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Habitat conditions and host tree properties affect the occurrence, abundance and fertility of the endangered lichen *Lobaria pulmonaria* in wooded meadows of Estonia

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Abstract: We assessed multiple environmental factors that might influence the population vitality of the epiphytic lichen *Lobaria pulmonaria* at the individual tree and habitat levels in partially overgrown wooded meadows in Estonia. A total of 301 trees of four species were sampled at nine study plots, using a stratified factorial scheme, 151 colonized by *L. pulmonaria* and 150 not colonized by *L. pulmonaria* forming the control group. We used the Generalized Linear Models (GLZ) to identify a complex of factors which predicts the probability of the lichen occurring on tree trunks and the presence of apothecia on its individuals. We employed the General Linear Mixed Model (GLMM) to study the relationship between cover of *L. pulmonaria* and environmental factors. The occurrence probability of *L. pulmonaria* on tree trunks increased with increasing light availability and height of deciduous shrubs near the trunk, and decreased with increasing distance to the nearest colonized tree. The host tree species and its trunk properties were also of importance, particularly the facilitating effect of the cover of bryophytes upon *L. pulmonaria*. The probability of occurrence of apothecia increased with maximum values of bark pH and cover of *L. pulmonaria* on the trunk. We conclude that partially overgrown wooded meadows are suitable habitats for *L. pulmonaria*. However, to maintain the vitality of these populations, a specific management scheme, preventing development of a dense stand, should be applied. Management requirements would include 1) selective cutting of overgrowing coniferous trees (particularly spruce), 2) preservation of adult and younger potential host trees within 10–20 m of colonized trees, 3) preservation of scattered deciduous shrubs in the vicinity of the host trees.

Key words: bark pH, bark roughness, bryophytes, dispersal distance, reforestation, semi-natural habitats, trunk diameter, woodland management

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Introduction

The detailed knowledge of the distribution and habitat requirements of threatened species is essential in improving conservation actions and policies (Hunter & Webb 2002; Berglund & Jonsson 2003). Most threatened species are rare or very locally distributed, which makes it difficult to obtain appropriately quantified information about their autecology, consisting of limiting factors and optimal ecological conditions for species survival (Scheidegger & Goward 2002; Glavich *et al.* 2005). In Europe, the epiphytic alliance *Lobarion*, which is confined to woodland habitats of long ecological continuity and to sub-neutral barked deciduous trees, consists of lichen species of great conservation concern (Rose 1988). The characteristic species of this alliance, *Lobaria pulmonaria* (L.) Hoffm., is a conspicuous foliose lichen which is used as a model organism to study the population biology of lichens at the stand and landscape levels (Scheidegger & Werth 2009).

Intensified forest management practices have influenced the distribution of *L. pulmonaria*, as a significant part of the modern European forest landscape is covered with mono-cultured and even-aged stands with short rotation cycles and a lack of suitable

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host trees (Rose 1988). In the boreal region, the species has mainly been preserved in small and fragmented old forest patches within managed forests (Gustafsson *et al.* 1992; Auzinš & Ek 2001; Gu *et al.* 2001; Andersson *et al.* 2003; Pykälä 2004; Jüriado & Liira 2009, 2010). Low connectivity among fragmented forest remnants is proposed as an essential limiting factor for cryptogamic epiphytes, including also *L. pulmonaria*, indicating a restricted dispersal range (Snäll *et al.* 2004, 2005).

Lobaria pulmonaria also grows in various semi-natural habitats with sparse cover of old trees, such as old parklands, pasture-woodlands and wooded meadows (e.g. Hallingbäck & Martinsson 1987; Rose 1992; Wolseley & James 2000; Kalwij *et al.* 2005; Carlsson & Nilsson 2009). Wooded meadows are a critical habitat in Estonia, because 19% of forest remnants with *L. pulmonaria* have become endangered by forest management and 6% have been cut during the last decade (Jüriado & Liira 2010).

At the tree scale the presence of *L. pulmonaria* is affected by various abiotic and biotic factors. In boreal forests the species prefers large diameter host trees (Gu *et al.* 2001; Riiali *et al.* 2001; Mikhailova *et al.* 2005; Öckinger *et al.* 2005). Tree bark pH is another factor limiting its distribution because even small changes in bark pH prevent the establishment of new individuals (Wolseley & James 2000). Large diameter deciduous trees with a well-buffered bark and a pH between 5·0 and 6·0 are the preferred hosts for *L. pulmonaria* (James *et al.* 1977; Gauslaa 1985).

On the tree bole, presence of lichen-feeding molluscs (Scheidegger *et al.* 1995; Asplund & Gauslaa 2008) and the extent of the bryophyte cover (Wolseley & James 2000; Öckinger *et al.* 2005) are important ecological drivers that influence the establishment and growth of *L. pulmonaria*. Air pollution also affects the vitality and fertility of *L. pulmonaria*; because of acid rain there are fewer fertile specimens now than is believed to have been the case in the past (Hawksworth *et al.* 1973; Hallingbäck & Martinsson 1987; Wirth 1995; Bruun 2000).

The aim of this study was to explore the role of tree- and stand-scale factors affecting the probability of occurrence, cover and fertility of the epiphytic lichen *L. pulmonaria* in the abandoned wooded meadows of Estonia. The role of these stand and tree trunk properties need to be evaluated for conservational application and restoration management of overgrown wooded meadows. Overgrowing of semi-open habitat, due to cessation of traditional land-use, causes significant changes in microhabitats of lichen communities on trees; the number of lichen species decreases and the species composition changes (Leppik & Jüriado 2008; Jönsson *et al.* 2011; Leppik *et al.* 2011). Highly intensive management activities may also threaten sensitive lichen species (Rose 1992, 2001). Observations from wooded meadows in Finland (Carlsson & Nilsson 2009) suggest that *L. pulmonaria* prefers intermediate conditions of partially overgrown wooded meadows to well lit and dry, continuously managed, wooded meadows.

Materials and Methods

Study area

Estonia is located in north-eastern Europe in the hemi-boreal sub-zone of the boreal forest zone (Laasimer & Masing 1995). It is characterized by significant seasonal variations in air temperature and in the amount of solar radiation (Arold 2005). The study area is located in north-eastern Estonia in the Pandivere Uplands, where the till plain is mostly 100–130 m high. The bedrock core of this upland is Ordovician limestone underlying a thin Quaternary glacial sediment cover with a thickness of 2–5 m. Although the upland is characterized by a cultural landscape with extensive fields and numerous rural settlements, the woodland area is still 40·5% (Arold 2005). In this region, a significant part of the forestland consists of abandoned overgrown fields or wooded meadows. Wooded meadows are semi-natural communities where traditional management has led to the formation of complexes of mosaic vegetation, consisting of scattered deciduous trees and shrubs alternating with mowed open areas (Kukk & Kull 1997). In the study area, wooded meadows accounted for approximately 20% of the upland's land cover in the mid-20th century (Arold 2005). After the rapid increase of intensive agriculture and collectivization of farming in Estonia in the second half of the 20th century, the mosaic wooded meadows were replaced by cultivated fields or woods (Kukk & Kull 1997; Kukk & Sammul 2006).

FIG. 1. Photograph of the Lasila wooded meadow illustrating the overgrowth of an oak tree by spruce (on the left side of the photograph) and the *Corylus*-shrub partially shading the trunk of the other oak tree (on the right side of the photograph). In the background, saplings of aspen colonize the open part of the meadow in front of the overgrown forest-like part.

Study sites and data collection

Based on the data from previous inventories (Andersson *et al.* 2003; Jüriado & Liira 2009), weselected three study sites with *L. pulmonaria* growing in partially overgrown wooded meadows (Fig. 1), located in Lääne-Viru County at the Lasila, Haavakannu and Suurekivi Nature Reserves. Each study site is characterized by a high abundance of *L. pulmonaria*.

Within each of the three study sites, three study plots were selected, each with an area of 0·5 ha, and each with different canopy closure (Appendix 1). The distance between the study plots was at least 200 m. The dominant tree species in the selected plots were *Quercus robur* L., *Populus tremula* L., *Acer platanoides* L., *Salix caprea* L., *Tilia cordata* Mill. and *Fraxinus excelsior* L. Some coniferous trees, such as *Pinus sylvestris* L. and *Picea abies* (L.) H. Karst., occurred also in the subcanopy. The shrub layer was dominated by *Corylus avellana* L. In addition, there grew *Sorbus aucuparia*, *Ribes alpinum* L., *Lonicerea xylosteum* L. and *Frangula alnus* Mill. The cover percentage of the shrub layer in each study plot was estimated according to the Braun-Blanquet scale (Jongman *et al.* 1995).

A spherical densiometer was used to estimate the forest canopy cover. The canopy cover in each study plot was estimated at the centre of the plot and at 20 m from the centre in every cardinal direction. The average of these five estimates was used in data analyses.

We applied a stratified factorial sampling methodology to maximize the efficiency of the analytical apparatus, in order to ensure factorial completeness and to obtain unbiased quantitative estimates for critical environmental factors at the tree and stand scales. First, we stratified samples by tree species occurring in the plot. Second, within each tree species, we sampled an equal number of trees with and without *L. pulmonaria* as local pairs. In the study plot, we recognized all trees with *Lobaria* as '*Lobaria*-trees'. Thereafter, for each individual *Lobaria*-tree we described a potentially suitable but uncolonized host tree for *L. pulmonaria* as a 'control tree'. The control tree was defined by two criteria: 1) the nearest neighbouring tree from the same tree species as the *Lobaria*-tree to avoid subjective selection of control trees and to increase the efficiency of revealing spatial neighbourhood effects; and 2) a trunk diameter of at least 8 cm to exclude tree saplings not suitable for establishment of *L. pulmonaria*. In our sample plots, *L. pulmonaria* was sometimes growing so abundantly that nearly all suitable deciduous trees without *Lobaria* were selected as control trees. Total sample size was 301 trees, consisting of 151 *Lobaria*-trees and 150 control trees (for one *Salix* there was no suitable match with acceptable size). We sampled the four most frequent tree species in the study stands: *Quercus robur* (n = 210), *Acer platanoides* (n = 34), *Populus tremula* (n = 32) and *Salix caprea* (n = 25). The number of sampled trees in the study plot varied from 23 to 50. The geographical coordinates of all trees were recorded by means of GPS (GPSmap 60Csx, Garmin) to assess the distance between the trees.

The circumference of each sampled tree was measured at breast height (*c.* 1·3 m above ground level), the vitality of each sampled tree (healthy or senescent, the latter including unhealthy, partly dead, dried or damaged trees) was determined and the presence of trees and shrubs around the sampled trees (within 1 m) was recorded (Appendix 1). The maximum height of shrubs, within 1 m of each sampled tree, was also measured, as was the inclination of the trunk of the sampled tree, in degrees, using a compass.

Lobaria pulmonaria usually grows unevenly around the tree trunk, frequently preferring only one side of the tree bole. To determine the reason for such one-sided preference, we sampled two sides of each *Lobaria*-tree: the side with *Lobaria* (or with the highest coverage) and the side opposite to it (without *Lobaria* or with lower coverage). In the case of the control trees, the two contrasting sides were subjectively defined based on the cover of other epiphytic lichens and bryophytes (maximum vs. least cover), light conditions (most vs. least well lit) and inclination of the trunk (upper side vs. lower side). The methodology designating contrasting sides gives information on the range of environmental variation on the trunk, as well as general conditions from averaging two extreme values. The rationale for this methodology, in contrast to traditional fixed cardinal directions, lies in the environmental complexity of mixed woodland. For instance, direction to the nearest gap or evergreen conifer tree affects environmental conditions on the trunk more than cardinal direction. Hence our methodology helps avoid biased estimation of average conditions on the trunk and provides an option to use maximum values in addition to average estimates per tree as factors in models. We determined the cardinal position of both sides. The cover percentage of *L. pulmonaria* and the cover of bryophytes were estimated at a height of 2 m above the ground on both sides of the trunk (in 10% intervals). The roughness of the bark was also measured on both sides, using a vernier caliper; measurements were made in triplicate, at *c.* 1·3 m above ground level, and the average value was used in data analysis. Light conditions on both sides of the tree were measured, using a spherical densitometer at 0·5 m from the trunk. The minimum values of the 'Light conditions' variable were used in data analysis (Appendix 1).

For measurement of bark pH, two samples of the bark free of lichens and bryophytes were removed with a knife from both sides of the trunk on each sampled tree. The bark samples were air-dried and stored in paper bags until laboratory analysis. Bark pH was measured with a flat head electrode (Consort C532), applying a technique suggested by Schmidt *et al.* (2001) and Kricke (2002), with slight modifications by Jüriado *et al.* (2009).

We also recorded the presence of apothecia on *L. pulmonaria* for each sampled tree and evaluated their presence relative to the cover value of *L. pulmonaria* and other environmental variables.

Statistical analyses

We used the main effects of ANOVA ($n = 301$) to test for the difference in the average estimates of the tree properties and the environmental factors between the study sites, the tree species and the sampled trees (*Lobaria*-trees vs. control trees), to make sure that sampling was adequately balanced.

We applied a generalized linear model (GLZ) with the two-way stepwise selection procedure to study the probability of presence/absence of *L. pulmonaria* ($n = 301$) as dependent on the environmental variables, implemented in the program package Statistica ver. 7 (StatSoft, Inc. 2005). The model was assembled from variables describing the site and tree properties listed in Appendix 1. In the model, we used the Binomial error distribution, logit link-function and Pearson correction coefficient to correct for overdispersion.

The GLZ analysis was also applied to evaluate the influence of 'Cover of *Lobaria*' and environmental variables on the probability of occurrence of the apothecia of *L. pulmonaria*, using the same model settings as in the model described above. Only the sides of the *Lobaria*-trees with the lichen were considered in this model ($n = 151$).

We tested the response of the cover of *L. pulmonaria* to the influence of the environmental variables ($n = 151$) using a general linear mixed model (GLMM; Littell *et al.* 1996) with the stepwise selection procedure, implemented in the program package SAS ver. 8.2 (proc MIXED, SAS Institute Inc. 1989). The categorical factor 'Sample tree' was considered the random factor and 'Tree side' was treated as repeated observations of *L. pulmonaria* per sample tree. In the model building, we also tested interactions with the categorical factors 'Tree species' and 'Tree side'; we also tested non-linear relationships between the factors. For multiple comparisons between the factors 'Tree species' and 'Tree side', we used the Tukey-Kramer adjustment. Akaike's information criterion (AIC; Akaike 1973) was used as an auxiliary tool to find an optimal model according to predictive power and to avoid overparameterization (Shao 1997). Only the final model is presented.

In ANOVA and GLMM, the cover values of *L. pulmonaria* and the variables 'Bark roughness', 'Circumference' and 'Distance' were log-transformed to obtain the Normal distribution of residuals.

Results

Study plots and sample tree characteristics

Among the nine investigated study plots, light availability (i.e. stand openness) varied between 6 and 39% and the cover of shrubs varied between 10 and 70%. The circumference of sampled trees varied between 28 and 238 cm, the inclination of the trunks was

TABLE 1. *The results of main effects of ANOVA for the difference in the average values of the environmental variables between colonized (*Lobaria*-tree) and uncolonized trees (control tree), study sites and tree species (*n *= 301).*

	Study sites		Tree species		Sample tree		*Lobaria*-tree	Control tree
Variable	*F*	*P*[*]	*F*	*P*[*]	*F*	*P*[*]	Mean (± SE)[†]	Mean (± SE)[†]
Inclination (°)	6·45	**0·002**	2·17	0·091	4·79	**0·029**	76·1 ± 0·76^{b}	77·8 ± 0·77^{a}
Circumference (cm)	67·11	**<0·0001**	4·30	**0·005**	1·97	0·162	88·8 ± 0·02	84·1 ± 0·02
Bark roughness (mm)	16·15	**<0·0001**	3·45	**0·016**	0·02	0·883	0·7 ± 0·03	0·6 ± 0·03
Bryophyte cover (%)	1·53	0·218	12·09	**<0·0001**	9·51	**0·002**	27·8 ± 1·75^{a}	22·1 ± 1·77^{b}
Bark pH	1·78	0·169	25·86	**<0·0001**	3·29	0·071	5·90 ± 0·05	5·81 ± 0·05
Height of shrubs (m)	18·30	**<0·0001**	4·05	**0·007**	5·46	**0·020**	192·7 ± 14·83^{a}	155·8 ± 15·02^{b}
Light conditions (%)	31·57	**<0·0001**	0·18	0·911	1·37	0·243	11·9 ± 0·52	11·3 ± 0·53

[*] Significant *P* values ($P < 0{\cdot}05$) in bold.
[†] Superscript letters denote homogeity groups.

50°–90°, and most of the tree boles were partially covered with mats of bryophytes (mean 26%). The pH of the tree bark varied from rather acid (4·63) to moderately basic (7·62) and the cracks in the bark were 0·2–2·3 cm deep. The mean cover of *L. pulmonaria* on colonized trees was 11% (Appendix 1). In the study area, *L. pulmonaria* was more common on *Quercus robur* (69·5%, $n = 105$), compared to *Acer platanoides* (11·3%, $n = 17$), *Populus tremula* (10·6%, $n = 16$) and *Salix caprea* (8·6%, $n = 13$). The geometric mean distance between the trees with *L. pulmonaria* was 6·5 m (quartile range, i.e. 50% of observations are between 3·9–11·6 m) and between the control tree and the nearest *Lobaria*-tree was 9·3 m (quartile range 6·1–14·7 m). According to the result of ANOVA, these means are significantly different ($P < 0{\cdot}0001$, $F = 16{\cdot}47$).

According to the main effects of ANOVA, the selected sites differed in their light conditions and height of shrubs (as prescribed in the sampling scheme) but also in some tree characteristics (average inclination, circumference and bark roughness) (Table 1). The characteristics of sampled trees and the height of shrubs near the trees differed also for the four deciduous tree species studied (Table 1), whereas light conditions were similar for all tree species ($P = 0{\cdot}911$). *Lobaria*-trees and control trees revealed statistically significant differences in the mean values of trunk inclination, bryophyte cover, and height of shrubs near the tree. However, these differences were minimal in the ecological sense and proved significant only because of the large sample size ($n = 301$) (Table 1). For example, on average, the cover of bryophytes was 5·7% larger on *Lobaria*-trees than on control trees, the trunks of colonized trees were 1·7° more inclined than the trunks of uncolonized trees, and shrubs were 34 cm taller near *Lobaria*-trees than near control trees.

Factors predicting the probability of occurrence, cover and fertility of *Lobaria pulmonaria*

The modelling results show that the presence of *L. pulmonaria* was positively correlated with light availability and, at the same time, with increasing height of shrubs around the trunk (Table 2, left half). The probability of occurrence of *L. pulmonaria* also increased with increasing cover of bryophytes on the trunk, up to 50%, but decreased thereafter according to a unimodal relationship (Fig. 2).

The probability of occurrence of *L. pulmonaria* was dependent on the host tree species and on the vitality of the tree. The probability of occurrence was also higher on the trunks of senescent trees (Table 2). The probability of occurrence of *L. pulmonaria* decreased with increasing distance from the nearest

TABLE 2. *The results of the Generalized Linear Model (GLZ*[†]*) analysis in terms of the dependence of presence/absence of* L. pulmonaria *on the environmental variables (*n = *301) and the results of the General Linear Mixed Model (GLMM) analysis about the effect of the environmental variables on the cover of* L. pulmonaria *(log-transformed) (*n = *151).*

Variable	GLZ of presence/absence				GLMM of cover				
	df	Wald statistic	P*	Coefficient	df	F	P*	Coefficient	Mean (±SE)
Intercept	1	0·04	0·306	2·005					
Study site			n.i.		2;143	2·00	0·140		
Study plot			n.i.		6;143	1·07	0·381		
Tree species	3	9·09	**0·028**		3;143	0·57	0·636		
Tree side			n.i.		1;143	235·02	**<0·0001**		
Tree side - *Lobaria*									14·4% (±0·12)^{a}
Tree side - Opposite									1·2% (±0·12)^{b}
Tree species*Tree side			n.i.		3;143	3·45	**0·018**		See Fig. 4
Distance	1	11·14	**0·001**	−3·146			n.i.		
Tree species*Distance	3	8·74	**0·033**	See Fig. 3			n.i.		
Height of shrubs	1	5·67	**0·017**	0·002			n.i.		
Light conditions	1	4·24	**0·039**	0·067			n.i.		
Senescent tree	1	9·98	**0·001**	1·765			n.i.		
Bark roughness			n.i.		1;143	5·21	**0·024**	−0·806	
Bryophyte cover	1	11·73	**0·001**	0·082	1;143	28·47	**<0·0001**	0·016	
(Bryophyte cover)^2	1	6·77	**0·009**	−0·001	1;143	19·31	**<0·0001**	−0·0001	

df, degree of freedom; Wald statistic, the value of Wald test statistic; *F*, value of F-criterion; *P**, significant values (*P* <0·05) in bold; Coefficient, parameter estimate for a continuous variable in the model; n.i., not included.

[†] The specifications of the GLZ model are: Binomial error distribution, log-link function and Pearson correction-coefficient for overdispersion. In the GLMM model, the factor 'Sample tree' is treated as the random factor and 'Tree side' is treated as repeated observations per sample tree. The variables 'Bark roughness' and 'Distance' are log-transformed; 'Tree side: '*Lobaria*' – tree side with *Lobaria*, 'Opposite' – tree side without *Lobaria* or lower cover of *Lobaria*. Model coefficient estimates are presented for continuous variables; within-group mean values are presented for categorical variables, letter labels in superscript denote homogeneity groups according to the results of the Tukey-Kramer multiple comparison test. Factors not included in either model can be found in Appendix 1.

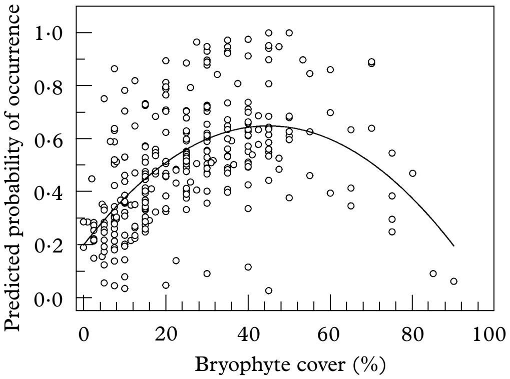

FIG. 2. Predicted probability of occurrence of *Lobaria pulmonaria* on the mean cover of bryophytes according to the generalized linear model (GLZ) (see Table 2).

colonized tree. The probability of its occurrence was less than 50% when the neighbouring *Lobaria*-tree was at a distance of more than 10 m and less than 25% when the neighbouring *Lobaria*-tree was at distance of *c.* 20 m (Fig. 3). The significant term of interaction between host tree species and distance to the nearest neighbour tree indicated tree species-specific patterns (Table 2, Fig. 3), revealing the weakest effect of distance in the case of *Quercus robur* and strongest effect of distance in the case of less common trees such as *Acer platanoides* and *Populus tremula*.

Targeting in the GLMM analysis on factors predicting the cover of *L. pulmonaria* on trunks and taking into consideration the effect of site and intentionally sampled contrast between the tree sides, 'Tree side' identity and the effect of tree species in interaction with 'Tree side' were significant (Table 2). Comparison between the tree side with the highest abundance of *L. pulmonaria* and the opposite side revealed the most contrasting cover values in the case of *Acer platanoides* and *Salix caprea*, and the most uniform distribution of cover values in the case of *Quercus robur* (Fig. 4). Additionally, the cover of *L. pulmonaria* on the tree trunk was negatively correlated with bark roughness (Table 2, Fig. 5A) and had a unimodal relationship with the cover of bryophytes (Table 2, Fig. 5B). The cover of *L. pulmonaria* increased with increasing cover of bryophytes up to 50–70%, thereafter the cover of *L. pulmonaria* decreased. This suggests that colonization by *L. pulmonaria* might be supported by bryophytes on tree trunks up to a certain limit, but in the case of a profusion of bryophytes, spatial competition between *L. pulmonaria* and bryophytes will determine the relationship (Table 2, Fig. 5B).

According to the results of the model building procedure, the probability of occurrence and cover of *L. pulmonaria* were not influenced by mean canopy cover of the stand, mean cover of shrubs in the study plot, presence of trees near the sample tree, tree-level parameters such as inclination and circumference of the tree trunk, pH of the tree bark or cardinal position of the trunk side, as these factors were insignificant in the models.

We observed apothecia at all three study sites and in almost every study plot. The percentage of trees with fertile thalli in the population was the highest at Haavakannu (36%) and less at Lasila (22%) and Suurekivi (14%). The probability of occurrence of apothecia was the highest at the maximum values of bark pH and increased with increasing cover of *L. pulmonaria* on the trunk (Table 3).

Discussion

Partly overgrown wooded meadows in the Pandivere Uplands support one of the largest populations of *L. pulmonaria* in Estonia (Andersson *et al.* 2003; Jüriado & Liira 2010). In this area, the presence of *L. pulmonaria* depends on light conditions near the trunk of host trees rather than on general light conditions in the habitat (e.g. average canopy cover). The presence of deciduous shrubs around the tree trunk is also a predictor of its higher probability of occurrence. Sheltering by shrubs could be especially important during the establishment of diaspores of *L. pulmonaria*. Hilmo *et al.* (2011) have reported that establishment success decreases with increasing canopy openness.

It has been reported that the occurrence and growth of *L. pulmonaria* is controlled by a delicate balance between light availability

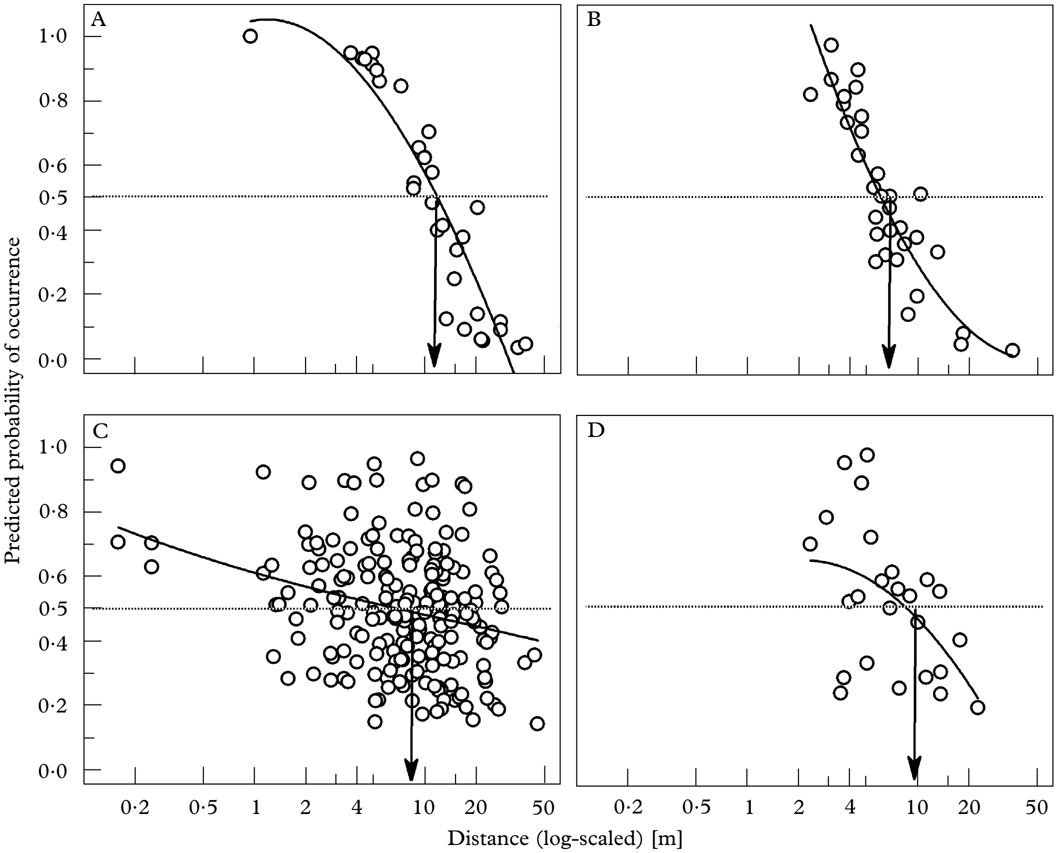

FIG. 3. Predicted probability of occurrence of *Lobaria pulmonaria* depending on the distance to the nearest source tree, according to the generalized linear model (GLZ) (see Table 2). A, *Acer platanoides*; B, *Populus tremula*; C, *Quercus robur*; D, *Salix caprea*. The arrow denotes the derivation of the distance between the target tree and the nearest neighbouring tree with *L. pulmonaria* at which value the occurrence probability of *L. pulmonaria* on the target tree is 50%.

and desiccation risk, showing physiological trade-offs between the growth potential and fatal desiccation damage, both of which increase with increasing light (Gauslaa *et al.* 2006, 2007). For *L. pulmonaria* in open habitats, there is a long-term risk of being killed by high light intensity during long periods with no rain (Gauslaa *et al.* 2006). In Estonia, this is the period of mid-summer. Such a risk probably occurs in managed wooded meadows with open canopies and few shrubs. Deciduous shrubs, mainly *Corylus avellana*, around the tree trunk could help maintain a favourable moisture regime on the tree bole as they protect the tree trunk from desiccating winds and direct sunlight during the summer period. In moist periods (spring and autumn), however, leafless deciduous shrubs provide improved light conditions for growth.

In a forested landscape, the occurrence of *L. pulmonaria* within a stand is most frequently found to depend on the diameter of host trees (Gu *et al.* 2001; Riiali *et al.* 2001; Mikhailova *et al.* 2005; Öckinger *et al.* 2005; Edman *et al.* 2008; Belinchón *et al.* 2009). However, in the Estonian wooded meadows we studied, the species grew on a large variety of tree species with a large variation in trunk diameters. For example, we found it growing on large oak trees (*Quercus robur*), representing substratum continuity during several

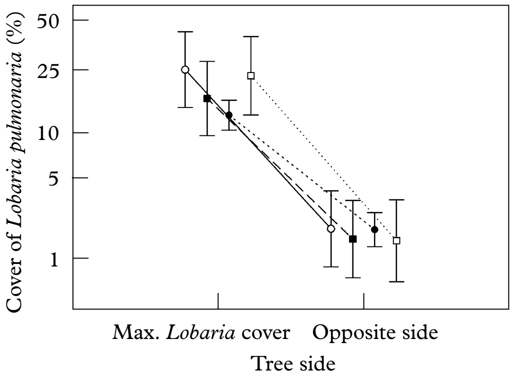

FIG. 4. Cover (log-scale) of *Lobaria pulmonaria* on two sides of the trunk for different tree species according to the general linear mixed model (GLMM) (see Table 2). Trunk sides are defined as the side with maximum *L. pulmonaria* cover and the side opposite to it. ○ *Acer platanoides*; ■ *Populus tremula*; ● *Quercus robur*; □ *Salix caprea*.

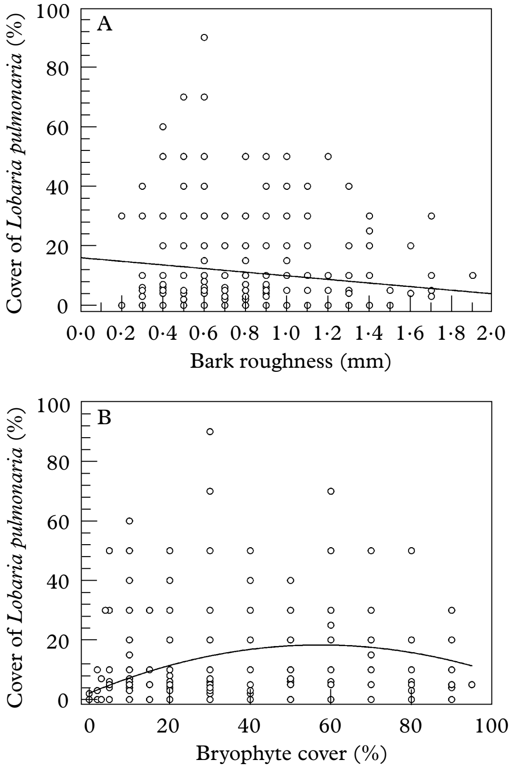

FIG. 5. Relationships between cover of *Lobaria pulmonaria* and A, bark roughness and B, bryophyte cover (GLMM, see Table 2).

TABLE 3. *The results of the Generalized Linear Model (GLZ) analysis about the dependence of presence/absence of apothecia of* L. pulmonaria *on the maximum values of bark pH and cover of* L. pulmonaria *(log-transformed) on a sample tree (*n *= 151).*

Variable	df	Wald statistic	*P*	Coefficient
Intercept	1	21·07	<0·0001	−11·91
Bark pH (max)	1	12·32	<0·001	1·38
Cover of *Lobaria*	1	11·72	<0·001	1·90

df, degrees of freedom; Wald statistic, the value of Wald test statistic; Coefficient, parameter estimate for a continuous variable in the model.

hundred years, as well as on small-diameter trees, such as *Salix caprea* and *Sorbus aucuparia*. It has been reported that, under optimal climate and habitat conditions where *L. pulmonaria* is abundant, the species can grow on various trees, even those with small diameters, and even on moss-covered large stones (Hakulinen 1964; James *et al.* 1977; Wolseley 1991; Istomina 1996; Carlsson & Nilsson 2009).

In the current investigation, bark pH like the trunk diameter, was not correlated with the probability of occurrence and cover of *L. pulmonaria*. However, it has already been shown that bark pH is an important factor limiting the establishment of *L. pulmonaria* from propagules (Scheidegger *et al.* 1998; Wolseley & James 2000). In habitats where *L. pulmonaria* is abundant, it seems that the pH of the substratum is less important, as in the studied stands *L. pulmonaria* was also growing on lower shaded twigs of spruce (*Picea abies*) (bark pH of 3·70–4·50) and on the coniferous shrub *Juniperus communis* (bark pH 3·60–3·99). The specimens growing on spruce and juniper had obviously fallen from deciduous trees and attached to coniferous branches.

Regarding the colonization success of lichens on trunks, bark roughness is reported to facilitate the attachment of lichen diaspores to the substratum (Ranius *et al.* 2008). In the case of *L. pulmonaria*, neither transplantation studies (Scheidegger *et al.* 1998) nor field surveys (Öckinger *et al.* 2005) have found any correlation with bark structure. In the current investigation, bark structure did not differ between *Lobaria*-trees and control trees, nor did it predict the probability of occurrence of *L. pulmonaria* on trees. It is possible that, at our study sites, *L. pulmonaria* was too common to reveal the bark structure-establishment relationship. We did find, however, that *L. pulmonaria* was more abundant on trunks with lower bark roughness, which indicates that the lichen has some preference for the bark of middle-aged trees with low or medium bark roughness. Regrettably, we did not record the abundance of juveniles on tree trunks, which would more directly indicate establishment success.

We also found that the probability of occurrence of *L. pulmonaria* and its cover on the host tree was positively correlated with cover of bryophytes, that is bryophytes facilitated the growth of *L. pulmonaria*. Yet this relationship was only valid up to a certain abundance of bryophytes, as we observed a unimodal relationship between cover of bryophytes and occurrence and cover of *L. pulmonaria*. It has been shown that some bryophytes may out-compete *L. pulmonaria* (Wolseley & James 2000) and a dense bryophyte mat can also hinder the establishment of diaspores (Scheidegger *et al.* 1995). At the same time, a moss mat on tree trunks helps maintain suitable humidity conditions on the bole (Veneklaas *et al.* 1990) and supports more suitable growing conditions for cyanolichens in comparison to the bare bark (Sillett & McCune 1998). Nonetheless, the presence of mosses on the tree bole is not always obligatory for *L. pulmonaria* colonization, as it grows well also on the bare bark (Öckinger & Nilsson 2010).

An interesting additional finding of our case survey is the higher probability of occurrence of *L. pulmonaria* on damaged or senescent trees, which might be interpreted as its preference for mineral-rich microsites (Gauslaa 1995). It has been shown that many lichens and mosses survive well around wounds or on nutrient streaks that have higher pH than the rest of the trunk (Gilbert 1970). We suggest that *L. pulmonaria* might profit from improved light conditions and flow of rainwater on the tree trunk, as the crown of these damaged or senescent trees is incomplete and the canopy above the trunk is open.

Population genetics studies of *L. pulmonaria* in wooded meadows of Estonia showed a high rate of clonal spread within distances of 15 to 30 m (Jüriado *et al.* 2011). Evidence for source-sink dynamics (Gaggiotti 1996) was found; it was concluded that old trees harbour a higher number of different multilocus genotypes and act as a source of vegetative diaspores, while younger trees between the old ones can be considered sink substrata (Jüriado *et al.* 2011). Their low estimate for the dispersal range was confirmed by the present study: probability of occurrence of *L. pulmonaria* decreased with increasing distance from the nearest colonized tree and dropped below 50% even at a distance less than 10 m (Fig. 3). This estimate of the limiting distance might be slightly underestimated because the spatial relationship was studied under conditions of multiple source trees in the sample plot. At the same time, actual sources might have been located at greater distances. Our observed effective dispersal distance is several times shorter than that suggested by previous studies (Kalwij *et al.* 2005; Öckinger *et al.* 2005).

The results of the current study and our previous study (Jüriado *et al.* 2011) suggest that sub-optimal host trees can be colonized only if they are situated very close to other colonized trees. Hence, dispersal success profits from the 'mass-effect' (Shmida & Wilson 1985). Consequently, in order to preserve and support the viability of *L. pulmonaria* populations in woodlands, suitable host trees must grow in the vicinity of 10–20 m from the source tree and from each other, so that further dispersal is enhanced.

In many of the previously investigated populations of *L. pulmonaria* elsewhere, fertile specimens were either absent (Gu *et al.* 2001) or the number of apothecia found was low (Gauslaa 2006; Öckinger & Nilsson 2010). In the populations studied in north-eastern Estonia, trees with fertile individuals accounted for 14–36% of all *Lobaria*-trees. This is consistent with the results of fertility studies carried out in North America, where the described within-population frequency of fertile thalli was up to 25% (Denison 2003) or even 30% (Edman *et al.* 2008). Similarly, in Northern Europe, in Åland Islands (SW Finland), about 25–30% of trees harboured fertile individuals in some luxuriant populations of *L. pulmonaria* (Carlsson & Nilsson 2009).

On the tree scale, like Edman *et al.* (2008), we found that the presence of apothecia correlated significantly with abundance of the lichen. Environmental conditions also play an important role in determining the presence of apothecia. Edman *et al.* (2008) have noted that fertile individuals are more frequent in uncut stands while Öckinger & Nilsson (2010) failed to find any correlation between fertility of *L. pulmonaria* and habitat characteristics. We found that the presence of apothecia increased with increasing bark pH. In combination with the results of an earlier study (Jüriado *et al.* 2011) we suggest, therefore, that bark pH plays a role in the production of apothecia, but this effect is evidently related to population size, continuity of the stand and suitability of growing conditions.

Conclusions

The results of our study show that partially overgrown wooded meadows provide favourable environmental conditions for *L. pulmonaria* in the region of hemi-boreal forests, serving as important habitats with high conservation concern. However, during the secondary succession of these wooded meadows into deciduous woods, increasing canopy cover with low light conditions beneath will undoubtedly restrict the growth of *L. pulmonaria*. To maintain optimal light conditions for this species, moderate management of the habitat by means of tree and shrub thinning is needed, particularly of conifers. *Lobaria*-trees and potential host trees for *L. pulmonaria* should be spaced, on average, 10–20 m from each other. The potential host trees in such areas include, primarily, *Quercus robur*, as well as other deciduous trees with subneutral bark pH and a moderate cover of bryophytes on the tree trunk. Also, in long-term conservation planning, regrowth of potential host trees should be promoted to ensure the continuity and vitality of the *L. pulmonaria* population. When thinning the shrub layer, some deciduous shrubs near the trunk of colonized tees and near potential host trees should also be preserved.

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Appendix 1. Explanatory variables used in data analyses.

A. Categorical variables*

Variables	Scale	Number of levels	Comments
Study site	stand	3	Haavakannu (59°11′N; 26°24′E), Lasila (59°15′N; 26°12′E) and Suurekivi (59°13′N; 26°25′E) Nature Reserves
Study plot	stand	9	Each with an area of 0·5 ha, nested at three study sites
Presence of *Lobaria* on sample tree	tree	2	Trees with *Lobaria* ("*Lobaria*-trees", $n = 151$) and trees without *L. pulmonaria* ("control tree", $n = 150$), total 301 trees
Tree species	tree	4	*Acer platanoides* ($n = 34$), *Populus tremula* ($n = 32$), *Quercus robur* ($n = 210$) and *Salix caprea* ($n = 25$)
Senescent tree	tree	2	Levels: (1) healthy tree or (2) senescent, partly dead, dried or damaged tree
Presence of trees	tree	2	Levels: (1) presence or (2) absence of neighbouring trees within 1 m around a sample tree
Tree side	tree side	2	Levels: (1) the side with *Lobaria* (or with higher coverage) and (2) the side without *Lobaria* (or with lower coverage)
Cardinal position	tree side	4	Levels: north, east, south and west

B. Continuous variables†

Variables	Scale	Mean (±SD)	Range (min-max)	Comments
Distance	stand	7·5 (±0·6)	0·1–38·7	Distance between the sampled trees (m), used log-transformed in analyses
Shrub cover	stand	36·8 (±18·8)	10–70	Cover percentage (%) of the shrub layer in a study plot
Stand openness	stand	15·7 (±8·5)	6–39	Average openness of a study plot measured with a spherical densiometer
Height of shrubs	tree	146·7 (±153·9)	0–800	Maximum height of shrubs within 1 m around a sample tree (cm)
Circumference	tree	97·5 (±38·7)	28–238	Circumference of a sample tree measured at breast height *c.* 1·3 m above ground level (cm)
Inclination	tree	77·2 (±7·2)	50–90	Inclination of a sample tree (°) measured at a height of *c.* 1·3 m above ground with a compass
Light conditions	tree side	11·5 (±6·5)	3·1–58·3	Light conditions measured at 0·5 m from both sides of the trunk using a spherical densiometer
Bark roughness	tree side	0·7 (±0·3)	0·2–2·3	Roughness of the bark measured with a vernier caliper at a height of *c.* 1·3 m above ground level (cm) on both sides of the trunk
Bark pH	tree side	5·8 (±0·5)	4·63–7·62	Bark pH measured with a flat head electrode *c.* 1·3 m above ground level on both sides of the trunk
Bryophyte cover	tree side	26 (±17·3)	0–90	Cover of bryophytes (%) estimated at a height of 0·5–2 m above ground level on both sides of the trunk
Cover of *L. pulmonaria*	tree side	11·2 (±10·1)	1–90	Cover of *L. pulmonaria* (%) on colonized trees estimated at a height of 0·5–2 m above the ground on both sides of the trunk

* A, categorical variables: number of levels.

† B, continuous variables: mean values with standard deviation (SD) and the minimum–maximum range.