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## Research

### Epiphytic lichen synusiae and functional trait groups in boreo-nemoral deciduous forests are influenced by host tree and environmental factors

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Deciduous forests with temperate broad-leaved tree species are particularly important in terms of biodiversity and its protection, but are threatened habitats in northern Europe. Using multivariate analyses we studied the effect of forest site type, environmental variables and host tree properties on epiphytic lichen synusiae as well as on the composition of species-specific functional traits. Epiphytic lichens were examined on *Acer platanoides*, *Fraxinus excelsior*, *Quercus robur*, *Tilia cordata*, *Ulmus glabra* and *U. laevis* in two types of forests: *Humulus*-type floodplain forests and *Lunaria*-type boreo-nemoral forests on the talus slopes of limestone escarpment (klint forests). Klint forests located near the seashore were under greater maritime influence compared to floodplain forests located in inland Estonia which experience stronger air temperature contrasts. In addition to stand level and climatic variables, tree level factors (bark pH, trunk circumference and cover of bryophytes) considerably affected the species composition of the lichen synusiae. Overall, 137 lichen species were recorded, including 14 red-listed species characteristic of deciduous trees. We defined 13 lichen societies and showed their preference to forests of a specific site type and/or host tree properties. In forests of both types, most of the epiphytic lichens were crustose, and had apothecia as the fruit bodies and chlorococcoid algae as the photobiont. However, the proportion of lichens with a foliose or fruticose growth form, as well as the proportion of lichens with vegetative diaspores, were higher in floodplain forests. In klint forests with a stronger influence from the wind, crustose species completely dominated, while species with vegetative diaspores were rare and most species dispersed sexually. Lichens with *Trentepohlia* as the photobiont were characteristic of these forests, and lichens with lirellate ascomata were prevailing, indicating the great uniqueness of the kint forests for epiphytic lichens in the boreo-nemoral region.

Keywords: ash, elm, floodplain forests, lime, *Trentepohlia*, cyanolichens, growth form, oak, temperate broad-leaved trees



## Introduction

Lichens contribute significantly to the biodiversity of forest ecosystems (Timonen et al. 2011, Ellis 2012) and are sensitive indicators of their function, state and quality in terms of structure, air pollution and climate (McCune 2000, Nimis et al. 2002, Pinho et al. 2011, Ellis 2015). Without information about the lichens species composition and synusiae, the knowledge of forest communities is incomplete; nevertheless, lichens have often been ignored in vegetation analysis, mainly because of the paucity of specialists (Bültmann et al. 2015). At the same time, studies of lichen species assemblages can provide ample information for solving several problems in phytocoenology, i.e. those connected to vegetation classification, succession theory and bioindication (Bültmann et al. 2015, Mucina et al. 2016).

Due their peculiar life history and growth forms, lichen assemblages are usually treated as synusiae and classified as autonomous syntaxa (Gams 1918, Lippmaa 1935, Trass 1964, Du Rietz 1965, Korchagin 1976, Martin 2013). Lichen assemblages differ in their degree of independence from the surrounding vascular plant vegetation. For example, lichen synusiae on rocks are indisputably independent (Bültmann 2012), whereas terricolous lichen assemblages in northern boreal forests, which constitute essential and sometimes dominating components of the vegetation understorey, are one of the major ecosystem drivers (Nilsson and Wardle 2005, Hart and Chen 2006). Epiphytic and epixylic lichen synusiae make up discrete assemblages on a single host tree. However, in old forest expanses, epiphytic lichen synusiae on trees may recur with similar compositions and quantitative proportions between species on several hundreds of trees (Barkman 1958, 1973, Trass 1981, Ellis et al. 2015). The formation and taxonomic composition of epiphytic lichen synusiae depend, first of all, on host tree properties (Gauslaa 1985, Ellis et al. 2015). Still, the characteristics of surrounding plant communities, created mainly by higher plants, largely determine the local moisture regime and light conditions which influence epiphyte communities (McCune 1993, Dymytrova et al. 2016, Sales et al. 2016).

In Estonia, forest dwelling lichens have been the subject of numerous studies (Sõmermaa 1972, Martin and Martin 1998, Trass et al. 1999, Lõhmus 2003, Jürjado et al. 2003, Marmor et al. 2017, Randlane et al. 2017). However, studies of the composition of the functional traits of epiphytes as related to habitat conditions and the distribution of synusiae are almost lacking. In the current study, we will focus on the lichen synusiae of temperate broad-leaved trees, i.e. ash *Fraxinus excelsior* L., common oak *Quercus robur* L., small-leaved lime *Tilia cordata* Mill., wych elm *Ulmus glabra* Huds. and spreading elm *Ulmus laevis* Pall., growing on screes of the north-Estonian limestone escarpment (klint) and on Estonian floodplains. Forests of these site types have a high diversity of both species and communities (Paal 1998). They include microhabitats harbouring numerous unique vascular plant species, as well as rare bryophyte and lichen species (Paal et al. 2007, 2008, Paal 2009, Jürjado et al. 2009a, b).

In different biogeographical regions, lichen synusiae on broad-leaved trees have been studied quite intensively (Klement 1955, Nimis 1982, Gauslaa 1985, Romanova 2009, Ellis et al. 2015, Vicol 2015). Still, regional studies of lichen syntaxa and synecology continue to be of interest as the composition of lichen assemblages on trees depends on regional climatic conditions (Aragón et al. 2012, Prieto et al. 2017), as well as on the connectivity and ecological continuity of forests (Ellis and Coppins 2007a, Wolseley et al. 2017) and local environmental conditions (Ellis 2012, Ellis et al. 2015). This is especially important in the light of ongoing climatic changes, but also for biodiversity and its protection. Moreover, a better understanding of the ecological mechanisms driving species assemblages in forests may be gained if lichen life history traits are also considered (Ellis and Coppins 2006, Giordani et al. 2012, Bässler et al. 2016, Randlane et al. 2017, Degtjarenko et al. 2018). For example, lichens with *Trentepohlia* as their photosynthetic partner thrive at higher temperatures and, as a result of climate warming, presently expand their distribution in Europe (Aptroot and van Herk 2007). However, lichens with *Trentepohlia* are rare in areas with intensive land use (Stofer et al. 2006) and need further monitoring and study, taking into account ongoing climatic changes as well as increasing anthropogenic impact.

The objectives of the current study were: 1) to establish the types, i.e. societies sensu Du Rietz (1936, 1965), of epiphytic lichen synusiae in Estonian floodplain and klint forests, 2) to identify the main factors determining the distribution of epiphytic lichen synusiae in these deciduous forests and, 3) to identify the main factors determining the composition of lichen species and their functional groups on the studied trees.

## Nomenclature

The nomenclature of lichens follows the checklist of the lichenized, lichenicolous and allied fungi of Estonia (<<http://esamba.bo.bg.ut.ee/checklist/est/home.php>>, ver. 31 December 2016).

## Material and methods

### Study area and study sites

Estonia is located in northeastern Europe on the eastern coast of the Baltic Sea in the boreo-nemoral sub-zone of the boreal forest zone. The topography of Estonia is flat: in the western and southwestern regions, absolute altitude rarely reaches above 20 m, while the southeastern part reaches to a few hundreds of metres above sea level (Raukas 1996). The climate of Estonia is temperate with warm summers and moderately cold winters (Jõgi and Tarand 1995). The average air temperature is 17°C in July, and -6.5°C in January (Jaagus 1999). The climate is milder on the coast than in the inland because of the influence of the sea. The amount of precipitation is higher on the uplands of the northeastern

and southeastern regions (650–700 mm per year) compared with the coastal areas and the islands (500–550 mm per year) (Jõgi and Tarand 1995).

Forests on the North-Estonian limestone escarpment (klint) grow under ecological conditions that are relatively specific in temperate boreo-nemoral zone. The North-Estonian Klint stretches along the southern coast of the Gulf of Finland, forming a part of the Baltic Klint. Its maximum relative height is 56 m in northeastern Estonia, descending gradually westwards and eastwards (Raukas 1996). The foot of the escarpment usually constitutes a talus slope (scree), consisting of limestone or sandstone blocks partly covered with finer weathered material, clay or primitive soil which is amply inundated with calcareous and nutrient-rich seeping ground water or springs. The talus slopes are covered with broad-leaved forests. In places, due to inaccessibility, they are thought to be among the very few primary forest stands that have survived in Estonia (Kalda 1962). *Fraxinus excelsior*, *Tilia cordata*, *Ulmus glabra* and *Acer platanoides* are the dominating tree species in the forests on the talus slope of the escarpment. The most characteristic species of the herb layer are *Lunaria rediviva* and *Mercurialis perennis* (Paal et al. 2001) and this forest type is named after the first species (Paal 1997). According to the EU Habitats Directive (EC 1992), the klint forests represent habitat type 9180 ‘*Tilio-Acerion* forests of slopes, screes and ravines’ with priority rank for all Europe (Paal 2007b, 2009). Based on the tree species composition of these stands (Paal 2001, 2007a, Paal et al. 2001), 12 study sites along the talus slope of the escarpment from west to east were selected for the current study (Fig. 1), avoiding

the area affected to some extent by alkaline air pollution (Jüriado et al. 2009a).

The floodplain forests represent habitats intermediate between terrestrial and aquatic ecosystems where the water table is usually at or near surface, and land is periodically covered with shallow water (Hager and Schume 2001, Klimo 2001). In Estonia, like in most European countries, the area of floodplain forests has greatly decreased and therefore these forests are included in Annex I of the EU Habitats Directive (EC 1992) under type 91E0 ‘Alluvial forests with *Alnus glutinosa* and *Fraxinus excelsior*’ (*Alno-Padion*, *Alnion incanae*, *Salicion albae*) (Paal 2007b). We restricted our study to forests of the *Humulus* site type (Paal 1997). For the lichenological study, we selected 16 stands of floodplain forests in Estonia (Paal et al. 2007). All studied stands were located in a continuous forest landscape near Laiksaare in southwestern Estonia (two stands), in the Soomaa National Park in central Estonia (six stands) and in the Alam-Pedja Nature Reserve in eastern Estonia (eight stands) (Fig. 1).

### Data collection

Climatic data recorded by the Estonian Weather Service (<www.ilmateenistus.ee/>) were obtained from six meteorological stations located close to the study sites. We used average maximum air temperature, average minimum air temperature, average precipitation (mm), average wind speed ( $\text{m s}^{-1}$ ), and average sunshine duration (h) calculated over 1981–2010 (Table 1). The field data were collected in 2000–2002 as part of a project aimed to describe the typology and soils of Estonian floodplain and klint forests

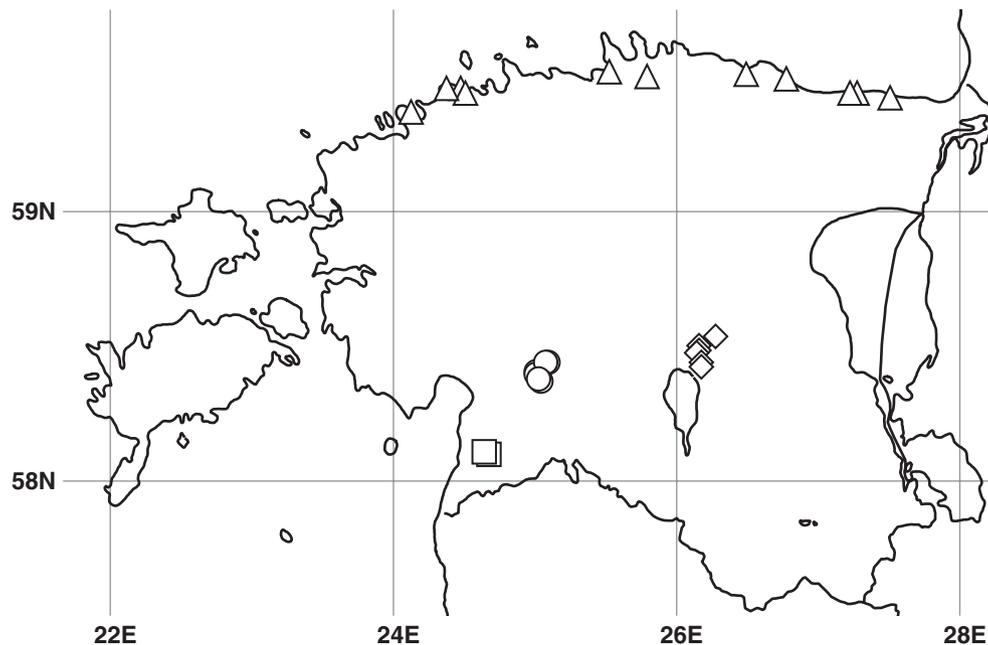


Figure 1. Location of the study sites in klint forests in northern Estonia and in floodplain forests in three regions of southern Estonia. Notations: triangles denote the study sites in klint forests, quadrates denote foodplain forests near Laiksaare, circles denote the foodplain forests in the Soomaa National Park, and diamonds denote the foodplain forests in the Alam-Pedja Nature Reserve.

Table 1. Environmental variables.

Variables	Notation	Comments
Climatic variables*		
Maximum air temperature	temp max	average maximum air temperature
Minimum air temperature	temp min	average minimum air temperature
Precipitation	precipitation	average precipitation (mm)
Wind speed	wind	average wind speed (m s <sup>-1</sup> )
Sunshine duration	sunshine	average sunshine duration (h)
Stand level variables		
Forest type	floodplain klint	floodplain forest study sites (n=16) in three study regions of southern Estonia klint forest study sites (n=12) along the coast in northern Estonia
Habitat lightness	lightness	mean of the corresponding indicator values per 0.1 ha sampling area according to Ellenberg (1979) and Paal et al. (2007)
Soil fertility	soil fertility	mean of the corresponding indicator values per 0.1 ha sampling area according to Ellenberg (1979) and Paal et al. (2007)
Soil moisture	soil moisture	mean of the corresponding indicator values per 0.1 ha sampling area according to Ellenberg (1979) and Paal et al. (2007)
Tree level variables		
Tree species	Ace pla, Fra exc, Que rob, Til cor, Ulm gla, Ulm lae	tree species studied: <i>Acer platanoides</i> (n=28), <i>Fraxinus excelsior</i> (n=63), <i>Quercus robur</i> ** (n=20), <i>Tilia cordata</i> (n=39), <i>Ulmus glabra</i> (n=42) and <i>Ulmus laevis</i> ** (n=21)
Canopy cover	can cov	percentage of canopy cover on the scale zero to one around each sample tree
Bryophyte cover	bry cov	mean cover of bryophytes on a 20 × 20 sample quadrat on the bole
Bark pH	bark pH	bark pH in a sample quadrat on the bole
Circumference	circum	circumference of a sample tree at a height of 1.3 m above ground

\* Climatic data was obtained from the Estonian Weather Service (<www.ilmateenistus.ee/>), the meteorological data were recorded in six study regions of Estonia in the time period 1981–2010.

\*\* *Quercus robur* and *Ulmus laevis* were only present in floodplain forests.

(Paal 2001, 2007a, Paal et al. 2001, 2007). In every forest stand (study site) one circular 0.1 ha sample plot was used for describing the composition of plant species in the tree and herb layers (Paal et al. 2001, 2007a). The sample plot was established within a homogenous forest area using a 'Suunto' height and distance measuring instrument: one tree stem was marked as the central point from which a radius of 17.8 m was measured in different directions. The ground vegetation was described using randomly located sample quadrats of 1 × 1 m; their number was 15–20 per plot. The number of stems of shrub layer species was registered from five randomly located 2 × 2 m sample quadrats in every stand. The tree layer was characterized by the mean basal area of each species, obtained as an average of 3–5 measurements (Paal et al. 2001, 2007a). For each sample plot, habitat lightness, soil moisture and fertility conditions were evaluated by means of calibration (Jongman et al. 1995), using the ecological indicator values of the herbaceous plant species (Ellenberg 1979), their abundance values and a weighted averaging algorithm (for details, see Paal et al. 2001, 2007a) (Table 1).

At each study site (sample plots) in klint forests, usually two sample trees of four temperate broad-leaved species (*Acer platanoides*, *Fraxinus excelsior*, *Tilia cordata* and *Ulmus glabra*) were studied; altogether 80 trees were sampled. At the 16 study sites (sample plots) in floodplain forests, altogether 133 sample trees, representing the same species as in klint forests, were studied; in addition, *Ulmus laevis* and *Quercus robur* were included in the study (Table 1). In every sample

plot, where available, five or six trees from each species were sampled.

The sample trees, with a diameter more than 20 cm, were chosen subjectively within the 0.1 ha sample plots. The circumference of each sample tree was measured at breast height (1.3 m above ground level) and the canopy cover was estimated visually near each sample tree on a scale from zero to one (Table 1). Epiphytic lichen synusiae were described on two sides of tree trunks at a height of 1.3 m above ground level using a 20 × 20 cm plastic sample quadrat. In floodplain forests the quadrats were set on the northern and southern sides of the tree trunk (Jüriado et al. 2009b), while in klint forests the quadrats were set on two aspects of the trunk, one facing and the other opposite the escarpment (Jüriado et al. 2009a). To estimate the cover percentage of each lichen species and the total cover of bryophytes, the sample quadrat was divided into 100 sub-quadrats using a grid. In addition, lichen species were recorded from tree trunks at a height of 0.6 m to 1.3 m above ground level. The specimens that were not identified in the field were collected for indoor investigation.

For measurement of the pH of the bark surface, two small samples of bark (ca 1.5 cm<sup>2</sup>) were removed from each 20 × 20 cm sample quadrat on both sides of the tree trunk. Regarding the bark samples of klint forests, a bark sample (1 g) was incubated in distilled water for 24 h and the pH of the solution was then measured with a standard pH meter (E6121) (for details see Jüriado et al. 2009a). For measuring the bark pH of the samples from floodplain forests, a flathead electrode (Consort C532) was used. A small amount

of solvent (0.01 M KCl) was dropped in a small petri dish and a bark sample was placed into the solvent with the outer surface downward to soak only its uppermost part (for details see Jürriado et al. 2009b). In statistical analyses the pH of two bark samples was averaged for each sample tree. The bark pH values measured by using solvents H<sub>2</sub>O or KCl were strongly correlated but the pH<sub>KCl</sub> values were generally lower than pH<sub>H<sub>2</sub>O</sub> values (Farmer et al. 1990, Kricke 2002).

For identification of lichens in the laboratory, a stereo-microscope, a light microscope, 'spot tests', UV light and standardized thin-layer chromatography (TLC) were used (Randlane and Saag 2004). Because of their complicated taxonomy, species of the genus *Arthopyrenia* and small specimens of the genus *Collema* were treated at the generic level. Reference materials are deposited in the lichenological herbarium at the Natural History Museum of the University of Tartu (TU). The red-listed lichen species are indicated following Randlane et al. (2008).

Information about the functional traits of the species was derived from the literature (Randlane and Saag 2004, Smith et al. 2009). We addressed the characteristics growth form, presence/absence of soredia and isidia, type of ascocarp (apothecia or perithecia), frequency of ascocomata, and photobiont type. Frequency of ascocomata was treated as frequent (ascocomata usually present) or infrequent (ascocomata usually absent). Type of apothecium was described as lecidine or lecanorine, lirellate, or stalked apothecium usually with mazedium. Three groups of lichen growth forms were considered: crustose, foliose and fruticose. Three types of photobionts were distinguished: chlorococcoid algae (e.g. *Trebouxia* spp.), *Trentepohlia* spp. and

cyanobacterium (e.g. *Nostoc* spp. in the thallus or in cephalodia) (Table 2).

## Data processing

### Ordination analyses

Prior to data analysis, some explanatory variables were transformed to improve the assumptions of homoscedacity and to render the units of the variables comparable. The cover values of bryophytes were square-root transformed and the variable 'circumference' was log-transformed. The bark pH values of the trees of both site types, measured with different methods and solvents, were standardized. For each forest sample plot, habitat lightness, soil moisture and fertility conditions were characterized (Paal 2001, Paal et al. 2001, 2007a) using the indicator values of the species of the herb layer (Ellenberg 1979) and a weighted averaging algorithm. For ordination analyses, a species list was combined per sample tree using the lichen records from both sides of the sample tree within the quadrats, as well as the records of the species from the same sample tree outside the quadrats at a height of 0.6 m to 1.3 m above ground level.

Canonical correspondence analysis (CCA), implemented in CANOCO ver. 5.0 (ter Braak and Šmilauer 2012), was used to examine the relationships between species composition and environmental variables. In the data matrix for the species used for ordination, the species recorded on less than three tree trunks were removed from the data to reduce the information noise caused by rare species. Altogether, the presence-absence records of 86 lichen species on the sample trees were used for the ordination analyses. The forward

Table 2. Functional traits of species considered in the redundancy analysis (RDA) and their number of occurrence (No) and frequency (%) in the total species list. Relative frequencies of species' traits are presented also by forest types (floodplain and klint forest).

Species trait	Trait class	Notation	No	Frequency (%) (n=137)	Frequency (%)	
					Floodplain forest (n=121)	Klint forest (n=78)
Growth form	crustose	crustose	107	78.1	75.2	88.5
	foliose	foliose	19	13.9	15.7	6.4
	fruticose	fruticose	11	8.0	9.1	5.1
Ascocarp	frequent	ascoc_freq	88	64.2	62.0	73.1
	infrequent	ascoc_infreq	43	31.4	33.9	21.8
	inapplicable*		6	4.4	4.1	5.1
Types of ascocarp	lecidine or lecanorine apothecia	lec_apot	100	73.0	76.0	65.4
	lirellate apothecia	lirellate	11	8.0	7.4	14.1
	stalked apothecia	stalked_apot	11	8.0	8.3	6.4
	perithecia	perithecia	9	6.6	4.1	9.0
	inapplicable*		6	4.4	4.1	5.1
Soredia	present	soredia_present	45	33	34.7	26.9
	absent	soredia_absent	92	67	65.3	73.1
Isidia	present	isidia_present	12	9	9.1	3.9
	absent	isidia_absent	125	91	90.9	96.1
Photobiont	chlorococcoid algae (e.g. <i>Trebouxia</i> spp.)	chloroco	102	74.5	77.7	66.7
	<i>Trentepohlia</i>	Trentepohlia	28	20.4	17.4	29.5
	cyanobacterium (e.g. <i>Nostoc</i> spp.)	cyano	5	3.6	4.1	2.6
	photobiont absent		2	1.5	0.8	1.3

\*Species (*Lepraria* spp.) reproducing only asexually.

selection procedure with randomization tests (Monte Carlo permutation test, 1000 unrestricted permutations) was employed to select the most important environmental variables affecting the species composition of lichens, retaining the variables with an independent significant contribution at the  $p \leq 0.05$  level. The Monte Carlo permutation test was used to determine the statistical significance of the first and hereafter all canonical axes together.

To relate variation in the functional traits of epiphytic lichens in floodplain and klint forests to environmental variation, a community-based approach was used (Šmilauer and Lepš 2014). First, the community-weighted means (CWM) of the traits for each tree trunk were calculated. Then the CWMs of the traits (response data) were related to the environmental data (explanatory variables) by means of redundancy analysis (RDA) (Šmilauer and Lepš 2014). An interactive forward selection procedure with randomization tests was employed to select the most important environmental variables, retaining the variables with an independent significant contribution at the  $p \leq 0.05$  level.

### Analyses of lichen synusiae

Although several authors have pointed out that conditions for the growth of lichens on the opposite sides of a tree are often different and there will develop synusiae with different compositions (Barkman 1958, Sõmermaa 1972), preliminary cluster analysis demonstrated that the sample quadrats (respect synusiae) of the same tree were quite frequently clustered in couples. For this reason, in order to avoid pseudoreplication due to the autocorrelation of the data recorded from the opposite sides of the same tree, we used only the data from the quadrat with the higher species number within each couple. Altogether, the data of 213 quadrats were included. To reduce the disproportionate effects of the dominating species, the cover values of the lichen species in the quadrats were square-root transformed (McCune and Grace 2002).

For cluster analysis, the chord distance and the flexible  $\beta$  algorithm ( $\beta = -0.6$ ) were used. The chord distance eliminates differences in the total abundance of species among sample units and compares them according to the species abundance proportions (McCune and Grace 2002). To reduce noise, the species appearing in less than three samples were removed from the data set prior to clustering. To test for differences in species composition among the clusters, a non-parametric multi-response permutation procedure (MRPP; Mielke 1984) based on the Euclidean distance (McCune and Mefford 1999) was used. The indicator values of the species in the clusters (respect societies) were calculated using the Dufrière and Legendre (1997) method (McCune and Mefford 1999). For each species, the relative abundance and relative frequency in every cluster were calculated using this method. Multiplication of these two values, expressed in percentages, yields an indicator value for a particular species in a particular cluster. The statistical significance of the obtained indicator values was evaluated by using the Monte Carlo permutation test.

## Data deposition

Data available from the Estonian Natural Museum digital repository eBiodiversity: <www.natmuseum.ut.ee/en/content/ebiodiversity> (Jüriado and Paal 2018).

## Results

### Composition of lichen species in relation to environmental variables

In total, 137 lichen species were found on the trunks of the six broad-leaved tree species studied. Among these, 121 species were recorded in floodplain forests and 78 species in klint forests (Supplementary material Appendix 1). The most frequent lichen species were *Arthothelium ruanum*, *Graphis scripta*, *Lepraria lobifigans*, *Lecidella elaeochroma*, *Phlyctis argena* and *Pseudoschismatomma rufescens*, occurring on more than 55% of the sampled trees. Altogether, 14 red-listed lichen species were recorded, nine of them growing on broad-leaved trees in floodplain forests and ten in klint forests (Supplementary material Appendix 1).

The eigenvalues of the first, second and third ordination axes were 0.35, 0.18 and 0.16, respectively. In the CCA forward selection procedure twelve variables revealed a significant ( $p \leq 0.05$ ) contribution to the results of the ordination (Fig. 2), i.e. all variables except for 'canopy cover' and the tree

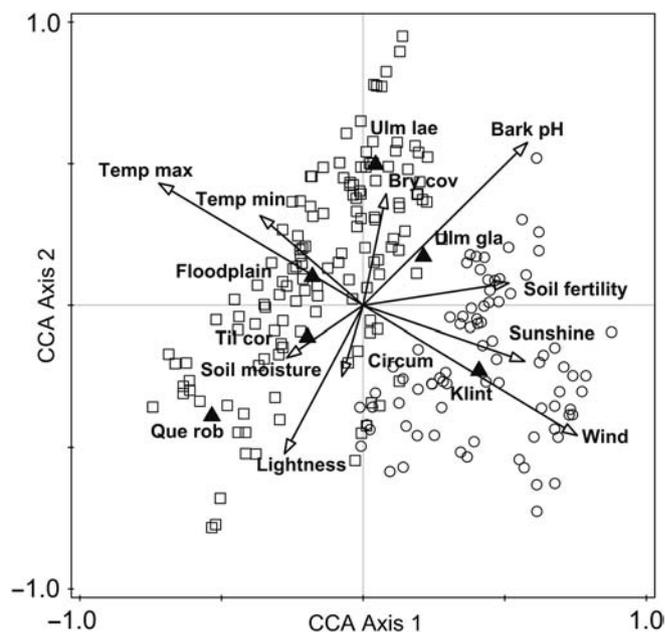


Figure 2. CCA ordination diagram of the sampled trees and significantly correlated environmental variables along the first and second ordination axes. Circles denote the sample trees from klint forests and quadrats denote the sample trees from floodplain forests. The dummy variables 'tree species' and 'forest type' are represented by their centroids. For abbreviations and explanations of the environmental variables see Table 1.

species *Acer platanoides* and *Fraxinus excelsior*. The final CCA model with all significant predictors explained 22.4% of the total variance in the species data while total inertia was 6.467.

In the ordination plot, two groups are clearly evident (Fig. 2): trees from floodplain forests on the left and trees from klint forests on the lower right (Fig. 2). Klint forests are exposed to stronger winds and more sunny days per year compared to floodplain forests. Floodplain forests are growing under more continental climatic conditions with larger variation in air temperature compared to klint forests (Fig. 2). Soil fertility is higher in klint forests, whereas the soils of floodplain forests are more moist. The species in the lower right part of the ordination plot, such as *Alyxoria ochrocheila*, *Anisomeridium bifforme*, *Arthonia atra*, *Lecania naegelii* and *Opegrapha vulgata*, occurred exclusively or more frequently in klint forests (Fig. 3A); while *Lepraria jackii*, *Buellia griseovirens*, *Micarea prasina*, *Ochrolechia arborea* and *Parmelia sulcata*, located in the upper left part of the ordination plot, were more common in floodplain forests.

Of the host tree (substrate) variables, bark pH is the most strongly positively correlated with both the first and second ordination axes, while cover of bryophytes is strongly positively correlated with the second axis only (Fig. 3A). Lichen species favoured by the subneutral or basic bark of *Ulmus glabra* and *U. laevis*, e.g. *Acrocordia gemmata*, *Bacidia rubella*, *Biatoridium monasteriense* and *Phaeophyscia orbicularis*, are located in the upper right part of the ordination plot. Species that are correlated with higher cover of bryophytes on trunks (e.g. *Bacidia subincompta*, *Lobaria pulmonaria* and *Mycobilimbia epixanthoides*) are also situated in the upper part of the ordination plot. Lichen species most frequently found on the acid bark of *Quercus robur* and *Tilia cordata* (e.g. *Arthonia vinosa*, *Lecanora pulicaris*, *Hypogymnia physodes* and *Ochrolechia androgyna*), are located in the lower left part of the ordination plot. *Arthonia byssacea* and *Pyrrhospora quernea* are favoured by good light conditions on oak trees whose trunks are usually only modestly or almost not at all covered by bryophytes (Fig. 3A). The same species, as well as *Buellia schaeereri*, *Chaenotheca trichialis* and *Pertusaria flavida* were more frequently found on larger tree trunks; according to the ordination analysis, they are located in upper left part of the biplot of the first and third axes (Fig. 3B). Lichen species occurring frequently on stems with a smaller diameter (e.g. *Arthonia radiata*, *Cliostomum griffithii*, *Lecanora exal lens* and *Lecidella elaeochroma*) are placed in the lower part of the same ordination plot (Fig. 3B).

### Functional trait groups of epiphytic lichens in relation to environmental variables

Most of the epiphytic lichens (74.5%) found in floodplain and klint forests contained chlorococcoid algae (e.g. *Trebouxia* spp.) as the photobiont in their thallus; 20.4% of the lichens had *Trentepohlia* spp., and only 3.6% of the lichens had a cyanobacterium as the photobiont (Table 2). Lichens with *Trentepohlia* as the photobiont were more common in klint forests (29.5%) than in floodplain forests (17.4%) (Table 2).

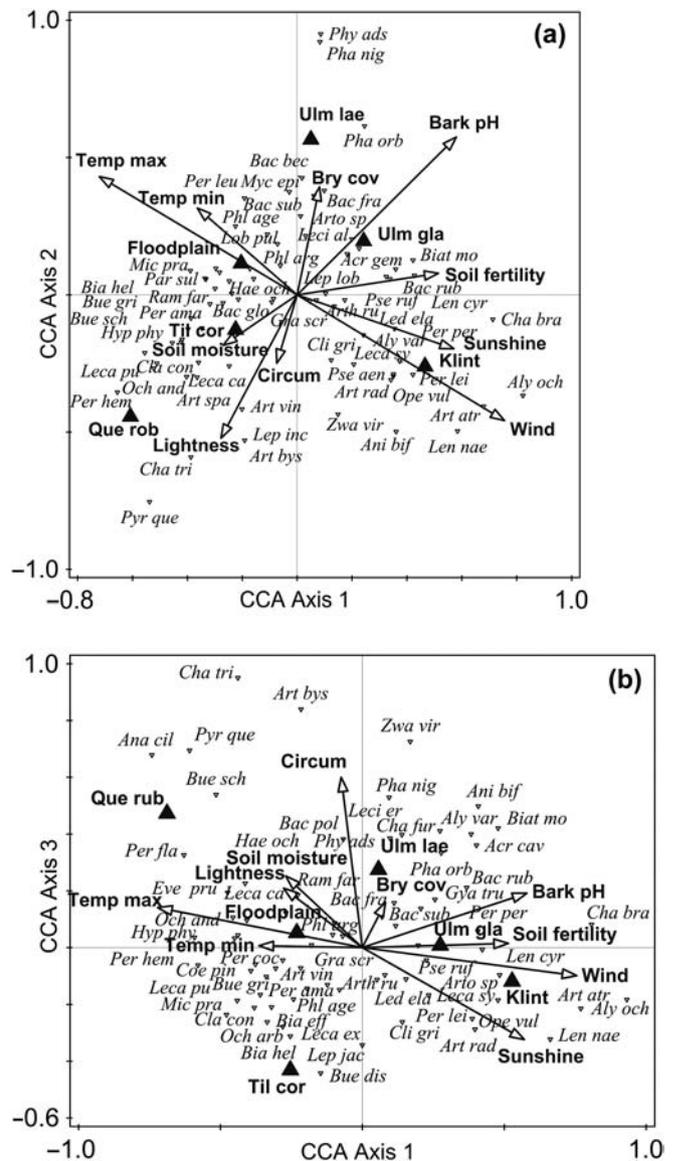


Figure 3. CCA ordination diagram of the species and environmental variables for axes 1 and 2 (a), and for axes 1 and 3 (b). Full names of lichen species are found in Supplementary material Appendix 1. For abbreviations and explanations of the environmental variables see Table 1.

The largest fraction of the recorded lichens (78%) have a crustose growth form, most of the species have ascomata (60.6%), and lecideine or lecanorine apothecia (73%) were the most common type of ascocarps (Table 2). Other types of apothecia (lirellate and stalked apothecia) were present in 16% of the studied lichens, and 6% of the lichens had perithecia (Table 2). Lichens with lirellate apothecia were found more frequently in klint forests (14.1%) than in floodplain forests (7.4%).

According to the results of the interactive forward selection of explanatory variables by RDA, climatic variables ('wind' and 'temp min' = minimal air temperature), forest soil fertility and tree level variables ('bark pH' and 'circumference'),

contributed significantly to the explanation of variation in the response data and accounted altogether for 41.0% of the variation. Most of the variation was explained by the first ordination axis (eigenvalue 0.36), the second and the third axes contributed only marginally (eigenvalues 0.03 and 0.02, respectively). Eutrophic klint forests are under stronger maritime influence (wind speed) and hosted lichen communities with specific combinations of functional traits. The proportion of crustose species forming epiphytic lichen synusiae was very high there; the most common photobiont was chlorococcoid algae, but lichens with *Trentepohlia* as the photobiont were also characteristic (Fig. 4). Epiphytic lichens in klint forests disperse mostly sexually, having different types of apothecia (stalked apothecia, lirellae) and the proportion of vegetatively dispersing sorediate or isidiate species was lower than in the other stands. In contrast, epiphytic lichens common in floodplain forests most frequently have chlorococcoid algae as the photobiont in the thallus and a foliose or fruticose growth form were more frequent than in klint forests (Fig. 4). Epiphytic lichens in inland forests had frequently soredia or isidia as vegetatively dispersing diaspores; and the characteristic type of ascocarp was the apothecium. Lichens with perithecia were most common on trees with a subneutral bark while the frequency of calicioid lichens with stalked apothecia was higher on large trees (Fig. 4).

### Epiphytic lichen societies

The analysed 213 sample quadrats/synusiae were classified into 13 clusters/societies. Their reliability was confirmed by the MRPP test: all established societies had significantly different species compositions ( $p < 0.05$ ), even when considering Bonferroni correction for multiple comparisons. Moreover, all societies had their own significant indicator species (Table 3) which also had the highest abundance in almost all cases (Supplementary material Appendix 2). Therefore, we labelled the established societies according

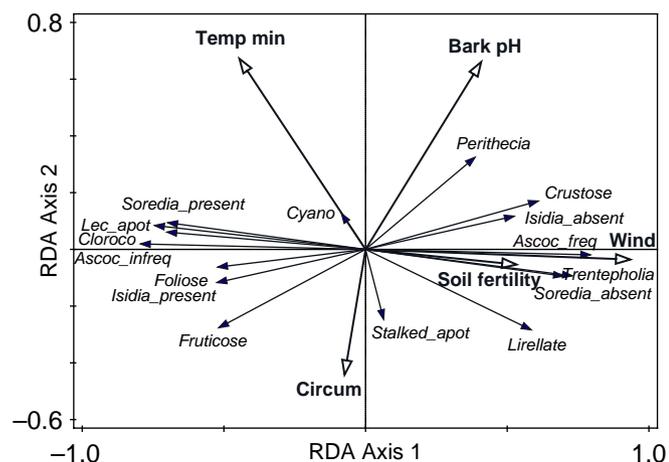


Figure 4. Functional traits of lichens and environmental variables on the biplot from redundancy analysis (RDA) of axes 1 and 2. Notations and abbreviations as in Table 1 and 2.

to the indicator species (Table 3). The synusiae of a certain society group differed significantly also by environmental conditions (i.e. soil fertility) and by the host three characteristics (bark pH, cover of bryophytes and trunk circumference) (Table 4). Eight societies, e.g. the synusiae of *Phlyctis argena* (1st), *Micarea prasina* (2nd), *Arthonia byssacea* (4th), were more common in floodplain forests, while the synusiae of the *Opegrapha vulgata* (5th), *Lecidella elaeochroma* (12th) and *Pseudoschismatomma rufescens* (13th) societies were more frequent on klint forest trees; the synusiae belonging to the *Bacidia rubella* (3rd) and *Graphis scripta* (11th) societies were represented in forests of both site types (Table 4). Moreover, the synusiae of the *Bacidia rubella* (3th), *Opegrapha vulgata* (5th) and *Bacidia subincompta* (10th) societies were mainly found in forests on the most fertile soils (Table 4). To get a better overview and ecological specification, the established societies are divided into two groups according to the increasing bark pH of the substrate (Wirth 1995): 1) moderately acid bark (pH 5.3–5.6) and 2) subneutral bark (pH 5.7–7).

### Synusiae on moderately acid bark (pH 5.3–5.6)

Mature trees (diameter 20–40 cm), moderately acid bark (pH 5.3–5.5) and a low cover of bryophytes – these substrate features supported the synusiae of the 1st, 2nd and 6th societies (Table 4). The synusiae of the 1st society were dominated by *Phlyctis argena*. Common species were also *Bacidia subincompta*, *Buellia griseovirens*, *Graphis scripta*, *Micarea prasina* and *Phlyctis agelaea* (Supplementary material Appendix 2). Synusiae of this type were characteristic of floodplain forests where they occurred on almost all studied broad-leaved tree species (less frequently on *Acer platanoides*) (Table 4). *Micarea prasina* was one of the dominating species of the 2nd type synusiae. However, *Phlyctis argena* together with *Buellia griseovirens*, *Biatora helvola*, *Cladonia coniocraea*, *Ochrolechia androgyna* and *Pertusaria amara* were often intermixed (Supplementary material Appendix 2). The corresponding synusiae were usually found on the stems of *Fraxinus excelsior*, *Quercus robur* and *Tilia cordata* and were less frequent on *Acer platanoides* and *Ulmus* spp. (Table 4). The comparatively moist conditions of floodplain forests evidently supported also the synusiae of the 6th society, where *Phlyctis agelaea* was the dominating species (Supplementary material Appendix 2), but also *Bacidia globulosa*, *Hypogymnia physodes* and *Parmelia sulcata* were reliable indicator species (Table 3). These synusiae were found on all studied broad-leaved trees (Table 4).

In both forest site types the synusiae of the 11th society occurred on younger *Tilia cordata* trees with smaller circumference (mean 108 cm) and higher bark pH (5.6) (Table 4). The prevailing species in the corresponding synusiae was *Graphis scripta*, accompanied frequently by *Lecidella elaeochroma* and *Phlyctis argena* (Supplementary material Appendix 2).

In floodplain forests, mainly on old *Quercus robur* and *Fraxinus excelsior* trees (mean circumference 163 cm), with an average pH of 5.6 and a low cover of bryophytes, the

Table 3. Indicator species of the lichen societies on temperate broad-leaved trees in floodplain and klint forests and their indicator values. The species' names used to label the recognised societies are presented in bold. Notations: \* – marks the species' maximum indicator value in a corresponding society, p – significance level.

Species	p	Society type												
		1	2	3	4	5	6	7	8	9	10	11	12	13
<b>Phlyctis argena</b>	<0.001	34*	19	2	2	1	10	2	2	1	4	5	1	0
<b>Micarea prasina</b>	0.007	5	24*	0	0	0	1	1	0	0	0	1	0	0
<i>Ochrolechia androgyna</i>	0.015	0	22*	0	0	0	1	0	0	0	0	0	0	0
<i>Cladonia coniocraea</i>	0.021	0	17*	0	0	0	0	0	0	0	0	0	0	0
<i>Buellia griseovirens</i>	0.031	9	18*	0	0	0	4	0	0	0	0	11	0	0
<i>Pertusaria amara</i>	0.046	1	15*	0	8	0	5	0	0	0	0	0	0	0
<i>Biatora helvola</i>	0.049	2	15*	0	1	0	0	0	0	0	0	3	0	0
<b>Bacidia rubella</b>	<0.001	0	0	76*	0	1	0	0	4	0	0	0	0	2
<b>Arthonia byssacea</b>	0.001	0	0	0	33*	0	0	0	0	0	0	0	0	0
<i>Haematomma ochroleucum</i>	0.040	0	0	0	20*	0	1	0	0	0	0	0	0	0
<b>Opegrapha vulgata</b>	0.003	0	0	0	1	28*	0	0	0	0	0	2	0	0
<i>Lecidea albohyalina</i>	0.012	0	0	0	0	24*	0	0	0	0	0	0	0	0
<i>Anisomeridium biforme</i>	0.013	0	0	0	0	22*	0	0	0	1	0	0	0	0
<b>Phlyctis agelaea</b>	<0.001	1	0	0	0	0	45*	0	0	0	1	0	1	0
<i>Bacidia globulosa</i>	0.001	1	0	2	0	1	32*	0	0	0	0	1	1	0
<i>Hypogymnia physodes</i>	0.036	0	9	0	0	0	19*	0	0	0	0	0	0	0
<i>Parmelia sulcata</i>	0.042	1	1	0	0	0	16*	0	0	0	0	2	0	0
<b>Lepraria lobificans</b>	<0.001	0	2	1	1	0	5	54*	5	0	0	0	0	0
<i>Acrocordia gemmata</i>	0.007	0	0	11	0	1	0	23*	3	6	1	0	0	4
<b>Alyxoria varia</b>	<0.001	0	0	0	1	1	0	0	82*	0	0	0	0	1
<i>Arthopyrenia</i> spp.	<0.001	0	0	1	0	0	0	0	0	87*	0	0	0	0
<b>Mycobilimbia epixanthoides</b>	<0.001	0	0	0	0	0	0	0	0	81*	0	0	0	0
<b>Bacidia subincompta</b>	<0.001	2	0	0	0	0	0	2	0	0	80*	0	0	0
<b>Graphis scripta</b>	<0.001	2	2	1	1	2	3	0	0	0	1	60*	1	4
<b>Lecidella elaeochroma</b>	<0.001	1	0	0	0	0	3	0	0	1	0	5	66*	5
<i>Lecanora chlarotera</i>	0.004	0	1	0	0	0	0	0	0	0	0	5	24*	2
<b>Pseudoschismatomma rufescens</b>	<0.001	1	2	3	0	0	1	0	3	0	0	0	12	56*
<i>Pertusaria leioplaca</i>	0.009	0	1	1	0	11	0	0	0	0	0	0	2	21*

synusiae of the *Arthonia byssacea* (4th) society were found (Table 4). The indicator species of this society, in addition to *Haematomma ochroleucum* (Table 3), were frequently also *Biatoridium monasteriense* and *Lecanora argentata* (Supplementary material Appendix 2).

### Synusiae on subneutral bark (pH 5.7–7)

In klint forests, on younger to mature trees (diameter 20–40 cm) with subneutral bark (pH 5.9–6.0) and a low cover of bryophytes, the synusiae of the 12th and 13th societies were frequent (Table 4). The synusiae of the 12th type were dominated by *Lecidella elaeochroma*; a significant indicator species was also *Lecanora chlarotera*. In the synusiae of the 13th society, *Pseudoschismatomma rufescens* prevailed, besides the significant indicator species *Pertusaria leioplaca* (Table 3). The synusiae belonging to the 5th type were common on all mature broad-leaved tree species of the same forest type (mean bark pH 5.7, Table 4). Characteristic species of this society were *Anisomeridium biforme*, *Lecidea albohyalina* and *Opegrapha vulgata* (Table 3).

The synusiae of *Mycobilimbia epixanthoides* (9th society) and *Bacidia subincompta* (10th society) were common on mature trees (diameter 20–40 cm) with higher bark pH (average pH 6.1–6.2) and a high cover of bryophytes

in floodplain forests (Table 4). Important indicators of the *Mycobilimbia epixanthoides* society were also species of the genus *Arthopyrenia* (Table 3). The synusiae dominated by *Bacidia subincompta* (10th type) were found both on trunks of *Ulmus glabra* and *U. laevis* (Table 4). On mature or old big trees (diameter >40 cm) with subneutral bark (average pH 6.1–6.2), moderately to rather abundantly covered by bryophytes, the synusiae of the 3rd and 7th societies were common. The synusiae of the 3rd type were frequently recorded in both klint and floodplain forests. They had mostly formed on quite big mossy stems of *Ulmus* spp. and *Fraxinus excelsior*. *Bacidia rubella* was a significant indicator species of this type (Table 3) while *Acrocordia gemmata*, *Arthopyrenia* spp. and *Pseudoschismatomma rufescens* were also frequent (Supplementary material Appendix 2). The synusiae of the 7th type were common in floodplain forests. The corresponding synusiae were characterized by *Acrocordia gemmata* and *Lepraria lobificans* (Table 3), which occurred on large *Fraxinus* trunks (mean circumference 132 cm), with the highest cover of bryophytes (Table 4) which were more abundant than epiphytic lichens.

In floodplain forests, on the oldest *Fraxinus* trees (diameter >40 cm) with an average pH of 6.6 and a low cover of bryophytes, the synusiae of the 8th society were the most frequent. The mean circumference of these trees was 214 cm

Table 4. Mean values of the environmental variables of lichen societies and significance level of their difference according to univariate ANOVA. Similar groups of values by the Fisher LSD test are marked with superscript letters ( $p < 0.05$ ). For abbreviations and explanations of the environmental variables see Table 1. Notations: Bark pH – phorophyte bark pH mean standardized value and mean original value in the parentheses (pH measured in  $H_2O$ ), Bry cov – square root transformed mean value of bryophyte cover and mean original value in the parentheses ( $cm^2$ ), Circum – log transformed mean value of phorophyte girth and mean original value in the parentheses (cm).

Society type	Soil														
	Ace pla	Fra exc	Que rob	Til cor	Ulm gla	Ulm lae	Floodplain	Klint	Can cov	Lightness	fertility	moisture	Bark pH	Bry cov	Circum
p	0.316	0.328	0.003	<0.001	<0.001	0.005	<0.001	<0.001	0.383	0.066	<0.001	0.119	<0.001	<0.001	<0.001
1	<0.1	0.2	0.1 <sup>abc</sup>	0.2 <sup>a</sup>	0.2 <sup>bc</sup>	0.3 <sup>cd</sup>	0.9 <sup>f</sup>	0.1 <sup>a</sup>	0.83	4.7	5.6 <sup>a</sup>	6.2	-0.41 <sup>a</sup> (5.5)	2.5 <sup>b</sup> (6)	2.07 <sup>ab</sup> (119)
2	<0.1	0.3	0.2 <sup>bc</sup>	0.4 <sup>bc</sup>	<0.01 <sup>a</sup>	0.1 <sup>ab</sup>	0.9 <sup>f</sup>	0.1 <sup>a</sup>	0.80	4.7	5.5 <sup>a</sup>	6.3	-0.69 <sup>a</sup> (5.4)	1.9 <sup>ab</sup> (3)	2.11 <sup>bc</sup> (129)
3	0.1	0.3	0.0 <sup>a</sup>	0.0 <sup>a</sup>	0.4 <sup>c</sup>	0.2 <sup>bcd</sup>	0.4 <sup>abc</sup>	0.6 <sup>def</sup>	0.78	4.5	6.3 <sup>cd</sup>	6.0	0.65 <sup>f</sup> (6.2)	3.0 <sup>bc</sup> (9)	2.15 <sup>cd</sup> (141)
4	0.2	0.3	0.3 <sup>c</sup>	0.1 <sup>a</sup>	0.1 <sup>abc</sup>	0.1 <sup>ab</sup>	0.7 <sup>cde</sup>	0.3 <sup>bcd</sup>	0.77	5.0	6.0 <sup>abc</sup>	6.3	-0.37 <sup>ab</sup> (5.6)	1.8 <sup>ab</sup> (3)	2.20 <sup>d</sup> (163)
5	0.2	0.3	0.0 <sup>a</sup>	0.2 <sup>ab</sup>	0.3 <sup>c</sup>	0.0 <sup>a</sup>	0.2 <sup>a</sup>	0.8 <sup>f</sup>	0.80	4.6	6.4 <sup>cd</sup>	5.9	-0.17 <sup>abce</sup> (5.7)	1.8 <sup>ab</sup> (3)	2.09 <sup>abc</sup> (124)
6	0.1	0.4	0.2 <sup>abc</sup>	0.1 <sup>a</sup>	0.1 <sup>abc</sup>	0.1 <sup>abc</sup>	0.9 <sup>f</sup>	0.1 <sup>ab</sup>	0.78	4.8	6.0 <sup>abc</sup>	6.6	-0.80 <sup>a</sup> (5.3)	0.9 <sup>a</sup> (0.5)	2.07 <sup>abc</sup> (119)
7	0.2	0.5	0.0 <sup>a</sup>	0.1 <sup>a</sup>	0.2 <sup>abc</sup>	0.1 <sup>abc</sup>	0.8 <sup>def</sup>	0.2 <sup>abc</sup>	0.75	4.1	6.0 <sup>abcd</sup>	6.1	0.38 <sup>cdef</sup> (6.1)	6.4 <sup>d</sup> (40)	2.12 <sup>bcd</sup> (132)
8	0.0	0.5	0.0 <sup>ab</sup>	0.2 <sup>ab</sup>	0.2 <sup>abc</sup>	0.2 <sup>abcd</sup>	0.7 <sup>cdef</sup>	0.3 <sup>abcd</sup>	0.78	4.4	5.9 <sup>abcd</sup>	6.3	1.11 <sup>f</sup> (6.6)	1.8 <sup>ab</sup> (3)	2.33 <sup>e</sup> (214)
9	0.0	0.2	0.0 <sup>ab</sup>	0.0 <sup>a</sup>	0.0 <sup>abc</sup>	0.0 <sup>abc</sup>	0.8 <sup>def</sup>	0.2 <sup>abc</sup>	0.75	3.8	5.9 <sup>abcd</sup>	5.8	0.67 <sup>ef</sup> (6.2)	5.6 <sup>d</sup> (32)	1.96 <sup>a</sup> (92)
10	0.2	0.1	0.0 <sup>a</sup>	0.0 <sup>a</sup>	0.4 <sup>d</sup>	0.4 <sup>d</sup>	0.8 <sup>def</sup>	0.2 <sup>abc</sup>	0.83	4.0	6.2 <sup>bcd</sup>	6.2	0.43 <sup>cdef</sup> (6.1)	4.3 <sup>ac</sup> (19)	2.05 <sup>abc</sup> (114)
11	0.2	0.2	0.0 <sup>a</sup>	0.6 <sup>c</sup>	0.0 <sup>ab</sup>	0.0 <sup>a</sup>	0.5 <sup>bcd</sup>	0.5 <sup>cd</sup>	0.84	4.8	5.7 <sup>ab</sup>	6.2	-0.33 <sup>abc</sup> (5.6)	1.7 <sup>ab</sup> (3)	2.03 <sup>ab</sup> (108)
12	0.2	0.5	0.0 <sup>a</sup>	0.1 <sup>a</sup>	0.2 <sup>abc</sup>	0.0 <sup>a</sup>	0.3 <sup>ab</sup>	0.7 <sup>ef</sup>	0.79	4.6	5.9 <sup>abc</sup>	5.7	0.17 <sup>bcd</sup> (5.9)	1.5 <sup>ab</sup> (2)	2.06 <sup>abc</sup> (116)
13	0.2	0.5	0.0 <sup>a</sup>	0.1 <sup>a</sup>	0.2 <sup>abc</sup>	0.0 <sup>a</sup>	0.2 <sup>a</sup>	0.8 <sup>f</sup>	0.76	5.0	6.6 <sup>d</sup>	6.2	0.13 <sup>bcd</sup> (6.0)	1.7 <sup>ab</sup> (3)	2.08 <sup>abc</sup> (122)

(Table 4). These synusiae were dominated by *Alyxoria varia*, but *Acrocordia gemmata*, *Bacidia rubella* and *Lepraria lobifera* were also frequently found intermixed (Supplementary material Appendix 2).

## Discussion

The results of our study showed that the composition of epiphytic lichen species and their synusiae on temperate broad-leaved trees in floodplain and klint forests are strongly influenced by host tree properties, stand level environmental variables and climatic conditions. On six temperate broad-leaved tree species, we distinguished 13 societies that occur in largely different microhabitats differing by substrate acidity (bark pH), tree age (stem circumference) and abundance of bryophytes on the tree bole. Moreover, there was a significant correlation between synusiae of some societies and particular tree species, which indicates that other tree species-specific bark properties (Ellis 2012) are important as well.

Of the tree level factors, bark pH appeared to be the most important factor affecting the species composition of lichen synusiae on broad-leaved trees in *Humulus* site type floodplain forests and in *Lunaria* site type klint forests; a gradient in lichen species composition from *Quercus robur* and *Tilia cordata*, with the most acid bark, to *Ulmus glabra* and *U. laevis*, with a subneutral bark, was revealed. The bark pH gradient was correlated also with cover of bryophytes on the tree bole, which in turn, had a significant impact on the development of epiphytic lichen synusiae. Changes in the composition of lichen synusiae on broad-leaved trees occur mainly due to the combined influence of several environmental variables, e.g. covariation of cover of bryophytes with bark pH or tree size (circumference) (Jüriado et al. 2009b, Ellis 2012). However, in forests, conditions at the habitat scale also have some impact on the composition of lichen species, e.g. degree of canopy cover directly determines light and moisture conditions on the tree bole (Gauslaa 2014). The effect of canopy closeness can also be indirect as light and humidity conditions of the stand may favour the growth of bryophytes on the tree bole (Hong and Glime 1997, Frahm 2003). Moreover, an indirect effect of soil properties on epiphytic communities has been shown in several studies: for example, tree size depends on soil fertility, or bark pH is influenced by soil pH (Gauslaa 1985, 1995, Gustafsson and Eriksson 1995).

### Epiphytic lichen societies on temperate broad-leaved trees

In Estonia, Trass (1981) described several lichen synusiae occurring on the bark of deciduous trees in conditions of low anthropogenic impact, but without specifying the tree species or other ecological characteristics. The societies of *Graphis scripta* (11th) and *Lecidella elaeochroma* (12th), established in the current study, correspond well to the unions (resp. synusiae) *Graphis scripta*–*Arthonia radiata* and *Lecidea*

*euphoria*–*Lecanora carpineae* established by Trass (1981). Some affinity occurs also between the *Phlyctis argena* (1st) and *Micarea prasina* (2nd) societies distinguished by us, and the union of *Phlyctis argena*–*Pertusaria amara* recognised by Trass. Although he treated the lichen species of different growth forms (crustose, foliose, and fruticose) as belonging to different synusiae (Trass 1964, 1981), most phytosociological studies tend to consider lichen assemblages of different growth forms as belonging to the same synusiae (Barkman 1958, Nimis 1982, Romanova 2009). Indeed, Gams (1918) and Du Rietz (1936, 1965), the authors who defined the synusiae as one-layer plant assemblages belonging to one or close life forms, considered the life forms (resp. growth forms) according to Raunkjær (1907, 1934), i.e. all epiphytic lichens represented one life form – the epiphytes.

Some similarity can be observed between the lichen societies identified in the current study and the epiphytic lichen community types in Scottish woodlands established by Ellis et al. (2015). Despite the different geographic, climatic and habitat conditions in Scotland and Estonia, the *Graphis scripta* (11th), *Lecidella elaeochroma* (12th) and *Pseudoschismatomma rufescens* (13th) societies, described from younger trees by us, have, according to the characteristic species, certain similarity with Scottish epiphytic lichen community types A and B, i.e. the early successional (pioneer) communities of mesotrophic smooth-bark microhabitats. In mesotrophic microhabitats and in conditions of a continental climate, A-type (*Arthonia radiata*–*Lecidella elaeochroma*) and B-type (*Graphis scripta*) lichen communities are replaced with the D-type communities of *Phlyctis argena*–*Ramalina farinacea* during succession (Ellis et al. 2015). In Estonian klint and floodplain forests, the analogous societies are *Phlyctis argena* (1st), *Micarea prasina* (2nd) and *Phlyctis agelaea* (6th) on trees with acid-bark.

In the maritime climate of Scotland several bryophyte-dominated communities on old trees are been formed with cyanobacterial macrolichens, e.g. *Lobaria virens* and *L. pulmonaria* (Ellis et al. 2015). In contrast, in Estonian broad-leaved forests, on mossy tree trunks, microlichens of the crustose growth form are common, represented, e.g. by synusiae of the *Mycobilimbia epixanthoides* (9th) and *Bacidia subincompta* (10th) societies. On older trees with subneutral bark and a moderate to high cover of bryophytes, the synusiae of *Bacidia rubella* (3th society), *Alyxoria varia* (8th society) and *Lepraria lobificans* (7th society) are frequently found.

### Factors associated with the functional groups of epiphytic lichens

In general, the lichen synusiae occurring on temperate broad-leaved trees in the studied forests were relatively homogenous in terms of their growth form and photobiont: of the corresponding synusiae, 75% in floodplain forests and even 88.5% in klint forests were formed of crustose lichens, and of the lichens 75% had chlorococcoid algae as the photobiont. Nevertheless, it appeared that tree properties had a specific

impact on certain groups of lichens with particular life-history traits. Like Johansson et al. (2009), we found that pin-lichens, i.e. the lichens with stalked apothecia (e.g. *Calicium viride*, *Chaenotheca* spp.), preferred older and larger trees, while the pyrenolichens, i.e. the lichens with perithecia as the ascocarp (e.g. *Acrocordia* spp., *Pyrenula* spp., *Pseudosagedia aena*), were growing mostly on trees with subneutral bark (Smith et al. 2009).

We also established that the composition of the functional traits of lichens is different for the different forest site types, i.e. it is determined by the particular habitat and climatic conditions of floodplain and klint forests. In klint forests, with a stronger influence of the wind, the proportion of crustose species is overwhelming, diaspores for vegetative dispersal (soredia and isidia) are not common and epiphytic lichens disperse mostly sexually. In these forests, lichens with *Trentepohlia* as the photobiont are characteristic and lichens with lirellate ascocarp are common. The proximity of the sea creates milder climatic conditions in klint forests than in floodplain forests located in inland Estonia; the solar radiation is also slightly higher and average winter temperatures are considerably higher on the coast than in inland (Jõgi and Tarand 1995). Moreover, in klint forests, due to the proximity of the sea, strong winds can have a destructive effect on loosely attached fruticose lichens (Essen and Renhorn 1988), whereas the shade provided by the almost perpendicular high klint may support the growth of shade adapted crustose microlichens (Lakatos et al. 2006). In addition, the shade provided by the klint may be another reason why lichens with *Trentepohlia* as the photobiont are characteristic of klint forests and are more common there than in floodplain forests. Lichens with *Trentepohlia* have their photosynthetic optimum in shaded warm conditions, being more sensitive to freezing than lichens with other types of photobiont (Nash et al. 1987, Kappen 1993). In Italy, for example, the richness of lichens with *Trentepohlia* also increases in wet regions and/or in areas exposed to maritime influence and decreases in continental areas (Marini et al. 2011).

Sexually reproducing lichens may have an advantage in open or fragmented landscapes (Jüriado et al. 2006, Ellis and Coppins 2007b, Hedenås and Ericson 2008) as they have more effective long-distance dispersal compared to lichens propagating mainly by vegetative diaspores (soredia or isidia) (Johansson et al. 2012, Ronnäs et al. 2017). Therefore, it has been suggested that a greater proportion of asexual lichen species may occur in landscapes with a relatively continuous forest cover (Stofer et al. 2006, Randlane et al. 2017). We suppose that differences in the proportions of vegetatively and sexually dispersed lichen species in klint and floodplain forests is determined by the location and connectivity of forest stands in the landscape. Estonian klint forests stretch as a narrow stripe (usually 10–100 m wide) on the talus slopes of the limestone escarpment along the northern coastline of Estonia (Paal 2009) and are usually separated by grasslands from the larger forest massifs located on the klint southwards. The studied floodplain forests are typically situated within

or beside bigger forest massifs, which might account for the higher proportion of vegetatively dispersed species in the forests of this site type. Also flooding and high water table create a humid mesoclimate in floodplain forests (Hager and Schume 2001, Paal et al. 2007, 2008), which could favour lichens of the foliose or fruticose growth forms as their thick and/or compact thalli need more time to become hydrated in humid air compared to crustose lichens with a thin thallus that take up humidity rapidly (Gauslaa 2014).

Fourteen red-listed species found in this study constitute half of the red-listed epiphytes characteristic of temperate broad-leaved trees in Estonia (Marmor et al. 2017). Nine of the recorded red-listed species have *Trentepohlia* as the photobiont (e.g. *Alyxoria ochrocheila*, *Arthonia atra*, *Eopyrenula leucoplaca*, *Pyrenula nitidella*, *Thelotrema lepadinum*, *Zwackhia viridis*), three have chlorococcoid algae as the photobiont (*Biatoridium monasteriense*, *Lecanora intumescens* and *Lecidea erythrophaea*) and there was found only one red-listed cyanobacterial lichen (*Lobaria pulmonaria*) (Supplementary material Appendix 1). Apparently, the red-listed lichens with *Trentepohlia* as the photobiont favoured the milder climatic conditions of klint forests compared to floodplain forests; in places, also *Biatoridium monasteriense* was quite abundant in klint forests.

It is notable that in studied forests the overall frequency and abundance of lichens with a cyanobacterium as the photobiont was very low, with only five recorded species (Supplementary material Appendix 1). In Europe, destructive forest management has greatly diminished the occurrence and diversity of cyanobacterial lichens (e.g. *Lobaria pulmonaria*) as they are characteristic of ancient woodlands or old-growth forests (James et al. 1977, Gauslaa, 1985, 1995, Rose 1988). Apart from forest management, cyanolichens are sensitive to atmospheric pollutants (SO<sub>2</sub>, O<sub>3</sub>) and acid rain (Gauslaa 1995, Goward and Arsenault 2000, Richardson and Cameron 2004). Considering also the low dispersal ability of cyanolichens (Gu et al. 2001, Jüriado et al. 2012), this functional group of lichens is among the most threatened groups of epiphytes (Jüriado and Liira 2010).

In northern Europe, where temperate broad-leaved trees have a limited distribution (Paal 2007b), from a lichenological perspective, floodplain and klint forests are very valuable habitats, hosting high species richness including a notable number of red-listed species. As pointed out already earlier (Jüriado et al. 2009a, b), these forests are high-ranked for the conservation of threatened epiphytes in the boreo-nemoral region (Thor 1998, Berg et al. 2002). We showed that the specific location and climatic conditions of klint forest create unique environmental conditions for this bioclimatic zone, favouring lichens with *Trentepohlia* as the photobiont.

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Supplementary material (online at <[www.nordicjbotany.org/appendix/njb-01939](http://www.nordicjbotany.org/appendix/njb-01939)>). Appendix 1–2.