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Diversity of lichens in semi-natural habitats of Estonia

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CONTENTS

LIST OF ORIGINAL PUBLICATIONS

The thesis is based on the following publications, which are referred to in the text by the Roman numerals:

I Leppik, E. & Jüriado, I. (2008) Factors important for epiphytic lichen communities in wooded meadows of Estonia. *Folia Cryptogamica Estonica* 44: 75–87.

II Leppik, E., Jüriado, I. & Liira, J. (2011) Changes in stand structure due to the cessation of traditional land use in wooded meadows impoverish epiphytic lichen communities. *The Lichenologist* 43: 257–274.

III Leppik, E., Jüriado, I., Suija, A. & Liira, J. (2013) The conservation of ground layer lichen communities in alvar grasslands and the relevance of substitution habitats. *Biodiversity and Conservation* 22: 591–614.

IV Leppik, E., Jüriado, I., Suija, A. & Liira, J. (2013). Drivers of epigeic lichens in alvar grasslands with regard to their functional traits. Manuscript submitted to *Fungal Ecology*.

The author was primarily responsible for data collection and identification of lichens, for surveying and examining the literature, and for the writing of papers **I–IV**. The author substantially contributed to analysing data in papers **I–IV**.

1. INTRODUCTION

1.1. General introduction

Semi-natural habitats appeared together with human settlements in the Mesolithic (9000–5000 BCE in Estonia) as tracks in forest and small expanses around settlements, but pastures came into being probably with the beginning of grazing by domestic animals in the Neolithic (5000–1800 BCE in Estonia) (Kriiska 2004). Human interference in semi-natural habitats, mainly grasslands, comprises mowing or grazing by livestock (Kukk & Kull 1997; Pärtel et al. 1999*b*). Moderate human interference reflects natural disturbances like the influence of big herbivores, fire (Vera 2000) or droughts (Rosén 1995). Therefore, it has been assumed that traditional extensive farming maintains the near-natural state of the nature (Vera 2000).

Wooded meadow is a type of semi-natural grassland; it is a mosaic vegetation complex which consists of small copses of deciduous trees and shrubs alternating more or less irregularly with open regularly mowed meadow glades (Hæggström 1983). Traditional management of wooded meadows includes raking and picking of fallen branches in spring, mowing in July, aftermath is grazed by cattle in autumn and clearing of trees and shrubs is carried out in late autumn or winter (Hæggström 1983; Kukk & Kull 1997; Mitlacher et al. 2002). Another type of semi-natural grassland is alvar. Alvars are calcareous grasslands on shallow skeletal soil (thickness < 20 cm) formed on Ordovician or Silurian calcareous sediments or on monolithic calcareous rock (Laasimer 1965; Rosén 1982; Zobel 1987). The sparse vegetation of alvars is traditionally managed by livestock grazing and occasional juniper harvesting, mowing is less known (Pärtel et al. 1999*b*; Rosén & van der Maarel 2000). In addition to historical grazing pressure, alvars are characterized by environmental stress and natural disturbances, because thin soil on monolithic rock is susceptible to extreme droughts in summer, frost-induced soil movements in winter and small-scale flooding in spring (Rosén 1995; Ott et al. 1997). As a result of continuous land use lasting for centuries or millennia, semi-natural grasslands, including alvars and wooded meadows, have developed to form species-rich ecosystems with specific biodiversity (Rosén 1982; Hæggström 1983; Kull & Zobel 1991; Poschlod & WallisDeVries 2002; Pärtel et al. 2007).

These semi-natural grasslands, alvars and wooded meadows are mainly distributed in the countries around the Baltic Sea, particularly on the islands (Hæggström 1983; Rosén 1982; Pärtel et al. 2007). Traditionally managed wooded meadows were prevailing in the cultural landscape of Estonia in the 18th century, covering roughly 20% (ca 850,000 ha) of the Estonian area at their peak (Kukk & Kull 1997). Alvars were not so widespread, they covered ca 1.2% (ca 50,000 ha) of the Estonian area in the 19th century (Pärtel et al. 1999*a*; Kukk & Sammul 2006). The area of these semi-natural habitats decreased greatly over the last century as a consequence of the cessation of traditional management. This rate of loss has even accelerated since the 1940s and 1950s (Eriksson et al. 2002; Poschlod & WallisDeVries 2002; Pykälä et al. 2005). Mosaic-structured wooded meadows have been replaced by cultivated fields or abandoned to brush-woods, and open alvar grasslands are overgrown by junipers (*Juniperus communis* L.) or Scots pines (*Pinus sylvestris* L.). Therefore, in present-day Estonia, traditionally-managed wooded meadows cover ca 1,500–2,000 ha and alvars cover ca 15,000 ha, accounting for 0.2% and 30% of their former territory, respectively (Kukk & Sammul 2006).

Estonian semi-natural habitats have some regionally specific singularities compared with other countries around the Baltic Sea. For example, Scandinavian tradition includes pollarding of trees in wooded meadows (Hæggström 1983; Moe & Botnen 2000), while this is not common in Estonia. There are also differences in the species pool as only about 58% of lichen species in wooded meadows are shared between the meadows in Gotland, Sweden and Estonia (Thor et al. 2010). Specific for Estonia, however, are low-productivity alvar areas with furrows and pits on ground, which were created by afforestation attempts in the 1950s–1980s (Laasimer 1975; Kaar 1986). Activities for military purposes and limestone (gravel) quarrying or afforestation practises have included partial or total removal of the soil layer along with exposing bare base rock or piling up of soil to promote tree plantation growth. In the last century non-agricultural activities in limestone areas have created suitable novel habitats for many ground layer lichens (Gilbert 1993).

Contemporary nature conservation policy in Europe considers the protection of semi-natural grasslands to be a central issue in halting biodiversity loss (Poschlod & WallisDeVries 2002). Primary attention in grasslands has been paid to vascular plants, however, a biodiversity conservation policy should apply an integrated approach and cover the demands of multiple taxonomic and ecological groups (WallisDeVries et al. 2002; Brown et al. 1994). For example, epigeic lichens constitute a specific guild under or instead of the herb and moss layer in calcareous grasslands of shallow skeletal soils (Dengler et al. 2006). Nevertheless, relatively little is known about the effects of the cessation of traditional land use practices and the encroachment of woody plants on ground layer lichen communities (During & Willems 1986; Gilbert 1993). Also, studies of epiphytic lichen communities in wooded meadows are scarce (Moe & Botnen 1997, 2000; Thor et al. 2010; Jönsson et al. 2011), although in the (hemi)boreal region, including in Estonia, the epiphytic lichen communities have received major attention (e.g. Hedenås & Ericson 2000; Lõhmus 2003; Johansson et al. 2007; Fritz et al. 2009; Jüriado et al. 2003, 2009*a*, *b*; Marmor et al. 2011, 2013; Lõhmus et al. 2012). Detection of environmental drivers, which determine the composition and richness of lichens in these semi-natural habitats, should be the first priority in the optimisation of conservation planning. However, each species is unique in its response to a changing environment and this response is dependent on a complex of species-specific traits, which determine its ecological niche. For example, species with contrasting functional traits tend to be distributed differently, and predictably, along a successional gradient (Ellis 2012). Moreover, species growth form composition can provide indicative information about microclimatic and biotic conditions in a particular habitat (McCune 1993; Eldridge & Rosentreter 1999; Warren & Eldridge 2003; Ott et al. 1997).

1.2. The objectives

The main objective of the current study was to contribute to the knowledge of lichen communities (systematically lichenized fungi, hereafter named as lichens) in Estonian semi-natural grasslands, namely wooded meadows (**I**, **II**) and alvar grasslands (**III**, **IV**).

The factors structuring local communities act on a multitude of spatial and temporal scales, moreover, delimiting of the processes influencing lichen communities is difficult as the factors are inter-correlated (Ricklefs 1987, 2004; McCune 1993; Loreau 2000; Ellis 2012). Therefore, a great number of environmental factors and different habitat and substratum characteristics were considered to assess their effects on epiphytic lichen communities in wooded meadows (**I**, **II**) and on ground layer lichen communities in alvar grasslands and alvar-like habitats (**III**, **IV**). Moreover, the effects of different factors on individual epiphytic (**II**) and ground layer lichen species (**IV**) were evaluated.

The main threats to the biodiversity of semi-natural habitats are cessation of traditional management and overgrowing by woody plants (Rosén & van der Maarel 2000; Eriksson et al. 2002; Poschlod & WallisDeVries 2002). As overgrowing intensifies (Rosén 1988, 2010; Pärtel & Helm 2007), there will arise an urgent need to estimate how encroachment by vascular plants (trees and shrubs) influences epiphytic lichen communities in wooded meadows at stand (**I**) and tree (**II**) levels and, similarly, how encroachment by shrubs and herbs influences ground layer lichen communities in alvars (**III**, **IV**). In seeking alternative solutions, it was attempted to find out whether disturbed areas can act as temporary substitution habitats for epigeic lichens. For this purpose, we intended to estimate to what extent the lichen communities of disturbance-induced alvar-like habitats resemble traditionally managed alvar communities (**III**).

Since statistical tools cannot be used to evaluate the ecology of low-occurrence species, an alternative approach is suggested, where drivers of rare species can be extrapolated from the driver-trait relationships established for frequently occurring species, assuming that these relationships are consistent regardless of rarity of species. It has been shown that lichen communities are controlled by functional traits in respect to different ecological factors (Jun & Rozé 2005; Johansson et al. 2006, 2007; Lewis & Ellis 2010; Koch et al. 2013).

Therefore, it was intended to draw parallels between the traits of common and rare alvar species to reveal the drivers that limit rare species (**IV**).

In summary, the aims of the present thesis are defined as follows.

- To evaluate the effect of different factors on (a) epiphytic lichen communities in wooded meadows, and (b) on ground layer lichen communities in alvar grasslands and alvar-like habitats.
- To determine the results of the cessation of traditional management in wooded meadows and alvars on the epiphytic and epigeic lichen communities in these habitats, and to propose alternative management practices for maintaining the richness of lichen species in the studied semi-natural habitats.
- To examine whether any (disturbed) areas could act as substitution habitats for (rare) epigeic lichens of calcareous grasslands.
- To define the species traits of common lichens in low-productivity alvars and to draw parallels between the traits of common and rare species to reveal the ecological drivers that limit rare species.

2. MATERIALS AND METHODS

2.1. Study area

Estonia is located in the hemi-boreal sub-zone of the boreal forest zone – this is the transitional area between the southern boreal forest subzone and the spruce-hardwood subzone (Laasimer & Masing 1995). Ca 50% of the country is covered by forest (Adermann 2009), and conifers *Picea abies* (L.) H. Karst. and *Pinus sylvestris* L. as well as birches *Betula pendula* Roth and *B. pubescens* Ehrh. are the dominant tree species (Adermann 2009). The proportion of deciduous woodland with temperate broad-leaved trees (e.g. *Quercus robur* L., *Acer platanoides* L., *Fraxinus excelsior* L., *Ulmus glabra* Huds.) is almost insignificant in Estonia, mainly because the soil conditions in the habitats of these tree species are suitable for agricultural land use (Kaar 1974; Paal 1998). Characteristic tree species in the wooded meadows of Estonia are temperate broad-leaved trees, e.g. English oak (*Quercus robur*) and European ash (*Fraxinus excelsior*), with common aspen (*Populus tremula* L.); birches and black alder (*Alnus glutinosa* (L.) Gaertn.) are also quite common (Kukk & Kull 1997). Historically, the islands and western Estonia were the regions, which were the richest in wooded meadows, while in central and eastern Estonia wooded meadows were never as widespread (Kukk & Kull 1997). Similarly, Estonian alvars are mainly distributed on the islands of the eastern coast of the Baltic Sea (57.3–59.5° N, 21.5–28.1° E); smaller fragments can be found on the western and northern parts of the Estonian mainland, in regions where the dominant soil types on limestone are rendzinas (Laasimer 1965; Kõlli & Lemetti 1999; Pärtel et al. 2007). The region has a mild maritime climate with a mean annual temperature of 6.2 °C and a precipitation of 600 mm (http://www.emhi.ee).

2.2. Study sites and sampling

The study sites were located on the western islands of Estonia and mainly in the western and north-eastern parts of the Estonian mainland. Wooded meadows were studied in papers **I** and **II**, and alvars and alvar-like habitats were studied in papers **III** and **IV** (Fig. 1).

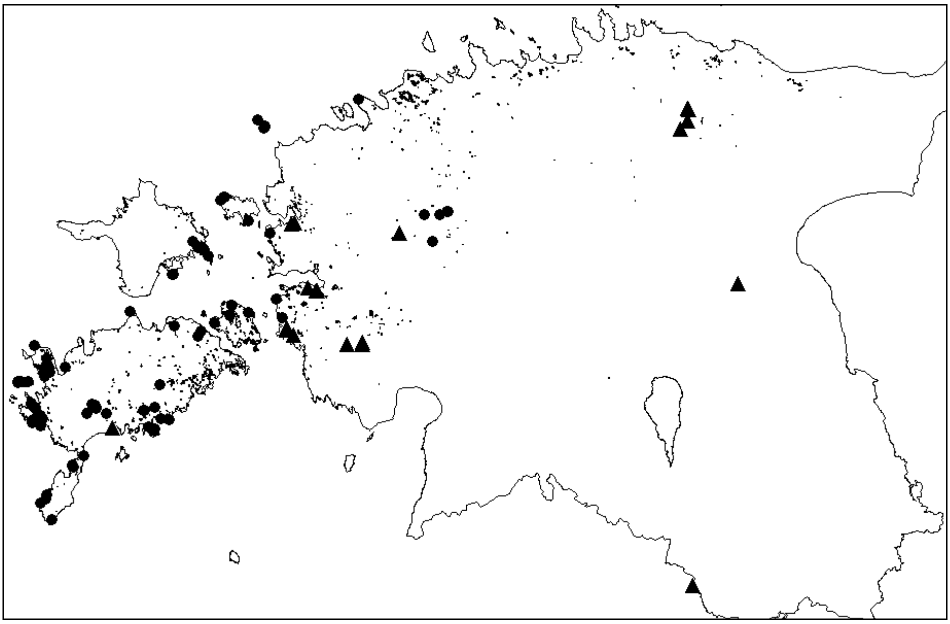

Figure 1. Black dots (●) denote the study areas in alvars (**III**, **IV**) and triangles (▲) denote the study areas in wooded meadows (**I**, **II**). Black areas on the map show the distribution of alvar grasslands in Estonia according to the database of the Estonian Seminatural Community Conservation Association in 2008.

2.2.1. Sampling of epiphytic lichens in wooded meadows

In wooded meadows (**I**, **II**) study sites were selected according to their management history: 'open' sites were regularly or irregularly mown and had no stand undergrowth (bushes and young trees), whereas 'overgrown' sites had not been mown or otherwise managed for approximately the last 50 years, and had dense undergrowth. Epiphytic lichens were sampled from 29 stands in paper **I** and from 12 stands in paper **II**. In a stand 12 trees were studied (tree species were selected proportionally to the tree layer) in an area of ca one hectare. In paper **I** the occurrence of lichen species on tree stems up to two metres was recorded and the species list per study stand was compiled and used in data analysis. Factors considered in paper **I** were: habitat type (open vs. overgrown), geographical coordinates, distance from a gravel road, no of tree species in a stand, percentage of neutral- and acid-barked trees and percentage of oak trees in a stand, mean diameter of the studied trees and the canopy cover. In paper **II** vertically elongated sample plots (10 × 50 cm with five unit areas of 10 × 10 cm each) were placed on trees in four cardinal directions, with the upper margin of plots at 1.5 m. The occurrence of lichen species in every unit area was recorded and summed for each sample tree (maximum abundance score is 20 per sample tree). This abundance measure of lichen species per tree was used in analyses in paper **II**. In paper **II** the primary goal was to determine the effect of the overgrowing of a wooded meadow by trees and brushwood on epiphytic lichens. For this purpose, we estimated, besides the percentage of the canopy cover, also the percentage of undergrowth within a range of 10 m around each sample tree and measured light conditions using hemispherical digital photographs taken around each studied tree trunk at four cardinal directions. For analysis, we used maximum radiation coefficient (proportional combination of direct and diffuse radiation) for each tree. To assess the effects of substrate properties on the composition of lichen species and on individual lichen species in wooded meadows, we recorded several tree scale parameters in paper **II**: tree species, tree diameter, bark pH, bark structure and bryophyte abundance.

2.2.2. Sampling of epigeic lichens in alvars

In alvar studies (**III**, **IV**) we distinguished four main types of alvar grassland: plate, ryhk, shingle and heath alvars. In addition, we studied alvar-like habitats that have the potential to be substitution habitats for epigeic lichens, like limestone quarry floors (**III**, **IV**), coastal areas with young shingle (**III**) and deforested areas on alkaline base rock (**III**). In paper **III** we determined 'reference' alvars as traditional alvars with a thin soil layer (< 6 cm), low shrub cover and without signs of intense disturbance (e.g. soil removal). Ground layer lichens from soil, bryophytes and plant debris were studied in a circular plot of 0.1 ha in 86 and in 76 study sites (Fig. 1), respectively, in papers **III** and **IV**. The lichen species list per 0.1 ha plot was compiled in two steps. First, we recorded the presence of lichens in ten randomly placed 20 × 20 cm quadrats. The frequency of each species within the study plot was calculated as the count of presence in these ten quadrats (value range 0–10). In the second step, we recorded additional lichen species within the 0.1 ha plot for 30 minutes, and these species were assigned a frequency value of 0.2 in data analysis. In paper **III** species with a conservation value (protected, red-listed and rare species with a maximum of ten records in Estonia) were distinguished. In paper **IV** genuinely rare species in alvars as well as in the study region (with a maximum of ten records in Estonia) were detected. Numerous environmental variables from the plot and different quadrat levels were considered in both alvar studies (**III**, **IV**). Herb layer parameters (e.g. vascular plant, bryophyte and stone cover) were measured in a 20 × 20 cm sample quadrat; within a 50 × 50 cm quadrat (placed over a 20 × 20 cm quadrat) we recorded small-scale disturbances (recent ground damage caused by animals or frost induced soil movements; small-scale trampling; animal excrements; mounds and depressions); and in a 1 × 1 m quadrat (placed over a 20 × 20 cm quadrat) we estimated quadrat openness. At the 0.1 ha plot level we recorded different types of former major disturbances, shrub cover and height, soil parameters and presence of different microhabitats (**III**, **IV**).

2.3. Statistical analyses

The effect of different factors on the richness of lichen species and on the abundance of individual lichen species was tested using the General Linear Model (GLM; **I**, **II, III**). The GLM was also used to estimate the effect of environmental drivers on the percentage of lichen growth form groups (**III**).

Multivariate analyses, indirect ordination methods Detrended Correspondence Analysis (DCA; **III**) and Non-metric Multidimensional Scaling (NMS; **I**) were carried out to find the main gradients in the composition of lichen species. Also, Two-Way Indicator Species Analysis (TWINSPAN) was performed to summarise variation in the species composition of frequent epigeic lichens in alvars (**IV)**. Indicator Species Analysis (ISA) was performed to find out indicator lichens for alvar and alvar-like habitat types and for areas with different disturbances (**III**). Multi-Response Permutation Procedure (MRPP) with the Euclidean distance was used to find out differences in the composition of lichen species among tree species and among regions (**II**), among alvar types, and between 'reference' alvars and sites with former major ground disturbances (**III**).

In order to minimize redundancy between individual variables describing potential drivers in the analyses, we combined them using Factor Analysis with the Varimax rotation of the principal components (**III, IV**). To establish the most important environmental factors for epigeic lichen species, Spearman rank order correlations were calculated between lichen species and studied environmental parameters (**IV**). In order to eliminate the confounding and dominating effect of alvar types from species data and from compound factors, we calculated the residuals in GLM for species data and for compound factors (**IV**). Thereafter Spearman rank order correlations were also calculated between epigeic species and compound factors to reveal the drivers of lichen species in conditions where the effect of alvar type was removed (**IV**).

To estimate the effect of ecological gradients on the composition of lichen species direct ordination analysis like Canonical Correspondence Analysis (CCA; **II**) was used. In order to evaluate the explanatory power of different sets of variables, the variation partitioning approach was employed (**II**). For this the variables were grouped and their explanatory power was estimated in two ways: as the main effect of a trait group without considering the explanatory effect of the other trait groups, and the 'unique' contribution of each trait group after conditioning the effect of the other factors (**II**).

Principal Component Analysis (PCA) was used to visualize the composition of species traits (**IV**). The proportional pattern of the species traits in each ecological group was tested against randomness with Log-linear analysis (**IV**).

The software applications Statistica ver. 7.1, PC-ORD ver. 4.25, CANOCO ver. 4.5, SAS ver. 8.2 were used for the statistical analyses.

3. RESULTS

3.1. Species richness

A total of 172 lichenized fungi were identified from trees in wooded meadows (**I**) and 122 lichenized fungi were found on soil, on epigeic bryophytes and on plant debris in alvars and alvar-like habitats (**III**). Forty-one and 44 rare (with less than 10 localities in Estonia) red-listed or protected lichen species were recorded from wooded meadows (**I**) and from alvars (**III**), respectively.

On average, 46 epiphytic lichen species per wooded meadow were recorded; the highest number of species per study plot was 59 and the lowest was 31 (**I**). Plate alvars and old limestone quarries had an average of 20 lichen species per study plot, and an average of eight species with a conservation value (**III**). The lowest species richness was observed in heath and old shingle alvars, where the average number of all lichen species was 12.6 and 15.4 per plot, respectively, and the number of species with a conservation value varied between one and three species per site (**III**).

3.2. Factors influencing epiphytic lichen communities in wooded meadows

The present study demonstrates that the variation in the epiphytic lichen species composition of wooded meadows is determined by a complex of factors, including regional, habitat and tree level variables (**I**, **II**). At the stand level, the composition of the lichen species of wooded meadows was mainly determined by canopy cover, followed by composition of tree species, mean DBH of trees and geographical location of wooded meadows (**I**). However, at the tree level (**II**) the most important variables were tree species-specific variables, i.e. the tree species and bark pH, which explained most of the variance in the composition of epiphytic lichen communities (10.3% of variation in the data set), followed by geographical variables (8.8%), the other tree level variables (bark structure, bryophyte abundance and DBH; 6.9%) and the set of environmental variables related to site openness and light conditions (canopy cover, max TSF and undergrowth; 6.5%) (Fig. 2; **II**). After controlling for the tree species-specific variables and the geographical location, canopy cover and tree species DBH determined differences in the composition of the lichen species (**II**).

The species richness of epiphytic lichens in wooded meadows was mainly determined by canopy cover; total number of lichen species and number of valuable lichen species decreased with increasing canopy cover (Fig. 3; **I**). The abundance of the most frequent epiphytic lichen species in wooded meadows was mainly determined by the geographical location of wooded meadows, followed by the canopy cover, the DBH of trees and the tree species (**II**).

Variables such as bark structure, bark pH and percentage of undergrowth around the tree appeared to be significant predictors for the abundance of some lichen species (**II**). The abundance of several common macrolichens, like *Evernia prunastri*, *Hypogymnia physodes*, *Melanelia subaurifera*, *Parmelia sulcata* and *Ramalina farinacea,* as well as microlichens, e.g. *Buellia griseovirens*, *Lecanora pulicaris* and *Tephromela atra*, were negatively influenced by increasing canopy cover (**II**). Only a few microlichens (*Biatora efflorescens*, *Chaenotheca trichialis* and *Lepraria incana*) preferred to grow in shady habitats with a denser canopy (**II**).

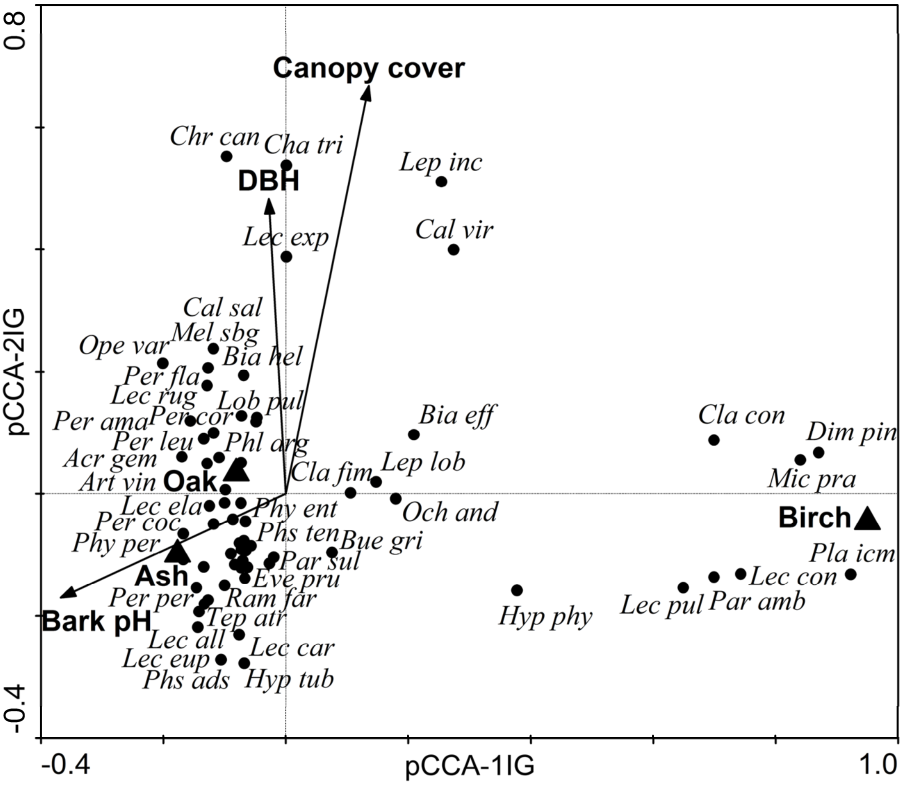

Figure 2. Lichen species and factors on the biplot of partial canonical correspondence analysis (pCCA) of the first and second axes. Symbol 'I' in the titles of the axes means conditioning, i.e. variable 'Region' (G) has been covaried out. DBH = diameter of tree trunk at breast height; the abbreviations of the species names are given in Appendix 1 in paper **II**.

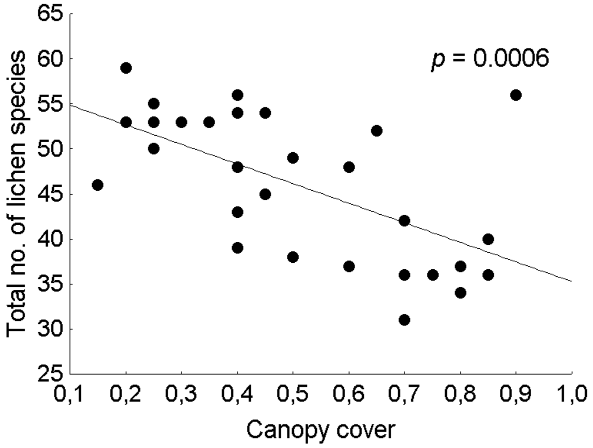

Figure 3. Relationship between canopy cover and total number of lichen species according to the general linear mixed model (see Table 2 in paper **I**).

3.3. Factors influencing epigeic lichen communities in alvar grasslands

According to the DCA ordination of the plots based on the composition of the lichen species, two habitat types, i.e. deforested alvars and young shingle alvars, were distinguished from the other types in that they formed two well-defined clusters (Fig. 4; **III**). As the ecology of the characteristic species of these two communities was in contrast to that for the other habitats (forest-dwelling species and species growing on decaying wood were characteristic of deforested alvars, and species growing on bryophytes and plant debris were characteristic of young shingle alvars), these two habitat types were excluded from further analyses as the outliers. The MRPP test revealed that there were also differences in the composition of the lichen species between the remaining five alvar and alvar-like habitat types (Fig. 4, $A = 0.081$, $p < 0.081$; **III**). Moreover, correlation analysis for the lichen species and potential drivers revealed that species were most commonly correlated with individual variables, which distinguished between the properties of the specific alvar types (**IV**). Among them, stone cover and soil pH were significantly correlated with more than half of the frequent species (**IV**).

After controlling for the effect of the habitat type, herb layer productivity was the most important environmental factor for the abundance of frequent species, followed by afforestation disturbance and shrub encroachment (**IV**). The encroachment of alvars by vascular plants had a negative influence on the ground layer lichens (**III**, **IV**), while herb layer productivity had a stronger negative effect on the richness of epigeic lichens than encroachment by shrubs. Herb layer productivity predicted species loss starting from cover value of 40–50% (**III**). The negative effect of herb layer productivity and shrub encroachment was evident for the richness of species with a conservation value, as the species richness of common lichen species did not show any correlation with the combined factors (**III**). In addition to the decrease in species richness, encroachment of alvars by vascular plants also altered species composition; it caused the replacement of crustose and squamulose species with fruticose species (Fig. 5; **III**).

Different disturbances revealed a positive effect on ground layer lichen communities in alvars (**III**, **IV**). Sites with historic ground disturbances, like sites involving afforestation attempts and areas with a peeled off soil layer, had a composition of the lichen species similar with that of traditionally managed open alvars with a thin soil layer (Fig. 6; **III**). In addition, 15 frequent lichen species out of 41 were influenced by different disturbances and 14 were correlated positively with either historical afforestation practices, former soil peeling and ground damages caused by vehicles, or recent small-scale ground disturbances or livestock grazing (**IV**). Half of these disturbance dependent species were also correlated negatively with high herb layer productivity, however, the other half did not show preference for site productivity (**IV**).

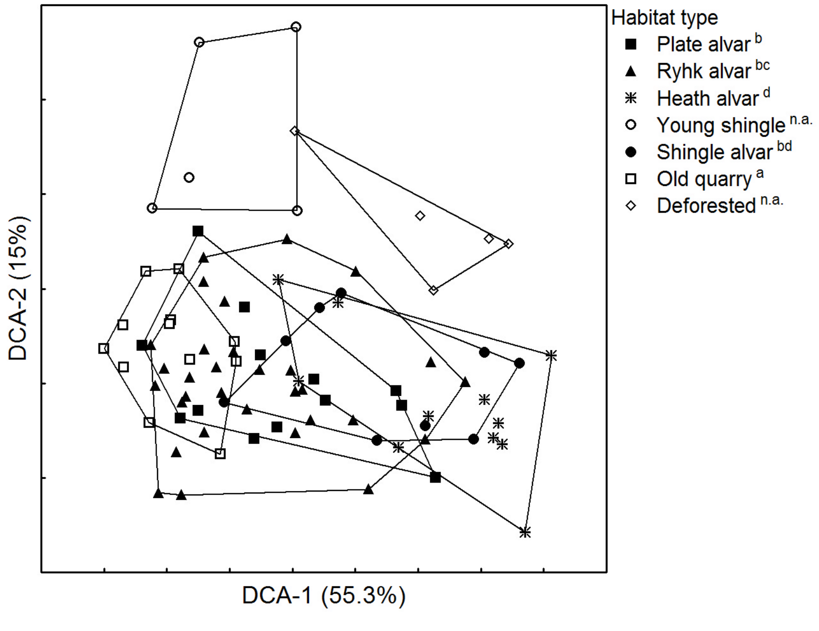

Figure 4. The DCA ordination of the study plots. Axis 2 is a compound view of DCA axes 2 and 3, as they have been rotated by 60 degrees for better viewing of the site groups on a single diagram. The sites are grouped according to habitat types. The compositional homogeneity groups among the five overlapping habitat types in the lower part of the graph are denoted with super-script labels according to the results of pair-wise comparisons within the MRPP test (labels a-d denote similarity groups, n.a. – not applied for analysis).

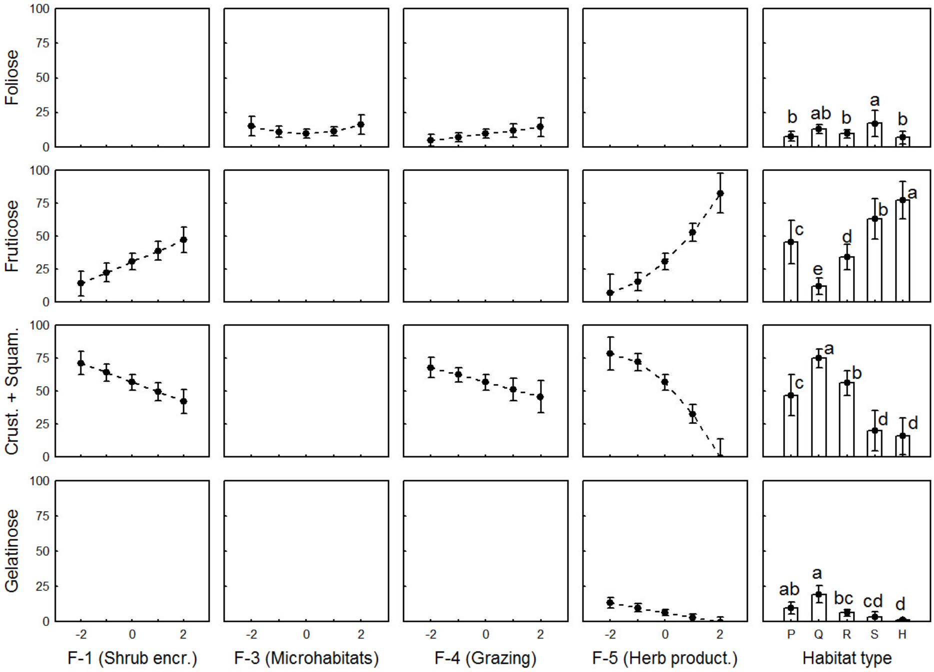

Figure 5. Model prediction profiles for the proportions of lichen growth forms based on the GLM results (Table 3 in paper **III**) after stepwise selection of generalized environmental factors (Table 2 in paper **III**). Only significant relationship profiles with the 95% confidence intervals are presented. The labels of the habitat types are: P – plate alvar, Q – old quarry floor, R – ryhk alvar, S – old shingle alvar, and H – heath alvar. The super-script labels denote the homogeneity groups according to the results of the Tukey HSD multiple comparison test. Please note that the growth forms crustose and squamulose are combined, and gelatinose species are treated as an overlapping growth form (Appendix 2 in paper **III**).

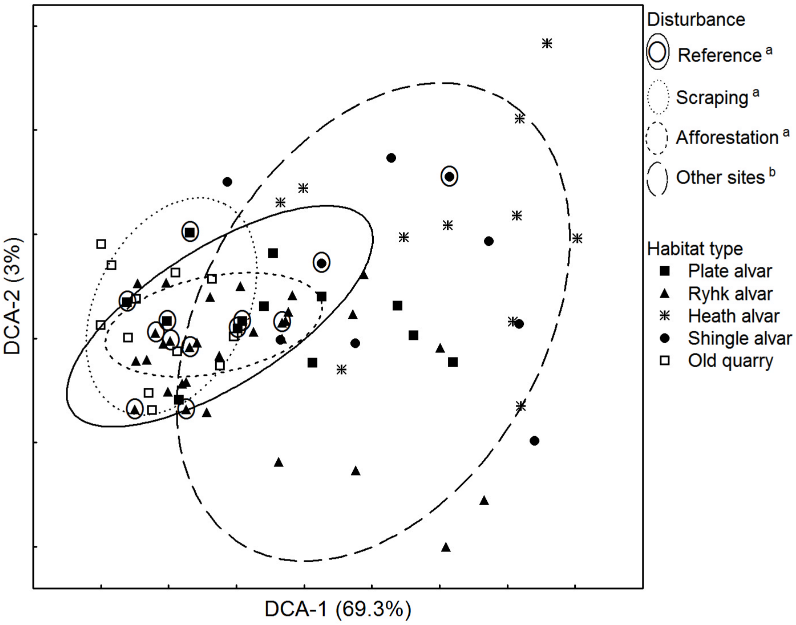

Figure 6. The DCA ordination of the study plots along axis 1 and axis 2. Young shingle alvars and deforested alvars are excluded. The plots are grouped on the basis of the habitat types (symbols). The ellipses denote the 95% range of the plots belonging to the respective disturbance group. 'Reference' alvars are meant for comparison; these are sites with thin soil layers, low shrub cover and without signs of intense disturbance. The compositional distinction between the disturbance groups and the 'reference' alvars are noted with super-script labels on the basis of the results of pair-wise comparisons within the MRPP test.

3.3.1. Species traits of common and rare epigeic lichens

Environmental factors with a similar effect were pooled and common alvar lichens were grouped taking into account positive and negative correlations between the species and the factors that formed two major groups, namely site productivity combined with encroachment and different disturbances. Altogether five response groups (RG) of species emerged (**IV**): RG 1 – species growing at low productivity sites; RG 2 – lichens preferring low productivity sites but are also influenced by different disturbances; RG 3 – species growing also in disturbed areas but do not reveal their preference for site productivity; RG 4 – lichens growing most abundantly at overgrown sites; RG 5 – undefined – species which do not show any preferences for the studied factors. The species characteristics of these groups of common lichens were compared with the group of rare lichens. It was found that rare lichens as a group resembled the lichens confined to sites with low herb-layer productivity (Fig. 7, RG 1 + 2; **IV**). Both groups can be characterized by being calciphilous, growing on soil and/or bryophytes, having crustose or squamulose growth form, reproducing sexually and having UV-protective pigments in the thallus or in the fruit bodies and containing rarely bitter or toxic secondary compounds. The only difference occurred in their distribution range: rare species had mostly arctic-alpine or montane distribution (53%, Table 3 in paper **IV**), while the lichens of RG 1 and RG 2 were more widely distributed (**IV**). Only three rare lichen species, namely *Flavocetraria cucullata*, *Cladonia grayi* and *C. novochlorophaea* had traits resembling the species of RG 3 and 4 (species of high productivity alvars and disturbed alvars without clear preference for site productivity, Rare-2 in Fig. 7; **IV**). The remaining rare species (Rare-1 in Fig. 7; **IV**) differed from those of RG 3 and 4 in their ability to grow on bryophytes (85%), dominance of sexual reproduction (95%), and general lack of lichen secondary compounds (10%, **IV**). In general, the lichens of RG 3 and 4 are generalists, mostly fruticose, disperse generally with conidia or thallus fragments and contain bitter or toxic secondary compounds (**IV**).

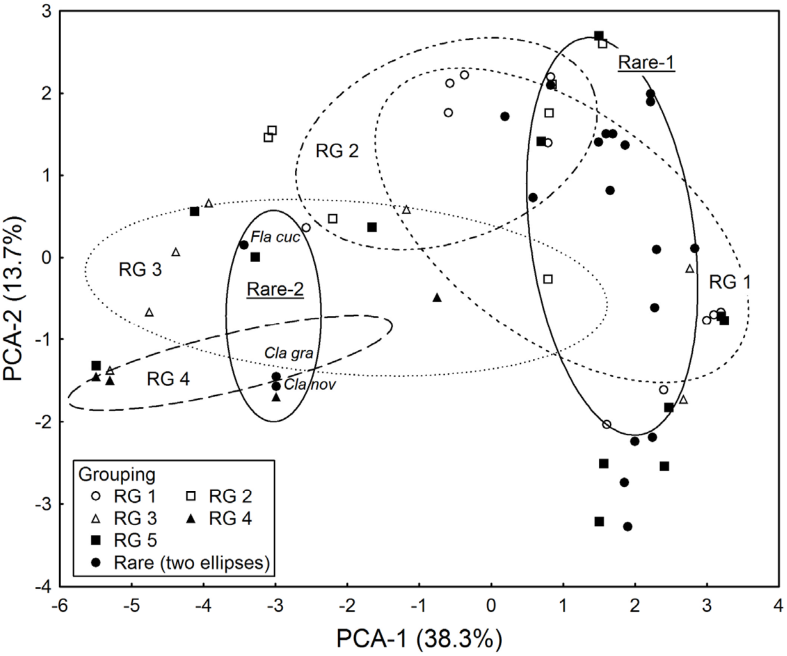

Figure 7. The PCA diagram of the species groups (Table 2 in paper **IV**) according to their trait composition (Table 3 in paper **IV**). The 95% range ellipses are added to each group, except RG 5 (undefined species). Rare species are presented in two sub-groups. The grouping of species according to Table 2 in paper **IV**: RG 1 – species growing at low productivity sites; RG 2 – lichens preferring low productivity sites but are also influenced by different disturbances; RG 3 – species growing also in disturbed areas, but do not reveal their preference for site productivity; RG 4 – lichens growing most abundantly at overgrown sites; RG 5 – undefined – species which do not show any preference for the studied factors; Rare – rare species in Estonia (with less than ten localities). For abbreviations of the lichen species, see Appendix 3 in paper **IV**.

4. DISCUSSION

4.1. Species richness and composition

Semi-natural habitats, wooded meadows and alvars harbour a specific and species-rich lichen biota. For example, rare, red-listed and protected lichen species constitute 24% and 36% of total species richness in wooded meadows and in alvars, respectively. In addition, several species new to Estonia were found in these semi-natural habitats. Three new epiphytic lichen species were found in wooded meadows, such as *Biatoridium delitescens*, *Leucocarpia dictyospora* and *Lecanora thysanophora* (**I**) and seven epigeic lichen species were found in alvar habitats, such as *Agonimia vouauxii*, *Catapyrenium daedaleum*, *Cladonia magyarica*, *Lecania sambucina*, *Lecanora zosterae*, *Leptogium intermedium* and *Polyblastia sendtneri* (Suija et al. 2011).

In wooded meadows of Estonia, 172 species of epiphytic lichen species have been recorded (**I**). The number of epiphytic lichens in Estonian wooded meadows accounts for ca 36% of all epiphytic lichens recorded in Estonia (Lõhmus 2003). The high species richness of epiphytic lichens in wooded meadows is probably the result of various combined factors of these ancient habitats.

Ground layer lichens (growing on soil, mosses and plant debris) found in alvars and alvar-like habitats constitute ca 59% of all species growing on soil, mosses and plant debris in Estonia (Randlane et al. 2002). High species richness in alvars is probably due to the specific conditions in alvars as hard limestone with poor drainage, shallow soils that dry throughout, strong irradiation in rock pavements, alternating drought and flooding, low temperatures and frost induced soil movements in winter (Rosén 1982; Ott et al. 1996, 1997). These conditions favour growing together of different species that rarely co-occur in calcareous habitats of Central Europe (Dengler et al. 2006). Species with oceanic, continental, arctic-alpine or submediterranean distribution, as well as acidophytic or basiphytic and xerophytic or hygrophytic species may frequently grow intermingled in Nordic alvar grasslands (Ott et al. 1996; Dengler et al. 2006).

4.2. The influence of habitat management and site openness

The study demonstrates that habitat openness is a significant factor of both epiphytic as well as epigeic lichen communities in semi-natural habitats (**I**, **II**, **III**, **IV**). Cessation of traditional management consisting in mowing of hay and selective cutting (i.e. the abandonment of wooded meadows) causes changes in stand structure and in the openness of wooded meadows, which subsequently impoverishes and alters the epiphytic lichen community (**I**, **II**; Jönsson et al.

2011). Light demanding epiphytic lichen communities, rich in foliose and fruticose lichens, will be replaced with impoverished shade-tolerant crustose lichen dominated communities due to overgrowing (**II**). Changes in the microclimate could be the main reason for the difference of the epiphytic lichen communities of open and dense canopy wooded meadows. The results of our study support the statement of Barkman (1958) that most epiphytic macrolichens with a green photobiont and with a foliose and fruticose growth form are highly dependent on good illumination conditions. However, the growth of epiphytic lichens (e.g. protected and red-listed lichen *Lobaria pulmonaria*) is controlled by a delicate balance between light availability and desiccation risk (Gauslaa et al. 2006) and is therefore supported by the semi-open structure of wooded meadows (Jüriado et al. 2012). It has been suggested that traditionally managed wooded meadows resemble pre-agricultural wooded ecosystems in northern Europe (Vera 2000; Eriksson et al. 2002). Today, when forests are intensively managed, mostly mono-cultured, even-aged, with dense canopies, and lacking many natural elements of old-growth stands such as gaps and large-diameter old trees (Esseen et al. 1992; Bengtsson et al. 2000; Liira & Sepp 2009), managed wooded meadows could be potential refugia for species originating from ancient semi-opened landscapes (Rose 1992; Svenning 2002).

Similarly, the epigeic lichen communities of semi-natural alvar grasslands are strongly affected by the cessation of grazing and juniper cutting (**III**, **IV**). Considering the diversity of epigeic lichens, we found that increased abundance of herbs and mosses suppressed ground layer lichens most, and the increased shrub cover was only of secondary importance (**III**). Also, Löbel et al. (2006) demonstrated negative relationships between richness of lichen species and vascular plant cover. Higher species richness in plate alvars and old quarry floors (**III**) is probably due to the availability of bare rock and skeletal soils for colonization (Tomlinson et al. 2008, Jeschke 2012). Lichens with crustose and squamulose growth forms and lichens with a conservation value were particularly sensitive to the abandonment-induced encroachment of herbs and shrubs (**III**). Only large cushion-shaped *Cladonia* species were common in shady conditions under shrub boundaries and between clumped shrubs, as was also noted by Ott et al. (1996).

In open alvars herb and shrub growth is suppressed by drought sensitive thin soil and by grazing of domestic animals (Rosén 1995; Schaefer & Larson 1997; Rosén & van der Maarel 2000). Such conditions favour crustose/squamulose lichens that are outcompeted in denser communities (**III**; Ott et al. 1996; Cornelissen et al. 2001). The reproduction strategy of these lichens is targeted for maintaining their evolutionary potential and capability for long distance dispersal via sexual reproduction (Seaward 2008). As an adaptation to intensive UV-radiation, they have photoprotective dark pigments, secondary compounds or pruina (Lawrey 1986; Gauslaa & Solhaug 2001; Nybakken et al. 2004; Hauck et al. 2007). Species of low productivity habitats often grow on bryophyte cushions, probably in order to escape seasonal flooding; and also, mosses may serve as a water reservoir for lichens during drought (Ott et al. 1996, 1997). These species and their trait composition is characteristic of the crust forming early successional xerothermic communities of *Fulgensietum fulgenetis* and/or *Cladonietum symphycarpae* (James et al. 1977; Gilbert 1993; Belnap et al. 2003; Büdel 2003). In contrast, the lichens of overgrown alvars (RG 4) or sites with moderate productivity (RG 3) can be regarded as habitat generalists without special preference to soil type, having a fruticose growth form or a bigger thallus in general, with mostly vegetative reproduction (**IV**). The composition of these traits is characteristic of late successional species with competitive strategies (Ahti & Oksanen 1990; Rogers 1990; Lawrey 1991).

4.3. The influence of tree level variables on epiphytic lichen communities

In wooded meadows, as well as in forest communities (Aude & Poulsen 2000; Belinchón et al. 2007; Jüriado et al. 2009*a*), the tree level variables explained most of variation in the composition of epiphytic lichens (**II**). Particularly, the difference between the epiphytic lichen communities on birches (*Betula pendula* and *B. pubescens*) and on other deciduous tree species in the temperate region is quite well known (Barkman 1958; Cieśliński 1996; Lõhmus 2003). The most probable cause of such difference between tree species is the lichens' response to tree-species-specific bark properties (Culberson 1955; Barkman 1958; Rose 1974; Bates & Brown 1981). More specifically, the physical and chemical properties of bark, e.g. bark pH and bark roughness, define the epiphytic communities of trees (Ellis & Coppins 2007; Ellis 2012). Tree diameter, but also bark roughness and pH, are known to be age-dependent factors for trees (Johansson et al. 2007; Fritz et al. 2009; Ellis & Coppins 2007; Ranius et al. 2008). The observed variation in the composition of lichen communities along the gradient of trunk diameter (i.e. tree age) is in accordance with that observed in many other studies (Hedenås & Ericson 2000; Friedel et al. 2006; Fritz et al. 2009; Jüriado et al. 2009*a*, *b*; Jönsson et al. 2011; Thor et al. 2010).

4.4. The effect of disturbances on epigeic lichen communities

It was found that the species composition of habitats with historic soil disturbances (afforestation attempts, peeling off soil, e.g. in old limestone quarry floors or in military training areas) resembled that of traditionally managed alvar grasslands (**III**). Earlier, human-induced alvar-like habitats have been referred to as hotspots of lichen biodiversity in general, and especially for species with a conservation value (Wells et al. 1976; Gilbert 1993; Tomlinson et al. 2008). Ground layer disturbance due to grazing has been a characteristic environmental driver in alvars. However, in contrast with earlier studies of grazed grasslands, none of the species were negatively correlated with grazing (Rogers & Lange 1971; Warren & Eldridge 2003). At the same time, we did find one species (*Cladonia arbuscula*, **IV**) that was favoured by grazing. This can be explained by generally low grazing intensity in Estonian alvars during the last decades. Instead, Estonian low productivity alvars were extensively disturbed by afforestation attempts in the 1950s–1980s (Laasimer 1975; Kaar 1986) or by military training. Still, evident open patches, furrows and pits on the ground are the consequence of these activities. These disturbances, however, have increased areas with the lichen-dominated soil crust in Estonia (**III**, **IV**). Two response groups of lichens (RG 2 and 3, **IV**) showed positive correlations with these disturbances; crust-forming species of RG 2, such as *Cladonia foliacea, C. symphycarpia*, *Collema tenax, Fulgensia bracteata, Placidium squamulosum* and *Psora decipiens* and various species of RG 3 in which the majority of species have fruticose growth form, like *Cetraria islandica*, *C. macroceras* and *Cladonia rangiformis.* The last three species are reproductively plastic by producing different types of diaspores: complex diaspores such as thallus fragments, conidia (mitospores) and occasionally also ascospores (meiospores). Such a mixed reproductive strategy is a useful adaptation in environments with stochastic disturbances (Eldridge & Rosentreter 1999). The RG 3, in particular is characterized by higher proportion of species with conidia. Conidia allow rapid colonization of suitable patches within a habitat as well as long distance dispersal between habitats (Wicklow 1981; Geml et al. 2010) and therefore this can be seen as an adaptation to stochastically changing conditions.

4.5. Rare species vs. common species

Drawing parallels between common and rare species revealed that the trait composition of the rare lichens largely overlapped with the traits of lichens growing on low productivity alvars (RG 1 and 2, **IV**), except their limited geographic distribution in arctic-alpine or montane regions. Such phenotypic resemblance indicates that rare alvar species prefer low productivity open habitats where (seasonal) extremes of environmental conditions are common (Billings & Mooney 1968; Ott et al. 1996; Longton 2008) and can benefit from small or large-scale disturbances, which destroy the vegetation and expose base rock. Most probably, rare species have similar ecological niche optimums, but their niche is more restricted than that of the common species of low productivity alvars (RG 1 and 2, **IV**). This accounts for their higher sensitivity to changes that take place after grassland falls out of use. The rare alvar species also have some traits common with the species of overgrown alvars (RG 4) or with the species of disturbed sites with intermediate productivity (RG 3) or with all response groups **(IV)**, which indicates that these traits cannot be used to explain their rarity. For instance, they grow mainly on soil and only seldom on plant debris, are hardly ever foliose in growth form, and have only rarely perithecia.

4.6. Management implications

The main principle of conservation of semi-natural grassland is the maintenance of millennia-old land use traditions ensuring the preservation of these dynamic quasi-equilibrium habitats, wooded meadows and alvars (Laasimer 1981; Rosén & van der Maarel 2000; Poschlod & WallisDeVries 2002). These semi-natural habitats in northern Europe are of great importance for nature conservation because of their high contribution to biodiversity (**I**, **III**, Dengler et al. 2006; Thor et al. 2010; Jönsson et al. 2011). Moreover, several rare, red-listed and protected lichens need the preserving of these habitats (**I**, **III**, Thor 1998). In the last century, habitat loss and degradation were evident processes because of major changes in land use practices (Willems 2001; Rosén & Bakker 2005). As the recovery of the grassland community in reforested areas or cropland is a slow process, preservation and enlargement of existing habitat fragments should be the primary focus of conservation efforts (Pärtel et al. 2007; Piqueray et al. 2011).

Preservation of tree species diversity and different age (diameter) groups is vital in order to maintain the high diversity of epiphytic lichens in wooded meadows (**I**, **II**). Selective cutting of trees and undergrowth, retaining a mosaic of semi-open structure with trees of various species and age classes and some clumps of bushes, is proposed, which will create heterogeneous microclimatic conditions for a diverse community of epiphytic lichens. To increase heterogeneity and to maintain favourable moisture regime for some demanding epiphytes (e.g. protected *Lobaria pulmonaria*), deciduous shrubs should be preserved around some tree trunks of a wooded meadow (Jüriado et al. 2012). In addition to controlling the tree layer of the stands, management of wooded meadows in terms of annual mowing or grazing has been prescribed as vitally important actions preserving the semi-open structure, and particularly high species diversity (Pykälä et al. 2005; Aavik et al. 2008; Jönsson et al. 2011; Jüriado et al. 2012). Grazing, however, might enrich the epiphytic lichen community with nitrophytic species as a result of fertilization of tree trunks by cattle (Benfield 1994; van Herk 1999; Ruisi et al. 2005). Therefore, it is suggested that grazing is only beneficial for overall lichen diversity if it has been undertaken with limited intensity (Rose 2001; Sanderson & Wolseley 2001).

For optimisation of alvar and its species, conservation planning and different management (moderate grazing) and restoration (felling shrubs out, pealing off thick turf and soil layer) practices should be applied to enhance the probability of occurrence of calciphilous lichens, especially rare lichens (**III**, **IV**). Disturbances that lead to partial removal of soil or exposing of bare rock sound drastic, but would restore epigeic lichen diversity (Gilbert 1993; Jeschke & Kiehl 2006; Tomlinson et al. 2008; Jeschke 2012). Both the species richness of lichens as well as bryophytes has shown to be higher at topsoil removal sites than at sites without topsoil removal (Jeschke & Kiehl 2006). The recovery of the richness of vascular species may take a longer time (Jeschke & Kiehl 2006). Tomlinson et al. (2008) found that quarry floors comprise about half of characteristic alvar species. Also, transfer of hay to topsoil removal sites promotes the growth of vascular plant species and pleurocarpous mosses, whereas only some fruticose *Cladonia* species will benefit from this method Jeschke 2012). Alternative habitats created as a result of large-scale human disturbances can be considered to be novel habitats for ground layer lichens, including lichens with a high conservation value (**III**, **IV**). Therefore, old abandoned limestone quarries and former military areas should be considered as temporary substitution habitats or refugia for ground layer lichens, particularly in regions of historic alvars.

CONCLUSIONS

1) Wooded meadows, alvars and alvar-like habitats in northern Europe are of great importance for nature conservation according to their high contribution to biodiversity including new, rare, red-listed, and protected lichens for the studied region (**I**, **II**, **III**, **IV**). Species-rich and specific lichen communities in semi-natural habitats are the result of specific habitat conditions and human influence.
2) The present study demonstrates that habitat openness and hence also habitat management are significant drivers of both epiphytic (**I**, **II)** and epigeic (**III**, **IV**) lichen communities in semi-natural habitats. Cessation of traditional management consisting in hay mowing and selective cutting (i.e. abandonment of wooded meadows) causes changes in stand structure and in the openness of wooded meadows, which impoverishes and alters epiphytic lichen community (**I**, **II**). Light-demanding lichen communities, rich in foliose and fruticose lichens, will be replaced with impoverished shade-tolerant crustose lichen dominated communities due to encroachment of wooded meadows with trees and shrubs (**II**). Similarly, epigeic lichen communities of semi-natural alvar grasslands are strongly affected by cessation of grazing and cutting of junipers (**III**, **IV**). With the increasing herb and shrub cover, the species richness of epigeic lichens is diminished (**III**), species composition is altered, the proportions of species growth forms change, and crustose and squamulose species are replaced with fruticose species (**III**, **IV**). Lichens with a conservation value, especially rare species, are particularly sensitive to the abandonment-induced encroachment of herbs and shrubs (**III**, **IV**).
3) Lichens of open low productivity alvars are characterised as being primarily calciphilous, growing on soil as well as on bryophytes, having a squamulose or crustose growth form, mainly sexual reproduction, containing dark pigments or photoprotective compounds for the defence against intensive (UV) radiation and making low investment in chemical defence with bitter or toxic secondary compounds (**IV**).
4) Study of the functional traits of rare epigeic lichens revealed that rare lichens resembled species that were confined to sites with low herb layer productivity, the only difference being their mostly arctic-alpine or montane distribution (**IV**). Therefore, rare epigeic alvar lichens prefer presumably open low productivity alvars and disappear with alvar encroachment.
5) In wooded meadows epiphytic lichens are affected by regional (geographical location), habitat (tree species composition, canopy cover) as well as tree specific properties (bark pH, bark roughness) (**I**, **II**). Therefore, it is important to preserve wooded meadows in different regions, to cut trees and undergrowth selectively, retaining a mosaic of semi-open structure with trees of various species and age classes, and some clumps of bushes, which will

create heterogeneous microclimatic conditions for a diverse community of epiphytic lichens (**I**, **II**).

6) Old abandoned limestone quarries, former military areas or wastelands of failed afforestation attempts appeared to be alternative or temporary substitution habitats (refugia) for ground layer lichens including lichens with a high conservation value (**III**, **IV**). To support the lichen biodiversity of alvar grasslands and particularly rare and/or crust forming lichens, scarcely vegetated low productivity habitats on exposed limestone should be maintained or created (**III**, **IV**). Therefore, in addition to conventional recommendations for alvar restoration including moderate grazing and removal of shrubs, it is suggested to promote various ground cover disturbances and patchy peeling off of the soil layer to expose base rock. Conservational management of alvars should create a mosaic of microhabitats, which makes alvar a suitable habitat for both early and late successional species (**III**, **IV**).

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SUMMARY IN ESTONIAN

Samblike mitmekesisus Eesti poollooduslikes kooslustes

Eesti poollooduslikud kooslused – puisniidud ja loopealsed (alvarid) – on meie tänapäeva kultuurmaastikult kadumas. Poollooduslike rohumaade pindala drastiline vähenemine nii Eestis kui kogu Euroopas on tingitud eelkõige traditsioonilise majandamisviisi lakkamisest. Puisniidud on võsastunud või haritud üles põllumaaks ning looniidud ja -karjamaad on asendunud tihedate kadastikega, kuna loomade karjatamine madala produktiivsusega alvaritel pole eriti tulus. Poollooduslike koosluste pindala vähenemine mõjutab eelkõige nende kooslustega koos kujunenud ja seal elavaid/kasvavaid organisme. Antud töös uuriti poollooduslike koosluste samblike elustikku. Samblikud ehk lihheniseerunud seened (edaspidi kasutatakse terminit ‘samblik’) moodustavad olulise osa nii loopealsete maapinnaelustikust kui puisniitude puude epifüütidest. Peamine eesmärk oli välja selgitada, kuidas puisniitude võsastumine (**I**, **II**) ja loopealsete kadastumine (**III**, **IV**) mõjutab sealseid samblikukooslusi. Otsides alternatiivseid lahendusi loopealsete samblikukoosluste säilimiseks huvitas mind, kas häiritud mullapinnaga jäätmaad (vanad karjäärid, militaaralad, metsastamise katse alad) võiksid sobida ajutiseks asendusalaks loopealsete samblikele ja kuivõrd nende samblikuelustik sarnaneb traditsiooniliste loopealsete samblikukooslustele (**III**). Looduskaitse seisukohalt on oluline teada, millised keskkonnategurid organismidele enim mõju avaldavad, seetõttu uuriti, millised on olulisimad tegurid puisniidu epifüütsele samblikuelustikule (**I**, **II**) ja mis mõjutab enim loopealsete maapinnasamblikke (**III**, **IV**). Kuna keskkonnategurite mõju harva esinevatele haruldastele liikidele on raske hinnata, siis prooviti leida paralleele haruldaste ja sagedaste liikide omaduste vahel ja laiendada sagedastele liikidele mõjuvaid tegureid sarnaste omadustega haruldastele liikidele (**IV**).

Puisniidud ja loopealsed on Euroopas levinud peamiselt Läänemere ümbruses, eriti saartel. Proovialad Eestis hõlmasid peamiselt läänesaari ja mandri lääneosa, Ida-Eestisse jäid mõned puisniidualad. Puisniitudel uuriti samblikuelustikku ja keskkonnategureid ca 1 ha suurusel alal, puutüvedel kuni kahe meetri kõrgusele (**I**, **II**). Loopealsetel uuriti 0.1 ha suurusel alal maapinnal, mullal, samblal ja taimejäänustel kasvavat samblikuelustikku (**III**, **IV**). Uuringusse võeti nii avatud kui juba kinni kasvanud puisniidud, samuti erinevates kadastumise staadiumites loopealsed. Maapinnasamblikke uuriti erinevatel lootüüpidel (plaat-, räha-, klibu- ja nõmmlool) ning loopealsetega sarnastel aladel nagu vanad lubjakivikarjäärid (**III**, **IV**), rannaäärsed noored klibulood (**III**) ja endised loometsa alad paeplaadil (**III**).

Uuritud poollooduslikel kooslustel tuvastati rikas ja omapärane samblikuelustik. Kokku registreeriti puisniitudel kasvavatel puudel 172 lihheniseerunud seeneliiki (**I**), mis moodustab umbes 36% kõigist epifüütsetest samblikest Eestis. Loopealsetelt ja neile sarnastelt kooslustelt leiti 122 mullal, samblal ja taimejäänustel kasvavat samblikuliiki (**III**), mis moodustab umbes 59% kõigist samadel substraatidel registreeritud liikidest Eestis. Poollooduslike koosluste olulisust samblike kasvukohana rõhutab ka suur haruldaste, punasesse nimistusse kuuluvate ja kaitsealuste liikide osakaal, 24% ja 36% vastavalt puisniitudel (**I**) ja loopealsetel registreeritud samblikest (**III**). Lisaks leiti puisniitudelt kolm (**I**) ja loopealsetelt seitse Eestile uut liiki (**III**).

Poollooduslike koosluste majandamine, eelkõige nende kasvukohtade avatus on üks olulisemaid tegureid nii puisniidul kasvavatele epifüütsetele kui loopealsetel kasvavatele maapinnasamblikele. Traditsioonilisest majandamisest loobumine aga on toonud kaasa puisniitude võsastumise ja kinnikasvamise, mistõttu on muutunud sealsed klimaatilised tingimused, eelkõige valgustingimused (**I**, **II**). See omakorda on muutnud ja vaesustanud puisniitudele omaseid epifüütseid samblikukooslusi (**I**, **II**). Valgusnõudlikud liigirikkad samblikukooslused on asendunud liigivaeste varju taluvate samblike kooslustega (**I**, **II**). Ka loopealsete maapinnasamblikud on mõjutatud traditsioonilise majandamise (karjatamise, kadakate harvendamise) lakkamisest (**III**, **IV**). Maapinnasamblike liigirikkus väheneb (**III**) ja liigiline koosseis muutub (**III**, **IV**) rohu- ja põõsarinde katvuse suurendes. Muutub ka samblike kasvuvormide proportsioon, koorikja ja soomusja kasvuvormiga liigid asenduvad põõsasja kasvuvormiga liikidega (**III**, **IV**). Rohu- ja põõsarinde pealetungi suhtes on eriti tundlikud haruldased ja kaitset väärivad liigid (**III**, **IV**).

Avatud loopealsete samblikke iseloomustab lisaks koorikjale ja/või soomusjale kasvuvormile veel kaltsiumilembus, kasvamine nii mullal kui sammaldel, paljunemine peamiselt sugulisel teel (et edendada kauglevi), liigse UV-kiirguse kaitseks tumedate pigmentide või UV-kaitsega samblikuainete sisaldus talluses või viljakehades ja samal ajal vähene panustamine keemilisse kaitsesse ehk kibedate ja toksiliste samblikuainete puudumine (**IV**).

Uurides haruldaste samblike (kuni 10 leiukohta Eestis) tunnuseid, leiti, et haruldased maapinnasamblikud sarnanevad enim samblikega, kes kasvavad madala produktiivsusega avatud loopealsetel, ainsaks erinevuseks oli nende leviala, mis haruldastel liikidel asub peamiselt arktoalpiinses või montaanses vöötmes (**IV**). Seetõttu võime eeldada, et haruldased samblikud eelistavad tõenäoliselt kasvada madala soontaimede produktiivsusega avatud alvaritel ja kaovad nende kinnikasvamisel.

Epifüütsete samblike liigiline koosseis puisniidul on mõjutatud nii regionaalsete (geograafiline asukoht), kasvukoha (puuliigiline koosseis, puude liituvus) kui ka puu tasemel (koore pH ja krobelisus) mõjuvate tegurite komplekti poolt (**I**, **II**). Seetõttu tuleks puisniite säilitada Eesti eri piirkondades, raiuda puid ja järelkasvu valikuliselt, jättes kasvama eri vanuses ja erinevat liiki puid. Säilitada tuleks puisniitude mosaiikset poolavatud struktuuri jättes kasvama erinevaid puude- ja põõsastegruppe, et luua epifüütsetele samblikele võimalikult heterogeensed klimaatilised tingimused. Puisniitude majandamine peaks lisaks puurinde korrastamisele hõlmama ka niitmist või karjatamist, et tagada selle avatud struktuuri.

Erinevad maapinnahäiringud mõjusid positiivselt loopealsete samblikukooslustele (**III**, **IV**). Seetõttu tuleks loopealsete taastamisel ja majandamisel rakendada lisaks traditsioonilstele majandamisvõtetele (karjatamine ja kadakate harvendamine) ka drastilisemaid võtteid nagu mullapinna laiguti eemaldamine aluspõhjani välja. Loopealsete samblikele alternatiivsed kasvukohad, nagu vanad lubjakivikarjäärid, endised sõjaväealad või nurjunud metsastamise katsega jäätmaad, on kujunenud loopealsete samblikele omamoodi ajutisteks asendusaladeks või refuugiumiteks (**III**, **IV**).

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Conference presentations:

Leppik, E.; Jüriado, I.; Suija, A.; Liira, J. “Ground layer lichen communities in alvar grasslands and alvar-like habitats in Estonia – habitat degradation and temporary substitution habitats”. Oral presentation in the 7th International Association for Lichenology Symposium 2012, Bangkok, Thailand.

Leppik, E.; Jüriado, I.; Suija, A.; Liira, J. “Ground-layer lichen communities on alvars of western Estonian islands”. Poster presentation in XXIII Conference-Expedition of the Baltic Botanists 2010, Haapsalu, Estonia.

Leppik, E.; Jüriado, I.; Liira, J.; Suija, A. "Lichens on alvar grasslands in Estonia". Oral presentation in the meeting of Nordic Lichen Society 2009, Snæfellsnes peninsula, Iceland.

Leppik, E.; Nõmm, M. "Lichen communities in cultural landscapes of Saaremaa". Oral presentation in The XVII Symposium of Baltic Mycologists and Lichenologists 2008, Saaremaa, Estonia.

Awards and scholarships:

Margalith Galun Award 2012 for the best student oral contribution at IAL7 in Bangkok

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Publikatsioonid:

Leppik, E.; Jüriado, I.; Suija, A.; Liira, J. (2013). The conservation of ground layer lichen communities in alvar grasslands and the relevance of substitution habitats. Biodiversity and Conservation, 22(3), 591–614.

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Suija, A.; **Leppik, E.**; Jüriado, I.; Lõhmus, P.; Marmor, L.; Saag, L. (2011). New Estonian records and amendments: Lichenized, lichenicolous and allied fungi. Folia Cryptogamica Estonica, 48, 154–158.

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Suija, A.; Jüriado, I.; **Leppik, E.**; Randlane, T. (2006). New lichens and lichenicolous fungi. Folia Cryptogamica Estonica, 42, 103–105.

Konverentsiettekanded:

Leppik, E.; Jüriado, I.; Suija, A.; Liira, J. “Ground layer lichen communities in alvar grasslands and alvar-like habitats in Estonia – habitat degradation and temporary substitution habitats”. Suuline ettekanne 7. Rahvusvahelisel Lihhenoloogide Ühingu Sümpoosionil, 2012, Bangkok, Tai.

Leppik, E.; Jüriado, I.; Suija, A.; Liira, J. “Ground-layer lichen communities on alvars of western Estonian islands”. Posterettekanne Balti Botaanikute XXIII konverents-ekspeditsioonil, 2010, Haapsalu, Eesti.

Leppik, E.; Jüriado, I.; Liira, J.; Suija, A. “Lichens on alvar grasslands in Estonia”. Suuline ettekanne Põhjamaade Lihhenoloogide Koosolekul, 2009, Snæfellsnes poolsaar, Island.

Leppik, E.; Nõmm, M. “Lichen communities in cultural landscapes of Saaremaa”. Suuline ettekane Balti Mükoloogide ja Lihhenoloogide XVII Sümpoosionil, 2008, Saaremaa, Eesti.

Saadud uurimistoetused ja stipendiumid:

Margalith Galun nimeline auhind 2012. aastal parima tudengi ettekande eest IAL7 konverentsil Bangkokis

Välissõidu toetused Ökoloogia ja maateaduste doktorikoolilt 2010 ja 2012

Muu teaduslik organisatsiooniline ja erialane tegevus:

Põhjamaade Lihhenoloogide Ühingu liige alates 2007

Eesti Looduseuurijate Seltsi liige alates 2006

Pärandkoosluste Kaitse Ühingu liige alates 2004

Osalemine kursustel:

Suvekool “Pool-looduslikud kooslused”, 19–23 juuli, 2010 Haapsalu, Eesti

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