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Distribution of *Lepraria* in Latvia in relation to tree substratum and deciduous forest type

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The aim of the study was to evaluate the distribution of *Lepraria* lichen species in dry deciduous forests, in relation to tree substratum and forest characteristics. In total, 34 localities with 1020 trees (13 tree species) were studied in different parts of Latvia. *Lepraria* spp. were found on 642 trees: *L. eburnea* on 8 trees, *L. incana* on 80 trees, and *L. lobificans* on 568 trees. *Lepraria eburnea* was recorded for the first time in Latvia. Tree species, tree bark crevice depth, inclination, pH and forest type were the most important variables explaining the presence of *Lepraria* species. *Lepraria incana* was associated with *Quercus robur* and *Tilia cordata*, while *L. lobificans* was associated with *Betula pendula*. The occurrence probability of *L. lobificans* increased with tree inclination and tree bark pH, and that of *L. incana* with bark crevice depth and tree bark pH.

Introduction

Epiphytic lichens are an important component of the biodiversity in deciduous forests. Several crustose lichens, such as *Acrocordia gemmata*, *Bacidia rubella* and *Lecanactis abietina* are indicators of forest primevity (Nordén *et al*. 2007). Lichen species have different preferences regarding the tree species on which they grow (Loppi & Frati 2004, Lõhmus *et al*. 2007, Mežaka *et al*. 2008, Meier & Paal 2009, Jüriado *et al*. 2009). Some crustose lichen species prefer deciduous trees with a basic bark (Loppi & Frati 2004, Hedenås & Hedström 2007), while others prefer more acidic coniferous bark (Marmor & Randlane 2007). Based on the relationship of epiphytic species to tree bark pH, Barkman (1958) suggested dividing tree species into three groups: (1) rich bark (pH 5.00–7.00), (2) medium rich bark (pH 4.00–5.00), and (3) poor bark (pH < 4.00).

The richest lichen diversity in Latvia is found on deciduous trees, such as *Acer platanoides*, *Alnus glutinosa*, *A. incana*, *Carpinus betulus*, *Fraxinus excelsior*, *Populus tremula*, *Sorbus aucuparia*, *Tilia cordata*, *Ulmus* spp., and *Quercus robur* (Piterāns 2001, Mežaka *et al*. 2008).

It can be assumed that *Lepraria* species also differ in niche requirements, but due to identification problems in the field unidentified species of the genus have often been grouped together as "*Lepraria* spp." (Kuusinen 1994, Loppi &

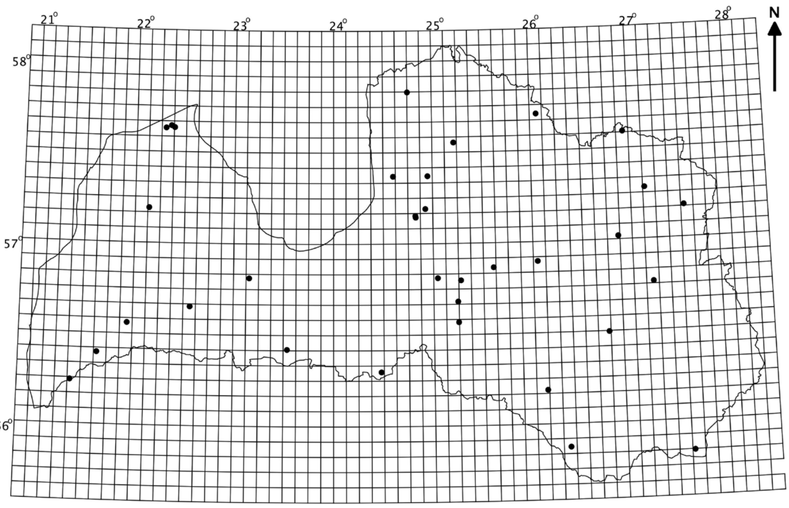

Fig. 1. Locations of the studied forest stands in Latvia. Scale 1:500 000.

Frati 2004, Perhans *et al.* 2007, Caruso *et al.* 2008). Recently, *Lepraria* species have been taxonomically studied worldwide. Kümmerling *et al.* (1991) found chemical differences between *L. incana* and *L. lobificans*, which have been used to verify species identifications in the laboratory. Different thallus types and subtypes in the *Lepraria* species can be recognized based on micro- and macro-characters (Lendemer 2011). However, field identification is still difficult, particularly when the thallus is small. A world survey of 57 *Lepraria* species was compiled by Saag *et al.* (2009), and a review of the genus in Poland was made by Kukwa (2006). Recent studies have shown that the species can be good indicators of the forest environment, as different *Lepraria* species with different ecological preferences can be found within a small area (Lõhmus *et al.* 2003, Jüriado *et al.* 2003, Saag 2007).

Previously, only two *Lepraria* species (*L. incana* and *L. lobificans*) have been reported from Latvia (Piterāns 2007). The aim of the present study was to evaluate the distribution of *Lepraria* species in the Latvian dry deciduous forests in relation to tree bark characteristics and forest type.

Material and methods

Study areas

Latvia is located in the hemiboreal vegetation zone, with mixed deciduous–coniferous forests being typical for this area. The mean annual temperature is +5.56 °C and the mean amount of annual precipitation is 600 mm (Temņikova 1975).

The present study was conducted in 34 seminatural deciduous forest stands in Latvia (Fig. 1), all of which corresponded to Woodland Key Habitat (WKH) criteria (Ek *et al.* 2002). The study was conducted in WKHs, as these areas are considered to support high biodiversity. In Latvia, WKH is defined as an area hosting habitat specialist species that cannot sustainably survive in stands managed for timber production (Ek *et al.* 2002). Most of the studied localities were classified in the WKH inventory as dry broad-leaved WKHs, and some of these were riparian forests. Also some aspen WKHs were included due to the high biological value of these forests.

Each selected forest stand also corresponded to one of five protected forest habitat types in the European Union (European Commission 2007): (1) Sub-Atlantic and medio-European oak or oak-hornbeam forests of the Carpinion betuli (euQ), (2) Fennoscandian hemiboreal natural old broad-leaved forests (*Quercus*, *Tilia*, *Acer*, *Fraxinus* or *Ulmus*) rich in epiphytes (eubrl), (3) riparian mixed forests of *Quercus robur*, *Ulmus laevis* and *U. minor*, *Fraxinus excelsior* or *F. angustifolia*, along big rivers (eucoast), (4) western taiga, (5) forests of slopes, screes and ravines (eusr). The selected stands were located in different geographical regions in Latvia. In our study, we considered only a subset of the western-taiga habitat, i.e. *Populus tremula* stands, which represent a successional stage of boreal forests. *Ulmus minor* and *Fraxinus angustifolia* are not native to Latvia, but nevertheless, the riparian mixed forest habitat type with a different tree species composision is found in the country (European Commission 2007). The most common tree species in the studied forest stands were *Acer platanoides*, *Fraxinus excelsior*, *Populus tremula*, *Tilia cordata* and *Ulmus glabra*.

Field work

Data in the field were collected from 2006 to 2008. Stands for sampling were selected from the inventory data on WKH obtained from the Latvian State Forest Service. To avoid edge effects, plots were sampled in the middle of forest stands. Different forest types were selected to maximize the habitat diversity for *Lepraria* spp. occurrence. The size of the sample plots was 20 × 20 m. In each plot 30 trees with DBH > 0.05 m were selected randomly.

The tree stem with the largest DBH was chosen if a tree had a stem branched at base. If more than 30 trees were found in a selected sample plot, trees with a larger DBH were sampled. For each tree, its species, height (m), DBH (m), inclination (degrees), bark pH and bark crevice depth (mm) were recorded.

A total of 137 tree stems were cored with a Prestler borer and the annual rings were counted for determination of tree age. Tree inclination was measured with a surveying compass at 0.5 m to 2.0 m height, in the place where the maximum inclination was observed. If a tree was straight up to 2.0 m, it was considered vertical. Tree height was measured with a Sunto relascope. Tree bark samples for pH measurements in the laboratory were collected with a knife to a depth of 3.0 mm from the north side of stems up to 1.3 m height. Bark crevice depth was measured with a ruler on the north side of a tree at 1.2 m height. The north side was selected for sampling as suggested by Barkman (1958), to provide standardized samples.

Specimens were collected for species identification in the laboratory. Samples of *Lepraria* were taken from the largest visible patch of *Lepraria* on each tree, at heights up to 2.0 m. The lichen species nomenclature follows Saag (2009). The samples of *Lepraria* were submitted to the Herbarium Universitatis Latviensis (RIG).

Laboratory work

Bryophytes and lichens were removed from tree bark samples before pH measurements. Bark samples were air-dried for one week at room temperature and then cut into pieces (< 2 mm diameter) with a knife. Each bark sample weighed approximately 0.5 g, one sample consisting of many bark pieces. Some samples, however, weighed less than 0.5 g due to difficulties with bark removal from some old individuals of *Populus tremula* whose bark was thick and hard. Each bark sample was shaken in 20 ml of 1 M KCl for 1 h and then pH was determined with a pH meter (GPH 014, Greisinger Electronic). All bark pH values were converted to H^+ concentrations before calculating the mean values. For the pH measurement, we used a modified version of the Kermit and Gauslaa (2001) method without wax treatment of one side of the bark pieces.

The *Lepraria* spp. samples were extracted with acetone. Thin Layer Chromotography (TLC) was conducted following Orange *et al*. (2001) (solvents A, B and C).

Data analysis

A chi-square (χ^2) test with Yate's continuity correction was used to (1) determine if the frequency occurrence of a *Lepraria* species on a particular tree species differed from the overall frequency on all trees, and (2) to determine positive or negative relationships between *Lepraria* species occurrence and binomial variables (tree species and forest type). The chi-square analysis was performed using the R program package (freely available at http://www.r-project.org/).

A Generalized Linear Model (GLM) with binomial families in the R program package was used to determine significant factors affecting *L. incana* and *L. lobificans* occurrence on trees. *Lepraria eburnea* was not included in the analysis due to a low number of replications. Four models were employed: (1) tree height, DBH, bark crevice depth, bark pH, tree inclination; (2) tree species; (3) forest habitat; and (4) tree species plus forest habitat. Percentage of deviance was used (available in BiodiversityR package) to estimate the explanatory power of each model.

GLM in the program Canoco ver. 4.7 for Windows was used to derive probability response curves for *L. incana* and *L. lobificans* in relation to significant explanatory factors. A logit function with a binomial distribution was used. Canoco offers a simpler means for managing graphical options than the R program. The factors tested were tree height, DBH, bark crevice depth, bark pH, tree inclination. Monte Carlo Permutation tests were used to identify the significant variables.

Results

In total, three *Lepraria* species (*L. eburnea*, *L. incana*, *L. lobificans*) were found in the Latvian dry deciduous forests. *Lepraria eburnea* was found on 8 trees, *L. incana* on 80 trees and *L. lobificans* on 568 trees. A summary of the characteristics of the studied trees is given in Table 1. In comparison with the other tree species, *Quercus robur* had the largest mean DBH, bark crevice depth, tree height and tree age. The highest bark pH values were found for *Acer platanoides* and *Ulmus laevis*, and the lowest for *Alnus glutinosa* (Table 1).

Lepraria eburnea was recorded for the first time in Latvia on one *Alnus incana*, three *Populus tremula* and four *Ulmus glabra*. Differences were found in *Lepraria* spp. distribution on the tree species. *Lepraria lobificans* had a lower frequencies of occurrence than expected on *Alnus incana* ($\chi^2 = 8.82, p < 0.01$), *Populus tremula* ($\chi^2 = 3.28, p < 0.01$), *Quercus robur* ($\chi^2 = 4.147, p = 0.042$) and *Sorbus aucuparia* ($\chi^2 = 7.306, p < 0.01$) and higher frequency than expected on *Betula pendula* ($\chi^2 = 19.927, p < 0.01$). The correlations between *L. incana* and *Quercus robur* ($\chi^2 = 75.18, p < 0.01$) and *Tilia cordata* ($\chi^2 = 3.94, p = 0.04$) were significant and higher than expected. The frequencies of occurrence of *L. incana* on *Fraxinus excelsior*, *Populus tremula*, *Quercus robur* and *Ulmus glabra* were significantly lower than the overall frequency on the other tree species (Fig. 2). The low number of *L. eburnea* records did not allow for generalizations (Fig. 2).

Tree inclination was a statistically significant factor for *L. lobificans* occurrence, but the explanatory power was very low (0.3% of variance). Tree bark crevice depth and pH were significant factors for *L. incana*, but they explained only 9.95% of the variance (Table 2). The presence of *Tilia cordata* and *Quercus robur* explained 15.23% of variance in the occurrence of *L. incana*. In comparison, a model with five tree species explained only 6.33% of the vari-

Table 1. Measured characteristics of the studied tree species. Mean values ± SD are given.

Tree species	DBH (m)	Bark crevice depth (mm)	pH	Tree inclination (degrees)	Tree height (m)	Tree age (years)
Acer platanoides	0.31 ± 0.15	3.9 ± 3.5	5.79 ± 0.77	10.5 ± 11.1	20.9 ± 7.1	93 ± 32
Alnus glutinosa	0.22 ± 0.06	4.1 ± 1.9	3.92 ± 0.34	4.8 ± 4.5	20.7 ± 5.0	65 ± 22
Alnus incana	0.18 ± 0.07	1.1 ± 2.0	4.73 ± 0.55	6.3 ± 7.4	41.8 ± 5.3	54 ± 8
Betula pendula	0.36 ± 0.15	7.5 ± 5.5	3.80 ± 0.68	16.0 ± 13.5	25.8 ± 7.6	not cored
Carpinus betulus	0.33 ± 0.04	1.5 ± 0.6	4.69 ± 0.35	0.6 ± 0.5	22.8 ± 7.6	103 ± 27
Fraxinus excelsior	0.34 ± 0.18	4.3 ± 4.0	5.25 ± 0.01	8.8 ± 10.5	24.0 ± 7.8	68 ± 23
Populus tremula	0.38 ± 0.11	4.3 ± 2.9	4.86 ± 0.77	6.4 ± 7.1	26.9 ± 6.6	not cored
Quercus robur	0.49 ± 0.21	9.7 ± 6.7	4.35 ± 0.93	7.1 ± 7.1	23.3 ± 7.0	139 ± 45
Salix caprea	0.16 ± 0.03	3.8 ± 3.3	4.34 ± 0.38	9.0 ± 11.5	13.3 ± 5.7	not cored
Sorbus aucuparia	0.14 ± 0.06	1.6 ± 0.7	5.02 ± 0.47	13.2 ± 11.6	12.7 ± 8.1	not cored
Tilia cordata	0.30 ± 0.16	4.3 ± 3.7	4.59 ± 0.72	12.2 ± 11.0	20.4 ± 7.6	80 ± 53
Ulmus glabra	0.25 ± 0.18	4.8 ± 3.6	5.43 ± 0.76	8.6 ± 9.4	15.6 ± 8.1	75 ± 18
Ulmus laevis	0.29 ± 0.19	5.2 ± 3.4	5.97 ± 0.68	3.4 ± 6.5	15.4 ± 6.0	55 ± 9

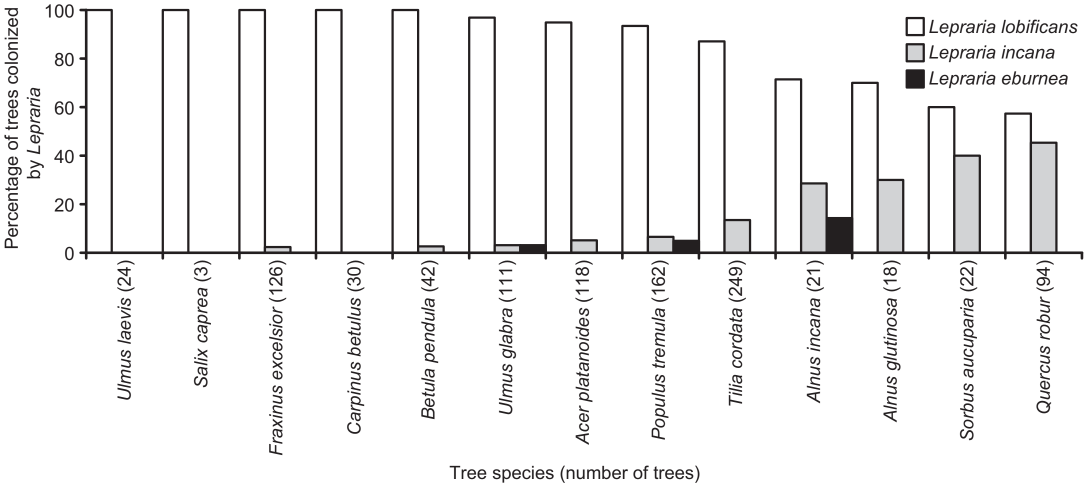

Fig. 2. Percentage of trees colonized by *Lepraria* spp.

ance in *L. lobificans* occurrence (Table 2). The occurrence of *Lepraria lobificans* was partly explained by the forest type, (8.79% of variance), but *L. lobificans* showed no significant preference for any particular forest type (χ^2-test: $p > 0.05$). Forest type explained 10.07% of the variance in occurrence of *L. incana*. Percentage of variance increased for both *Lepraria* species in model 4, when tree species and forest type were included together (Table 2).

Only significant continuous variables were employed to derive GLM response curves

Table 2. *Lepraria* species occurrence in relation to tree variables and forest type in Generalized Linear Model. *Lepraria eburnea* was not included in the analysis as only eight records were found for this species. Abbreviations: euQ = Sub-Atlantic and central-European oak or oak–hornbeam forests of the *Carpinion betuli*; eubrl = Fennoscandian hemiboreal natural old broad-leaved forests (*Quercus*, *Tilia*, *Acer*, *Fraxinus* or *Ulmus*) rich in epiphytes; eusr = forests of slopes, screes and ravines; eucoast = riparian mixed forests of *Quercus robur*, *Ulmus laevis* and *U. minor*, *Fraxinus excelsior* or *F. angustifolia*, along large rivers.

Models	*Lepraria incana*	*Lepraria lobificans*
Model 1 (tree characteristics)		
Percentage of variance	9.95	0.3
Significant variables ($p < 0.05$)	tree bark crevice depth, pH	inclination
Model 2 (tree species)		
Percentage of variance	15.23	6.33
Significant variables ($p < 0.05$)	*Tilia cordata*, *Quercus robur*	*Alnus incana*, *Quercus robur*, *Populus tremula*, *Sorbus aucuparia*, *Betula pendula*
Model 3 (forest type)		
Percentage of variance	10.07	8.79
Significant variables ($p < 0.05$)	euQ	eubrl, eusr, eucoast
Model 4 (tree species and forest type)		
Percentage of variance	18.13	14.27
Significant variables ($p < 0.05$)	*Tilia cordata*, *Quercus robur*, euQ	*Alnus incana*, *Quercus robur*, *Populus tremula*, *Sorbus aucuparia*, *Betula pendula*, eubrl, eusr, eucoast

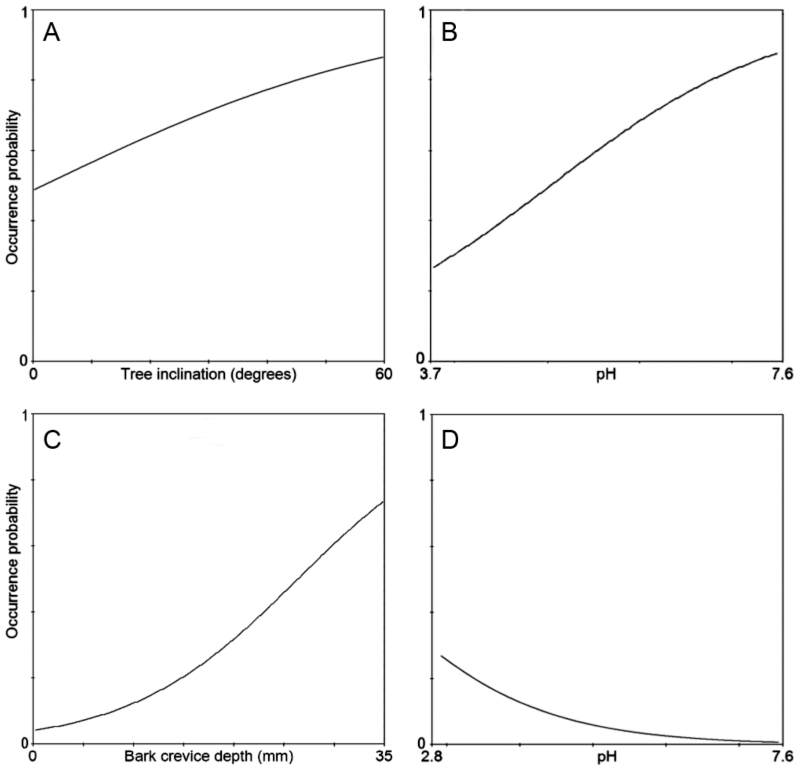

Fig. 3. Occurrence probabilities of *Lepraria* spp. in relation to tree variables as indicated by GLM. — **A**: *L. lobificans* and tree inclination ($F = 23.43$, $p < 0.01$). — **B**: *L. lobificans* and bark pH of *Acer platanoides* ($F = 9.09$, $p < 0.01$). — **C**: *L. lobificans* and bark crevice depth ($F = 30.66$, $p < 0.01$). — **D**: *L. incana* and bark pH ($F = 35.74$, $p < 0.01$).

(Fig. 3). Presence of *L. lobificans* showed positive correlation to tree inclination (Fig. 3A) while its occurrence probability increased with increasing tree bark pH only on *Acer platanoides* (Fig. 3B). *Lepraria incana* occurrence probability increased with bark crevice depth (Fig. 3C) and decreased with increasing bark pH (Fig. 3D). However, the probability of occurrence for *L. incana* was very low for all pH values.

Discussion

The occurrence of *Lepraria* species was best explained by tree species and not so much by other parameters, such as bark crevice depth, pH or inclination which covary with tree species (Table 2). For example, *Quercus robur* has deeper bark crevices and a lower bark pH. Tree inclination may also depend more on habitat features than on tree species. In forests on slopes, screes and in ravines, trees are more inclined in comparison with trees in forests in flat areas. Nevertheless, a correlation between *Lepraria* species occurrence and tree inclination was very weak (Fig. 3A). Olsen (1917) and Barkman (1958) noted that, when a thick bryophyte cover has developed on the upper part of inclined trees, a lack of water supply promotes the occurrence of *Lepraria* spp. (not identified to species level).

The differences in the occurrence of *Lepraria* species in different forest types might be due to differences in microclimate or dominance of different tree species. However, the amount of explained variance for the studied factors was low (13%–15%). Possibly, the intensity of sampling was insufficient, as we collected only the largest visible patch of *Lepraria* spp. from each tree, i.e. the incidence of different *Lepraria* species might have been higher. Lõhmus *et al.* (2003) found that several *Lepraria* species may be present on small pieces of bark.

Lepraria lobificans, the most common species in the present study, was found on all 13 tree species. It is one of the most common epiphytic sorediate crustose lichens in central and northern Europe (Tønsberg 1992, Wirth & Heklau 1995, Dietrich & Scheidegger 1996). Occurrence of

L. lobificans on *Alnus incana*, *Populus tremula*, *Quercus robur* and *Sorbus aucuparia* was less frequent. It has previously been reported that *L. lobificans* is more common on trees with higher bark pH, such as *Acer platanoides*, *Fraxinus excelsor* and *Ulmus glabra* (Jüriado *et al*. 2009), but our results do not support this. This difference may have resulted from the fact that tree species occur with different frequencies in habitats with different environmental conditions, such as light and/or humidity.

Lepraria lobificans was mostly found in the European protected habitat "Fennoscandian hemiboreal natural old broad-leaved forests rich in epiphytes", as well as in forests on slopes, screes and in ravines, where the presence of brooks, dead wood and various tree species ensure heterogenous microclimatic conditions. This suggests that *L. lobificans* prefers moderate humidity and moderately shady conditions. Perhaps habitat type is the main factor explaining the presence of *L. lobificans*, and in the preferred habitat types *L. lobificans* lacks a preference for any particular tree species. However, to test this, a larger number of plots with a stratified design are needed to objectively distinguish habitat and tree species effects.

Lepraria incana was found on ten of the studied tree species (Fig. 2) and it was more common than expected on *Tilia cordata* and *Quercus robur* (Table 2). This might explain the correlation with Sub-Atlantic and medio-European oak or oak–hornbeam forests of the Carpinion betuli, where *Quercus robur* is more common (the highest number of *L. incana* records). *Lepraria incana* has been described as a common species in Europe (Tønsberg 2002, Kukwa 2006, Saag 2007) and it thrives on a wide range of substrates (Baruffo *et al*. 2006, Kukwa 2006), such as *Quercus robur*, *Betula pendula* and *Sorbus aucuparia* (Wirth & Heklau 1995, Tønsberg 1992). We found *Lepraria incana* to prefer trees with relatively low bark pH (Fig. 3D). Jüriado *et al*. (2009) also observed *L. incana* to be associated with more acidic substrata, such as *Betula* spp. and *Alnus glutinosa*.

Lepraria eburnea was found only on eight trees (Fig. 2). However, it is a common lichen in Estonian old-growth forests (Saag 2007). Wirth and Heklau (1995) reported *L. eburnea* mostly on *Quercus* spp., but Tønsberg (1992) found it more common on *Alnus incana*, *Sorbus aucuparia* and rare on *Populus tremula* and *Quercus* spp. Its low occurrence in our study did not allow for statistical analyses, but Baruffo *et al*. (2006) found that *L. eburnea* was indifferent to substratum, as it was observed to grow on mosses as well as on acidic and sub-neutral tree bark, and those authors described it as a common colonizer on stems of deciduous tree.

Probably the studied forest fragments in sample plots were too small to be representative of the *Lepraria* spp. distribution in the Latvian deciduous forests, as lichen communities may change considerably within a forest stand.

Conclusions

This study presents preliminary data on the ecology of *Lepraria* spp. in Latvia. More detailed studies are necessary to reliably evaluate *Lepraria* spp. diversity. There are probably more than three *Lepraria* species in Latvia, as in the neighboring Estonia there are eight species associated with forests (Saag 2007). Furthermore, the study localities were selected subjectively. Studies including a greater variety of habitats (e.g. coniferous forests) and not only WKH, but also managed forest stands and different substrata (e.g sandstone) are necessary to further evaluate the distribution of *Lepraria* spp. in Latvia. However, the present study demonstrates that *L. incana* and *L. lobificans* differ slightly in their ecological demands. *Lepraria lobificans* prefers deciduous forests with moderate humidity and shady conditions and trees with higher bark pH, while *L. incana* is more common on trees with deeper bark crevices and lower bark pH. Tree species and forest type preferences explained the highest amount of variance of *Lepraria* species distribution in Latvian deciduous forests. Future research on *Lepraria* spp. distribution should consider a wider range of habitat types and increase the number of studied localities to decipher the preference of the different species for habitat type *versus* tree species substratum. *Lepraria elobata* has been found in the coniferous forests in Estonia and Lithuania, both bordering Latvia (Motiejūnaitė 1999, Saag 2007), but it has not yet been reported from Latvia.

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