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The distribution of epiphytic bryophyte and lichen species in relation to phorophyte characters in Latvian natural old-growth broad leaved forests

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Abstract: Epiphytic bryophyte and lichen species distribution was studied in representative natural old-growth broad leaved forests in Latvia. Overall 120 epiphytic bryophyte and lichen species were found in 13 forest stands. Seven Latvian red-listed bryophyte (*Antitrichia curtipendula, Lejeunea cavifolia, Metzgeria furcata, Neckera complanata, Neckera pennata, Dicranum viride, Jamesoniella autumnalis*) and four red-listed lichen species (*Lobaria pulmonaria, Opegrapha viridis, Pertusaria pertusa, Thelotrema lepadinum*) were recorded. The relationships of total epiphytic bryophyte and lichen species richness and red-listed epiphytic bryophyte and lichen species richness with substrate factors (phorophyte species, DBH (diameter at breast height), tree bark crevice depth and tree bark pH) were evaluated.

Kokkuvõte: Epifüütsete sambla- ja samblikuliikide leviku seos forofüüdi omadustega Läti vanades looduslikes laialehistes metsades

Epifüütsete sambla- ja samblikuliikide levikut uuriti tüüpilistes Läti vanades looduslikes laialehistes metsades. Kokku leiti kolmeteistkümnel uurimisalal 120 epifüütset sambla- ja samblikuliiki, nende seas seitse punase raamatu samblaliiki (*Antitrichia curtipendula, Lejeunea cavifolia, Metzgeria furcata, Neckera complanata, Neckera pennata, Dicranum viride, Jamesoniella autumnalis*) ja neli samblikuliiki (*Lobaria pulmonaria, Opegrapha viridis, Pertusaria pertusa, Thelotrema lepadinum*). Hinnati kogu sambla ja sambliku liigirikkuse ning punasesse raamatusse kuuluvate sammalde ja samblike liigirikkuste seoseid substraadi omadustega (forofüüdi liik, DBH (tüve diameeter rinna kõrgusel), korba lõhede sügavus ja korba pH).

INTRODUCTION

Broad leaved forests reached their maximum distribution area in Latvia in the Atlantic period, approximately 7400 years ago (Zunde, 1999). Latvia is located in the hemiboreal vegetation zone on an ecotone between the boreal and nemoral biomes, resulting in a mixture of coniferous and deciduous forests. The present forest cover is close to 55% (VMD, 2007) of Latvian territory and broad leaved forests cover 1 % of the total forest area (Priedītis, 1999). Due to agricultural intensification, the coverage of broad leaved forests has decreased in Latvia in the past (Dumpe, 1999). The loss and fragmentation of natural habitats, by agriculture, forestry and urbanization are the main causes decreasing biodiversity at local, regional and global scales (Hanski 2005). Due to fragmentation, broad leaved forests in Latvia are mostly restricted to river valleys, lake islands and slopes (Priedītis, 1999). A number of protected broad leaved forest habitats in the European Union are found in Latvia: Fennoscandian natural old broad leaved forests, Subatlantic oak-hornbeam forests of the Carpinion betuli, Tilio-Acerion forests of slopes, screes and ravines, riparian mixed forests of *Quercus robur*, *Ulmus glabra* and *Fraxinus excelsior* (Council Directive 92/43/EEK, 1992). In these nutrient-rich forests with an abundance of deciduous tree species and characteristic high transpiration rates, rich epiphytic bryophyte cover and lichen species diversity have been observed (Āboliņa, 1968; Priedītis, 2000; Bambe, Lārmanis, 2001; Ek et al., 2002; Anonymous 2003; Mežaka et al., 2008).

Studies on epiphytic bryophyte and lichen species are not complete in Latvia and are based mostly on species-focused taxonomic works (Āboliņa, 1968; Piterāns, 2001; Āboliņa. 2001; Bambe & Lārmanis, 2001; Bambe, 2002; Znotiņa, 2003). Epiphytic bryophytes in Latvia have been more studied in forests of slopes, screes and ravines (Mežaka & Znotiņa, 2006), but complete studies about epiphytic bryophyte and lichen ecology in other types of broad leaved forests are lacking.

Substrate has an important role in determining distribution of epiphytic species (Barkman, 1958; Āboliņa, 1968; Weibull, 2001;

Snäll et al., 2004; Mežaka & Znotiņa, 2006; Paltto et al., 2006; Marmor & Randlane, 2007). Earliest studies about Latvian bryophytes (Āboliņa, 1968) indicate particular tree species importance in bryophyte species distribution. Epiphytic bryophyte and lichen species composition varies depending on tree species and it is highly related with bark chemical and physical properties (Barkman, 1958). However, little is known about epiphytic bryophyte and lichen community composition on various broad leaved tree species in Latvia (Āboliņa, 1968).

Epiphytic bryophytes prefer trees with larger diameter at breast height (Ingerpuu & Vellak, 2007; Hazell et al., 1998). Bark crevice depth is a significant factor affecting epiphytic species distribution (Slack, 1976; Gustafsson & Eriksson, 1995; Snäll et al., 2004, creating various microhabitats for epiphytes on a small scale.

Tree bark pH is one of the most important factors affecting bryophyte (Weibull, 2001) and lichen species distribution (Barkman, 1958). In Latvia bryophyte species were classified into ecological groups based on substrate acidity since the beginning of the 20th century (Apinis & Diogucs, 1935; Apinis & Lācis, 1936). The relationship between lichen species richness and tree bark pH has not been studied in Latvia.

The aim of the present study is to provide information about the total and red-listed epiphytic bryophyte and lichen species richness in relation to main characteristics of the phorophyte in Latvian broad leaved forests.

MATERIALS AND METHODS

Study areas

Epiphytic bryophytes and lichens were studied in 13 old-growth broad leaved forest stands located in various parts of Latvia (Fig. 1). The mean annual precipitation in Latvia is 600 mm and the annual air temperature is 5.56 °C (Temņikova, 1975). The studied territories were selected based on the Woodland Key Habitat (WKH) inventory data (Ek et al., 2002; Anonymous, 2003).

All selected forest stands were located in old-growth forests, having trees with different diameter, dead wood in various decay stages and crown openings. The most common were Fennoscandian natural old broad leaved forests (Table 1).

Field work

The present study was conducted from summer 2006 to autumn 2007 in spring, summer and autumn seasons. Studied sample plot in forest stand was selected randomly in a representative place characterizing whole forest stand. One sample plot 20×20 m was established in each studied forest stand. Epiphytic bryophytes and lichens were studied on 30 tree stems with a minimal DBH (diameter at breast height) of 10 cm in each sample plot. In cases of insufficient number of trees, an adjacent sample plot (20×20 m) was made.

Epiphytic bryophyte and lichen presence and absence was recorded up to a 2 m height all around the tree in total of 390 trees. Unknown bryophyte and lichen specimens were collected for identification in the laboratory. Bryophyte species nomenclature follows Grolle & Long (2000); Smith (2004), Āboliņa (2001), and lichen species nomenclature after Piterāns (2001).

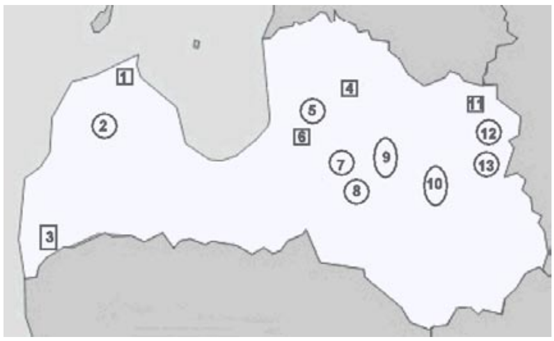

Fig. 1. Studied areas in Latvia. 1 – Zilie kalni in Slitere National Park, 2 – Moricsala Nature Reserve, 3 – Dunika Nature Reserve, 4 – Zilais kalns Nature Reserve, 5 – Lauri forest stand, 6 – Nurmiži Ravine Reserve in Gauja National Park, 7 – Laubere microreserve, 8 – Aizkraukles purvs un meži Nature Reserve, 9 – Vērenes gobu un vīksnu audze Nature Reserve, 10 – Pededzes lejtece Nature Reserve, 11 – Korneti-Peļļi Nature Reserve, 12 – Jaunanna Nature Reserve, 13 – Vjada Nature Reserve. Squares – Tilio-Acerion forests of slopes, screes and ravines, circles – Fennoscandian natural old broad leaved forests, rectangular – Subatlantic and medio-European oak-hornbeam forests of Carpinion betuli, ovals – Riparian mixed forests of *Quercus robur, Ulmus glabra, Fraxinus excelsior.*

Table 1. Studied forest characteristics. Mean DBH – mean tree diameter at breast height.

Study area	Mean DBH (m)	Studied tree species	Forest stand area (ha)
Aizkraukles purvs un meži Nature Reserve	0.28	*Betula pendula, Quercus robur, Tilia cordata, Ulmus glabra*	4.8
Dunika Nature Reserve	0.34	*Carpinus betulus*	1.8
Jaunanna Nature Reserve	0.36	*Betula pendula, Tilia cordata, Ulmus glabra*	1.8
Korneti-Peļļi Nature Reserve	0.37	*Acer platanoides, Quercus robur, Sorbus aucuparia, Tilia cordata*	3.4
Laubere microreserve	0.26	*Acer platanoides, Alnus incana, Fraxinus excelsior, Tilia cordata*	1.9
Lauri forest stand	0.33	*Acer platanoides, Alnus incana, Quercus robur, Tilia cordata, Sorbus aucuparia*	5.9
Moricsala Nature Reserve	0.39	*Acer platanoides, Quercus robur, Tilia cordata*	2.0
Nurmiži Ravine Reserve in Gauja National Park	0.27	*Acer platanoides, Fraxinus excelsior, Populus tremula, Ulmus glabra, Ulmus laevis*	5.9
Pededzes lejtece Nature Reserve	0.26	*Quercus robur, Ulmus glabra, Betula pendula, Alnus incana, Salix caprea, Alnus glutinosa, Fraxinus excelsior*	4.8
Vērenes gobu un vīksnu audze Nature Reserve	0.30	*Alnus incana, Sorbus aucuparia, Ulmus glabra, Ulmus laevis*	1.2
Vjada Nature Reserve	0.26	*Acer platanoides, Fraxinus excelsior, Tilia cordata, Ulmus glabra*	0.3
Zilais kalns Nature Reserve	0.35	*Populus tremula, Quercus robur, Tilia cordata*	7.3
Zilie kalni in Slitere National Park	0.39	*Acer platanoides, Fraxinus excelsior, Populus tremula, Ulmus glabra*	5.0

Tree diameter at breast height (m), bark pH, and bark crevice depth (mm) were measured. Samples for tree bark pH measurements were collected and bark crevice depth was measured at 1.20m height on north exposure on all studied trees, one measurement per tree.

pH measurements

In total 390 tree bark samples were measured for bark pH. Bryophyte and lichen remnants were removed from tree bark to avoid their influence on pH value. Tree bark samples were cut in small pieces (medium size 0.001 g). An amount of 0.5 g of bark pieces was shaken in 20 ml 1M KCl (pH 5.50) solution for one hour in 100 ml flasks and pH measured with a pHmeter (GPH 014, Greisinger Electronic).

Data analysis

Prior to data analysis, outliers (z-score value ≥ 3) for quantitative data were removed based on distribution of residuals. Univariate GLM (General linear model) was used to determine significant factors (*Acer platanoides, Alnus incana, Carpinus betulus, Fraxinus excelsior, Populus tremula, Quercus robur, Tilia cordata, Ulmus glabra, Ulmus laevis* as tree species, DBH, tree bark crevice depth and tree bark pH) affecting total epiphytic species richness, epiphytic bryophyte and lichen species richness, total red-listed epiphytic species richness, red-listed lichen species richness.

Multiple Comparisons after Post-Hoc Scheffe test were used for checking differences between epiphytic species richness and tree species. Spearman rank correlation was used for check of autocorrelations. Four tree species consisting less than 10 tree individuals (*Sorbus aucuparia, Betula pendula, Alnus glutinosa* and *Salix caprea*) were removed from this analysis. A total of 352 trees were included in data analysis by GLM and Multiple Comparisons after Post-Hoc Scheffe test. Data were analysed using SPSS for Windows, Release 15.0.0, SPSS Inc.

RESULTS

In total 120 epiphytic (63 bryophyte and 57 lichen) species were found on 390 trees from 13 species – *Carpinus betulus, Fraxinus excelsior, Acer platanoides, Ulmus glabra, Tilia cordata, Ulmus laevis, Sorbus aucuparia, Alnus incana, Populus tremula, Betula pendula, Quercus robur, Alnus glutinosa, Salix caprea* (Table 2). *Tilia cordata* was the most common tree species. The most common bryophyte species (>200 records on trees) were *Hypnum cupressiforme, Homalia trichomanoides*, *Radula complanata* and lichens were *Lepraria* spp. and *Phlyctis argena*. Seven red-listed Latvian bryophyte species (vulnerable species – *Antitrichia curtipendula, Lejeunea cavifolia, Metzgeria furcata, Neckera complanata, Neckera pennata,* rare species – *Dicranum viride, Jamesoniella autumnalis* (Āboliņa, 1994)) and four red-listed lichen species (vulnerable species – *Lobaria pulmonaria,* rare species – *Opegrapha viridis, Pertusaria pertusa, Thelotrema lepadinum,* (Piterāns & Vimba, 1996)) were found.

Some bryophyte and lichen species were found exclusively on one tree species. For example, *Antitrichia curtipendula* was found only on *Carpinus betulus*, and *Opegrapha viridis* on *Tilia cordata*. Several bryophyte species common on soil were also found on tree stems: *Climacium dendroides*, *Hylocomium splendens*, *Pleurozium schreberi*, *Rhodobryum roseum* and *Thuidium tamariscinum*.

The species richness of various epiphytic bryophyte and lichen species varied among tree species (Fig. 2a). The highest total epiphytic species (mean 11.7) and bryophyte species richness (mean 8.1) were found on *Populus tremula* and lichen species richness on *Sorbus aucuparia* (mean 6.2 species) and *Tilia cordata* (mean 4.5 species).

Significant differences were found in total species richness between *Acer platanoides* and *Populus tremula* and bryophyte species richness varied significantly between *Tilia cordata* and *Fraxinus excelsior* (Table 3).

Latvian red-listed species (mean 1.7) were more common on *Carpinus betulus* (Fig. 2b), as well as on *Fraxinus excelsior* and *Acer platanoides* compared with other tree species. Significant differencies were found in red-listed epiphytic bryophyte and lichen species richness between *Carpinus betulus*, *Fraxinus excelsior, Acer platanoides* and other tree species (Table 3). Red-listed lichen species were not found on *Sorbus aucuparia, Ulmus laevis, Betula pendula* and *Alnus incana*. Tree species was the most significant factor explaining various groups of epiphytic bryophyte and lichen species richness (Table 4). Red-listed bryophyte species richness was removed due to high autocorrelation (r=0.960) with total red-listed species richness after Spearman rank correlation.

Bark pH value varied among tree species (Fig. 3). The highest mean pH (6.13) was found for *Ulmus laevis* and the lowest (3.53) for *Betula pendula*.

DBH explained total and red-listed bryophyte and lichen species richness, but tree bark pH affected significantly only lichen species richness. Bark crevice depth did not explain epiphytic bryophyte or lichen species richness (Table 4).

DISCUSSION

In the present study *Hypnum cupressiforme*, an ubiquitous species, *Radula complanata* and *Homalia trichomanoides* were the most common bryophyte species. *Radula complanata* is one of the most frequent epiphytic bryophyte species in Central Sweden (Hazell et al., 1998). *Homalia trichomanoides* was the most common indicator species in the WKH inventory data in Latvia (Anonymous, 2003), *Lepraria* spp, and *Phlyctis argena* were the most common lichens in the present study, as described previously (Piterāns, 2001). The most common red-listed bryophyte species in Latvia were *Metzgeria furcata* and *Neckera pennata* as also found in the WKH inventory (Anonymous, 2003), but *Lejeunea cavifolia* and *Neckera complanata* common in the WKH inventory, were not frequent in the present study. The WKH inventory was conducted in various forest types in Latvia, but the present study was focused on old – growth broad leaved forests exclusively. *Thelotrema lepadinum*, one of the rarest species in the present study, was common in the WKH inventory. On the other hand *Pertusaria pertusa*, the most common red-listed lichen species in the present study, was one of the rarest lichen species observed in the WKH inventory (Anonymous, 2003). Probably there is a need to update the information on species in the Latvian bryophyte and lichen red-lists based on data in the present study and in the WKH inventory. The most recent data on red-

Table 2. Epiphytic bryophyte and epiphytic lichen species occurrence. Number of tree stems for species is given in brackets. ^{v} – vulnerable and ^{r} – rare red-listed species in Latvia.

Epiphyte species	Tree species													
Bryophytes	*Carpinus betulus* (30)	*Fraxinus excelsior* (45)	*Acer platanoides* (38)	*Ulmus glabra* (51)	*Tilia cordata* (118)	*Ulmus laevis* (16)	*Sorbus aucuparia* (5)	*Alnus incana* (12)	*Populus tremula* (14)	*Betula pendula* (8)	*Quercus robur* (47)	*Alnus glutinosa* (5)	*Salix caprea* (1)	Total
Amblystegium serpens	1	13	15	30	28	16	2	3	7	-	11	1	-	127
Amblystegium subtile	-	1	1	1	1	-	-	-	-	-	-	-	-	4
Amblystegium varium	-	-	1	-	-	-	-	-	-	-	-	-	-	1
Anomodon attenuatus	-	6	-	4	2	2	-	1	1	-	2	5	1	24
Anomodon longifolius	-	4	10	4	1	5	-	-	7	-	-	-	-	31
Anomodon viticulosus	-	2	1	3	13	-	-	-	-	-	2	-	-	21
Antitrichia curtipendula^{v}	4	-	-	-	-	-	-	-	-	-	-	-	-	4
Blepharostoma trichophyllum	-	-	-	-	1	-	-	-	-	-	-	-	-	1
Brachythecium glareosum	-	-	1	-	-	1	-	-	-	-	-	-	-	2
Brachythecium oedipopodium	3	-	-	3	6	-	-	-	-	-	3	2	-	17
Brachythecium populeum	-	8	2	4	8	-	-	-	-	-	2	-	-	24
Brachythecium rutabulum	2	17	16	17	28	-	-	3	6	-	16	3	1	109
Brachythecium salebrosum	-	1	2	2	3	-	-	-	-	1	3	-	-	12
Brachythecium velutinum	-	-	1	-	1	-	-	-	-	-	-	-	-	2
Campylium chrysophyllum	-	-	-	-	-	1	-	-	-	-	-	-	-	1
Cirriphyllum piliferum	-	2	1	2	1	1	-	1	1	-	1	-	-	10
Climacium dendroides	-	-	-	-	1	-	-	-	-	-	-	-	-	1
Dicranum montanum	2	-	1	3	47	-	-	2	-	7	26	5	-	93
Dicranum scoparium	1	-	-	-	10	-	-	1	-	2	3	-	-	17
Dicranum viride^{r}	-	4	-	1	7	-	-	-	-	-	3	-	1	16
Eurhynchium angustirete	1	4	5	10	20	1	-	1	1	1	3	-	-	47
Eurhynchium hians	-	4	-	9	3	7	-	1	9	-	2	1	-	36
Eurhynchium pulchellum	-	-	-	1	-	2	-	-	-	-	-	-	-	3
Eurhynhium striatum	7	8	5	1	9	2	-	4	1	-	-	-	-	37
Fissidens adianthoides	-	-	-	-	-	-	-	-	-	-	1	-	-	1
Fissidens bryoides	-	-	-	1	-	-	-	-	-	-	-	-	-	1
Frullania dilatata	15	20	4	5	7	1	1	-	4	-	-	-	1	58
Homalia trichomanoides	11	41	31	43	50	7	1	7	12	2	18	5	1	229
Homalothecium sericeum	10	2	8	4	7	1	-	-	-	-	-	-	-	32
Hylocomium splendens	-	-	-	-	1	-	-	-	-	-	-	-	-	1
Hypnum cupressiforme	28	26	12	24	93	5	3	9	14	8	42	2	1	267
Isothecium alopecuroides	20	9	7	5	8	-	-	-	1	-	3	-	-	53
Jamesoniella autumnalis^{r}	-	-	-	-	2	-	-	-	-	1	-	-	-	3
Jungermannia leiantha	-	-	-	-	-	-	-	-	-	-	1	-	-	1
Lejeunea cavifolia^{v}	-	4	1	4	1	1	-	-	1	-	-	-	-	12
Leucodon sciuroides	5	21	16	21	13	15	-	1	3	-	6	-	-	101
Lophocolea heterophylla	-	-	1	-	3	-	-	1	1	1	1	-	-	8
Metzgeria furcata^{v}	17	19	13	16	39	2	1	4	1	1	2	-	-	115
Mnium hornum	-	-	-	-	7	-	-	-	1	-	7	-	-	15
Mnium stellare	-	-	1	1	2	-	-	-	-	1	-	-	-	5

Table 2 (continued)

Epiphyte species	Tree species													
Bryophytes	*Carpinus betulus* (30)	*Fraxinus excelsior* (45)	*Acer platanoides* (38)	*Ulmus glabra* (51)	*Tilia cordata* (118)	*Ulmus laevis* (16)	*Sorbus aucuparia* (5)	*Alnus incana* (12)	*Populus tremula* (14)	*Betula pendula* (8)	*Quercus robur* (47)	*Alnus glutinosa* (5)	*Salix caprea* (1)	Total
Neckera complanata″	14	10	11	3	1	-	1	-	1	-	-	-	-	41
Neckera pennata″	1	11	15	23	11	6	1	-	-	-	3	-	-	71
Orthotrichum affine	4	2	2	5	2	3	2	2	1	-	2	-	-	25
Plagiochila asplenioides	2	2	3	4	4	-	-	2	1	-	-	-	-	18
Plagiochila porelloides	1	-	1	-	5	-	-	-	-	-	-	-	-	7
Plagiomnium affine	-	4	4	5	10	-	-	2	-	1	1	-	-	27
Plagiomnium cuspidatum	-	3	2	2	7	-	-	-	-	1	2	-	-	17
Plagiomnium undulatum	-	1	-	3	5	1	-	-	-	-	-	-	-	10
Plagiothecium cavifolium	-	1	-	1	1	-	-	-	-	-	2	-	-	5
Plagiothecium laetum	1	3	-	-	8	-	-	2	-	1	6	-	-	21
Plagiothecium latebricola	-	-	-	-	2	-	-	-	-	-	1	-	-	3
Platygyrium repens	4	14	2	10	36	-	2	4	5	1	19	4	1	102
Pleurozium schreberi	-	-	-	-	2	-	-	-	-	-	-	-	-	2
Pseudoleskeella nervosa	-	4	6	8	32	3	3	3	2	-	24	-	1	86
Ptilidium pulcherrimum	-	-	-	-	3	-	-	-	-	2	-	-	-	5
Pylaisia polyantha	4	16	2	17	10	6	2	1	9	1	8	-	-	76
Radula complanata	21	33	25	44	59	16	4	8	13	1	16	5	1	246
Rhytidiadelphus triquetrus	-	1	1	-	8	-	-	-	-	-	1	-	-	11
Rhodobryum roseum	-	-	-	-	1	-	-	-	-	-	-	-	-	1
Sanionia uncinata	-	2	2	5	10	1	-	-	5	-	2	1	-	28
Thuidium delicatulum	-	5	1	2	5	-	-	-	2	-	2	-	-	17
Thuidium tamariscinum	2	-	-	-	-	-	-	-	-	-	-	-	-	2
Ulota crispa	7	6	3	5	13	2	1	3	4	-	3	-	-	47
Lichens														
Acrocordia gemmata	-	6	3	5	2	5	-	-	13	-	8	1	-	43
Arthonia byssacea	-	-	-	-	1	-	-	-	-	-	-	-	-	1
Arthonia radiata	-	10	2	4	-	-	1	1	3	-	1	1	1	24
Arthonia vinosa	-	-	3	1	3	-	-	-	-	-	-	-	-	7
Arthothelium ruanum	1	-	-	-	-	-	1	-	-	-	3	-	-	5
Bacidia friesiana	-	-	1	-	1	-	-	-	-	-	-	-	-	2
Bacidia rubella	-	2	-	7	-	3	-	-	3	2	1	-	-	18
Buellia griseovirens	-	4	-	3	1	-	-	3	-	1	-	-	1	13
Calicium abietinum	-	-	-	-	1	-	-	-	-	-	-	-	-	1
Chaenotheca brunneola	-	-	-	-	-	-	-	-	-	-	1	-	-	1
Chaenotheca ferruginea	-	1	1	-	-	-	-	-	-	-	3	1	-	6
Chrysotrix candelaris	-	1	-	-	3	-	-	-	-	-	-	-	-	4
Cladonia coniocraea	-	2	1	3	43	-	-	1	1	7	16	2	-	76
Dimerella lutea	-	-	2	-	1	-	-	-	-	1	-	-	-	4
Evernia prunastri	-	-	1	-	2	3	1	-	-	-	-	-	-	7
Graphis scripta	7	13	12	21	65	2	5	11	-	1	6	4	1	148
Gyalecta truncigena	-	-	-	-	-	1	-	-	-	-	-	-	-	1

Table 2 (continued)

Epiphyte species	Tree species													
Bryophytes	*Carpinus betulus* (30)	*Fraxinus excelsior* (45)	*Acer platanoides* (38)	*Ulmus glabra* (51)	*Tilia cordata* (118)	*Ulmus laevis* (16)	*Sorbus aucuparia* (5)	*Alnus incana* (12)	*Populus tremula* (14)	*Betula pendula* (8)	*Quercus robur* (47)	*Alnus glutinosa* (5)	*Salix caprea* (1)	Total
Hypocenomyce scalaris	-	-	-	-	-	-	-	-	-	1	-	-	-	1
Hypogymnia physodes	-	-	1	-	54	-	1	2	-	6	11	-	-	75
Lecanactis abietina	-	-	-	-	-	-	-	-	-	-	1	-	-	1
Lecanora allophana	1	-	1	-	-	-	-	-	-	-	1	-	-	3
Lecanora argentea	-	-	1	-	6	-	-	-	-	-	-	-	-	7
Lecanora carpinea	-	1	-	2	5	1	-	-	1	-	1	-	-	11
Lecanora glabrata	23	-	-	-	-	-	-	-	-	-	-	-	-	23
Lecanora rugosella	-	1	-	-	-	-	-	-	-	-	-	-	-	1
Lecanora subrugosa	-	5	4	2	4	-	1	-	-	-	1	-	-	17
Lecidella elaeochroma	1	9	4	3	4	1	2	3	2	-	2	-	-	31
Lecidella euphorea	-	7	-	6	6	5	1	-	-	-	-	1	1	27
Lepraria spp.	30	30	33	34	87	5	4	5	10	6	45	4	-	293
Lobaria pulmonaria[r]	-	1	1	1	3	-	-	-	1	-	1	-	-	8
Melanelia exasperata	-	-	1	-	-	-	-	-	-	-	-	-	-	1
Melanelia glabratula	-	6	5	8	43	2	2	7	-	-	3	1	-	77
Melanelia olivacea	-	1	-	1	3	2	1	1	-	-	-	-	-	9
Ochrolechia androgyna	-	-	-	-	-	-	-	-	-	-	2	-	-	2
Opegrapha rufescens	5	5	7	4	6	6	-	-	1	-	3	-	-	37
Opegrapha varia var. varia	-	2	6	2	6	2	-	-	-	-	8	-	-	26
Opegrapha viridis[r]	-	-	-	-	1	-	-	-	-	-	-	-	-	1
Opegrapha vulgata	-	-	-	1	-	-	-	-	-	-	-	-	-	1
Parmelia saxatilis	-	-	-	-	1	-	-	-	-	-	-	-	-	1
Parmelia sulcata	-	3	4	2	23	3	2	2	-	-	2	-	-	41
Peltigera praetextata	-	5	2	-	5	-	-	-	-	-	5	-	-	17
Pertusaria albescens	-	-	-	1	-	1	2	-	-	-	-	-	-	4
Pertusaria amara	-	5	5	6	62	-	2	2	1	1	18	-	-	102
Pertusaria leioplaca	-	-	1	2	3	-	-	-	-	-	-	-	-	6
Pertusaria multipuncta	3	-	-	-	-	-	-	-	-	-	-	-	-	3
Pertusaria pertusa[r]	16	1	1	1	2	-	-	-	-	-	1	-	-	22
Phlyctis agelaea	-	2	-	-	1	1	-	-	-	-	-	-	-	4
Phlyctis argena	10	29	19	45	82	12	5	11	14	1	29	1	1	259
Physcia dubia	-	-	-	-	-	-	-	-	-	1	-	-	-	1
Porina aenea	2	-	-	-	-	-	-	-	-	-	-	-	-	2
Pyrenula laevigata	-	1	-	-	-	-	-	-	-	-	-	-	-	1
Pyrenula nitida	4	-	-	1	-	-	-	-	-	-	-	-	-	5
Pyrenula nitidella	5	-	-	-	-	-	-	-	-	-	-	-	-	5
Ramalina farinacea	-	-	1	2	10	-	1	2	-	-	6	-	-	22
Sclerophora nivea	-	-	-	1	-	1	-	-	-	-	-	-	-	2
Thelotrema lepadinum[r]	-	-	1	1	2	-	-	-	-	-	-	-	-	4
Vulpicida pinastri	-	-	-	-	1	-	-	-	-	-	-	-	-	1

Table 3. Post-Hoc Multiple Comparisons after Scheffe between tree species and epiphytic bryophyte and lichen species richness. Ac – *Acer platanoides*, Ai – *Alnus incana*, C – *Carpinus betulus*, F – *Fraxinus excelsior*, P – *Populus tremula*, Q – *Quercus robur*, T – *Tilia cordata*, U – *Ulmus glabra*, Ul – *Ulmus laevis*, To – total bryophyte and lichen species richness, B – bryophyte species richness, L – lichen species richness, ToR– total red-listed bryophyte and lichen species richness, LR – red-listed lichen species richness, (noted if significant (p<0.05) difference between tree species was found), - – no significant difference (p>0.05).

	Ac	Ai	C	F	T	U
Ai	-	-	LR	-	-	-
C	LR	ToR	-	-	-	-
F	-	-	LR	-	B, L	-
P	To	-	ToR, LR	-	-	-
Q	ToR	-	ToR, LR	ToR	-	ToR
T	ToR	-	ToR, LR	ToR	-	-
U	-	-	LR	-	L	-
Ul	-	-	ToR, LR	-	-	-

listed bryophyte species was published in 1994 (Āboliņa, 1994), and red-listed lichen species in 1996 (Piterāns & Vimba, 1996).

Tree species was one of the most important factors explaining epiphytic species distribution. The highest number of epiphytic bryophyte and lichen species were found on *Populus tremula*, as found in several other studies from Nordic countries (Hazell et al., 1998; Snäll et al., 2004; Hedenås & Ericson, 2003). Epiphytic lichen species richness was highest on *Sorbus aucuparia*, but replication for this tree was low (6 trees) in our study. However, this agrees with studies of Pykälä et al. (2005) in Finland and Barkman (1958) in Central Europe. Jüriado et al. (2003) in Estonian natural forests observed the highest lichen species richness on *Populus tremula* and the lowest on *Sorbus aucuparia*. However, in that study boreo-nemoral forests and coniferous forests were considered together, where *Populus tremula* was more distributed among tree species.

Tree bark pH is known to be associated with epiphytic cryptogam species richness (Weibull, 2001; van Herk, 2001; Mežaka & Znotiņa, 2006; Löbel et al., 2006). Lichen species richness was lower on trees with higher bark pH, but epiphytic species richness in other epiphytic species groups were not explained significantly by bark pH in our study. Bark pH of *Populus tremula* (Gustafsson & Eriksson, 1995), *Tilia cordata* (Marmor & Randlane, 2007) and other broad leaved tree species (Loppi & Frati, 2004) were not found to be associated with epiphytic species richness. Thus the differences in cryptogamic species distribution associated with species richness might be due to some differences among tree species other than tree bark pH. Clearly also differences in the host of tree species sampled and the range of pH obtained will affect results obtained.

Relatively high lichen species richness was found on *Tilia cordata* (mean 4.65 species). *Tilia cordata* bark pH (mean 4.38) was lower compared with other studied tree species and a relatively low pH was associated with higher lichen species richness. Probably, *Tilia cordata* bark pH is too low for high bryophyte or red-listed species richness. Specific bark physical properties of *Tilia cordata* might ensure the lichen species diversity on this tree species.

Red-listed species were more common on *Carpinus betulus*. In literature *Carpinus betulus* is not described as having high epiphytic species diversity (Szövényi et al., 2004). *Antitrichia*

Table 4. Epiphytic bryophyte and lichen species depend on studied variables. Univariate GLM. - – non significant factor (p<0.05), Crev – bark crevice depth, DBH – tree diameter at breast height, pH – tree bark pH, epiphytic species group abbreviations as in Table 3.

Variables	Tests of Between-Subjects effects									
	F					p				
	To	B	L	ToR	LR	To	B	L	ToR	LR
Crev	-	-	-	-	-	-	-	-	-	-
DBH	6.628	14.96	-	5.747	-	0.01	0.0001		0.017	-
pH	-	-	16.902	-	-	-	-	0.0001	-	-
Tree species	-	2.654	-	10.656	10.497	-	0.008	-	0.0001	0.0001

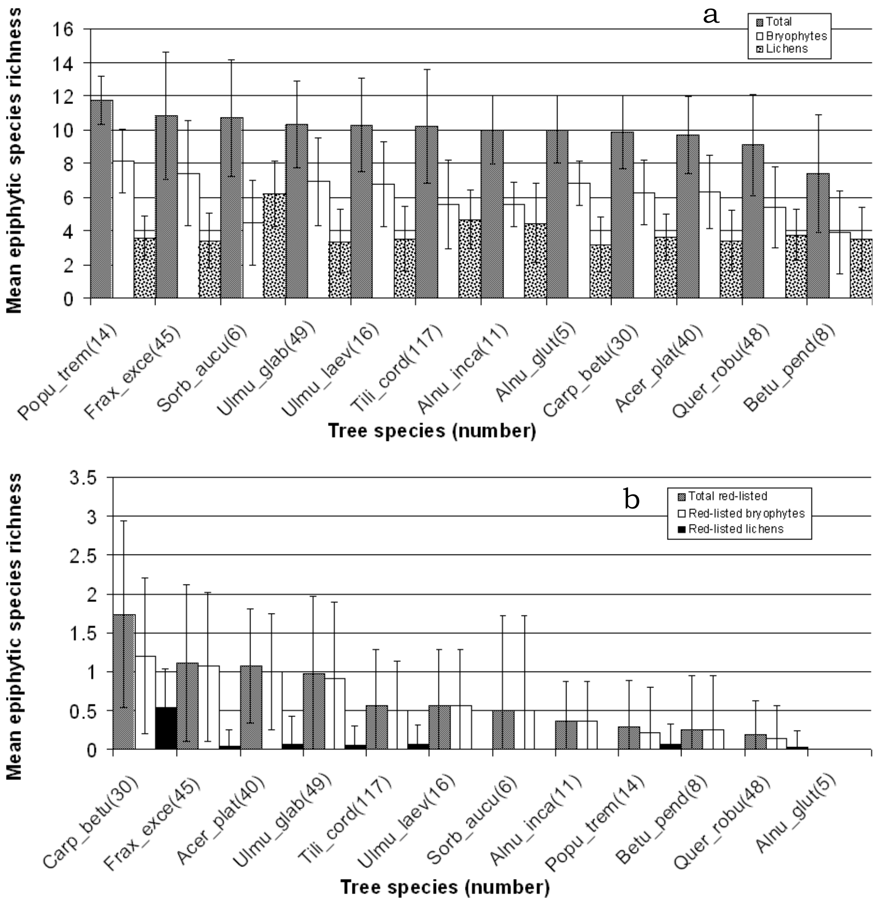

Fig. 2. Epiphytic bryophyte and lichen species richness within groups. Tree species arranged based on total epiphytic species richness (bryophytes and lichens) (a) and total red-listed epiphytic species (bryophytes and lichens) (b) among various tree species. *Salix caprea* was removed from analysis due to only one occurrence for this species. Abbreviations: Acer_plat – *Acer platanoides*, Alnu_glut – *Alnus glutinosa* Alnu_inca – *Alnus incana*, Betu_pend – *Betula pendula*, Carp_betu – *Carpinus betulus*, Frax_exce – *Fraxinus excelsior*, Popu_trem – *Populus tremula*, Ulmu_glab – *Ulmus glabra*, Ulmu_laev – *Ulmus laevis*, Quer_robu – *Quercus robur,* Sorb_aucu – *Sorbus aucuparia.* Number of tree individuals in brackets.

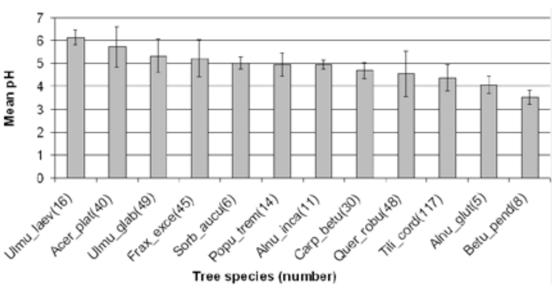

Fig. 3. Tree bark mean pH among tree species. Tree species abbreviations after Fig. 2.

curtipendula, which is red-listed in Latvia, was recorded only on *Carpinus betulus*, which is distributed only in the south-west part of Latvia (Mauriņš & Zvirgzds, 2006), where probably specific suitable conditions for *Carpinus betulus* consequently also exist for *Antitrichia curtipendula*. Probably climatic factors are the most important as *Antitrichia curtipendula* is distributed in western part of Latvia (Āboliņa, 1968). *Fraxinus excelsior*, *Acer platanoides* and *Ulmus glabra* were also rich in red-listed epiphytic bryophyte and lichen species, probably since broad leaved trees have relatively higher bark pH compared with other deciduous tree species (Barkman, 1958; Löbel et al., 2006; Mežaka & Znotiņa, 2006). *Acer platanoides* and *Fraxinus excelsior* bark is also porous with crevices, maintaining humidity (Barkman, 1958) for a longer time period, which can be an advantage for epiphytic bryophyte establishment.

DBH affected significantly positively the total epiphytic bryophyte and lichen, bryophyte and red listed species richness, but no significant relation was found between DBH and lichen species richness. Bark crevice depth was not associated significantly with any epiphytic cryptogam group species richness. This is in contrast to other studies, where these factors have been observed to be related to the lichen distribution (Stringer & Stringer, 1974; Riiali et al., 2001; Friedel et al., 2006). However, Löbel et al. (2006) concluded, that tree diameter was not significant factor in lichen species richness. Small diameter trees sometimes have deep bark crevices, for example *Ulmus glabra* (personal observations), which could create suitable conditions for epiphytic cryptogam species establishment.

Epiphytic bryophytes and lichens are important organism groups in the evaluation of forest continuity and connectivity (Ek et al., 2002). Lot of red-listed species have limited dispersal abilities and it could be the cause of using them as indicators of forest stand quality. There is still uncomplete information about cryptogam species distributions in boreal and temperate landscapes (Gustafsson et al., 2004) in Europe.

This is the first study on epiphytic bryophyte and lichen distribution in old-growth broad leaved forests in Latvia. Further studies are needed on landscape scale. In addition, experimental and survey studies investigating interactions between bryophytes and lichens need further research effort.

Conclusions

The results of the present study point to the need to update the bryophyte and lichen red-lists in Latvia, since numerous new localities for several of them were discovered.

Tree species and DBH were the most significant factors explaining most of epiphytic species groups, while tree bark pH affected significantly only lichen species richness.

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REFERENCES

Āboliņa, A. 1968. *Die Laubmoose der Lettischen SSR.* (In Russian, German summary). Riga, 332 pp.

Āboliņa, A. 1994. *Latvijas retās un aizsargājamās sūnas.* (In Latvian, English summary). Riga, 24 pp.

Āboliņa, A. 2001. Latvijas sūnu saraksts. (In Latvian, English summary). *Latvijas veģetācija* 3: 47–87.

Anonymous, 2003. *Dabisko meža biotopu inventerizācija Latvijas valsts mežos.* (In Latvian). 71 pp. [http://www.vmd1.gov.lv/doc_upl/Nosleguma_parskats.pdf]. 26.03.08.

Apinis, A. & Lācis, L. 1936. Data on the Ecology of Bryophytes 2. Acidity of the substrata of Musci. *Latvijas Botāniskā dārza raksti* 9(10): 1–100.

Apinis, A., & Diogucs A.M. 1935. Data on the Ecology of Bryophytes 1. Acidity of the substrata of Hepaticea. *Latvijas Universitātes Botāniskā dārza raksti* 1(3): 1–19.

Bambe, B. & Lārmanis, V. 2001. Specifics of forests and bryophyte flora in Nature Reserve Pirtslīcis – līkā atteka. (In Latvian). *Mežzinātne* 10 (43): 73–89.

Bambe, B. 2002. Dabas lieguma "Pilskalnes Siguldiņa" brioflora. (In Latvian). *Mežzinātne* 11(44): 111–124.

Barkman, J.J. 1958. *Phytosociology and ecology of cryptogamic epiphytes.* Van Gorcum. Assen. 628 pp.

Council Directive 92/43/EEK 1992. *On the protection of natural biotopes, wild plants and animal species.*

Dumpe, L. 1999. Mežu izmantošanas attīstība Latvijā. Latvijas mežu vēsture līdz 1940. In: *Latvijas mežu vēsture.* (In Latvian). Rīga, pp. 305–357.

Ek, T., Suško, U. & Auziņš, R. 2002. *Mežaudžu atslēgas biotopu inventarizācija. Metodika.* (In Latvian). Rīga, 76 pp.

Friedel, A., Oheimb, G.V., Dengler, J.& Härdtle, W. 2006. Species diversity and species composition of epiphytic bryophytes and lichens – a comparison of managed and unmanaged beech forests in NE Germany. *Feddes Repertorium* 117(1–2): 172–185.

Grolle R. & Long D. 2000. An annotated check-list of the Hepaticae and Anthocerotae of Europe and Macaronesia. *Journal of Bryology* 22: 103–140.

Gustafsson L., Hylander K. & Jacobson C. 2004. Uncommon bryophytes in Swedish forests-key habitats and production forests compared. *Forest Ecology and Management* 194:11–22.

Gustafsson, L. & Eriksson, I. 1995. Factors of Importance for the Epiphytic Vegetation of Aspen *Populus tre*mula with Special Emphasis on Bark Chemistry and Soil Chemistry. *The Journal of Applied Ecology* 32(2): 412–424.

Hanski, I. 2005. Landscape fragmentation, biodiversity loss and the societal response. *EMBO reports* 6(5): 388–392.

Hazell, P., Kellner, O., Rydin, H. & Gustafsson, L. 1998. Presence and abundance of four epiphytic bryophytes in relation to density of aspen *Populus tremula* and other stand characteristics. *Forest Ecology and Management* 107: 147–158.

Hedenås, H. & Ericson, L. 2003. Response of epiphytic lichens on *Populus tremula* in a selective cutting experiment. *Ecological Applications* 13(4): 1124–1134.

Ingerpuu, N. & Vellak, K. 2007. Growth of *Neckera pennata,* an epiphytic moss of old-growth forests. *The Bryologist* 110(2): 309–318.

Jüriado, I., Paal, J. & Liira, J. 2003. Epiphytic and epixylic lichen species diversity in Estonian natural forests. *Biodiversity and Conservation* 12: 1587–1607.

Lõbel, S., Snäll, T. & Rydin, H. 2006. Species richness patterns and metapopulation processes – evidence from epiphyte communities in boreo-nemoral forests. *Ecography* 29:163–182.

Lõbel, S., Snäll, T. & Rydin, H. 2006. Species richness patterns and metapopulation processes – evidence from epiphyte communities in boreo-nemoral forests. *Ecography* 29: 169–182.

Loppi, S. & Frati, L. 2004. Influence of tree substrate on the diversity of epiphytic lichens: comparison between *Tilia platyphyllos* and *Quercus ilex* (Central Italy). *The Bryologist* 107(3): 340–344.

Marmor, L. & Randlane, T. 2007. Effects of road traffic on bark pH and epiphytic lichens in Tallinn. *Folia Cryptog. Estonica* 43: 23–37.

Mauriņš, A. & Zvirgzds, A. 2006. *Dendroloģija.* (In Latvian). Riga, 448 pp.

Mežaka, A. & Znotiņa, V. 2006. Epiphytic bryophytes in old growth forests of slopes, screes and ravines in north-west Latvia. *Acta Universitatis Latviensis* (710): 103–116.

Mežaka, A., Strazdiņa, L., Brūmelis, G. & Piterāns, A. 2008. Epifītu flora un ekoloģija Dārznīcas pilskalnā. (In Latvian, English summary). *Latvijas veģetācija* 16: 19–34.

Paltto, H., Nordén, B., Götmark, F. & Franc, N. 2006. At which spatial and temporal scales does landscape context affect local density of Red data book and indicator species. *Biological Conservation* 133: 442–454.

Piterāns, A. & Vimba, E. 1996. *Red Data Book of Latvia. Rare and endangered species of plants and animals. Fungi and lichens.* Riga, 202 pp.

Piterāns, A. 2001. Latvijas ķērpju konspekts. (In Latvian, English summary). *Latvijas veģetācija* 3: 5–46.

Priedītis, N. 1999. *Latvijas mežs: daba un daudzveidība.* (In Latvian). Riga, 209 pp.

Priedītis, N. 2000. Habitats. In: Lārmanis V., Priedītis N. & Rudzīte M. *Handbook of woodland key habitats* (in Latvian). Riga, pp. 10–29.

Pykälä, J., Heikkinen, R.K., Toivonen, H. & Jääskeläinen, K. 2005. Importance of Forest Act habitats for epiphytic lichens in Finnish managed forests. *Forest Ecology and Management* 223: 84–92.

Riiali, A., Penttinen, A. & Kuusinen, M. 2001. Bayesian Mapping of Lichens Growing on Trees. *Biometrical Journal* 43(6): 717–736.

Slack, N.G. 1976. Host specificity of bryophytic epiphytes in Eastern North America. *Journal of Hattori Botanical Laboratory* 41:107–132.

Smith, A.J.E. 2004. *The moss flora of Britain and Ireland.* Cambrige, 1012 pp.

Snäll, T., Hagström, A., Rudolphi, J. & Rydin, H. 2004. Distribution pattern of the epiphyte *Neckera pennata* on three spatial scales – importance of past landscape structure, connectivity and local conditions. *Ecography* 27: 757–766.

Stringer, P.W. & Stringer, M.H.L. 1974. A quantitative study of corticolous bryophytes in the vicinity of Winnipeg, Manitoba. *The Bryologist* 77(4): 551–560.

Szövényi, P., Hock, Z.S. & Tóth, Z. 2004. Phorophyte preferences of epiphytic bryophytes in a stream valley in the Carpathian Basin. *Journal of Bryology* 26: 137–146 p.

Temņikova, A. 1975. Klimats. In: *Latvijas PSR ģeogrāfija.* (In Latvian). Riga, pp. 45–54.

van Herk C.M. 2001. Bark pH and susceptibility to toxic air pollutants as independent causes of changes in epiphytic lichen composition in space and time. *Lichenlogist* 33(5): 419–441.

VMD 2007. *Valsts meža dienests.* [http://www.vmd.gov.lv]. 26.03.08.

Weibull, H. 2001. Influence of tree species on the epilithic bryophyte flora in deciduous forests of Sweden. *Journal of Bryology* 23:55–66.

Znotiņa, V. 2003. Epiphytic bryophytes and lichens in boreal and northern temperate forests. *Proceedings of Latvian Academy of Sciences* 57:1–10.

Zunde, M. 1999. Mežainuma un koku sugu sastāva pārmaiņu dinamika un to galvenie ietekmējošie faktori Latvijas teritorijā. In: *Latvijas mežu vēsture.* (In Latvian). Riga, pp. 111–203.