

Distribution and habitat ecology of the threatened forest lichen *Lobaria pulmonaria* in Estonia

Inga Jüriado & Jaan Liira

Department of Botany, Institute of Ecology and Earth Sciences, University of Tartu, Estonia,
40 Lai st., Tartu 51005, Estonia.
E-mail: inga.juriado@ut.ee

Abstract: *Lobaria pulmonaria* is widely used as an indicator species of undisturbed old-growth forests ecosystems, but the knowledge about its habitat ecology is still highly fragmented. To quantify the distribution, habitat preference and host tree specificity of *Lobaria pulmonaria* we utilised data from databases and field surveys in Estonia. The number of *L. pulmonaria* localities is the highest in the densely forested regions, concentrated mainly in small forest patches defined as 'ecologically highly valuable'. The species grows mostly on deciduous trees, particularly on aspen (*Populus tremula*). *L. pulmonaria* is most common in oligo-mesotrophic boreal, eutrophic boreo-nemoral and in eutrophic paludifying forests, and prefers forests with an average age of trees more than 100 years. In addition, we found that younger stands could be suitable habitats for *L. pulmonaria* if the structure of the stand is comparable to mature stands. In spite of the many localities of *L. pulmonaria* in Estonia, the species is still threatened because (1) the rotation period of tree stands is short, (2) it is abundant in forest types which are rare or under strong economic pressure, (3) and it prefers host trees which have a restricted distribution in Estonia or are not favoured in forest management practice.

Kokkuvõte: Hariliku kopsusambliku (*Lobaria pulmonaria*), ohustatud metsasambliku levik ja kasvukohanõudlus Eestis.

Harilikku kopsusamblikku (*Lobaria pulmonaria*) on laialdaselt kasutatud looduslike vanade metsade indikaatorliigina, kuigi teadmised tema kasvukohanõudlustest on piiratud. Et saada ülevaadet h. kopsusambliku levikust, kasvukohaeelistustest ja puuliigi spetsiifilisusest Eestis, kasutasime erinevatesse andmebaasidesse koondatud andmeid. Hariliku kopsusambliku leiukohtade arv on kõrgeim suurema metsasusega piirkondades, peamiselt väikestes metsaosades, mis on defineeritud kui ökoloogiliselt väärtuslikud. See liik kasvab peamiselt lehtpuudel, eriti harilikul haaval (*Populus tremula*), olles kõige tavalisem palu-, salu- ja soostuvates metsades, ning eelistades puistuid, kus puude vanus on üle 100 aasta. Siiski võib h. kopsusamblik kasvada ka nooremates metsades, kui puistus on piisavalt suuri puid. Hoolimata h. kopsusambliku arvukatest leiukohtadest Eestis on see liik siiski ohustatud, kuna (1) metsade raiering on lühike, (2) ta on arvukas metsatüüpides, mis on Eestis haruldased või majandusliku surve all, (3) ning ta eelistab peremeespuid, mis on Eestis piiratud levikuga või mille kasvu ei soodusta metsamajandus.

INTRODUCTION

Lobaria pulmonaria (L.) Hoffm. is conspicuous and widely known epiphytic lichen species in the northern hemisphere. Within the range of distribution in boreal, temperate, montane and oceanic areas (Yoshimura, 1998), *L. pulmonaria* occurs in rather different forest types. In the boreal forest zone of northern Europe, *L. pulmonaria* is most often reported in forests dominated by *Picea abies* (Hakulinen, 1964; Istomina, 1996; Kuusinen, 1996). In the hemiboreal and temperate zones of Europe, it is more common in deciduous forests and woodlands (Andersson & Appelqvist, 1987; Gustafsson et al., 1992; Öckinger et al., 2005; Nascimbene et al., 2006), including semi-natural biotopes with a sparse cover of old trees (pasture-woodlands and wooded meadows) (Hallingbäck & Martinsson, 1987;

Rose, 1992; Wolseley & James, 2000). In spite of the occurrence of *L. pulmonaria* in a wide range of forest habitats in different light conditions, the species is high-light susceptible (Gauslaa & Solhaug, 1999) and favours habitats with high air humidity (Pannewitz et al., 2003).

In recent century, the distribution of *Lobaria pulmonaria* has become highly fragmented showing a decline across Europe, especially in densely populated and industrial areas, due to intensified forest management practice and air pollution (James et al., 1977; Wolseley & James, 2000). Therefore, *L. pulmonaria* has been included in national red lists in most European countries, including Estonia (Randlane et al., 2008). However, *L. pulmonaria* is still quite frequent in Fennoscandia and in the Baltic region,

where the lichen has been recorded mainly in small and fragmented old-growth patches in the landscape of managed forests (Auziņš & Ek, 2001; Gu et al., 2001; Andersson et al., 2003; Pykälä, 2004).

Lobaria pulmonaria has been widely used as an indicator species of undisturbed forest ecosystems and forest areas of a high ecological continuity (Rose, 1976; Andersson & Appelqvist, 1987; Nilsson et al., 1995; Andersson et al., 2003; Campbell & Fredeen, 2004; Liira & Sepp 2009), owing to the evidence of the low dispersal ability of the diaspores (Scheidegger, 1995; Walser et al., 2001) and long generation time (Scheidegger et al., 1998). During the long life-cycle of *L. pulmonaria*, in average 35 years, the dispersal by the vegetative diaspores (soredia, isidioid soredia) and by the thallus fragments predominates (Scheidegger et al., 1998; Scheidegger & Goward, 2002). That causes high density clustering of specimens within a habitat patch (Walser et al., 2003; Öckinger et al., 2005). In the later stage of the life cycle ascospores become available (Scheidegger et al., 1998; Scheidegger & Goward, 2002) and ensure long-distance dispersal (Wagner et al., 2006; Werth et al., 2006b).

The quality of the habitat, e.g. ecological conditions at stand and tree level may hinder successful establishment and colonization of *L. pulmonaria* (Werth et al., 2006a). Until now, the effect of the forest site type on the distribution of *L. pulmonaria* has received little attention (Gu et al., 2001; Nascimbene et al., 2006). Within a stand density of host trees and availability of large trees are positive predictors for presence of *L. pulmonaria* (Gu et al., 2001; Öckinger et al., 2005). At tree scale, colonization and re-establishment of individuals is dependent very specific pH levels of tree bark (Wolseley & James, 2000) and extent of bryophyte cover on host trees (Öckinger et al., 2005). The aim of this study is to evaluate the importance of different forest site types for the presence of *L. pulmonaria* in hemiboreal forests in north-eastern part of Europe. We also addressed our interest to assess some stand-scale habitat characteristics and the preference of the host tree species for the distribution of *L. pulmonaria* in forestland. We will provide an overview of the present distribution of *L. pulmonaria* in different habitats and forestland categories in Estonia and estimate the risk factors related to the forest management

for the long-term presence of *L. pulmonaria* in Estonia.

MATERIAL AND METHODS

Study area

Estonia has a flat topography: in the western and south-western regions, absolute altitude reaches mostly 20 m above the sea level, while in the south-east altitude reaches a few hundreds of metres. Average air temperature in Estonia is approximately 17 °C in July, and -6.5 °C in January (Jaagus, 1999). The amount of precipitation is higher on the uplands of the north- and south-eastern regions (650–700 mm per year) compared with coastal areas and islands (500–550 mm per year) (Jõgi & Tarand, 1995).

About a half of the mainland territory (51.5%) is covered by forests but most of them are clustered into certain regions (Kohava, 2001; Fig. 1). Estonian forests belong to the hemi-boreal subzone of the boreal forest zone of the northern hemisphere (Ahti et al., 1968). Scots pine (*Pinus sylvestris* L.), birches (*Betula pendula* Roth and *B. pubescens* Ehrh.) and Norway spruce (*Picea abies* (L.) H. Karst.) are the most common forest tree species in the region (Karoles, 1995). Speckled alder (*Alnus incana* (L.) Moench), black alder (*Alnus glutinosa* (L.) Gaertn.) and common aspen (*Populus tremula* L.) occur less frequently. The proportion of English oak (*Quercus robur* L.), small-leaved lime (*Tilia cordata* Mill.), Norway maple (*Acer platanoides* L.) and wych elm (*Ulmus glabra* Huds.) is almost insignificant (Kaar, 1974; Paal, 1998).

The conditions of anthropogenic disturbance of Estonian forests can be considered transitional between the almost natural conditions of forest areas of north-eastern Europe and the conditions of intensively managed forests of western Europe (Carlsson & Lazdinis, 2004). In Estonia clear-cutting of mature stands is the main management activity in commercial forests; therefore the stands are secondary by its origin, mostly intensively managed and monocultured (Sepp et al., 1999; Adermann, 2007). According to the methodology implemented by the Statistical Forest Inventory, only 4% of forests are in a near-natural status (*sensu* Kohv & Liira, 2005), about 79% are intensively used for commercial purposes, and 28% of forests are affected by edge-effect (Leemet & Karoles, 1995; Adermann, 2007).

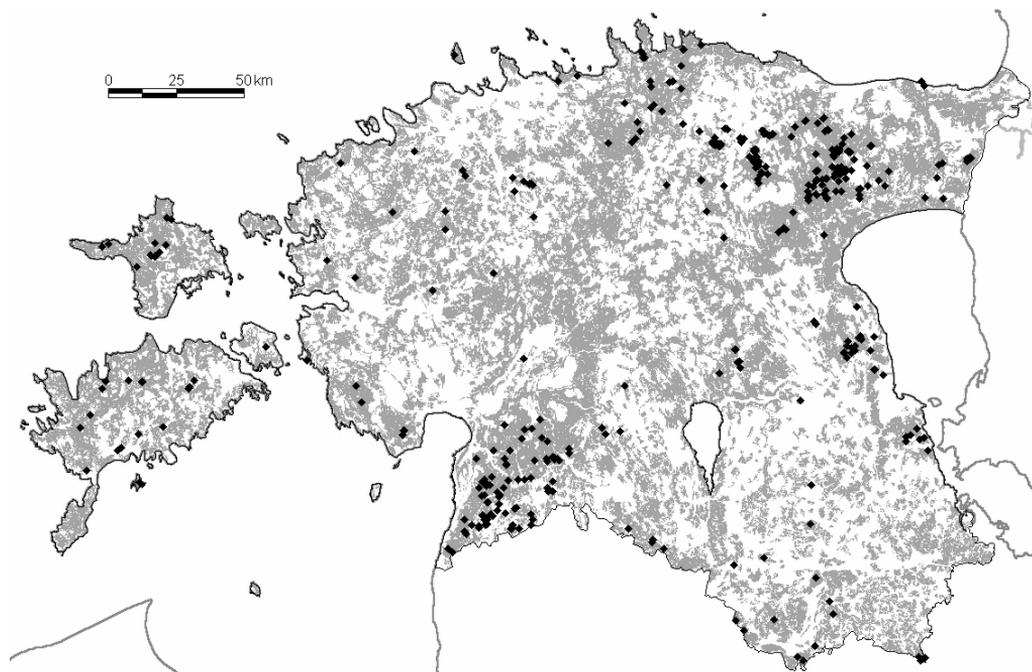


Fig. 1. Distribution map of *Lobaria pulmonaria* in Estonia. Filled signs denote exact localities of *L. pulmonaria* and grey areas represent forestland according to Peterson (2003).

Data sources

We used three data sets to give an overview of the distribution and habitat ecology of *L. pulmonaria* in Estonia. We combined the first data set of personal notes and the herbarium specimens deposited at the University of Tartu (TU). The data set consisted of 95 records from the period 1904–2002 including information about the location of specimens and about host tree species. We determined the locality coordinates based on the available descriptive information of the location. The second database is based on the survey “Estonian Forest Conservation Area Network” (Viilma et al., 2001) from the period 1999–2000, when forest inventory specialists registered 107 records of *L. pulmonaria* from state forests of Estonia. They provided host tree species and geographical coordinates for each locality. The third and largest data set concerning *L. pulmonaria* (302 records) is the Woodland Key Habitat Inventory (1999–2002) conducted in Estonian private and state forests and woodlands (Andersson et al., 2003). Inventory specialists registered the geographical coordinates of the locality but not the host tree species. Combining

the three data sets and pooling spatially overlapping records, we ended up with a database of 426 records of *L. pulmonaria* in Estonia. For 210 records out of 426, we obtained additional data of the forest type and of the stand variables from the State Forest Survey Database.

To describe the distribution and habitat ecology of *L. pulmonaria*, we used the following variables: (1) geographical location given by its coordinates ($n = 426$ records); (2) forest compartment area ($n = 426$); (3) habitat type ($n = 426$); (4) forest type ($n = 210$); (5) stand age ($n = 210$); (6) density of tree layer ($n = 210$); (7) main tree species in a stand ($n = 210$); and (8) host tree species ($n = 185$). The relative density of the tree layer is defined as the stand basal area gauge relative to the basal area gauge of standard stand. The main tree species in a stand is the economically most important tree species in the tree layer. The classification of habitat types consisted of three subtypes: forest, wooded meadow or park. Forest classification follows the classification by Lõhmus (2004). We used a five-group classification of forest site types: oligo-mesotrophic boreal (incl. *Vaccinium* and *Myrtillus* site types),

mesotrophic boreal (incl. *Oxalis* and *Hepatica* site types), eutrophic boreo-nemoral (incl. *Aegopodium* and *Dryopteris* site types), eutrophic paludifying forests (incl. *Filipendula*, *Equisetum* and *Carex* site types), and other forests. The last group combined all other forest types of Estonia where *L. pulmonaria* was found only a few times (eutrophic alvar forests, oligotrophic boreal heath forests, oligotrophic paludifying forests, eutrophic to meso-eutrophic swamp forests, mesotrophic bog forests, oligotrophic bog forests, and drained peatland forests).

We used the map of the distribution of forestland compiled by Peterson (2003) to illustrate the distribution of *L. pulmonaria* in Estonia. For the analysis of the distribution of *L. pulmonaria* in different forestland categories in Estonia (implemented in the program package Mapinfo 8.0), we used the map layers of commercial forest areas, protected forest areas (nature reserves, national parks) and valuable forest areas e.g. 'ecologically highly valuable' forests (Woodland Key Habitats and pre-selection areas of the Estonian Forest Conservation Area Network) from the Estonian Nature Information System (EELIS – Environmental Registry; Estonian Environment Information Centre). For estimation of the relatedness of *L. pulmonaria* with forest patch size, we classified the area of forest compartments and the area of protected forestland on a log-scale (0.1, 1, 10, 100, 1000, 10 000, or 100 000 ha).

We applied log-linear analysis to the most complete subset of data (210 records) to assess the non-randomness of the distribution of *L. pulmonaria* among the forest site types, stand age groups and relative stand density classes in the program package Statistica 6.5 (Statsoft Inc., 1989). We tested also the effects of the interaction between these variables on the frequency distribution of *L. pulmonaria*. We divided the continuous variables into classes: stand age ≤ 100 or > 100 years, relative density of the tree layer $\leq 60\%$ or $> 60\%$.

RESULTS

L. pulmonaria is a forest dependent species as 87% of the records were from forests, and only 10% from wooded meadows and 3% from parks. Mapping of all 426 records revealed that *L. pulmonaria* occurred most frequently in the north-eastern and south-western parts

of Estonia in regions with a large proportion of forestland (Fig. 1). However, sporadic locations were situated all over the mainland and larger islands, mostly in large patches of forestland. Map-analysis of records of *L. pulmonaria* showed that 23% of the records originated from protected areas (national parks, nature reserves), 61% from areas defined as 'ecologically highly valuable' and 16% from commercial forests or other habitats (Fig. 2). Most of the reserves and national parks where *L. pulmonaria* occurred were larger than 1000 ha, although extensive reserves form only a minor part of the protected areas in Estonia. The area of 'ecologically highly valuable' forest patches with *L. pulmonaria* was mostly less than 10 ha, reflecting the general size distribution of 'ecologically highly valuable' areas in Estonia (Fig. 2).

The largest number of the records of *L. pulmonaria* (37.8%) occurred in forests where *Picea abies* was the economically most important tree species, and 23.8% of the records were made from the stands where birches (*Betula pendula* or *B. pubescens*) were the main tree species (Fig. 3). The stands where *Alnus glutinosa*, *Fraxinus excelsior*, *Quercus robur* or *Tilia cordata* were the main tree species constituted 16.4% of the total list of *Lobaria* forests.

Within the large data set, there were 185 records including information about the host tree species. *L. pulmonaria* was found on 17 tree species, almost exclusively on deciduous trees (Fig. 4). One-third of the records (29%) were made from *Populus tremula*. *L. pulmonaria* was also common on temperate broad-leaved trees: 21% on *Fraxinus excelsior*, 13% on *Acer platanoides*, and 8% on *Quercus robur*. The presence of the lichen on coniferous trees was insignificant (approx. 1% of the records).

The results of log-linear analysis revealed that the frequency of *L. pulmonaria* differed for five forest site type groups ($P = 0.001$), for two stand age groups ($P = 0.001$), and for two stand density groups ($P = 0.005$; Table 1). *L. pulmonaria* was found more frequently in the oligomesotrophic boreal, eutrophic boreo-nemoral, and eutrophic paludifying forest site type groups (32, 30, and 20% of the records, respectively), and less frequently in the mesotrophic boreal and the other forest types (Table 2).

The average age of the *Lobaria* forest stands was 118 years ($n = 210$). In general, *Lobaria* preferred forests with stand age over 100 years

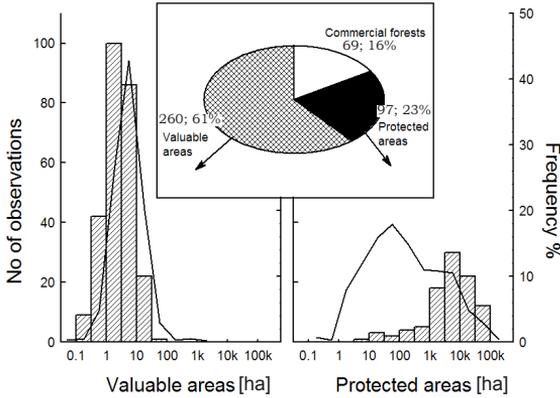


Fig. 2. The frequency of occurrence of *Lobaria pulmonaria* among three forestland categories (pieplot) and the number of observations of *L. pulmonaria* among the area size classes within Valuable areas and Protected areas (barplot and left axis). The overall frequency distribution (%) of the area size classes of Valuable areas and Protected areas is given by the lineplot (right-hand y-axis for count percentage). Protected areas = nature reserves, national parks, Valuable areas = ecologically highly valuable forests (Woodland Key Habitats and pre-selection areas of the Estonian Forest Conservation Area Network).

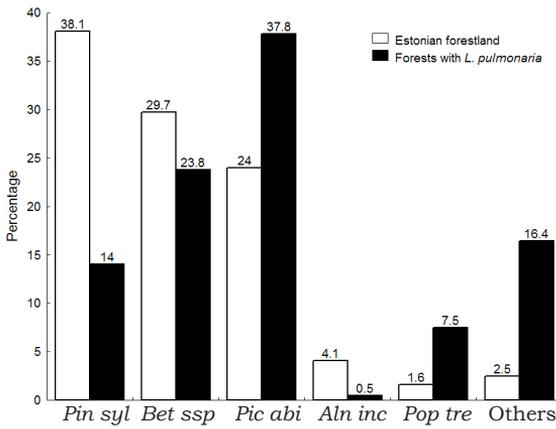


Fig. 3. The area-weighted frequency distribution of the economically most important tree species per stand on Estonian forestland (open bars; Karoles, 1995) and the frequency distribution of the main forest tree species in forests with *Lobaria pulmonaria* in Estonia (filled bars). *Pin syl* = *Pinus sylvestris*, *Bet ssp.* = *Betula pubescens* and *B. pendula*, *Pic abi* = *Picea abies*, *Aln inc* = *Alnus incana*, *Pop tre* = *Populus tremula*, Others = e.g. *Alnus glutinosa*, *Fraxinus excelsior*, *Quercus robur*, *Tilia cordata*.

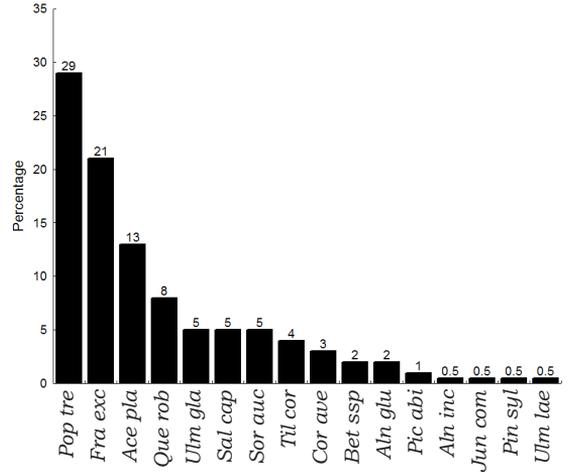


Fig. 4. The proportion (%) of *Lobaria pulmonaria* on different host tree species in Estonia. *Pop tre* = *Populus tremula*, *Fra exc* = *Fraxinus excelsior*, *Ace pla* = *Acer platanoides*, *Que rob* = *Quercus robur*, *Ulm gla* = *Ulmus glabra*, *Sal cap* = *Salix caprea*, *Sor auc* = *Sorbus aucuparia*, *Til cor* = *Tilia cordata*, *Cor ave* = *Corylus avellana*, *Bet ssp.* = *Betula pubescens* and *B. pendula*, *Aln glu* = *Alnus glutinosa*, *Pic abi* = *Picea abies*, *Aln inc* = *Alnus incana*, *Jun com* = *Juniperus communis*, *Pin syl* = *Pinus sylvestris*, *Ulm lae* = *Ulmus laevis*.

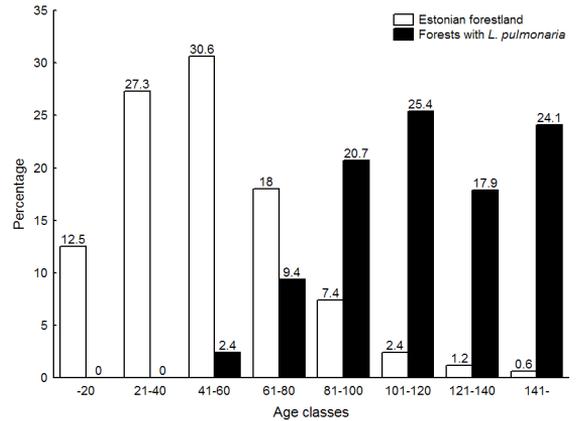


Fig. 5. The area-weighted frequency distribution of Estonian forests among the forest age classes (open bars; Karoles, 1995) and the frequency distribution of forests with *Lobaria pulmonaria* among the forest age classes (filled bars).

Table 1. Log-linear analysis of the interactions between the forest site type groups, stand age and density of the tree layer in forest stands for the occurrence of *Lobaria pulmonaria*. Forest classification follows the classification by Löhmus (2004). Continuous variables were divided into classes: stand age ≤ 100 or > 100 years, relative density of the tree layer $\leq 60\%$ or $> 60\%$.

| Factors | Degrees of freedom | Partial Chi-square | <i>p</i> |
|--|--------------------|--------------------|----------|
| Forest site type group | 4 | 52.53 | 0.001 |
| Stand age | 1 | 24.23 | 0.001 |
| Density of tree layer | 1 | 5.32 | 0.005 |
| Forest site type group* Stand age | 4 | 16.05 | 0.005 |
| Forest site type group* Density of tree layer | 4 | 0.86 | 0.930 |
| Stand age* Density of tree layer | 1 | 22.16 | 0.001 |
| Forest site type group* Stand age* Density of tree layer | 4 | 2.36 | 0.669 |

Note: *p* = significance level.

Table 2. Log-linear analysis of the interactions between the forest site type groups and stand age for the occurrence of *Lobaria pulmonaria*. Forest classification follows the classification by Löhmus (2004), group 'Others' refers eutrophic alvar forests, oligotrophic boreal heath forests, oligotrophic paludifying forests, eutrophic to meso-eutrophic swamp forests, mesotrophic bog forests, oligotrophic bog forests, and drained peatland forests

| Forest site type group | Observed number (percentage) of ≤ 100 yr-old stands | Observed number (percentage) of > 100 yr-old stands | Total |
|--------------------------|--|---|----------|
| Eutrophic boreo-nemoral | 31 (45%) | 31 (22%) | 62 (30%) |
| Eutrophic paludifying | 17 (25%) | 26 (18%) | 43 (20%) |
| Mesotrophic boreal | 6 (9%) | 18 (13%) | 24 (11%) |
| Oligo-mesotrophic boreal | 12 (17%) | 55 (39%) | 67 (32%) |
| Others | 3 (4%) | 11 (8%) | 14 (7%) |
| Total | 69 | 141 | 210 |

Table 3. Log-linear analysis of the interactions between stand age and density of the tree layer in forest stands for the occurrence of *Lobaria pulmonaria*

| Density of tree layer | Observed number (percentage) of ≤ 100 yr-old stands | Observed number (percentage) of > 100 yr-old stands | Total |
|---------------------------------|--|---|-----------|
| Density of tree layer ≤ 60 | 12 (17%) | 76 (54%) | 88 (42%) |
| Density of tree layer > 60 | 57 (83%) | 65 (46%) | 122 (58%) |
| Total | 69 | 141 | 210 |

(67% of the records, $n = 210$, $P = 0.001$; Tables 1 & 2), while the area-weighted frequency distribution of the age classes of Estonian state forests demonstrated the dominance of forests with stand age less than 80 years (Fig. 5). Stands of the forest age class of 41-60 years were the youngest where the species was recorded.

L. pulmonaria preferred forests with a high density of the tree layer (relative density class

61-100% accounting for 58% of the records, $P = 0.005$; Tables 1 & 3). However, stand density preference was dependent on stand age ($P = 0.001$; Table 1). The effect of the interaction between stand age and density of the tree layer was reflected by the fact that in the group of younger stands (stand age ≤ 100 years) *L. pulmonaria* was evidently more common in forests with a high relative density of the tree layer (83% of the

records), while in the group of old forests (stand age > 100 years), the presence of *L. pulmonaria* did not depend on the density of the tree layer (Table 3). According to the test of cross-tabulation between the forest type and the stand age group ($P = 0.0005$; Table 1), in the group of younger stands (stand age ≤ 100 years), 45% of the records of *L. pulmonaria* were ascribed to the eutrophic boreo-nemoral forest site type group and 25% of the records to the eutrophic paludifying forest site type group (Table 2). In the group of old stands (stand age > 100 years), the largest proportion of the specimens (39%) was found in oligo-mesotrophic boreal forests.

DISCUSSION

Distribution and habitat conservation

The highest density of localities of *L. pulmonaria* occurred in regions with the largest proportion of forest cover and historical continuity (Fig. 1). In other regions, suitable habitats are scarce as these are the areas of extensive long established agriculture with small fragments of forest or wooded meadows (Paal, 1998).

Only a quarter of specimens of *L. pulmonaria* were recorded from protected areas (nature reserves or national parks) (Fig. 2). Large unit area (mostly over 1000 ha), officially set restrictions on forest management activity and ban on clear cutting should ensure the continuity of the habitat and persistence of viable populations of *L. pulmonaria* in protected areas. However, the regeneration of suitable host trees is probably crucial in protected areas, especially in conifer dominated forests. For instance, Snäll et al. (2005) have predicted loss of *L. pulmonaria* in nature reserves of boreal old-growth forest due to the low regeneration rate of host trees (*Populus tremula* and *Salix caprea*).

A significant proportion of *L. pulmonaria* populations were found in small patches of mature and old-growth forest in a commercial forest landscape. Most of these patches are now defined as 'woodland key habitats' (Andersson et al., 2003). Nevertheless, a majority of the forest key habitats, particularly those situated on private land are not covered by definite protection regulations. Conservation of key habitats as hot spots of lichen diversity in a managed forest landscape is most essential for old-growth-forest-dependent lichen species (Berg et al., 2002; Peterson & McCune, 2003). On the

other hand, small remnant lichen populations in a managed forest landscape may reflect the delayed response between habitat fragmentation and the extinction of local population (Hanski, 1998; Gu et al., 2001), since small populations are presumably very vulnerable to disturbances (Scheidegger et al., 1998; Pykälä, 2004).

Preservation of *L. pulmonaria* populations in a commercial forest landscape is questionable as the species is sensitive to the short cutting rotation time (Snäll et al., 2005). The elongated rotation cycle of stands could promote the persistence of this species in a managed forest landscape. Recent studies (Kalwij et al., 2005, Werth et al., 2006b) have shown the ability of *L. pulmonaria* to colonize a habitat after 130 years of stand-replacing disturbance and to form a large population there. Small-scale disturbances, e.g. selective cutting of forest need not be harmful for individual specimens of *L. pulmonaria* if the host trees and the potential host trees remain intact; moreover, the increased amount of light might favour the lichen in the habitat (Coxson & Stevenson, 2007). However, at the stand level, selective cutting has a strong negative impact on the abundance, frequency and fertility of *L. pulmonaria* (Edman et al., 2008).

Host tree preference and forest stand characteristics

L. pulmonaria colonizes the bark of a variety of tree species. For example, it has been found on 28 tree species in Russia (Istomina, 1996), and on 17 tree species both in Finland (Hakulinen, 1964) and in Estonia. In northern Europe, the species sometimes occurs also on large mossy stones, cliffs and on soil (Hakulinen, 1964; Istomina, 1996).

Aspen (*Populus tremula*) is the main phorophyte for *L. pulmonaria* in Estonia (Fig. 4) and in boreal forests of northern Europe (Hakulinen, 1964; Kuusinen, 1996). Besides aspen, several temperate broad-leaved tree species (e.g. *Fraxinus excelsior*, *Acer platanoides*, *Quercus robur*, *Ulmus glabra*) are important host trees for *L. pulmonaria*. Despite the large proportion of *L. pulmonaria* in conifer dominated forests (Fig. 3), the presence of the species on coniferous trees was insignificant as is the case in most parts of Europe (Gauslaa & Holien, 1998; Goward & Arsenault, 2000). In the conditions of increasing acidification of the bark due to atmospheric

pollution, *L. pulmonaria* becomes restricted to trees with high bark pH and as well as to trees with a bark of high water retention capacity, e.g. *Populus tremula* (Gilbert, 1986; Gauslaa, 1995). As aspen is a more common tree species than temperate broad-leaved trees in hemiboreal forest (Kaar, 1974), the importance of preserving old aspen trees in forest management practice for maintaining biodiversity should be emphasized (Hanski & Hammond, 1995).

Analysing the frequency of *L. pulmonaria* in forest site types in more detail, we found that oligo-mesotrophic boreal (*Vaccinium* and *Myrtillus* site types) and mesotrophic boreal forests (*Oxalis* and *Hepatica* site types) provide favourable conditions for *L. pulmonaria*, which is confirmed by the presence of nearly half of the populations of *L. pulmonaria* in forests of these types (Table 2). These forests are dominated by pine or spruce trees and all suitable phorophytes (e.g. *Populus tremula*, *Salix caprea*, *Sorbus aucuparia*) appear as subdominants (Löhmus, 2004). However, *L. pulmonaria* is more frequent in old (more than 100 years) boreal forests (oligo-mesotrophic boreal and mesotrophic boreal forests) than in younger forests (Table 2). The occurrence of *L. pulmonaria* mainly in older forest age classes has been shown in several earlier studies (e.g. Campbell & Fredeen, 2004). The lichen evidently prefers a more humid mesoclimate in older conifer-dominated boreal forests. At the same time, gaps in the canopy structure of old forest (Esseen et al., 1992) could provide better light conditions for it.

Another important forest type for *L. pulmonaria*, the eutrophic boreo-nemoral forest site type group (*Aegopodium* and *Dryopteris* site types), includes the most productive and tree-species-rich mixed forests. Temperate broad-leaved trees suitable for *L. pulmonaria* (*Fraxinus excelsior*, *Quercus robur*, and *Ulmus glabra*) dominate in these highly fragmented stands (Löhmus, 2004). A considerable part of *Lobaria* populations occurred also in eutrophic paludifying forests (e.g. *Filipendula* site type). These forests are more humid because of the high groundwater table. In managed eutrophic paludifying forests, birch, spruce and black alder are the dominant trees (Löhmus, 2004), while *Fraxinus excelsior*, the potentially most important host tree for *Lobaria*, is only occasionally present as it is suppressed by management.

In several cases, especially in the eutrophic boreo-nemoral and eutrophic paludifying forest site type groups, *L. pulmonaria* was also present in younger stands (stand age less than 100 years). According to our field observations (unpublished data), the age of the trees colonized by *L. pulmonaria* in the eutrophic boreo-nemoral and eutrophic paludifying forests was generally higher than average stand age. In the eutrophic boreo-nemoral forests with temperate broad-leaved trees, old trees and part of the undergrowth are normally preserved during selective cutting (Kuuba, 2001a), which increases the probability for the host trees of *L. pulmonaria* remaining intact and may ensure the persistence of the lichen population (Edman et al., 2008). Also, these younger than 100-year-old eutrophic boreo-nemoral and eutrophic paludifying forests had higher relative stand density, i.e. their stand structure was almost similar to the maximum stand density in given environmental conditions. It means that *L. pulmonaria* can successfully use such a stand as suitable habitat, which structure is more mature than could be predicted on the basis of forest age. This suggestion is in accordance with the results of earlier studies (Gu et al., 2001; Öckinger et al., 2005; Edman et al., 2008) which demonstrate the preference of *L. pulmonaria* for large trees.

The other forest site type groups in Estonia, particularly, swamp forests, bog forests and oligotrophic boreal heath forests are dominated by *Pinus sylvestris*. These groups account for the largest proportion in the area of Estonian forestland (Karoles, 1995). Yet because of the absence of suitable phorophyte tree species, these forests cannot be considered important habitats for *L. pulmonaria*.

All forest types suitable for *L. pulmonaria* are faced with intensive anthropogenic disturbances and natural stands appropriate for *L. pulmonaria* are rare. Oligo-mesotrophic and mesotrophic boreal forests have been under intensive cutting pressure for centuries with a rotation cycle of 80-100 years (Kuuba, 2001b). As most boreo-nemoral forest areas with temperate broad-leaved trees have been transformed into agricultural fields, these forests have become the most heavily threatened habitats. Most eutrophic paludifying forests were drained in the last century and reforested with spruce or birch (Paal, 1998).

Conclusions

L. pulmonaria is threatened in the region, firstly, as it prefers over-mature and old-growth stands, threat derives from the short rotation period of stands (clear-cut cycle). Second threat is that *L. pulmonaria* is abundant in the forest types that are rare (e.g. eutrophic boreo-nemoral forests) or are under strong economic pressure (e.g. oligomesotrophic boreal forests). Third risk factor is that it prefers the host trees species which are not favoured by forest management practice (e.g. *Populus tremula* and *Fraxinus excelsior*), or which have a limited distribution in the hemiboreal zone (e.g. *Acer platanoides* and *Quercus robur*). On the other hand, the high number of the localities of *L. pulmonaria*, the presence of the species in managed forests, and in younger than 100-year-old forest age classes supports the opinion that *L. pulmonaria* is probably less dispersal-limited than previously proposed (Werth et al., 2007). Therefore, the current localities of *L. pulmonaria* (e.g. forest key habitats) should be preserved as potential sources of diaspores. In addition to old-growth forests, also middle-aged stands, particularly forests belonging to the oligo-mesotrophic boreal, eutrophic boreo-nemoral, eutrophic paludifying and mesotrophic boreal forests, with large deciduous trees should be considered potential habitats for *L. pulmonaria*. Such stands should be part of the forest networks connecting old-growth stands and provide possible dispersal corridors for vulnerable epiphytic species. From the point of view of forest management, growth of prospective host trees (e.g. *Populus tremula* and temperate broad-leaved tree species) should be promoted to provide the continuity of suitable phorophytes in forest stand.

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