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ORIGINAL PAPER

Tree and stand-scale factors affecting richness and composition of epiphytic bryophytes and lichens in deciduous woodland key habitats

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Abstract Conservation and sustainable forestry are essential in a multi-functional landscape. In this respect, ecological studies on epiphytes are needed to determine abiotic and biotic factors associated with high diversity. The aim of the present study was to evaluate relative sensitivity of conservation targets (epiphytic bryophytes and lichens) in relation to contrasting environmental variables (tree species, tree diameter at breast height, bark crevice depth, pH, tree inclination, pH, forest stand age, area and type) in boreo-nemoral forests. The study was conducted in Latvian 34 woodland key habitat (WKH) boreo-nemoral forest stands. Generalized linear mixed models and canonical correspondence analysis showed that tree species and tree bark pH were the most important variables explaining epiphytic bryophyte and lichen composition and richness (total, Red-listed, WKH indicator species). Forest stand level factors, such as stand size and habitat type, had only minor influence on epiphytic species composition and richness. The results of the present study indicate a need to maintain the diversity of tree species and large trees, particularly *Acer platanoides, Carpinus betulus, Fraxinus excelsior, Populus tremula, Tilia cordata, Ulmus glabra* and *Ulmus laevis* in conservation of epiphytic bryophyte and lichen communities in the future.

Keywords Epiphytes · Bryophytes · Lichens · Tree · Woodland key habitats

Introduction

In Northern Europe, commercial forestry has led to a decline of natural processes, structures and biodiversity (Brūmelis et al. 2011). Multi-functional landscape concept refers to landscapes, where ecological, socio-cultural and economical values are taken into account (Groot de 2006). Within such a landscape, knowledge of the factors associated with high biodiversity are important in setting conservation targets.

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Epiphytic bryophytes and lichens in forest ecosystems have been widely used as indicators of forest continuity and naturalness (Ek et al. 2002; Frego 2007), making them important part of forest biodiversity. Much is known about epiphyte relationships with environmental factors in natural boreal forests (Gustafsson et al. 1999; Pykälä et al. 2006), including boreo-nemoral forests (Prieditis 2002; Jüriado et al. 2003). Based on their ecological demands (e.g. poor dispersal ability and short-term woody substrate), epiphytes are used as woodland key habitat (WKH) indicators (Ek et al. 2002).

The particular tree species present in a stand constitute an important factor influencing epiphytic bryophyte and lichen community composition (Billings and Drew 1938; Barkman 1958; Mežaka et al. 2008). The tree factor is highly related to bark pH (Barkman 1958; Kuusinen 1996; Larsen et al. 2006). Other factors that affect epiphyte species richness and distribution are tree age (Abolin 1968; Uliczka and Angelstam 1999; Ranius et al. 2008), tree inclination (Barkman 1958; Smith 1982; Kuusinen 1994) and physical characteristics of bark (Barkman 1958; Bates 1992; Löbel et al. 2006). Tree diameter, which is a surrogate of tree age and is correlated with availability of space, is also known as a key factor (Barkman 1958; Trynoski and Glime 1982; Belinchòn et al. 2007).

The wider forest habitat can also be important in determining epiphyte distribution (Barkman 1958; Abolin 1968; Slack 1976), i.e. specific epiphytic species occur in specific habitat types with a unique local environment. Also size of the forest stand can affect distribution of epiphytic species (Ojala et al. 2000; Berglund and Jonsson 2003). Tree level variables have been found to be more important than stand level variables in explaining composition and richness of epiphytic lichen species (Jüriado et al. 2009a). This suggests that turnover within and among tree species is important to manage environmental heterogeneity and epiphyte diversity. However, as tree species composition might covary with stand-level variables, there is need to differentiate between these two sets of factors. Knowledge of the main factors affecting biological diversity is important in conservation management, as it can enable development of quantitative targets for both habitat structures and species (Villard and Jonsson 2009).

The present study was focused on evaluating a wide spectrum of environmental variables at tree and forest stand scales in nemoral tree species (*Acer platanoides*, *Carpinus betulus*, *Tilia cordata, Ulmus glabra, Ulmus laevis,* and *Quercus robur*) and *Populus tremula* stands, to determine the relative importance of environmental variables explaining different conservation targets (epiphytic bryophytes and lichens). The null hypothesis in our study was that different conservation targets (total richness, WKH indicator species, Red-listed species for epiphytic lichens and bryophytes) are sensitive to the same set of habitat factors.

Materials and methods

Field work

The studied stands were located in Latvia, which is found in the boreo-nemoral vegetation zone (Sjörs 1963). The forest area in Latvia is 54 % of the total land area. Coniferous forests have a slightly greater area than deciduous forests. The area of nemoral forests is only 1 % of the total forest area in Latvia (VMD 2009). The study was restricted to WKHs, as they represent stands that rank high in naturalness, i.e. they have evidence of natural disturbances, structures and species typical of old-growth woodland (Brūmelis et al. 2011). In Latvia, WKH are defined as areas that contain species that cannot survive in stands managed for timber production. The WKHs are identified by the presence of structures typical of natural forests and also indicator species (Ek et al. 2002).

Effort was made to select a subset of WKHs that encompassed the range of boreo-nemoral forest habitats and aspen *P. tremula* forest with replication of the forest types. Aspen WKHs were included due to the similarity of its epiphyte community composition with that in boreo-nemoral tree species forests and biological value of these forests (Hedenås and Ericson 2000). The study included five WKH types: (1) boreo-nemoral WKH—defined as a natural stand where at least 50 % of the stand volume consists of tree species, with clearly uneven tree size structure and pronounced gaps; (2) aspen WKH—a naturally regenerated stand, where at least 50 % of the stand volume consists of aspen, with evidence of a major natural disturbance (wind-throw, fire) or more often, human disturbance (clear-felling) which is followed by a natural succession favouring deciduous trees; (3) ravine WKH—a ravine, valley or brook gully formation, sometimes with a stream flowing in the ravine bottom, with ravine width over 10 m and depth at least 5 m (if there is a stream, width does not exceed 15 m; (4) slope WKH—a more or less steep slope with height over 10 m, which may face in any direction, often sloping towards a watercourse or lake, or located on the side of a moraine hill, or on a coastal or continental dune; and (5) riparian WKH—a variably forested, often fertile, riparian zone at the water's edge of rivers, streams and lakes, characterized by exposure to wind, ice, sun and in many cases periodic flooding, and by a terrain that is either flat or slightly sloping, sometimes with running ground water and seasonally high ground water level (Ek et al. 2002).

The data were collected in 2006–2008 in 34 stands designated as WKHs (Fig. 1), which were known to be rich in epiphytic species, based on data recorded in the WKH inventory. Effort was made to select stands in different geographical localities in Latvia. The forest stand age varied from 40 to 210 years and forest stand size from 0.5 to 12.6 ha. Forest stand size and age were taken from forest inventory data (VMD 2009). Forest stand age was assumed to be the age of the dominant tree species layer in the particular forest stand.

In total 30 trees in a sample plots (20 × 20 m) were selected in each of the 34 stands. If the number of trees in a 20 × 20 m plot was less than 30, then the plot size was increased to include 30 trees. If more than 30 trees were found in a selected sample plot, we selected trees randomly. Only trees with tree diameter at breast height (DBH) >0.05 m were selected. If a tree was branched from the base, the stem with the largest DBH was selected. Tree species was noted and DBH (m), inclination (°), bark pH and bark crevice depth (mm) were measured for each tree.

Tree inclination was measured at 0.5 m height with a surveying compass (actual angle from vertical), or at a higher height up to 2 m if the tree was vertical at 0.5 m height. If a tree was straight up to a 2 m height, the tree was evaluated as straight. Tree bark samples (0.5 g) with only dead bark tissue were collected from the north side up to a 1.30 m height on each tree stem for pH measurements in the laboratory. Bark thickness was up to 3 mm. Bark crevice depth was measured with a metal ruler on the north side at 1.20 m height on each tree.

Lists were made of epiphytic bryophyte and lichen species found on each tree ($n = 1020$) up to 2 m height by thorough examination. Most of the bryophyte and lichen species were identified in the field. Unknown specimens were collected for further identification in the laboratory. Bryophyte species nomenclature follows Grolle and Long (2000); Hill et al. (2006) and lichen species nomenclature follows Wirth (1995a, b) and Piterāns (2001).

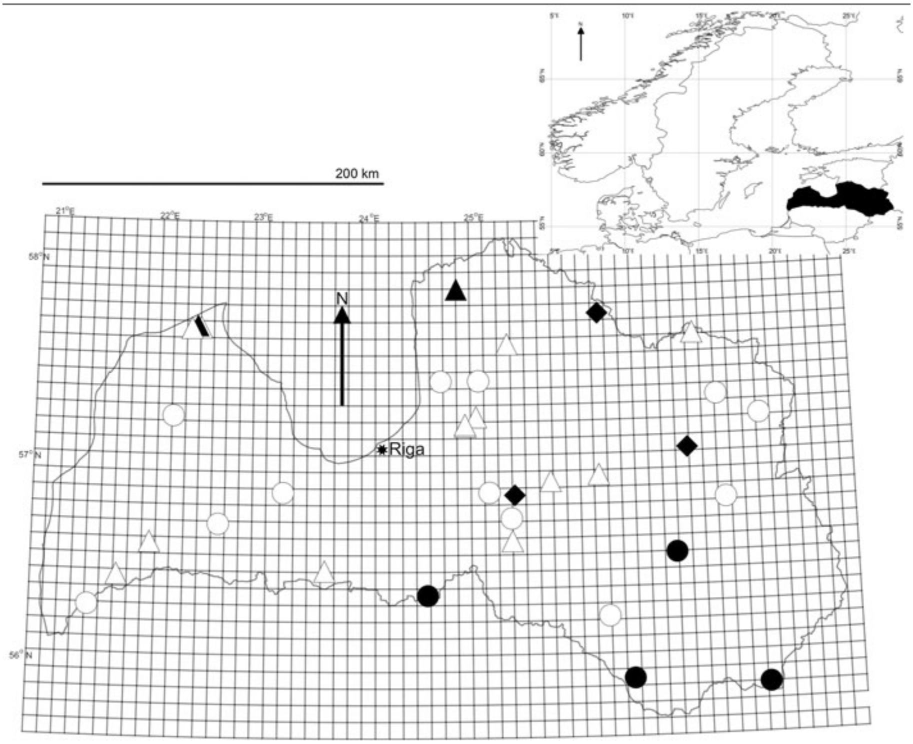

Fig. 1 Studied localities. *Open circles* nemoral tree species WKH, *filled circles* aspen WKH, *open triangles* slope WKH, *filled triangles* ravine WKH, *filled rombs* riparian WKH

Laboratory work

For pH measurement, tree bark was cleaned from bryophytes and lichens, air dried 1 week at room temperature and then cut into small pieces (medium size of one bark piece in a bark sample was 0.001 g). Some samples weighed less than 0.50 g due to difficulty of bark removal from *P. tremula*. Each bark sample was shaken in 20 ml 1 M KCl solution for 1 h and 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.

Several methods, such as 'spot tests', UV light and thin-layer chromatography were used for identification of lichen species in the present study (Orange et al. 2001). Some *Lepraria* samples were identified only to genus level (*Lepraria* sp.) due to insufficient material.

Data analysis

Species richness on each tree was determined separately for all epiphytes, Red-listed species, WKH indicator species, bryophytes, lichens, Red-listed bryophytes, Red-listed lichens, lichen WKH indicator species and bryophyte WKH indicator species. The red lists used were compiled by Āboliņa (1994) for bryophytes and by Vimba and Piterāns (1996) for lichens. Kendal's rank correlation coefficients were used to identify significant relationships between richness of the above mentioned epiphyte groups on trees. The Tukey HSD test was used for checking significant differences in species richness groups between tree species pairs.

A generalized linear mixed model (GLMM) was used to determine the effect of tree level variables (tree species, DBH, bark crevice depth, bark pH, intensity of tree inclination, and forest stand level variables (forest stand size, forest stand age, WKH type) on species richness for the above groups. Red-listed lichens were excluded from the analysis, as most trees lacked species from this group. GLMM with Poisson family, Laplace approximation and log link function was used for building models with the studied factors in relation to species richness. All tree and forest stand factors were considered as fixed effects and studied plot number as a random effect (Bolker et al. 2008). A full tree variable model and full tree plus forest stand variable model were developed for each of studied species groups. The power of each model was estimated by the akaike information criterion (AIC) and deviance. For evaluation of stand factor effect, ANOVA was used to test for significant differences between tree variable and stand variable models for each species richness group. AIC weights were used for selection of the best of the two models for each species richness group if a significant ($p < 0.05$) difference between models was found. Posterior correction of p values was not performed. The R program package 2.7.2. version (lme4 library) was used in the statistical tests (http://www.r-project.org/, Venables et al. 2008).

Mean epiphyte richness on a tree was also determined for each species group in plots. The Kruskall–Wallis rank sum test was used to test for significant differences in epiphyte species richness between WKH types.

Canonical correspondence analysis (CCA) was used to determine relationships between epiphytic bryophyte and lichen species composition and tree species, heterogeneity (number of tree species in studied sample plot/s, altogether 34 values), inclination, pH, bark crevice depth, tree diameter, forest type, size and age. CCA was conducted using the Canoco for Windows 4.53 program (Braak and Šmilauer 2002).

Results

Species richness

In total 148 (73 bryophyte and 75 lichen) epiphytic species were found in the present study on 1020 trees (Appendix Table 4). These included 15 Red-listed species in Latvia (ten bryophyte and five lichen species) and 21 WKH indicator species (12 bryophyte and nine lichen species) (Appendix Table 4). New localities were found for the bryophyte species *Dicranum viride*, which is a European Habitat Directive species (The Council of the European Communities 1992). The highest correlation coefficients were found between WKH and WKH bryophyte indicator species richness and all Red-listed species and Red-listed bryophyte species richness (Table 1). Significant correlations were shown by Red-listed lichen species richness with WKH indicator and WKH lichen indicator species richness.

The most common bryophyte species were *Hypnum cupressiforme* (on 737 of 1020 trees), *Radula complanata* (on 681 trees) and the WKH indicator species *Homalia trichomanoides* (on 548 trees). The most common lichen species were *Phlyctis argena* (on 768 trees), *Lepraria lobificans* (on 617 trees) and the WKH indicator species *Graphis scripta* (on 325 trees). *Metzgeria furcata* (on 228 trees) and *Lobaria pulmonaria*

Table 1 Epiphyte richness group pair-wise correlations after Kendal

	Red-listed species richness	Red-listed bryophyte species richness	Red-listed lichens species richness
WKH indicator species richness	0.564	0.574	0.096
WKH bryophyte indicator species richness	0.635	0.669	–
WKH lichen indicator species richness	–	–	0.169

Only significant correlations ($p < 0.05$) are shown

(on 14 trees) were the most common Red-listed species. The highest total, bryophyte, bryophyte WKH indicator and bryophyte Red-listed species richness was found in ravine WKH, and the highest lichen richness in riparian WKH. Slope WKH hosted the highest Red-listed lichen richness (Table 2). However, the Kruskall Wallis rank sum test did not show a significant habitat effect for any of the epiphyte species richness groups.

Total epiphytic species richness was rather similar among the studied tree species (Table 2). Total bryophyte species richness was highest on *U. laevis, Fraxinus excelsior* and *P. tremula*. *C. betulus* hosted the highest Red-listed species richness and bryophyte Red-listed species richness. The highest WKH indicator species richness was found on *U. laevis*. The highest lichen species richness was found on *T. cordata* and *Sorbus aucuparia* and highest WKH lichen indicator species richness on *Alnus incana*. Epiphytic species richness was generally low on *A. glutinosa* and *Q. robur.* Differences were found between tree species pairs in different epiphyte species richness groups. *U. glabra* showed significant differences between other tree species in seven epiphyte species richness groups and *F. excelsior, P. tremula, Acer platanoides, T. cordata, Q. robur*, *Betula pendula* showed differences in six epiphyte species richness groups (Table 2).

Tree and forest stand factors

In a CCA ordination, the gradients of species composition were best explained by pH and tree species (Fig. 2). The eigenvalues of CCA axes one and two were 0.195 and 0.165, respectively. Epiphytic species on the right side of the ordination, such as *Dicranum scoparium, D. montanum* and *Cladonia coniocraea*, were associated with tree species (*B. pendula, A. glutinosa, T. cordata and Q. robur*) that had lower pH. Epiphytic species on the left side of ordination, such as *Anomodon longifolius, M. furcata*, *Acrocordia gemmata*, were associated with *A. platanoides*, *F. excelsior* and higher pH. *Lecanora glabrata* was found more on *C. betulus* and therefore, the second axis can be considered to be due to an outlier effect.

Tree species was the main factor explaining species richness in all of the GLMM models for the epiphytic species groups. The tree species with the most significant influence in the models were *A. glutinosa*, *B. pendula, P. tremula, A incana, T cordata* and *F. excelsior*, but the effect was either positive or negative. *A. glutinosa* showed negative effect on total, bryophyte and bryophyte indicator species richness, while it had positive effect on lichen indicator species richness. A positive relationship was found between *F. excelsior* and Red listed as well as bryophyte Red-listed species richness. *Q. robur* showed negative influence on total species richness, while *B. pendula* showed negative relationship with total, bryophyte, bryophyte WKH indicator and bryophyte Red-listed

Table 2 Epiphytic bryophyte and lichen species richness among studied forest habitat types and tree species

WKH type	Bryophytes			Lichens			Total	WKH indicator species	Red-listed species
	Total	WKH indicator species	Red-listed species	Total	WKH indicator species	Red-listed species			
Ravine ($n = 2$)	7.40 ± 2.68	2.40 ± 1.25	1.07 ± 0.81	2.80 ± 1.29	0.48 ± 0.72	0.03 ± 0.18	10.20 ± 3.26	2.88 ± 1.53	1.10 ± 0.85
Riparian ($n = 3$)	5.99 ± 2.12	1.71 ± 1.06	0.34 ± 0.54	4.13 ± 1.96	0.86 ± 0.71	0.04 ± 0.21	10.12 ± 3.23	2.57 ± 1.31	0.39 ± 0.63
Slope ($n = 13$)	5.99 ± 2.89	1.31 ± 1.30	0.48 ± 0.77	3.98 ± 1.94	0.52 ± 0.66	0.07 ± 0.28	9.97 ± 3.39	1.83 ± 1.50	0.55 ± 0.85
Nemoral ($n = 12$)	6.09 ± 2.53	1.56 ± 1.21	0.64 ± 0.76	3.49 ± 1.66	0.49 ± 0.58	0.03 ± 0.19	9.59 ± 3.13	2.05 ± 1.28	0.67 ± 0.79
Aspen ($n = 4$)	6.63 ± 3.02	0.78 ± 0.74	0.15 ± 0.40	2.48 ± 1.17	0.35 ± 0.51	–	9.11 ± 3.34	1.13 ± 0.91	0.15 ± 0.40
Tree species									
Ulmus laevis ($n = 24$)	7.25 ± 2.42	1.88 ± 1.26	0.58 ± 0.65	3.42 ± 1.82	0.83 ± 0.70	0.04 ± 0.20	10.67 ± 3.09	**2.71** ± **1.52**	0.63 ± 0.71
Fraxinus excelsior ($n = 126$)	**7.17** ± **3.09**	2.08 ± 1.37	**0.80** ± **0.92**	**3.48** ± **1.80**	0.53 ± 0.71	0.06 ± 0.28	**10.65** ± **3.97**	**2.62** ± **1.71**	**0.87** ± **1.01**
Populus tremula ($n = 162$)	**7.53** ± **2.78**	1.25 ± 1.05	**0.44** ± **0.67**	**2.70** ± **1.39**	**0.29** ± **0.56**	0.01 ± 0.11	**10.23** ± **3.10**	**1.54** ± **1.28**	0.45 ± 0.67
Acer platanoides ($n = 118$)	**6.15** ± **2.70**	1.77 ± 1.38	**0.64** ± **0.79**	**3.75** ± **2.13**	**0.40** ± **0.53**	0.08 ± 0.29	9.90 ± 3.67	**2.18** ± **1.39**	**0.72** ± **0.81**
Carpinus betulus ($n = 30$)	6.27 ± 1.89	2.33 ± 1.15	**1.20** ± **1.00**	3.60 ± 1.38	**0.23** ± **0.43**	–	9.87 ± 2.19	**2.57** ± **1.19**	**1.20** ± **1.00**
Ulmus glabra ($n = 111$)	**6.60** ± **2.50**	1.72 ± 1.34	**0.70** ± **0.86**	**3.24** ± **1.57**	**0.63** ± **0.70**	0.05 ± 0.21	**9.84** ± **2.85**	**2.35** ± **1.46**	**0.75** ± **0.90**
Tilia cordata ($n = 249$)	**5.49** ± **2.52**	1.22 ± 1.12	**0.41** ± **0.62**	**4.33** ± **1.78**	**0.07** ± **0.27**	0.07 ± 0.27	9.82 ± 3.33	**1.94** ± **1.33**	**0.48** ± **0.73**
Salix caprea ($n = 3$)	5.33 ± 4.04	1.00 ± 1.00	0.33 ± 0.58	4.33 ± 1.15	0.33 ± 0.58	–	9.67 ± 4.04	1.33 ± 1.53	0.33 ± 0.58
Sorbus aucuparia ($n = 22$)	**4.41** ± **2.09**	0.55 ± 1.01	0.18 ± 0.66	**4.45** ± **2.48**	**0.91** ± **0.53**	0.05 ± 0.21	8.86 ± 3.23	1.45 ± 1.18	0.23 ± 0.69
Quercus robur ($n = 94$)	**5.42** ± **2.16**	1.12 ± 0.95	**0.30** ± **0.48**	3.37 ± 1.68	**0.25** ± **0.50**	0.02 ± 0.15	**8.78** ± **3.48**	**1.37** ± **1.02**	**0.32** ± **0.49**
Alnus incana ($n = 21$)	5.00 ± 2.00	1.19 ± 0.75	0.24 ± 0.44	3.67 ± 1.91	**1.05** ± **0.22**	–	8.67 ± 2.71	**2.24** ± **0.77**	0.24 ± 0.44

Table 2 continued

WKH type	Bryophytes			Lichens			Total	WKH indicator species	Red-listed species
	Total	WKH indicator species	Red-listed species	Total	WKH indicator species	Red-listed species			
Alnus glutinosa ($n = 18$)	**4.44 ± 2.18**	0.72 ± 0.39	–	3.83 ± 1.15	0.83 ± 0.62	–	**8.28 ± 2.14**	1.56 ± 1.20	–
Betula pendula ($n = 42$)	**4.71 ± 2.06**	0.50 ± 0.86	**0.12 ± 0.50**	3.05 ± 1.48	**0.26 ± 0.50**	–	**7.76 ± 2.71**	**0.76 ± 1.08**	**0.12 ± 0.50**

Mean richness and standard deviation are given. Values in *bold* indicate significant difference (Tukey HSD test) in pair-wise comparisons with at least two other tree species (lack of a value indicates no significant difference in pair-wise comparisons)

To total epiphyte species richness, *LI* lichen WKH indicator species, *I* WKH indicator species, *ToR* total Red-listed species, *BrR* bryophyte Red-listed species, *Br* bryophyte species richness, *L* lichen species richness

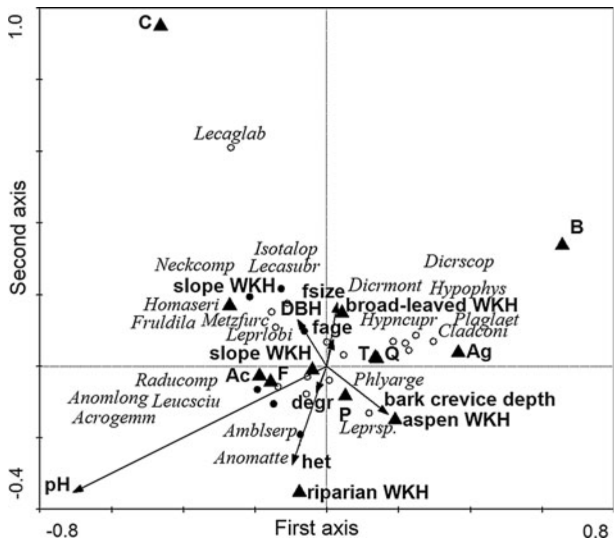

Fig. 2 CCA ordination in epiphytic species space. *Black dots* represent WKH indicator species and Red-listed species, *open circles* all other epiphytic species, *Black triangles* categorical variables tree species, WKH type (nominal factors), *arrows* other variables (vectors), *fage* forest age, *fsize* forest size, *Ac Acer platanoides*, *F Fraxinus excelsior*, *B Betula pendula*, *C Carpinus betulus*, *T Tilia cordata*, *Q Quercus robur*, *Ag Alnus glutinosa, P Populus tremula, degr* inclination of tree stem. Epiphytic species abbreviations are given in the Appendix Table 4. Only significant ($p < 0.05$) variables are included. The analysis was conducted using all species, but only species that occurred on >5 % of sampled trees were included in the ordination plot. This was done to restrict the interpretation of the ordination to the species showing the highest relationship to the derived gradients

species richness. *A. incana*, *T. cordata* and *S. aucuparia* showed positive relationship with lichen indicator species richness, while negative relationship was observed between *T. cordata* and bryophyte WKH indicator species as well as between *A. incana* and total species richness. *P. tremula* showed negative relationship with lichen and lichen WKH indicator species richness (Tables 2, 3). Heterogeneity influenced significantly only target species composition in CCA (Fig. 2).

Of the other tree-level factors, DBH had significant positive effect on three epiphyte species richness groups. Degree of inclination was positively related to bryophyte indicator species richness. Tree bark pH showed positive relationship with Red-listed, bryophyte WKH indicator species and bryophyte Red-listed species richness, but negative relationship was found with lichen richness. Bark crevice depth had negative effect on lichen WKH indicator species richness. The additional stand-level factors resulted in an improved GLMM models that significantly differed from the tree-scale models only for bryophyte WKH indicator species richness (Table 3). However, the difference in AIC of the two models for bryophyte WKH indicator species richness differed only slightly ($\Delta AIC = 2.7$).

Discussion

A significant correlation was observed between total WKH indicator species richness and total Red-listed species richness, as described earlier in Sweden (Gustafsson et al. 2004).

Table 3 GLMM models of epiphyte species richness groups explained by tree-scale variable and tree-scale plus stand-scale variables

Models	AIC	AIC weight	Deviance	Std. Error	Estimate	*p*
Total						
Tree species (Ag, Ai, B, Q) + DBH (+)	960.8		926.8	0.102	2.34	<0.01
Bryophytes						
Tree species (Ag, B) + DBH (+)	847.8		913.8	0.129	1.537	<0.01
Lichens						
Tree species (P, Ul) + pH (−)	671.7		637.7	0.168	1.934	<0.01
Total Red-listed						
Tree species (B, F) + pH (+)	648		614	0.501	−2.06	<0.01
Bryophyte indicator species						
Tree species (Ag, B, T) + degr (+) + DBH (+) + pH (+)	765.1	0.2	731.1	0.288	−0.698	<0.01
Tree species (Ag, B, T) + degr (+) + DBH (+) + pH (+) + forest type (coast, broadl) + fage (−)	762.4	0.799	718.4	0.464	−0.792	<0.01
Bryophyte Red-listed species						
Tree species (F) + pH (+)	607.7		573.7	0.528	−2.514	<0.01
Lichen indicator species						
Tree species (Ai, So, T) + crev (−)	685.3		651.3	0.461	−0.575	<0.01

Only the tree-scale variable model is shown in cases when there was no significant difference (ANOVA) between the models. Significant positive or negative parameter estimates are shown after continuous variable in brackets. Tree species and habitat type were categorical variables

Only significant ($p < 0.05$) factors in the models are shown. Only significant models ($p < 0.05$) included

Ag Alnus glutinosa, *B Betula pendula*, *F Fraxinus excelsior*, *Q Quercus robur*, *P Populus tremula*, *U Ulmus glabra*, *Ul Ulmus laevis*, *T Tilia cordata*, *Ai Alnus incana*, *So Sorbus aucuparia*, *degr* degrees of tree inclination, *area* size of forest stand, *DBH* tree diameter at breast height, *crev* tree bark crevice depth, *pH* tree bark pH, *ripar* riparian WKH, *broadl* nemoral WKH, *fage* forest stand age

These results confirm that the richness of indicator species used for identification of WKH can be used as a surrogate for estimation of richness of rare species. Paltto et al. (2006) did not find a significant correlation between WKH indicator species richness and Red-listed species richness in Swedish deciduous forests, but they had also included fungi and vascular plants in the analysis, which were not included in the present work.

Differences were found between several tree species in epiphyte richness. *P. tremula*, which had the highest bryophyte richness, is an important structure supporting high biological diversity in northern forests (Kouki et al. 2004; Madžule et al. 2012). *C. betulus* hosted the highest richness of two epiphyte groups—Red-listed species and bryophyte Red-listed species richness. Also Szövényi and Tóth (2004) found *C. betulus* rich in bryophytes the Carpathian Basin stream valley. The highest lichen species richness was found on *T. cordata*, as found in previous work in Estonian boreo-nemoral forests (Jüriado et al. 2009b). The difference in epiphyte species composition among trees in the CCA analysis indicates that heterogeneity in tree composition is related to stand diversity in epiphytes, and that diversity will be higher in stands with *P. tremula, C. betulus* and *T. cordata*.

Tree bark pH had a significant effect on epiphytic species composition in the CCA ordination and was a significant explanatory factor for richness of lichen species, Red-listed species, bryophyte WKH indicator species, and bryophyte Red-listed species in the GLMM analysis, in addition to the tree-species effect. *T. cordata*, which has low bark pH, supported high lichen species richness. At the other end of the tree species gradient,

F. excelsior, which has high bark pH, supported high richness of bryophytes. Other studies have shown that tree bark pH is one of the most important factors influencing epiphytic community composition and richness in boreal (Gustafsson and Eriksson 1995), boreo-nemoral (Löbel et al. 2006) and nemoral vegetation zones Cieslinski et al. (1996)

Tree inclination was a significant explanatory factor for bryophyte indicator species richness. Decreased risk of diaspore flush-off may explain species occurrence on moderately inclined trees, but this positive effect may decrease with increasing inclination. Highly inclined trees have lower substrate quality and more competitive species can be common (Snäll et al. 2005).

Tree diameter was a significant factor for total, bryophyte, bryophyte indicator species richness and epiphyte composition, which can be explained by increased substrate area for colonization (Glime 2007). Bark crevice depth was associated with epiphyte community composition and influenced lichen WKH indicator species richness negatively. Bark roughness was found to be a significant factor for epiphytic bryophyte and lichen composition in a *Fagus* forest (Aude and Poulsen 2000). Furthermore, Ranius et al. (2008) found that bryophyte and macrolichen occurrence has a negative relationship with bark crevice depth, while crustose lichens has a positive relationship. Our study partly agrees with earlier results of Stringer and Stringer (1974), who found bark roughness to be significant for lichen species cover and distribution and not for bryophyte species.

In the GLMM models, stand-scale variables, had little or no effect in epiphyte richness. This suggests that habitat quality, i.e. heterogeneity in trees species and presence of tree species high in epiphyte diversity, is the main factor determining richness of epiphytes in the relatively small WKH patches, as suggested also by the CCA analysis. In the CCA ordination, forest stand size had a significant effect on epiphyte composition, but which was confounded by tree-level factors. In contrast, Paltto et al. (2006) found that stand size was significantly related with both WKH indicator and lichen species occurrence. Also, Ojala et al. (2000) observed that total epiphytic bryophyte species occurrence and abundance were associated with stand size in old-growth *P. tremula* forests. The plot size used in our study might not have been representative of the whole stand, which might explain the lack of a stand area effect.

Forest stand age also showed little influence in epiphyte composition and affected significantly only bryophyte WKH indicator species richness (negatively). *Q. robur* had the oldest age in the stands, and hence this age effect may be explained by the lower bryophyte richness on this tree species. Jüriado et al. (2009a) found that stand age affects composition of lichens, but not lichen species richness. Threatened and vulnerable epiphytic lichen species did not show any relationship with forest stand age in coniferous forests (Holien 1996). Also, Baldwin and Bradfield (2007) did not find significant relationship between forest patch age and bryophyte species richness in temperate coastal rainforests.

In a study of WKHs in Sweden (Berg et al. 2002), epiphytic bryophyte and lichen richness was shown to differ between deciduous forest types; nemoral tree forests were more important for Red-listed bryophyte and lichen occurrence, while forests with *P. tremula* and *Picea abies* showed the lowest number of Red-listed bryophyte and lichen species. In forests of North Carolina (USA), forest type was more important in determining epiphytic bryophyte species community composition than particular tree species (Palmer 1986). In the present study, habitat-type effects seemed to be outweighed by the gradients explained by tree factors, and thus were likely due to covariation with the tree species effects. Thus, tree level effects alone explained most of the variation in bryophyte and lichen species composition and richness in nemoral tree species forests, as reported previously in Estonia (Jüriado et al. 2009a).

The obtained results indicate a need to maintain a range of tree species in conservation of epiphytic bryophyte and lichen communities. Management should aim to increase the habitat hetereogeneity of the existing WKHs by promoting regeneration of deciduous species in surrounding forest stands. A focus in restoration of nemoral woodland might be to maintain the presence of tree species (e.g. *A. platanoides, C. betulus, F. excelsior, P. tremula, T. cordata, U. glabra, U. laevis*) with high epiphyte diversity in the landscape. There is a risk that management to remove tree saplings around veteran trees, as is presently conducted in some protected areas in Lavia (Latvijas dabas fonds 2007), may serve to reduce epiphytic species diversity in the future by reducing tree substrate diversity.

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Appendix

See Table 4.

Table 4 Relative frequences of epiphytic bryophyte and lichen species on phorophytes.

Epiphytic species	Tree species													
Bryophytes	Abbrev.	Ul 24	F 126	P 162	Ac 118	C 30	U 111	T 249	Sa 3	So 22	Q 94	Ai 21	Ag 18	B 42
Amblystegium serpens	*Amblserp*	5.0	10.2	23.2	13.3	0.4	19.7	17.2	0.0	3.9	4.2	1.4	0.4	0.4
Amblystegium subtile		0.0	18.8	18.8	18.8	0.0	18.8	18.8	0.0	0.0	6.3	0.0	0.0	0.0
Anomodon attenuatus[a]	*Anomatte*	13.2	22.1	1.4	10.3	0.0	7.4	29.4	1.5	0.0	4.4	1.5	7.4	1.5
Anomodon longifolius[a]	*Anomlong*	4.9	17.3	9.9	32.1	0.0	21.0	9.9	0.0	0.0	4.9	0.0	0.0	0.0
Anomodon viticulosus[a]		11.3	13.2	0.0	13.2	0.0	11.3	43.4	0.0	0.0	7.6	0.0	0.0	0.0
Antitrichia curtipendula[b2]		0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Blepharostoma trichophyllum		0.0	0.0	0.0	0.0	0.0	0.0	25.0	0.0	0.0	0.0	0.0	50.0	25.0
Brachythecium rutabulum		0.4	16.3	21.5	13.2	0.7	9.4	17.7	0.4	1.0	14.9	1.4	1.7	1.4
Brachythecium salebrosum		1.5	7.7	43.1	10.8	0.0	10.8	10.8	0.0	1.5	9.2	3.1	0.0	1.5
Brachythecium velutinum		0.0	0.0	56.5	13.0	0.0	13.0	17.4	0.0	0.0	0.0	0.0	0.0	0.0
Bryum moravicum		0.0	0.0	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0
Campyliadelphus chrysophyllus		0.0	50.0	0.0	0.0	0.0	50.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cirriphyllum piliferum		1.6	23.0	42.6	8.2	0.0	3.3	11.5	0.0	3.3	3.3	3.3	0.0	0.0
Climacium dendroides		0.0	0.0	75.0	0.0	0.0	0.0	25.0	0.0	0.0	0.0	0.0	0.0	0.0
Dicranum montanum	*Dicrmont*	0.0	1.0	11.6	0.5	1.0	2.9	40.1	0.0	1.0	16.4	1.0	7.7	16.9
Dicranum scoparium	*Dicrscop*	0.0	0.0	30.6	2.8	1.4	1.4	36.1	0.0	0.0	8.3	0.0	1.4	18.1
Dicranum viride[ab3c]		0.0	25.0	10.0	0.0	0.0	5.0	40.0	5.0	0.0	15.0	0.0	0.0	0.0
Eurhynchiastrum pulchellum		7.7	0.0	42.3	19.2	0.0	23.1	3.9	0.0	0.0	0.0	0.0	0.0	3.9
Eurhynchium angustirete		0.8	22.1	18.9	10.2	0.0	8.7	29.9	0.8	0.8	3.2	0.8	2.4	1.6
Eurhynchium striatum		2.7	14.3	22.3	13.4	6.3	8.0	17.0	0.0	0.9	0.9	8.0	0.0	6.3
Fissidens adianthoides		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0
Fissidens bryoides		0.0	33.3	33.3	0.0	0.0	33.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Fissidens taxifolius		0.0	6.3	93.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Frullania dilatata	*Fruldila*	0.7	32.6	22.0	9.9	10.6	12.8	5.7	0.7	2.1	0.7	0.7	0.7	0.7

Table 4 continued

Epiphytic species	Tree species													
Bryophytes	Abbrev.	Ul 24	F 126	P 162	Ac 118	C 30	U 111	T 249	Sa 3	So 22	Q 94	Ai 21	Ag 18	B 42
Geocalex graveolens[b4]		0.0	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Herzogiella seligeri		0.0	0.0	0.0	0.0	0.0	0.0	50.0	0.0	0.0	0.0	0.0	0.0	50.0
Homalia trichomanoides[a]		2.6	17.9	16.6	12.4	2.0	11.9	21.0	0.4	0.9	9.9	2.7	0.9	0.9
Homalothecium sericeum	*Homaseri*	1.1	18.0	4.5	23.6	11.2	15.7	19.1	0.0	3.4	3.4	0.0	0.0	0.0
Hygroamblystegium varium		0.0	20.0	0.0	20.0	0.0	0.0	0.0	0.0	0.0	60.0	0.0	0.0	0.0
Hylocomium splendens		0.0	0.0	80.0	10.0	0.0	0.0	10.0	0.0	0.0	0.0	0.0	0.0	0.0
Hypnum cupressiforme	*Hypncupr*	1.8	10.3	17.9	8.0	3.8	7.6	27.8	0.4	1.2	11.9	1.8	2.0	5.4
Isothecium alopecuroides[a]	*Isotalop*	0.0	15.2	13.4	13.4	17.9	9.8	21.4	0.0	0.0	5.4	0.9	0.0	2.7
Jamesoniella autumnalis[a]		0.0	0.0	0.0	0.0	0.0	0.0	44.4	0.0	0.0	0.0	0.0	0.0	55.6
Jungermannia leiantha[a]		0.0	0.0	0.0	0.0	0.0	0.0	66.7	0.0	0.0	11.1	0.0	11.1	11.1
Lejeunea cavifolia[ab2]		3.6	46.4	25.0	3.6	0.0	17.9	3.6	0.0	0.0	0.0	0.0	0.0	0.0
Lepidozia reptans		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0
Leskea polycarpa		0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Leucodon sciuroides	*Leucsciu*	9.1	20.8	4.6	18.8	2.5	17.3	11.7	0.0	0.0	13.7	0.5	0.0	1.0
Lophocolea heterophylla		0.0	0.0	33.3	10.0	0.0	6.7	20.0	0.0	0.0	3.3	6.7	0.0	20.0
Metzgeria furcata[ab2]	*Metzfurc*	0.9	12.7	11.8	11.8	7.5	14.9	25.9	0.0	0.9	10.1	2.2	0.0	1.3
Mnium hornum		0.0	0.0	6.3	0.0	0.0	0.0	43.8	0.0	0.0	43.8	0.0	6.3	0.0
Mnium stellare		0	0	20	20	0	6.7	26.7	0	0	6.7	0	0	20
Neckera complanata[ab2]	*Neckcomp*	0	24.4	11.1	25.6	15.6	11.1	10	0	1.1	0	0	0	1.1
Neckera crispa[b3]		0	20	0	20	0	20	40	0	0	0	0	0	0
Neckera pennata[ab2]		5.4	20.9	19.4	17.8	0.8	20.9	10.9	0.0	0.8	2.3	0.0	0.0	0.8
Orthotrichum affine		2.2	16.3	38.0	12.0	4.4	9.8	6.5	0.0	5.4	2.2	3.3	0.0	0.0
Orthotrichum obtusifolium		0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Orthotrichum speciosum		4.7	11.6	11.6	44.2	0.0	18.6	9.3	0.0	0.0	0.0	0.0	0.0	0.0

Table 4 continued

Epiphytic species	Tree species													
Bryophytes	Abbrev.	Ul 24	F 126	P 162	Ac 118	C 30	U 111	T 249	Sa 3	So 22	Q 94	Ai 21	Ag 18	B 42
Oxyrrynchium hians		12.9	11.3	17.7	16.1	1.6	21.0	11.3	0.0	0.0	3.2	3.2	1.6	0.0
Plagiochila asplenioides		0	8.5	29.8	12.8	4.3	14.9	19.2	0	0	0	6.4	0	4.3
Plagiochila porelloides		0.0	8.7	26.1	8.7	4.4	4.4	43.5	0.0	0.0	0.0	0.0	0.0	4.4
Plagiomnium affine		3.6	9.1	36.4	9.1	0.0	12.7	20.0	0.0	1.8	3.6	1.8	1.8	0.0
Plagiomnium cuspidatum		1.4	9.7	40.3	11.1	0.0	6.9	22.2	1.4	0.0	5.6	0.0	0.0	1.4
Plagiomnium undulatum		2.9	26.5	20.6	5.9	0.0	17.7	20.6	0.0	0.0	0.0	2.9	2.9	0.0
Plagiothecium cavifolium		0.0	9.1	27.3	0.0	0.0	9.1	27.3	0.0	0.0	18.2	0.0	0.0	9.1
Plagiothecium denticulatum		0.0	0.0	80.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	20.0
Plagiothecium laetum	*Plaglaet*	0.0	5.0	18.3	1.7	1.7	5.0	26.7	0.0	1.7	8.3	1.7	5.0	25.0
Plagiothecium latebricola[b2]		0.0	0.0	0.0	0.0	0.0	0.0	40.0	0.0	0.0	40.0	0.0	0.0	20.0
Platygyrium repens		0.0	16.6	17.5	3.0	1.7	8.9	26.4	0.9	2.6	14.9	1.7	2.1	3.8
Pleurozium schreberi		0.0	0.0	50.0	0.0	0.0	0.0	50.0	0.0	0.0	0.0	0.0	0.0	0.0
Pseudoleskeella nervosa		5.3	8.0	4.4	14.2	0.0	16.8	33.2	0.4	4.4	11.1	1.8	0.0	0.4
Pterigynandrum filiforme[b1]		23.5	23.5	0.0	0.0	0.0	0.0	52.9	0.0	0.0	0.0	0.0	0.0	0.0
Ptilidium pulcherrimum		0.0	0.0	40.7	0.0	0.0	0.0	18.5	0.0	0.0	3.7	0.0	0.0	37.0
Pylaisia polyantha		5.0	15.4	20.9	11.6	1.5	15.4	19.3	0.0	1.9	6.2	1.2	0.4	1.2
Radula complanata	*Raducomp*	3.5	15.3	20.1	13.8	3.1	13.8	19.4	0.2	2.4	5.0	1.9	0.9	0.7
Rhodobryum roseum		0.0	0.0	62.5	0.0	0.0	12.5	25.0	0.0	0.0	0.0	0.0	0.0	0.0
Rhytidiadelphus triquetrus		0.0	12.1	36.4	6.1	0.0	6.1	30.3	0.0	3.0	3.0	0.0	0.0	3.0
Sanionia uncinata		1.9	16.7	22.2	5.6	0.0	16.7	27.8	0.0	3.7	3.7	0.0	1.9	0.0
Sciuro-hypnum oedipodium		0.0	3.1	47.7	6.2	0.0	7.7	20.0	0.0	1.5	7.7	0.0	3.1	3.1
Sciuro-hypnum populeum		0.0	16.2	26.5	11.8	4.4	10.3	22.1	0.0	0.0	2.9	4.4	0.0	1.5
Sciuro-hypnum reflexum		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0
Thuidium delicatulum		0.0	34.6	27.3	1.8	3.6	3.6	12.7	1.8	1.8	5.5	1.8	1.8	3.6

Table 4 continued

Epiphytic species	Tree species													
Bryophytes	Abbrev.	Ul 24	F 126	P 162	Ac 118	C 30	U 111	T 249	Sa 3	So 22	Q 94	Ai 21	Ag 18	B 42
Ulota crispa[a]		1.9	18.7	17.8	10.3	6.5	10.3	20.6	0.0	2.8	5.6	2.8	1.9	0.9
Lichens														
Acrocordia cavata		100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Acrocordia gemmata[a]	*Acrogemm*	10.0	16.7	22.2	10.0	0.0	25.6	4.4	0.0	0.0	8.9	1.1	1.1	0.0
Anaptychia ciliaris		0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Arthonia byssacea		0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Arthonia leucopellaea[a]		0.0	0.0	0.0	33.3	0.0	0.0	0.0	0.0	0.0	0.0	33.3	0.0	33.3
Arthonia radiata		10.0	36.7	10.0	6.7	0.0	20.0	0.0	3.3	3.3	3.3	3.3	3.3	0.0
Arthonia spadicea[a]		0.0	11.1	22.2	0.0	0.0	0.0	44.4	0.0	0.0	22.2	0.0	0.0	0.0
Arthonia vinosa[a]		0.0	0.0	5.0	20.0	0.0	10.0	30.0	0.0	5.0	10.0	0.0	5.0	15.0
Arthothelium ruanum		7.1	28.6	0.0	7.1	7.1	7.1	14.3	0.0	7.1	21.4	0.0	0.0	0.0
Bacidia friesiana		0.0	0.0	0.0	0.0	0.0	0.0	25.0	0.0	0.0	50.0	0.0	0.0	25.0
Bacidia rubella[a]		11.4	13.6	38.6	2.3	0.0	22.7	2.3	0.0	0.0	2.3	0.0	0.0	6.8
Buellia griseovirens		0.0	20.0	0.0	20.0	0.0	20.0	20.0	4.0	0.0	0.0	12.0	0.0	4.0
Calicium abietinum		0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Chaenotheca brunneola		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0
Chaenotheca ferruginea		0.0	0.0	0.0	0.0	0.0	0.0	33.3	0.0	0.0	66.7	0.0	0.0	0.0
Chaenotheca furfuracea		0.0	25.0	0.0	25.0	0.0	0.0	0.0	0.0	0.0	25.0	0.0	25.0	0.0
Chrysotrix candelaris		0.0	25.0	0.0	25.0	0.0	25.0	25.0	0.0	0.0	0.0	0.0	0.0	0.0
Cladonia chlorophea		0.0	0.0	71.4	0.0	0.0	28.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cladonia coniocrae	*Cladconi*	0.0	4.0	18.3	2.5	0.0	2.0	42.6	0.0	1.0	9.4	0.0	6.9	13.4
Dimerella lutea		0	0	0	100	0	0	0	0	0	0	0	0	0
Dimerella pineti		0	50	25	0	0	0	0	0	0	25	0	0	0
Evernia prunastri		18.8	12.5	6.3	12.5	0	0	25	0	12.5	12.5	0	0	0

Table 4 continued

Epiphytic species	Tree species													
Bryophytes	Abbrev.	Ul 24	F 126	P 162	Ac 118	C 30	U 111	T 249	Sa 3	So 22	Q 94	Ai 21	Ag 18	B 42
Graphis scripta[a]		1.5	11.4	1.5	9.9	2.2	9.2	44.6	0.3	5.5	1.9	6.5	4	1.5
Gyalecta truncigena		100	0	0	0	0	0	0	0	0	0	0	0	0
Hypocenomyce scalaris		0.0	0.0	0.0	11.1	0.0	0.0	55.6	0.0	0.0	0.0	22.2	0.0	11.1
Hypogymnia physodes	*Hypophys*	0.0	0.9	6.8	7.7	0.0	0.0	54.7	0.9	3.4	13.7	0.0	0.0	12.0
Lecanactis abietina[a]		0.0	0.0	0.0	0.0	0.0	9.1	63.6	0.0	0.0	27.3	0.0	0.0	0.0
Lecanora allophana		0.0	0.0	0.0	50.0	50.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lecanora argentata		0.0	0.0	0.0	40.0	0.0	0.0	60.0	0.0	0.0	0.0	0.0	0.0	0.0
Lecanora carpinea		5.9	5.9	5.9	5.9	0.0	11.8	52.9	0.0	5.9	5.9	0.0	0.0	0.0
Lecanora glabrata	*Lecaglab*	0.0	0.0	0.0	20.0	57.5	0.0	7.5	0.0	0.0	12.5	0.0	2.5	0.0
Lecanora leptyrodes		0.0	0.0	0.0	33.3	0.0	0.0	0.0	0.0	33.3	33.3	0.0	0.0	0.0
Lecanora rugosella		0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lecanora saligna		0.0	0.0	80.0	0.0	0.0	0.0	20.0	0.0	0.0	0.0	0.0	0.0	0.0
Lecanora subrugosa	*Lecasubr*	0.0	13.7	13.7	12.6	16.8	12.6	23.2	0.0	3.2	1.1	0.0	1.1	2.1
Lecidella euphorea		6.5	25.0	10.9	17.4	0.0	15.2	18.5	1.1	3.3	0.0	0.0	2.2	0.0
Lecidella olaeochroma		1.8	20.2	13.2	21.9	0.9	12.3	14.9	0.0	7.0	4.4	2.6	0.0	0.9
Lepraria lobificans	*Leprlobi*	0.7	13.8	9.2	12.3	4.9	10.2	28.2	0.3	1.6	10.4	1.1	1.1	6.2
Lepraria sp.	*Leprsp.*	2.8	7.4	32.4	3.7	0.0	12.0	15.7	0.0	0.0	17.6	0.0	6.5	1.9
Lobaria pulmonaria[b2]		7.1	7.1	7.1	42.9	0.0	7.1	21.4	0.0	0.0	7.1	0.0	0.0	0.0
Melanelia exasperata		0.0	0.0	0.0	62.5	0.0	12.5	0.0	0.0	0.0	0.0	0.0	0.0	25.0
Melanelia glabratula		0.7	9.0	9.0	11.6	0.0	10.3	40.0	1.3	2.6	5.2	6.5	1.3	2.6
Melanelia olivacea		7.7	7.7	0.0	3.9	0.0	7.7	53.9	0.0	15.4	0.0	3.9	0.0	0.0
Micarea prasina		0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ochrolechia androgyna		0.0	0.0	0.0	33.3	0.0	0.0	0.0	0.0	0.0	33.3	0.0	33.3	0.0
Opegrapha rufescens		7.5	16.3	5.0	25.0	6.3	8.8	26.3	0.0	0.0	3.8	0.0	1.3	0.0

Table 4 continued

Epiphytic species	Tree species													
Bryophytes	Abbrev.	Ul 24	F 126	P 162	Ac 118	C 30	U 111	T 249	Sa 3	So 22	Q 94	Ai 21	Ag 18	B 42
Opegrapha varia		1.9	16.7	0.0	25.9	0.0	9.3	24.1	0.0	0.0	16.7	0.0	3.7	1.9
Opegrapha viridis[b3]		0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Opegrapha vulgata		0.0	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Parmelia saxatilis		0.0	0.0	0.0	0.0	0.0	0.0	50.0	0.0	0.0	0.0	0.0	0.0	50.0
Parmelia sulcata		3.2	8.4	10.5	15.8	0.0	3.2	39.0	1.1	4.2	9.5	2.1	0.0	3.2
Parmeliopsis ambigua		0.0	0.0	0.0	0.0	0.0	0.0	50.0	0.0	0.0	0.0	0.0	0.0	50.0
Peltigera canina		0.0	0.0	50.0	0.0	0.0	50.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Peltigera praetextata		0.0	20.6	8.8	14.7	0.0	8.8	26.5	0.0	0.0	17.7	0.0	0.0	2.9
Pertusaria albescens		7.1	35.7	0.0	14.3	0.0	7.1	7.1	0.0	14.3	14.3	0.0	0.0	0.0
Pertusaria amara		0.6	11.2	7.3	11.7	0.0	2.8	44.7	0.0	2.2	16.8	1.7	0.6	0.6
Pertusaria hemisphaerica[b3]		0.0	0.0	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0
Pertusaria leioplaca		0.0	3.9	3.9	15.4	0.0	15.4	46.2	0.0	15.4	0.0	0.0	0.0	0.0
Pertusaria multipuncta		0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pertusaria pertusa[ab3]		0.0	23.8	4.8	4.8	0.0	19.1	38.1	0.0	4.8	4.8	0.0	0.0	0.0
Phaephyscia orbicularis		0.0	0.0	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0
Phlyctis agelaea[a]		14.3	42.9	14.3	0.0	0.0	0.0	28.6	0.0	0.0	0.0	0.0	0.0	0.0
Phlyctis argena	*Phlyarge*	2.6	11.9	19.0	10.7	1.3	12.6	24.9	0.4	2.3	8.9	2.6	1.7	1.2
Physcia dubia		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0
Physconia grisea		0.0	12.5	0.0	87.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Platismatia glauca		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0
Porina aenea		0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pyrenula laevigata		0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pyrenula nitida		0.0	25.0	0.0	0.0	50.0	12.5	0.0	0.0	0.0	0.0	0.0	0.0	12.5
Pyrenula nitidella		0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Table 4 continued

Epiphytic species	Tree species													
Bryophytes	Abbrev.	Ul 24	F 126	P 162	Ac 118	C 30	U 111	T 249	Sa 3	So 22	Q 94	Ai 21	Ag 18	B 42
Ramalina farinacea		0.0	10.0	10.0	18.3	0.0	5.0	28.3	0.0	3.3	18.3	3.3	0.0	3.3
Sclerophora nivea		50.0	0.0	0.0	0.0	0.0	50.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Thelotrema lepadinum[b]		0.0	25.0	0.0	0.0	0.0	25.0	50.0	0.0	0.0	0.0	0.0	0.0	0.0
Vulpicida pinastri		0.0	0.0	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0

Abbreviations are given for species referred to in Figure 2

Abbrev. – abbreviation, [a] – WKH indicator species, (Ek et al. 2002), [b] – Red-listed species in Latvia (Āboliņa 1994, Vimba, Piterāns 1996) with categories – 1 (Endangered), 2 (Vulnerable), 3 (Rare), [c] – protected species in European Union (EU 1992). Ul — *Ulmus laevis,* F — *Fraxinus excelsior,* P — *Populus tremula,* Ac — *Acer platanoides,* C — *Carpinus betulus,* U— *Ulmus glabra,* T — *Tilia cordata,* Sa — *Salix caprea,* So — *Sorbus aucuparia,* Q — *Quercus robur,* Ai —*Alnus incana,* Ag— *Alnus glutinosa,* B — *Betula pendula*. Number of trees next to each tree species. Relative frequency was calculated as the proportion of records on a tree species

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