lichen communities on *Qu* trunks are often quite similar to those of other trees within the same habitat type (Figs. 1, 5 and 6). Another comparison can be taken into account: parameters of *Fr* bark from the forest do not differ significantly from those determined for *Ul* outside the forest (Fig. 1). Nevertheless, the corresponding lichen compositions are basically distinct (Figs. 5 and 6), meaning that, regardless of the attributes of tree bark, there is another, more important factor responsible for the general pattern of epiphytic lichen distribution.

The size of the tree is considered an important factor affecting

the richness of epiphytes. This factor may be considered in the context of available space (Ranius et al., 2008; Kubiak and Osyczka, 2017) as well as of the length of time the tree was available for colonisation (Hilmo et al., 2009; Lie et al., 2009; Boch et al., 2013). Tree diameter proves to have a positive effect on both number of species and the Shannon index, which is likely associated with greater coverage of particular lichen species on the trunks of larger trees. The number of lichen species is usually positively related to tree size with the richest communities on older trees (Johansson et al., 2007, 2009; Ranius et al., 2008; Fritz et al., 2009; Lie et al., 2009; Nascimbene et al., 2009; Nordén et al., 2014). Diameter is often treated as a surrogate for tree age (Łukaszkiwicz et al., 2005; Łukaszkiwicz and Kosmala, 2008). This is, however, a simplistic approach, since the local conditions in which a tree develops, such as edaphic and climatic factors and inter-individual competition, can strongly modify its growth (Ford et al., 2017; Zhang et al., 2017). Regardless of the species, trees growing in close proximity to one another in forests tend to be considerably smaller in diameter (Fig. 2) than others. The richness of lichen species on tree trunks, except *Qu*, is greater, but only if the trunks are considered individually; however, the forest complexes generally provide greater diversity of lichens considering the entire pool of species (Fig. 3). This shows that the frequency of species in the forest is generally much less and signifies the importance of *Qu* in supporting the frequency of many species.

The richness of epiphytic lichen communities in a given area depends to a great extent on conductivity, pH value, and the water-holding capacity of bark. The first two parameters have a positive impact, the last a negative. The conductivity measured on the external part of bark is directly influenced by the proximity of internal tissues, which are rich in ions (Legrand et al., 1996). This parameter can also be considerably affected by pollution of various origins, agricultural treatments, or local microclimatic conditions (Poikolainen, 1997, 2004; Mustafa et al., 2009). Nevertheless, conductivity does not always correlate with pH values (Kuang et al., 2006). Although our study has shown some relationships



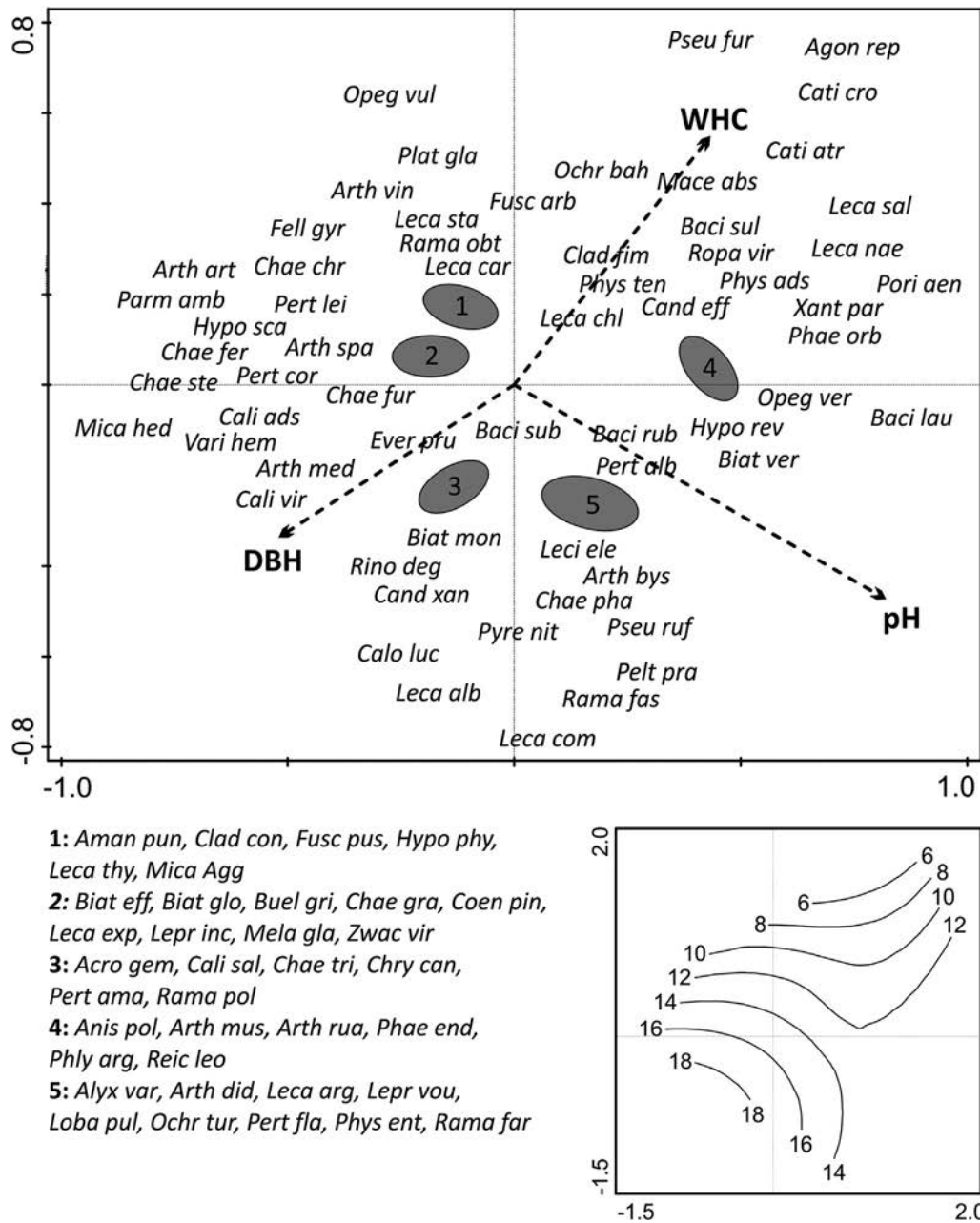
**Fig. 6.** Canonical correspondence analysis (CCA) ordination diagram based on data matrices of trees from non-forested habitat showing relationship between lichen species and significant variables (WHC – water holding capacity and pH) selected as a result of the forward selection procedure. Species richness contour lines are provided on inset graph; for lichen species abbreviations see Table S2.

between conductivity, tree species and with their habitat (Table 1), it is not an important factor that can regulate the occurrence of lichen in a given habitat type (Figs. 6 and 7; see also Mustafa et al., 2009). In contrast, the acidity and water retention capacity of the bark proved to be crucial factors for epiphytic lichens in both non-forested and forest areas.

Tree species differ in the amount and heterogeneity of light that they transmit (Sercu et al., 2017), due not only to their physiological and morphological properties but also to their surroundings. Light availability is very important for lichen growth and vitality (Loppi and Frati, 2004; Gauslaa et al., 2007; Hauck, 2011). The co-existence of various tree species in forest communities leads to denser filling of the canopy space than in the case of isolated or linear groups of trees which dominate in agricultural areas (Pretzsch, 2014). The intensity of light falling on the surface of tree trunks is the most significant factor differentiating between non-forested and forest areas (Table 1). Similarly, the studied host trees are distinctly separated into two main groups according to the habitat type (Figs. 5 and 6). Although only light intensity was quantified for each individual tree in the study, many other environmental variables are inherently related to this factor. In addition to their greater amount of sunlight, open areas differ from forest communities, which are characterised by lower humidity, greater variations in temperature and humidity, and higher wind speeds

(Chen et al., 1993, 1995; Matlack, 1993), making local climate conditions more variable within the daily cycle (see Li et al., 2015). Some lichens are negatively impacted by such wide microclimatic variability (Hauck et al., 2007; Király et al., 2013). On the other hand, the specific structure of a forest community shapes its own microclimate, which differs from the climate in a non-forested area or even from that accompanying single trees or trees growing in small assemblages (Stoutjesdijk and Barkman, 1992; Aussenac, 2000). The interior of a large forest provides more shade, slows down the wind, maintains higher humidity, and tempers fluctuations in temperature (Chen et al., 1999). Light is a key resource for photobionts and consequently determines the growth of lichen thalli (Nash, 2006). This is of particular importance in forest ecosystems, where the strong vertical structure leads to successive light interception from the canopy to tree trunks and to the forest floor. The study has shown that *Fr* and *Qu* trunks in forests are provided with significantly more light compared to the trunks of other tree species (Fig. S3). Nevertheless, these trees are still hosts mainly for lichens typically associated with forest ecosystems (Figs. 5 and 6). On the other hand, *Ti* trunks in open areas tend to be relatively more shaded than trunks of other trees (Fig. S3); this specificity is reflected somewhat in lichen composition (Fig. 4). Our results support the idea that light intensity is one of the most important determinants of the presence of particular epiphytic





**Fig. 7.** Canonical correspondence analysis (CCA) ordination diagram based on data matrices of trees from forest complexes showing relationship between lichen species and significant variables (WHC – water holding capacity, pH, DBH – diameter at breast height) selected as a result of the forward selection procedure. Species richness contour lines are provided on inset graph; for lichen species abbreviations see Table S2.

lichens. However, at the level of a specific habitat, where the differences in light intensity are more subtle (Fig. S3), this factor plays a less important role.

#### 4.2. Factors shaping epiphytic lichen composition in the non-forested habitat

Compared to trees of the forest interior, roadside trees constitute a habitat that is more homogeneous in terms of substrate characteristics and at the same time more extreme in terms of microclimate. As a result, some parameters, such as tree diameter, are not as important as in forest communities (Zahradníková, 2010). Outside protected forests, so-called ‘ancient’ or ‘veteran’ trees (Read, 2000; Lonsdale, 2013) are relatively rare (Hannah et al.,

1995; Niklasson et al., 2002). Moreover, removal of branches and entire trees that are dead, diseased, or irregular (particularly trees along roads) frequently occurs along roads. According to our observations, the various tree species from the non-forested area did not provide a more homogeneous habitat in terms of bark parameters than the same species growing in the forest (Fig. 1). Only two factors significantly affect species occurrence: WHC and bark pH (Fig. 6). The moisture retention ability, which varies between different tree species (Ilek et al., 2017), can potentially constitute an important variable for lichens that are poikilohydric (Barkman, 1958). Water retained in tree bark can affect the growth of epiphytic lichens by improving humidity in their close surroundings (Ilek et al., 2016). Water-holding capacity sometimes correlates positively with several other tree variables (e.g., age/DBH, bark

thickness), which makes it difficult to assess its direct significance for lichens (Fritz et al., 2009; Ilek et al., 2017; McDonald et al., 2017). Nevertheless, in the relatively dry environment of a non-forested landscape, trees with high WHC, especially *Ti* and *Ul* (Fig. 1), provide conditions suitable for lichens with greater humidity requirements, e.g. *Alyxoria varia*, *Anisomeridium polypori*, *Arthonia mediella*, *Bacidia rubella*, and *Biatora globulosa* (see also Nimis and Martellos, 2017). This may partly explain the low level of species diversity on *Qu*, whose bark is characterised by poor WHC, although this parameter increases with the size of *Qu* individuals (Osyczka and Kubiak, in print). Bark pH is generally considered the major substratum property to which epiphytic lichens respond, especially in areas transformed by humans (Barkman, 1958; Brodo, 1973; Kuusinen, 1996b). The pH of bark may also be affected by the proximity of other trees, especially those with clearly different chemistry (McDonald et al., 2017). The presence of other epiphytes may also be significant (Köhler et al., 2015). Generally, trees growing in open areas tend to have pHs higher than typical (Öztürk and Oran, 2011). This relationship seems particularly pronounced in the case of trees with a naturally low pH (Marmor and Randlane, 2007). In our study, this phenomenon was apparent especially in the case of *Ti*, and to some extent that of *Qu*. Consequently, the range of variability of this factor in open areas was somewhat narrower than in the forest (Fig. 1A) and the progressive unification of the composition of lichen communities and the decrease in lichen species richness in multi-species tree avenues may occur (Liška and Herben, 2008). Nevertheless, the presence of epiphytic lichens on the examined tree trunks is still determined by bark pH, given the limited role of other environmental factors and the low level of eutrophication (Spier et al., 2010).

#### 4.3. Factors shaping epiphytic lichen composition in the forest habitat

Natural deciduous or mixed forest communities are considered the most diverse and species-rich ecosystems in Central Europe (Czyżewska and Cieśliński, 2003; Loo, 2009). In north-eastern Poland, such forests have been preserved in a natural form, which can be attributed to their supraregional significance (Faliński, 1986; Peterken, 1996; Kubiak and Łubek, 2016; Guzow-Krzemińska et al., 2018). The forest community, in contrast to other forms of tree stands, provides many more structural elements and functional connections between trees, creating the potential for the appearance of lichen species with very different life requirements (Sillett and Antoine, 2004; van Stan and Pypker, 2015). This results in a high level of species richness; however, a relatively low frequency value is usually observed for most lichen species (Fig. 3). This is characteristic of many stenotopic organisms associated with primeval habitats (Czeszczewik et al., 2015; Czeszczewik and Walankiewicz, 2016).

Regardless of the complexity of the forest system, three main factors are most responsible for the occurrence of particular lichens (Fig. 7). Apart from the pH of bark and water-holding capacity, the size of trees is additionally of great importance (Johansson et al., 2009). The continuity and stability of conditions is frequently crucial for the existence of many sensitive species (Cieśliński et al., 1996; Esseen, 2006; Nordén et al., 2014). The presence of trees in various phases of life is one of the factors shaping the diversity of lichens in forests. In general, the occurrence of old trees within a stand favours the diversity of epiphytes (Lie et al., 2009, Fig. 7). A tree's size and structure, changing with age, result in the formation of many additional niches which enhance opportunities for the occurrence of epiphytic lichens with varied requirements. Among the analysed trees, only the periderm of *Qu* was evidently thicker and more deeply cracked compared to those of other trees,

especially in the case of individuals growing within the forest. Although the analysis did not return DPC as the main factor explaining the presence of particular lichens, the depth of cracks may depend on tree size, as in the case of *Ac* and *Qu* (Osyczka and Kubiak, in print). The association of many crustose species with old *Qu* specimens seems to be at least partly due to their preference for deep bark crevices (Ranius et al., 2008). Differences in bark acidity between species of trees growing in the forest (*Ti* and *Qu* vs *Ac*, *Fr*, and *Ul*) are more pronounced than in the case of trees from open areas (Fig. 1A). This may explain why trees and their lichen associations are slightly more separated in the forest habitat than in the non-forested area (Fig. 5). Water-holding capacity in the forest, as in open areas, is a very important factor for lichens. However, with increases in the value of WHC, the biodiversity of lichens is clearly diminished (Fig. 7). Epiphytic lichens usually populate niches where competition from other organisms is limited (During, 1992). Greater WHC promotes the development of bryophytes on trunks, which consequently inhibits the growth of lichens (Barkman, 1958; Sales et al., 2016). On the other hand, WHC is of great importance for typically hydrophilous lichen species, such as *Agonimia repleta*, *Catillaria croatica*, and *Catinarina atropurpurea*. These species are associated mainly with *Ul*, whose bark in forest specimens is characterised by a very high level of water capacity.

#### 4.4. Relicts of ancient forests

Deciduous primeval forests are biocenoses corresponding to natural ecological systems characterised by a complex spatial structure, shaped over a long period of time, and covering all phases of a tree's life (Czyżewska and Cieśliński, 2003; Johansson et al., 2009; Fritz et al., 2009; Nascimbene et al., 2009). As many as 19 species of epiphytic lichens are indicators of lowland old-growth forests in NE Poland and Lithuania (Czyżewska and Cieśliński, 2003; Motiejūnaitė et al., 2004), also defined as relicts of primeval/ancient forests (Cieśliński et al., 1996). It is assumed that such species are associated with aged deciduous trees and tend not to occur in habitats and substrates of anthropogenic origin (Cieśliński et al., 1996). Generally, this group of lichens corresponds to species classified in western and northern Europe as indicators of forest ecological continuity (Rose, 1976; Coppins and Coppins, 2002). The ecological continuity concept has been broadly applied for a relatively long time (Rose, 1974) but is still poorly defined (Rolstad et al., 2002). Nevertheless, recent research indicates that potential lichen indicators constitute an ecologically heterogeneous group, including species constrained in their distributions by microhabitat availability (niche specialists), time available for colonisation (dispersal limitation), or both (Fritz et al., 2008; Whittet and Ellis, 2013). The presence of a set of lowland old-growth forest indicators encompassing species with different requirements may be indicative of the ecological continuity of a forest. The following species may be involved as representatives (see also Nimis and Martellos, 2017): associated with old/large trees and preferring low-pH bark – *Calicium adpersum*, *Calicium viride*, *Micarea hedlundii*, *Varicellaria hemisphaerica*, *Chrysothrix candellaris*; linked to low-pH bark – *Arthonia arthonioides*, *Arthonia vinosa*, *Fellhanera gyrophorica*; characterised by a preference for neutral-pH bark – *Opegrapha vermicellifera*, *Lobaria pulmonaria*, *Pertusaria flavida*, *Arthonia byssacea*, *Hypotrachyna revoluta*; and requiring high water content in bark – *Agonimia repleta*, *C. croatica*, *C. atropurpurea*. Although the last-mentioned species have not previously been considered indicators of lowland old-growth forests, they may be helpful in this kind of environmental assessment. Some typical forest and hydrophilous lichens tend not to appear in managed forests planted in habitats typical of temperate deciduous forests (Kubiak et al., 2016) and are poorly tolerant to

eutrophication (see Hauck and Wirth, 2010). In addition, they do not necessarily require the presence of large trees in forest stands. All of the aforementioned lichens occur in the Białowieża Forest, the best-preserved forest complex in Europe (Faliński, 1986; Peterken, 1996).

#### 4.5. Importance of trees outside forest complexes

Although roadside trees do not constitute suitable habitat for typical forest lichens and appear to be hardly adequate to serve as effective ecological corridors, they can provide refuge for some other rare and endangered species (Coppins, 2001, Fig. 3B; Osyczka and Kubiak, in print). This mainly concerns photophilic, moderately hydrophilous or slightly nitrophilous macrolichens (Wirth, 2010) which currently do not find suitable conditions for growth in natural or commercial forest complexes, e.g. *Anaptychia ciliaris*, *Melanelia subargentifera*, *Parmelina tiliacea*, *Physcia aipolia*, *Physconia perisidiosa*, *Pleurosticta acetabulum*, *Ramalina fraxinea*. In the past, some of these species were probably associated with large-scale natural disturbances within forests (Frelich, 2016). Nowadays, set-aside forest areas affected by natural disasters (windfalls, forest fires, insect outbreaks) are rare in Central Europe (Szwagrzyk et al., 2018) and natural disturbances are usually limited to small spatial gaps created after the fall of individual trees (Bobiec, 2007). Therefore, as long as modern forest management does not reflect the full range of natural processes, a roadside multi-species tree planting system should certainly be continued. Any incentives for conservation efforts related to other forms of high greenery in forestless areas (wooded pastures, manor and rural parks, midfield woodlots) are also highly desirable.

#### 4.6. Conclusions

Based on data obtained from the natural deciduous lowland forest stands and forestless area of northern Poland, the following symptomatic relationships concerning trees and associated epiphytic lichens emerge from our study:

The prevailing conditions in the habitat where trees grow affect the parameters of their bark (Table 1). Most often, fluctuations in features are not greatly appreciable at the species level; however, changes in particular bark properties with regard to certain tree species are sometimes highly pronounced, e.g. pH in *Ti* (Fig. 1A), conductivity in *Qu* and *Ul* (Fig. 1B), WHC in *Ac* and *Ul* (Fig. 1C), and DPC in *Ac* and *Qu* (Fig. 1D). Moreover, trees growing in forest stands are smaller than those outside of forest stands (Fig. 2).

In general, the species richness of lichens on particular tree trunks is positively related to the conductivity and pH and negatively related to the water-holding capacity of the bark. Although the average number of lichen species on tree trunks from open areas is greater than on trees from forest stands, overall diversity, especially the number of endangered lichens, is definitely greater in deciduous forest habitats (Fig. 3).

Epiphytic lichen community composition in open areas and deciduous lowland forests is different (Figs. 5 and 6), as both habitat types are characterised by too many exclusive species (Osyczka and Kubiak, in print), and the relatively small group of species common to both types does not compensate for the compositional difference.

Although the presence of certain tree species is crucial for the occurrence of stenotopic epiphytic lichens (see Osyczka and Kubiak, in print), microclimatic factors likely differentiate lichen community composition in non-forested and forest areas to a greater extent than tree species. Factors related to bark properties, such as pH and WHC, gain in importance at the level of a specific habitat.

*Ul* and *Ti* are characterised by the most distinctive lichen

communities among all tree species in the forest habitat. The lichen composition on *Ti* in open areas most closely corresponds to the compositions observed on tree trunks from forest stands (Fig. 4).

Bark pH and WHC are the most important factors explaining the composition of lichens on trees in both habitat types; additionally, the tree size is significant factor in forests (Figs. 6 and 7).

Multi-species tree avenues, while undoubtedly constituting a valuable habitat for many lichens, cannot serve as ecological corridors for lichens typically associated with mixed deciduous lowland forest communities.

In shaping the structural environment, we must not only deliver optimal substrates for various epiphyte species, but also create forest stands that will provide appropriate microclimatic conditions. Future actions should be based on the reconstruction of certain structural elements derived directly from natural forests.

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#### Supplementary data

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