Host Tree Preferences of Red-listed Epiphytic Lichens in Estonia

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Abstract

Trees are the only or main growth substrate for thousands of lichen species, including many endangered ones. The present study gives an overview of the diversity of red-listed (belonging to the IUCN categories CR, EN, VU and NT) lichens on Estonian trees based on nearly 1300 herbarium samples collected during ca. 150 years. According to the results, altogether 75 threatened and near-threatened lichen species are known from Estonian trees. The highest number of red-listed species are accounted for *Fraxinus excelsior* (34 red-listed species), followed by *Quercus robur*, *Populus tremula*, *Betula* spp., *Picea abies* and *Acer platanoides* (30 to 26 species per each host tree). In addition to the importance of different tree species as host trees for the red-listed lichens, we also discuss, taking into account the frequency of the tree species and predicted changes in the age structure of their stands in Estonia, the future perspectives of the epiphytes associated with them. *Populus tremula* can be considered as the best possible alternative phorophyte for the greatest part of threatened lichen species that are growing on temperate broadleaved trees.

Key words: lichens; endangered species; biodiversity conservation; broadleaved trees; deciduous trees; conifers.

Introduction

Trees are the only or main growth substrate for thousands of lichen species as the heterogeneous bark conditions of different tree species provide variable habitats for a wide range of epiphytes. Epiphytic lichens have received a lot of attention in the ecological and conservational studies (Ellis 2012, Nascimbene et al. 2013). The importance of different tree species, for example common aspen (*Populus tremula* L.), wych elm (*Ulmus glabra* Huds.) and English oak (*Quercus robur* L.) (e.g. Hedenås and Ericson 2000, Berg et al. 2002, Jüriado et al. 2003, Thor et al. 2010), has been emphasised for the maintenance of diverse lichen communities in boreal and temperate forests, while a high species richness can be sustained in the landscape matrix of habitat types with varying tree species composition. Also, the importance of old trees and habitats with long continuity is well known (e.g. Tibell 1992, Uliczka and Angelstam 1999, Fritz et al. 2008, Marmor et al. 2011), along with the fact that many lichen species cannot be found in young managed stands (e.g. Kuusinen and Siitonen 1998, Nascimbene et al. 2010, Pykälä 2004). The pressure of forest management and consequent changes in the compositional and age structure of stands may lead to the decreasing frequency of many lichen species. Due to this and some additional reasons, like outbreaks of tree-specific fungal diseases, e.g. Dutch elm disease and ash dieback (Watson et al. 1988, McKinney et al. 2014), the most vulnerable lichen species have been set to threat and might be facing local extinction. Data about the proportion of different tree species as phorophyte species for the endangered lichens is highly important for biodiversity conservation. At the same time, most of the threatened species are more or less rare, which makes the research of their substrate preferences at field not rational, due to time-consuming data collection, and also conservational issues. The present overview of the host trees of threatened epiphytic lichens is based on the herbarium samples that have been collected in Estonia during last 150 years. The main aim of the study is to find out how many threatened lichen species have been recorded on different trees, which would allow pointing out the most critical tree species for the maintenance of high lichen diversity in Estonian forests. Taking into account the frequency of these tree species in Estonia and predicted changes in the age structure of their stands, we also discuss the future perspectives of the lichen species associated with them.

Materials and Methods

Estonian forests

Estonia is lying in the moderate climate zone; the monthly mean temperature varies from –5 °C to +17 °C (the annual mean is ca 6 °C), and the mean precipitation is ca. 650 mm (Estonian Weather Service). The country is situated in the hemiboreal forest zone, which is a transitional zone between the boreal coniferous and temperate deciduous forests (European Environment Agency 2007). About half of the territory is covered with forests, the proportion of coniferous and deciduous forests (by dominant tree species) being more or less equal (Pärt 2011). The proportion of tree species by volume on forest land is presented in Table 1. The most frequent tree species are *Pinus sylvestris* L. – 30.3%, *Picea abies* (L.) H. Karst. – 23.4%, *Betula* spp. (*B. pendula* Roth or *B. pubescens* Ehrh.) – 22.9%, *Populus tremula* – 7.4%, and *Alnus incana* (L.) Moench – 7.1%; the proportion of other tree species is less than 5% (Pärt et al. 2013). *Larix* spp. are the only introduced trees with some, although very small, importance in Estonian forestry. The average age of forests is 56 years, whereas only ca. 5% of forests are over 100 years old (Pärt et al. 2013).

Red-listed lichens in Estonia

The latest, the fourth, Red List of Estonia was prepared during 2006–2008, and it was, for the first time, based on the categories and criteria of the International Union for Conservation of Nature (IUCN) (Standards and Petitions Working Group 2006, Randlane et al. 2008). From 942 lichen species that are recorded in Estonia at present (Randlane et al., 2015), 464 species were evaluated (others either remained in the category Not Evaluated or were not yet nationally recorded during the preparation period of the Red List). The number of lichen species in the categories relevant to present study (155 altogether) is as follows, 13 species in Critically Endangered (CR), 32 in ENdangered (EN), 68 in VUlnerable (VU), and 42 in Near Threatened (NT). When compiling the list of threatened lichens for the present study, we also added the category NT to the traditional threatened categories (CR, EN, and VU); NT includes the species, which did not qualify for a threatened category during the evaluation, but were close to it and might become threatened with extinction in the near future.

Studied material and data analyses

The present study is based on the herbarium samples that have been collected in Estonia; the majority of them belongs to the lichenological collections of the University of Tartu (TU). The databases eSamba and PlutoF were used to get the label information of the collected specimens; the latest collections included in this study are from 2013 (the latest database queries were performed in September 25, 2013), while the earliest samples taken into consideration had been collected in 1860s. Although air pollution and other environmental conditions have changed considerably within the limits of this time period (ca. 150 years), the recording of lichens has been temporally irregular. For example, in the Estonian lichen herbarium database eSamba (http://www.eseis.ut.ee/), containing over 45,000 entries altogether, only less than 20% of data (8,539 entries) are from the period 1860–1950. Therefore, we included in our study all samples of threatened lichen species (IUCN categories CR, EN, VU, and NT) that were labelled to be epiphytic (leaving out the species that were reported from the decorticated woody parts of trees or from unspecified tree genus/species) and collected in Estonia during this period without any time-related segregation.

Most of the trees were studied at the species level; in case only the genus was marked, we regarded it to belong to the (only) native tree species, e.g. *Picea* spp. was included in the study as *Picea abies*. The phorophyte genera that include more than one native species in Estonia, viz. *Betula*, *Salix* and *Ulmus*, were studied at the genus level as the exact species remained unknown in many cases (the most frequently reported species among these genera were *Betula pendula*, *Salix caprea* L. and *Ulmus glabra*). The genus *Alnus* including two native tree species was exceptionally studied at the species level (the few samples that were reported from *Alnus* spp. were left out from the study). The tree species that hosted only 1–2 threatened lichen species were left out from the data analyses.

Substrate preferences of threatened epiphytic lichen species were determined if more than 50% of their records were from a specific group of trees or from one tree species (only the lichen species that were represented by at least 10 samples in the study were considered).

Nonmetric Multidimensional Scaling (NMS) in PC-ORD™ 5.0 (McCune and Mefford 1999) was used for the ordination of tree species based on the presence/absence of threatened lichen species (all lichen species were included). NMS analysis was run in autopilot mode, using slow and thorough settings (comparing 1 to 6-dimensional solutions, 50 runs with real data, 250 runs with randomized data, stability criterion 0.00001 and maximum number of iterations 500). Pearson squared correlations (r^2) were calculated for the axes to express total variation in lichen community composition (McCune and Mefford 1999).

Results

Epiphytic lichens, both macro- and microlichens, are generally well studied in Estonia (e.g. Jüriado et al. 2009a, b, 2011, 2015, Leppik et al. 2011, Lõhmus and Lõhmus 2011, Lõhmus and Runnel 2014, Marmor et al. 2010, 2011, 2013), while some difficult taxa, viz. calicioid lichens (Lõhmus and Lõhmus 2011), genera *Lepraria* (Lõhmus et al. 2003) and *Usnea* (Tõrra and Randlane 2007) or certain species, e.g. *Lobaria pulmonaria* (Jüriado and Liira 2009, 2010, Jüriado et al. 2011, 2012), have been an object of special research. Data about 1286 herbarium samples belonging to 75 threatened species of epiphytic lichens in Estonia have been accumulated into the national databases of lichens (eSamba and PlutoF) during last 150 years (from 1860s to 2013). Five epiphytic lichen species belonged to CR, eleven to EN, 30 to VU, and 29 to NT categories. Nineteen lichen species were represented only by a small number of herbarium samples (among them both very rare epiphytic taxa and a few species, which usually inhabit other substrates, like wood, rocks or ground), while five or more samples had been collected for 56 lichens species. *Lobaria pulmonaria* and *Usnea barbata* appeared the most frequently collected threatened lichen taxa, with 166 herbarium samples each.

Threatened epiphytic lichens have been recorded from 22 phorophyte species in Estonia, but only 16 tree taxa hosted seven or more threatened species (Table 1), and were included in further analyses. *Fraxinus excelsior* L. and *Quercus robur* hosted the highest numbers of threatened lichen species, 34 and 30 species respectively, followed by *Populus tremula, Betula* spp., *Acer platanoides* L. and *Picea abies*, with more than 20 lichen species each (Table 1). Altogether fifty threatened epiphytic lichen species (out of 75 such taxa) were recorded on temperate broadleaved trees (*Acer platanoides*, *Fraxinus excelsior, Quercus robur, Tilia cordata* Mill., and *Ulmus* spp.), while more than half of them (27) preferred these broadleaved trees as substrate. Other taxa of deciduous trees (*Alnus glutinosa* (L.) Gaertn., *A. incana, Betula* spp., *Corylus avellana* L., *Populus tremula, Salix* spp., and *Sorbus aucuparia* L.) harboured the biggest number of threatened lichens (53), but only twelve lichen species exhibited preference towards these phorophyte species (Tables 2 and 3). 38 lichen species inhabited coniferous trees (*Juniperus communis* L., *Larix* spp., *Picea abies,* and *Pinus sylvestris*), and ten of them preferred this substrate (Tables 2 and 3).

Table 1. The number of recorded threatened lichen species (categories CR, EN, VU and NT according to Randlane et al. 2008) on Estonian trees, and the volume of tree species on forest land (according to Pärt et al. 2013)

Tree species	No. of threatened lichen species	% of tree volume on forest land in Estonia
Fraxinus excelsior	34	1.0
Quercus robur	30	0.5
Populus tremula	27	7.4
Betula spp.	27	22.9
Picea abies	26	23.4
Acer platanoides	26	0.2
Ulmus spp.	20	0.1
Alnus glutinosa	20	4.9
Tilia cordata	20	0.2
Pinus sylvestris	17	30.3
Juniperus communis	13	<0.2
Salix spp.	12	1.0
Alnus incana	9	7.1
Sorbus aucuparia	9	0.3
Larix spp.	9	<0.2
Corylus avellana	7	<0.3

Analyzing the composition of lichen species with NMS, the best solution was a two-dimensional configuration. Proportion of variance in lichen community composition represented by those two axes was 77% (Figure 1). Pearson squared correlation coefficients (r^2) were 0.53 and 0.24 for the first and second axis, respectively. NMS analysis revealed the similarities in the composition of endangered lichen biota between the tree species (Figure 1). Common subneutral barked deciduous tree, *P. tremula,* is located in the left side of the ordination diagram together with temperate broadleaved trees, *A. platanoides, Q. robur, T. cordata* and *Ulmus* spp. It reveals that, *P. tremula* together with *A. platanoides, T. cordata* and *Ulmus* spp., appeared as suitable alternative substrates for lichens that grow on *F. excelsior,* the phorophyte which is the richest in threatened epiphytic lichens (Table 1). In the right side of the ordination diagram are the acid-barked coniferous trees (e.g. *Picea abies* and *Pinus sylvestris*) together with the most acid-barked deciduous taxa (*Betula* spp.). Other common deciduous trees (e.g. *A. glutinosa*, *Salix caprea*, *Sorbus aucuparia*) are located in the centre of the ordination diagram and amongst them, *A. glutinosa*, shows to be the most important host tree for lichens growing both in almost neutral or acid-barked tree species (Figure 1).

Discussion

Temperate broadleaved trees

Lichen diversity studies have frequently indicated the importance of temperate broadleaved trees (*Acer platanoides*, *Fraxinus excelsior*, *Quercus robur*, *Tilia cordata*, *Ulmus glabra* and *U. laevis* Pall.) in northern Europe (Löbel et al. 2006, Jüriado et al. 2009a, b, Hauck et al. 2013). Habitats dominated by these broadleaved trees are harbouring the highest numbers of threatened cryptogams in Sweden (Berg et al. 2002), where *Fraxinus excelsior*, *Quercus robur* and *Ulmus* spp. appeared among the most species rich host trees concerning endangered lichens (Thor et al. 2010). This

Table 2. The substrate preferences of threatened epiphytic lichen species. The species have been listed if ≥ 50% of their records are from a specific group of trees or from one tree species (in this case the tree name has been added); only the lichen species that were represented by at least 10 samples in the study have been considered

Groups of lichen species according to their substrate preferences	Number of lichen species in the substrate group, and the species	Tree species
Lichens growing mainly on temperate broadleaved trees (*Acer platanoides, Fraxinus excelsior, Quercus robur, Tilia cordata* and *Ulmus* spp.)	27 species:	
	Arthonia byssacea	*Quercus robur*
	Arthonia didyma	
	Bacidia laurocerasi	
	Biatoridium monasteriense	*Ulmus* spp.
	Caloplaca lucifuga	*Quercus robur*
	Chaenotheca cinerea	
	Coenogonium luteum	*Fraxinus excelsior*
	Eopyrenula leucoplaca	
	Gyalecta ulmi	*Ulmus* spp.
	Lecanora intumescens	
	Lecidea erythrophaea	
	Lobaria pulmonaria	
	Nephroma parile	*Quercus robur*
	Nephroma resupinatum	*Quercus robur*
	Opegrapha atra	
	Opegrapha ochrocheila	*Ulmus* spp.
	Opegrapha viridis	
	Parmelina tiliacea	
	Physconia detersa	
	Physconia grisea	
	Pyrenula laevigata	*Fraxinus excelsior*
	Pyrenula nitidella	*Fraxinus excelsior*
	Ramalina calicaris	
	Sclerophora coniophaea	*Quercus robur*
	Sclerophora farinacea	
	Sclerophora peronella	
	Xanthoria fallax	*Acer platanoides*
Lichens growing mainly on other deciduous trees (*Alnus glutinosa, A. incana, Betula* spp., *Corylus avellana, Populus tremula, Salix* spp. and *Sorbus aucuparia*)	12 species:	
	Bacidia biatorina	*Populus tremula*
	Cetrelia cetrarioides	
	Chaenotheca gracilenta	
	Collema nigrescens	*Populus tremula*
	Collema subnigrescens	*Populus tremula*
	Leptogium saturninum	*Populus tremula*
	Leptogium teretiusculum	*Populus tremula*
	Megalaria grossa	*Populus tremula*
	Menegazzia terebrata	*Alnus glutinosa*
	Nephroma laevigatum	
	Parmeliella triptophylla	*Populus tremula*
	Thelotrema lepadinum	
Lichens growing mainly on coniferous trees (*Juniperus communis, Larix* spp., *Picea abies* and *Pinus sylvestris*)	10 species:	
	Alectoria sarmentosa	*Picea abies*
	Evernia divaricata	*Picea abies*
	E. mesomorpha	*Pinus sylvestris*
	Ramalina thrausta	*Picea abies*
	Usnea barbata	
	Usnea diplotypus	
	Usnea fulvoreagens	*Pinus sylvestris*
	Usnea glabrata	*Picea abies*
	Usnea wasmuthii	
	Vulpicida juniperinus	*Juniperus communis*

is confirmed also by our results, regarding *Fraxinus excelsior* and *Quercus robur* (Table 1), while *Ulmus* spp. is less important as a substrate for epiphytic threatened lichens in Estonia, probably because of its very low frequency. All temperate broadleaved trees make up only 2% of tree volume in Estonian forests (Pärt et al. 2013). This can be explained by the high utilisation rate of the fertile soils, on which these forests grow, as agricultural land. Different broadleaved forest communities are at their northern distribution range in Estonia and they also dominate the list of most endangered and rare forest habitats in Estonia (Paal 1998). Therefore, other biotopes with temperate broadleaved trees, such as wooded meadows or historical manor parks, offering suitable alternative habitats to epiphytic lichens should be valued (Thor et al. 2010, Leppik et al. 2011).

Of all the temperate broadleaved tree species, *Fraxinus excelsior*, which hosts the highest number of threatened lichen species in Estonia, is at the present time seriously endangered itself as its populations are decreasing rapidly due to the ash dieback. The invasive pathogenic fungus, *Hymenoscyphus pseudoalbidus* Queloz et al., causing this disease, has spread through most of the natural range of *F. excelsior* in Europe within two decades (Ellis et al. 2012, Lõhmus and Runnel 2014); in Estonia, the fungus was identified in 2003, and currently over 80% of trees have died already in the forests, where *F. excelsior* appears as dominant species in the tree layer (Tee 2014). Therefore, the lichens associated with this phorophyte are under urgent threat (Ellis et al. 2012, Jönsson and Thor 2012). Out of 27 threatened lichens, which preferred to grow on temperate broadleaved trees, only a few (*Coenogoinium luteum, Pyrenula laevigatum* and *P. nitidella*) preferred specifically *F. excelsior* (Table 2). Lõhmus and Runnel (2014) proposed that old *Populus tremula* and late-successional deciduous trees may function as 'backup' for lichens against the ash dieback, which is in accordance with our results (Figure 1). The most suitable alternative tree species for lichens growing on *F. excelsior* are *A. platanoides*, *Q. robur* and *Ulmus* spp. (Figure 1). However, as these species are less frequent than *F. excelsior* in Estonian forests, the occurrence of many threatened lichens is still likely to decrease. For mitigating the situation, temperate broadleaved trees, including the young ones in understory, should be preserved in Estonian forests as much as possible. Similarly, Mežaka et al. (2012) have highlighted the need to maintain temperate broadleaved trees and *P. tremula* in Latvian forests, especially in the surroundings of existing woodland key habitats, for preserving high lichen diversity in the landscape. According to Lõhmus (2003), the general lichen spe-

Table 3. The list of threatened (belonging to the IUCN categories CR – critically endangered, EN – endangered, VU – vulnerable, and NT – near threatened) lichen species on Estonian trees; the numbers indicate studied herbarium samples per each species according to the databases eSamba and PlutoF

Lichen species	Threat category	Tree species																No of samples per lichen species
		Acer platanoides	*Alnus glutinosa*	*Alnus incana*	*Betula* spp.	*Corylus avellana*	*Fraxinus excelsior*	*Juniperus communis*	*Larix* spp.	*Picea abies*	*Pinus sylvestris*	*Populus tremula*	*Quercus robur*	*Salix* spp.	*Sorbus aucuparia*	*Tilia cordata*	*Ulmus* spp.	
Alectoria sarmentosa (Ach.) Ach.	NT									9								9
Arctoparmelia incurva (Pers.) Hale	EN							1										1
Arthonia apatetica (A. Massal.) Th. Fr.	VU									1			2					3
Arthonia byssacea (Weigel) Almq.	NT	1					3			1		1	23	1		3	3	36
Arthonia didyma Körb.	NT	5		1			6					5	4			3	5	29
Arthothelium spectabile Flot. ex A. Massal.	VU			3											1		1	5
Bacidia biatorina (Körb.) Vain.	EN											5	1					6
Bacidia laurocerasi (Delise ex Duby) Zahlbr.	NT	1	1				8			2		5					3	20
Biatoridium monasteriense J. Lahm ex Körb.	NT	4			1		9						1				15	30
Bryoria furcellata (Fr.) Brodo & D. Hawksw.	VU				1						1							2
Caloplaca lucifuga G. Thor	NT						1						8					9
Caloplaca ulcerosa Coppins & P. James	VU	1																1
Cetrelia cetrarioides (Delise ex Duby) W.L. Culb. & C.F. Culb.	VU	1		1	1		1			1		1		2				8
Cetrelia olivetorum (Nyl.) W.L. Culb. & C.F. Culb.	VU											1		1				2
Chaenotheca cinerea (Pers.) Tibell	EN						4										1	5
Chaenotheca gracilenta (Ach.) Mattsson & Middelb.	VU				2					1		4						7
Cladonia parasitica (Hoffm.) Hoffm.	NT							1			1							2
Cladonia pocillum (Ach.) Grognot	NT							1										1
Coenogonium luteum (Dicks.) Kalb & Lücking	VU						5					4						9
Collema nigrescens (Huds.) DC.	VU											10						10
Collema subnigrescens Degel.	NT											8	3					11
Cyphelium inquinans (Sm.) Trevis.	NT				1				2				4					7
Eopyrenula leucoplaca (Wallr.) R.C. Harris	EN	1					1						1				3	6
Evernia divaricata (L.) Ach.	VU				1			1	1	43	3							49
Evernia mesomorpha Nyl.	NT				6					3	12							21
Flavoparmelia caperata (L.) Hale	EN		1		3			1										5
Gyalecta ulmi (Sw.) Zahlbr.	VU						2						1			1	12	16
Lecanora impudens Degel.	VU						1			1			1			1		4
Lecanora intumescens (Rebent.) Rabenh.	VU	2			1	1	3							2	1	2		12
Lecidea erythrophaea Flörke ex Sommerf.	NT	1	1				7					4	10	1			2	26
Leptogium saturninum (Dicks.) Nyl.	NT					1	2					15	2			1		21
Leptogium teretiusculum (Wallr.) Arnold	VU						1					6						7
Lobaria pulmonaria (L.) Hoffm.	NT	21	2		3	3	29			2	1	52	19	9	5	9	11	166
Lobaria scrobiculata (Scop.) DC.	CR			1														1
Megalaria grossa (Pers. ex Nyl.) Hafellner	NT	2	1				11					34	1				1	50
Melanelixia glabra (Schaer.) O. Blanco et al	CR	1																1
Melanohalea elegantula (Zahlbr.) O. Blanco et al	EN												1					1
Melanohalea septentrionalis (Lynge) O. Blanco et al	NT				1					1	1			2				5
Menegazzia terebrata (Hoffm.) A. Massal.	NT		15		6					2	1	1				1		26
Micarea hedlundii Coppins	VU				1					1	2							4
Nephroma bellum (Spreng.) Tuck.	CR					1												1
Nephroma laevigatum Ach.	VU		1		1	2	6			1		5	1		1	1		19
Nephroma parile (Ach.) Ach.	VU		2	1		3		1					8					15

Table 3. (Continued)

Lichen species	Threat category	*Acer platanoides*	*Alnus glutinosa*	*Alnus incana*	*Betula* spp.	*Corylus avellana*	*Fraxinus excelsior*	*Juniperus communis*	*Larix* spp.	*Picea abies*	*Pinus sylvestris*	*Populus tremula*	*Quercus robur*	*Salix* spp.	*Sorbus aucuparia*	*Tilia cordata*	*Ulmus* spp.	No of samples per lichen species
		Tree species																
Nephroma resupinatum (L.) Ach.	EN				1					1			5					7
Opegrapha atra Pers.	NT	4	2				16	1				4	4		1	1	5	38
Opegrapha ochrocheila Nyl.	VU	1					3	1					1				7	13
Opegrapha sorediifera P. James	VU		1		1		1						3					6
Opegrapha viridis (Pers. ex Ach.) Behlen & Desberger	VU	1	1				6							1		2	4	15
Parmeliella triptophylla (Ach.) Müll. Arg.	VU						3			1		7				1		12
Parmelina tiliacea (Hoffm.) Hale	NT	8			2		4						3		1	11	4	33
Peltigera collina (Ach.) Schrad.	CR															2		2
Peltigera horizontalis (Huds.) Baumg.	NT															1		1
Peltigera hymenina (Ach.) Delise	NT										1							1
Physcia leptalea (Ach.) DC.	VU		1									1						2
Physconia detersa (Nyl.) Poelt	NT	1		2			1	1				1	5			1		12
Physconia grisea (Lam.) Poelt	NT	10					3		1				3			13	1	31
Pyrenula laevigata (Pers.) Arnold	VU				1		8					1						10
Pyrenula nitidella (Schaer.) Müll. Arg.	VU			2			8										2	12
Ramalina calicaris (L.) Fr.	VU	1	1		2		10	1		1		2	2		1			21
Ramalina sinensis Jatta	EN	1	1				1					1				1		5
Ramalina thrausta (Ach.) Nyl.	NT	1	1		6			1	1	29	3							42
Sclerophora coniophaea (Norman) Mattsson & Middelb.	NT												20				1	21
Sclerophora farinacea (Chevall.) Chevall.	VU	1					4						2				3	10
Sclerophora peronella (Ach.) Tibell	VU	2					1										3	6
Thelotrema lepadinum (Ach.) Ach.	NT	2	10	1	3	2	7			4		1	1	3	2	5		41
Usnea barbata (L.) Weber ex F.H. Wigg.	NT		4	1	25			1	7	82	38	1	3	4				166
Usnea chaetophora Stirt.	EN									2								2
Usnea diplotypus Vain.	NT	2			4				2	5	1			1				15
Usnea fulvoreagens (Räsänen) Räsänen	EN				2				2	7	14							25
Usnea glabrata (Ach.) Vain.	CR				1					7	1							9
Usnea substerilis Motyka	EN		1		2				2	1	1			1	1	1		10
Usnea wasmuthii Räsänen	VU		2		4				5	5	2							18
Vulpicida juniperinus (L.) J.-E. Mattsson & M.J. Lai	NT							5										5
Xanthoria calcicola Oxner	VU										1							1
Xanthoria fallax (Arnold) Arnold	VU	6	1				1					2						10

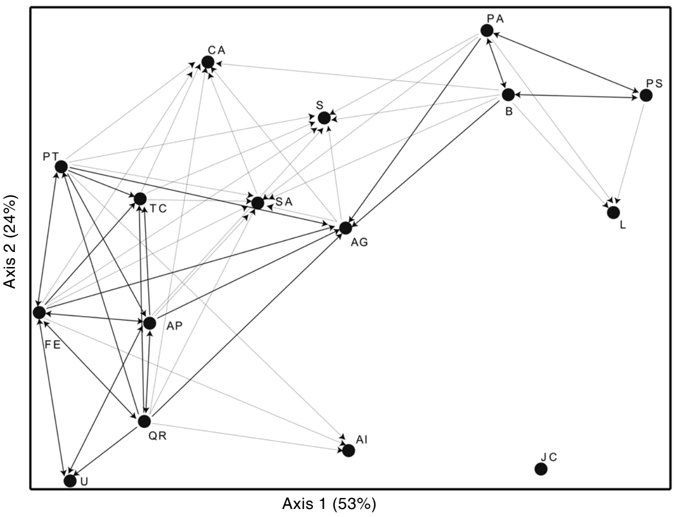

Figure 1. The similarities in the composition of threatened lichen biota between the tree species. Trees are situated on the NMS ordination plot (based on the presence/absence data of lichen species). The arrow from tree species 1 to species 2 indicates that ≥50 % of lichen species that have been collected from tree 2 are present also on tree 1; in case there are ≥10 species in common between the two trees the arrow line has been marked bold, and in case of < 10 common species the arrow line has been marked thin. Abbreviations of tree names: AG – *Alnus glutinosa*, AI – *Alnus incana*, AP – *Acer platanoides*, B – *Betula* spp., CA – *Corylus avellana*, FE – *Fraxinus excelsior*, JC – *Juniperus communis*, L – *Larix* spp., PA – *Picea abies*, PS – *Pinus sylvestris*, PT – *Populus tremula*, QR – *Quercus robur*, S – *Salix* spp., SA – *Sorbus aucuparia*, TC – *Tilia cordata*, U – *Ulmus* spp.

cies composition on *P. tremula* in Estonian forests is more similar to temperate broadleaved than to other deciduous trees. Regarding the frequency of this tree species in the region, *P. tremula* can be considered as the best possible alternative phorophyte for the greatest part of threatened lichen species that are growing on temperate broadleaved trees.

Other deciduous trees

Among other deciduous, except temperate broadleaved, trees, *Populus tremula* and *Betula* spp. belong to the top of valuable phorophytes, each of them hosting 27 threatened epiphytic lichen species (Table 1). The significance of *P. tremula* for the high lichen diversity in the region has been highlighted in several studies (e.g. Uliczka and Angelstam 1999, Jüriado et al. 2003, Hedenås and Hedström 2007). According to our results, *P. tremula* shares several threatened lichens with *F. excelsior*, *A. platanoides*, *T. cordata*, and *Q. robur* (Figure 1), which could be explained by their similarly high bark pH values. Still, there are several other taxa, mainly the cyanolichens (e.g. *Collema nigrescens*, *Leptogium saturninum* and *Parmeliella triptophylla*) that prefer *P. tremula* to other trees (Table 2) confirming its high importance as phorophyte species for the threatened epiphytes; this tree species is also the main substrate for *Lobaria pulmonaria* in Estonia (Jüriado and Liira 2009). The abundance of cyanobacterial lichens on large old *P. tremula* trees has been noticed also in Fennoscandia and Russia (Kuusinen 1994, Hedenås and Ericson 2000, Mikhailova et al. 2005). Many lichen species, especially those with conservation value, are known to grow mainly on older trees in the case of several tree species. This is explained by the changes in bark structure and microhabitat qualities but also by the longer time available for the colonisation of the tree (Ranius et al. 2008, Fritz et al. 2009, Nascimbene et al. 2009). The high growth speed of *P. tremula* is supporting the rather fast formation of microhabitats, like bark crevices. At the same time, its comparatively short lifespan, 120–150 years, and suggested short rotation period, 30–50 years (Forest Act 2015), might be problematic for the lichen species that are slow colonisers due to their short dispersal distances, high rarity or some other reason. For example, it has been found that the vegetative dispersal distance of *L. pulmonaria* is only up to 30 meters (Jüriado et al. 2011). Therefore, the spatial and temporal continuity of *P. tremula* stands deserves extra attention in the conservational context, especially in the circumstances, where the average age of *P. tremula* stands is going to decrease during the next decades, as it has been predicted by the Estonian Environment Information Centre (2011).

The most common deciduous tree genus, *Betula* (with *B. pendula* as the most frequent species) in Estonia, also hosts a very high number of threatened lichens, 27 species (Table 1). However, according to present data, there are no species that prefer *Betula* spp. to other trees (Table 2), and the composition of threatened lichen species of *Betula* spp. is more similar to that of *Picea abies* and *Pinus sylvestris* than any of the deciduous trees (Figure 1). For example, *Evernia mesomorpha* generally preferring *Pinus sylvestris*, and *Ramalina thrausta* preferring *Picea abies*, have been collected also from *Betula* several times (Table 3). The close resemblance of the epiphytic lichen biota on *Betula* and on the conifers *P. abies* and *P. sylvestris* is widely known in the boreal forest zone, mainly explained by their similar acid bark (Barkman 1958, Kuusinen 1996, Uliczka and Angelstam 1999, Leppik and Jüriado 2008). Taking into account that the genus *Betula* is very frequent in Estonia (ca. 25% of tree volume on forest land; Pärt et al. 2013) and the area of its old stands is likely to increase significantly in the next decades (Estonian Environment Information Centre 2011), *Betula* spp. should be a highly sustainable phorophyte for the lichens.

Altogether 20 threatened lichen species have been collected from another deciduous tree, *Alnus glutinosa,* that thrives in moist habitats. A lot of its epiphytic species are shared with various other trees (Figure 1), and only one taxon, *Menegazzia terebrata*, can be mainly found on *A. glutinosa* (Table 2). This lichen has been associated with *A. glutinosa* marsh forests also in Sweden (Thor 1998). Twelve threatened lichen species are known from *Salix* spp. (Table 1). According to Kuusinen (1996), old *S. caprea* trees are due to their high epiphyte richness and abundance of cyanobacterial lichens of great importance for the lichen conservation in boreal Finland; for example, it is, besides *P. tremula,* the main phorophyte for *L. pulmonaria* (Snäll et al. 2005). Our results do not indicate such great importance of *Salix* in Estonia. All other deciduous trees hosted less than ten endangered species (Table 1).

Coniferous trees

Of the two most frequent coniferous trees in northern Europe, *Picea abies* and *Pinus sylvestris* (ca. 22% and 25%, accordingly, of tree volume on forest land in Estonia; Pärt et al. 2013), *P. abies* harbours 26 threatened lichen species while only 13 such species have been recorded from *P. sylvestris* (Table 1). Several lichen species, predominantly beard-like macrolichens, prefer coniferous trees (Table 2). For example, *Alectoria sarmentosa* and *Evernia divaricata* can be most often found hanging on *P. abies* branches, while the bushy *Evernia mesomorpha* is most frequent on *P. sylvestris*. With its high richness of endangered lichens and several specialised species, *P. abies,* which is preferred by several beard-like macrolichens, such as *Alectoria sarmentosa, Evernia divaricata, Ramalina thrausta,* and *Usnea glabrata* (Table 2), can be regarded as a very important phorophyte for lichen conservation in Estonia. The two conifers have also a lot of shared threatened lichens with each other and with *Betula* spp., while *P. abies* shares comparatively many lichens also with some other deciduous trees, like *Alnus glutinosa* (Figure 1).

Future perspectives of lichens associated with *Picea abies* and *Pinus sylvestris* in Estonia depend on controverting factors. Both phorophytes are locally among the most harvested tree species, however, many new young trees are planted in state forests every year supporting their high frequency in Estonian forests also in future. The average age of *P. abies* and *P. sylvestris* is likely to decrease in the managed and increase in protected forests. For these two species, the age changes have been predicted to sum up in an increase of old stands (Estonian Environment Information Centre 2011). Still, for the protection of lichen species with poor dispersal ability, like *Alectoria sarmentosa* or *Evernia divaricata* that mostly disperse with thallus fragments, the spatial and temporal continuity of habitats should also be considered in conservation management. Previous studies in Estonian coniferous forests have shown that not only the age of trees but also the historical continuity of the forest is affecting epiphytic lichen communities, and several species can be foremost found in old forests (Marmor et al. 2011). For example, *A. sarmentosa* clearly prefers old trees in the remnants of old forests to the mature trees in the surrounding managed forests (Uliczka and Angelstam 1999).

One more native conifer, *Juniperus communis*, rather a shrub than a tree, deserves attention in the conservation of lichens. A recent study revealed that a total of 140 lichen species were recorded from junipers on Estonian calcareous grasslands, alvars (Jüriado et al. 2015). According to our results, it hosts 13 endangered lichen species (Table 1). One species, *Vulpicida juniperinus*, can be exclusively associated with *J. communis* (it grows additionally on limestone rich ground). Most species that have been found on *J. communis* are also known from other trees; but there is no high proportion of shared lichen species with any specific tree species (Figure 1). *J. communis* with its relatively acid bark (pH ca. 5.2) is a suitable host for acidophilic lichens (Ellis and Coppins 2009), whereas in alvars they may also host a rich assemblage of acidophobic epiphytes common usually on subneutral bark of broadleaved trees as well as species usually growing on ground mosses in calcareous soil (Jüriado et al. 2015). The cover of *J. communis* increases rapidly after the abandonment of grazing in these semi-natural habitats. As the semi-open alvars are first and foremost highly valuable habitats for many ground-dwelling threatened lichen species (Leppik et al. 2013), the overgrowing with *J. communis* should not be favoured; however, protection of some old and senescent junipers during restoration activities on overgrown calcareous grasslands is advocated (Jüriado et al. 2015).

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