The Lichenologist **45**(1): 51–63 (2013)
doi:10.1017/S0024282912000564

Lichens on *Picea abies* and *Pinus sylvestris* – from tree bottom to the top

Liis MARMOR, Tiiu TÕRRA, Lauri SAAG, Ede LEPPIK and Tiina RANDLANE

Abstract: The vertical gradient of the community structure of epiphytic lichens in forest canopies was studied in southern Estonian coniferous forests. All lichen species on 15 Norway spruces and 15 Scots pines were recorded; age of trees ≥100 years. Species were sampled in height ranges on entire trees from the bottom to the top. The number of lichen species on pine trunks decreased with height from the ground, whereas the number of species on branches increased. There was no significant vertical change in the number of lichen species on spruce trunks; number of species on spruce branches was highest in mid canopy. The mean number of lichen species on a tree was 41 in spruces and 34 in pines; the mean number of species on the first 2 m was 14 in spruces and 12 in pines. According to the results, about two thirds of a tree's lichen species remain unrecorded if only the first 2 m near the ground are surveyed. Many lichen species were found only higher than 2 m, including several common species (e.g. *Buellia griseovirens*, *Lecanora pulicaris*, and *Melanohalea exasperatula*), but also some locally rather rare (*Fellhanera subtilis*, *Micarea nitschkeana*, *Rinodina efflorescens*) or red-listed ones (*Evernia mesomorpha*, *Usnea barbata*, *U. fulvoreagens*, *U. substerilis*, *U. wasmuthii*) and one new species for Estonia, *Lecanora farinaria*. There were also some species, such as *Chaenotheca stemonea*, *Cladonia cenotea* and *C. norvegica*, that were restricted to the lowest 2 m. The results indicate that canopy lichens form a significant part of lichen diversity in coniferous forests, and could add valuable information when estimating forest lichen diversity for conservation and other purposes.

Key words: biodiversity, canopy, epiphyte, pine, spruce, vertical zonation

Accepted for publication 31 *July* 2012

Introduction

Most lichenological studies exclusively consider epiphytic lichens that grow on the first 2 m from the ground, the height reachable without climbing or logging the trees. Often, lichens are recorded only on tree trunks, sometimes in the limited area of sample grids. The clear advantages of such methods are the substantially better feasibility of fieldwork and higher comparability of trees sampled. At the same time, much of the information concerning species diversity on trees studied remains unavailable. This missing information might be useful for estimating the lichen species richness of forest sites, also for purposes of conservation and bioindication. For example, Fritz (2009) has cautioned that surveying only the lowest 2 m in old beech forests can lead to the underestimation of the number of lichen species with conservation concern and their population sizes. Marmor *et al.* (2010) found that lichen composition in the upper canopy of spruce and pine forests is a far more informative dust pollution indicator than species composition in the lower canopy.

The great variety of different microhabitats on trees, from root cavities to treetop twigs, provides suitable conditions for lichen species with various ecological requirements. Many epiphytic lichen species are associated with specific substrata, such as trunks or branches (e.g. Holien 1997; Caruso & Thor 2007; Lie *et al.* 2009). Lichen communities also change on trees with height from the ground. Although there are relatively few

L. Marmor, T. Törra, L. Saag, E. Leppik and T. Randlane: University of Tartu, Institute of Ecology and Earth Sciences, Lai Street 40, Tartu 51005, Estonia. Email: marmor@ut.ee
L. Saag is also at: Estonian Biocentre, Riia 23b, Tartu 51010, Estonia.

studies dealing with the diversity of canopy lichens, the existing studies have clearly proved that the occurrence and biomass of many lichen species change vertically on trees, and some species are more abundant in the mid or upper canopy (e.g. McCune 1993; McCune *et al.* 2000; Rosso *et al.* 2000; Campbell & Coxson 2001; Ellyson & Sillet 2003). According to Williams & Sillett (2007), many epiphytic species show distinct distribution patterns across the height strata and substratum types in redwood canopies. It can be derived that the total diversity of lichens on trees can be covered only if all substrata and height ranges are studied.

Picea abies (L.) H. Karst. (hereafter 'spruce') and *Pinus sylvestris* L. (hereafter 'pine') are the most common tree species in boreal Europe. So far lichen communities have been studied in spruce canopies (e.g. Kermit & Gauslaa 2001; Caruso & Thor 2007; Lie *et al.* 2009) where lichens have been sampled mostly at selected heights rather than across the whole height gradient; and only macrolichens have been studied in pine canopies (Marmor *et al.* 2011). In the present work the entire lichen biota is surveyed from the bottom to the top of the tree on all available substrata on spruce and pine. Sampling lichens in height ranges provides information about the vertical changes in lichen species richness on tree trunks and branches, and also about the occurrence of individual species. The main aims are to find out 1) how large the differences in lichen species richness are between the lowermost 2 m near the ground and the whole trees, that is how many species are missed if only the first 2 m are studied, and 2) how does the occurrence of individual lichen species change with height in the canopy, that is, which species are missed if only the lowermost 2 m are studied. We hypothesize that a high proportion of lichen species growing on trees remains unrecorded if only the lowermost metres of trees are sampled.

Materials and Methods

Study area

The study was carried out in Estonia, located in Northern Europe on the eastern shores of the Baltic Sea. The mean annual temperature is *c.* 5°C (monthly mean varies from −6°C to 16°C), and the mean precipitation is *c.* 630 mm (EMHI). About half of the territory of the country is covered with forests. Estonian forests belong to the hemiboreal subzone of the boreal forest zone, lying in the transitional area where the southern taiga forest subzone changes into the spruce-hardwood subzone (Ahti *et al.* 1968; Laasimer & Masing 1995). Pine, spruce and birch (*Betula pendula*) are the most abundant tree species in the area.

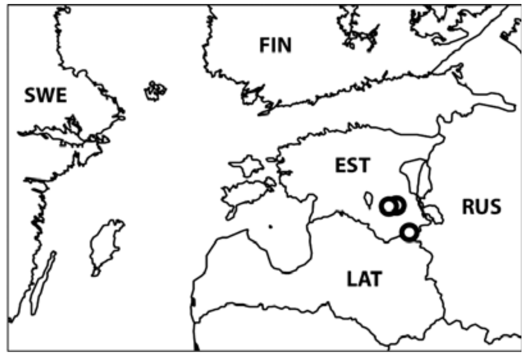

FIG. 1. Location of sample plots.

Our sample plots were located in the coniferous forests in southern Estonia. Lichens were studied in three plots: 1) 58·1113°N, 27·0314°E; 2) 58·1134°N, 26·9965°E; 3) 57·6957°N, 27·3622°E (Fig. 1). Spruce and pine were the main tree species in all sites; *Vaccinium myrtillus*, *V. vitis-idaea* and *Oxalis acetosella* dominated the undergrowth. The sites were located in forest-agricultural landscape and were surrounded by variously-aged forests from young growths to mature stands. Sample trees were chosen inside the forest stand in order to reduce the effect of sidelight. All sample plots were located in planned clear-cut stands where trees were going to be cut down anyway.

Field methods

Fieldwork was carried out in autumn 2008. Five spruce and five pine trees were cut down for the study in every site, making a total of 30 trees. The age of trees was measured by counting the annual rings on tree stumps. For studying the vertical gradient of lichens, all trees were divided into height ranges, first range extending from the ground up to 2 m (the height reachable without additional equipment or logging) and all the following ranges being 4 m long. The treetops which were $\leq$2 m long were included in the previous height range, and treetops which were $>$2 m long in the next height range. The attachment point was used for defining the height range of branches. Lichen presence or absence was recorded separately in every height range. All lichen species growing within a height range on tree trunks, branches or twigs were recorded at site or collected for later identification. Specimens collected were identified using a microscope and spot tests. Thin-layer chromatography with solvent A (Orange *et al.* 2001) was used for identifying secondary compounds in sterile crusts and some *Usnea* specimens.

Statistical analysis

Software applications STATISTICA 7 and PC-ORD 5 were used for the statistical analysis. Data were analyzed separately according to the tree species. A *t*-test was used for comparing the total lichen species richness on trees with species richness on the lowest 2 m near the ground. Pearson correlation analysis was used for finding out whether the number of lichen species on the first 2 m of trees is correlated with the number of species on entire trees. Spearman's correlation coefficient was calculated for describing the vertical changes in lichen species richness separately for tree trunk and branches; when calculating the mean number of lichen species on branches the height ranges with no branches were included in analyses with 0 species.

Indicator Species Analysis with Monte Carlo test of significance was used for finding out the preferred height range(s) of lichen species, jointly for trunks and branches. In addition, detrended correspondence analysis (DCA; axes rescaled, no down-weighting of rare species or any prior data transformations) was used for describing lichen species composition in the height ranges. Infrequent lichen species that were recorded only on 1–2 trees were left out from the Indicator Species Analysis and DCA. Fisher exact test (one-tailed) was used to determine the trunk-branches preferences of lichen species.

Results

Tree characteristics

Lichens were recorded on 15 spruces and 15 pines. Height of spruces varied from 22–35 m with an average of 29 m, and height of pines from 26–36 m with an average of 32 m. Age of spruces varied from 100–147, average age 123 years, and age of pines varied from 100–149, average 125 years. Depending on tree height, 6–9 height ranges were separated for trees studied.

Lichen communities

A total of 96 lichen species were found on the trees studied: 86 on spruces and 69 on pines (Table 1). The total number of lichen species found on the lowermost 2 m near the ground was 49 on spruces and 33 on pines. Eleven species were restricted to the lowest height range on spruces and five on pines; the most frequent being *Cladonia cenotea*. Thirty-seven lichen species were recorded only higher than 2 m on spruces and 36 on pines, the most frequent being *Buellia griseovirens*, *Lecanora pulicaris*, *L. symmicta*, *Lecidella subviridis*, *Melanelixia subaurifera*, *Melanohalea exasperatula*, *Micarea denigrata*, *Ochrolechia arborea*, and *Trapeliopsis flexuosa*. One species, *Hypogymnia physodes*, was found on all trees studied in nearly all height ranges.

The mean number of lichen species on entire spruces was 41 and on pines 34, whereas the mean number of species on the lowermost 2 m was 14 in spruces and 12 in pines (Fig. 2). There was a significant correlation between the total lichen species richness on a tree and species richness on its lowest 2 m in the case of pines ($r = 0{\cdot}80$; $n = 15$; $P = 0{\cdot}0003$); in spruces the correlation was insignificant ($r = 0{\cdot}22$; $n = 15$; $P = 0{\cdot}43$). Comparing vertical changes in lichen species richness between trunk and branches, a clear difference was found in the case of pines. Mean number of species on pine trunks decreased significantly with height ($R_s = -0{\cdot}75$; $n = 126$; $P \ll 0{\cdot}001$), whereas the number of species on branches increased ($R_s = 0{\cdot}76$; $n = 126$; $P \ll 0{\cdot}001$; Fig. 3A & B). There was no significant vertical change in lichen species richness on spruce trunks; the number of species on spruce branches was highest in mid canopy (Fig. 3C & D).

According to the results of DCA, height from the ground had a major impact on lichen species composition; correlation (r^2) between DCA axis 1 and height was 0·73 in spruces and 0·90 in pines (Figs 4 & 5). Indicator Species Analysis revealed that many species preferred some specific height range(s). Some species were associated with the lowest height range, whereas several species occurred only in mid or upper canopy (Fig. 6). New species not present in previous height ranges were discovered with increasing height until the treetops (Fig. 7).

One species, *Lecanora farinaria*, was recorded for the first time for Estonia during this study. It was found higher than 2 m (up to 22 m) on spruce branches in all three sample plots, on six trees altogether. Six of the lichen species recorded, *Fellhanera subtilis*, *Lecanora albellula*, *Lecidea hypopta*, *L.*

Table 1. *The frequency (percentage of occurrences) of lichen species at heights ≤2 m and >2 m; the statistically significant substratum preferences of species (according to Fisher test) have been added: T – trunk, B – branches*

		Spruce			Pine		
Species*	Abbrevation	≤2	>2		≤2	>2	
Arthonia mediella			7				
A. vinosa		7					
Bacidina phacodes			7				
Bryoria capillaris	Bry_capi	27	100		13	93	
B. fuscescens	Bry_fusc	7	100		7	93	
B. implexa			13				
B. nadvornikiana			13			13	
B. subcana	Bry_subc		40				
Buellia griseovirens	Bue_gris		53	B		33	B
Calicium glaucellum			7			7	
C. parvum	Cal_parv				13	60	
Cetraria sepincola						7	
Chaenotheca ferruginea	Cha_ferr	53	87		27	53	
C. chrysocephala	Cha_chry	67	80	T	27	13	
C. stemonea	Cha_stem	20					
C. trichialis		7					
Cladonia bacillaris	Cla_baci					27	
C. bacilliformis		7					
C. cenotea	Cla_ceno	20			33		T
C. coniocraea	Cla_coni	87	7	T	93	53	T
C. cornuta					7		
C. digitata	Cla_digi	60		T	87	47	T
C. fimbriata	Cla_fimb	20			20	33	
C. macilenta	Cla_maci	7			33	47	T
C. norvegica	Cla_norv	7			27		T
C. ochrochlora	Cla_ochr	13			7	13	
Cliostomum griffithii	Cli_grif	20	13			13	
Coenogonium pineti					7		
Evernia mesomorpha			7				
E. prunastri	Eve_prun	20	100			40	B
Fellhanera subtilis			7				
Fuscidea pusilla	Fus_pusi	7	40	B		33	B
Hypocenomyce friesii	Hyp_frie	13	47	T		7	
H. scalaris	Hyp_scal	20	53		27	33	T
Hypogymnia physodes	Hyp_phys	100	100		100	100	
H. tubulosa	Hyp_tubu	13	100		7	100	
Imshaugia aleurites	Ims_aleu	7	20			60	
Lecanora albellula	Lec_albe		33		7	40	
L. conizaeoides			7				
L. expallens	Lec_expa	27	33				
L. farinaria	Lec_fari		40	B			
L. hagenii			7				
L. norvegica	Lec_norv					20	
L. pulicaris	Lec_puli		100			100	B
L. symmicta	Lec_symm		40	B		33	
Lecidea hypopta	Lec_hypo	20	67		7	40	
L. leprarioides	Lec_lepr	13	27	T			
L. nylanderi	Lec_nyla	60	100		73	100	T
L. turgidula	Lec_turg	47	100			67	
Lecidella subviridis	Lec_subv		53			13	
Lepraria celata			7				
L. incana	Lep_inca	87	93		53	13	
L. jackii	Lep_jack	87	100		87	73	T
L. lobificans	Lep_lobi	27	20	T	27		T

TABLE 1. *Continued*

Species*	Abbrevation	Spruce			Pine		
		≤2	>2		≤2	>2	
Loxospora elatina	Lox_elat	33	33	T	40	20	T
Melanelixia subaurifera	Mel_suba		47	B		20	
Melanohalea exasperatula	Mel_exas		100	B		100	B
Micarea denigrata	Mic_deni					73	
M. elachista	Mic_elac				27	20	
M. melaena	Mic_mela	7			73	40	T
M. nitschkeana	Mic_nits		13			27	
M. prasina s.lat.	Mic_pras	67	80		60	80	
Mycoblastus fucatus	Myc_fuca	13	100	B	13	100	
Ochrolechia androgyna			7				
O. alboflavescens			7				
O. arborea	Och_arbo		73	B		20	
O. microstictoides	Och_micr	13	60		7	13	
Parmelia sulcata	Par_sulc	13	100			73	
Parmeliopsis ambigua	Par_ambi	53	60	T	87	100	T
P. hyperopta	Par_hype		13		20	20	T
Pertusaria amara	Per_amar		33	B		7	
Phlyctis argena	Phl_arge	7	47	B			
Physcia adscendens			7				
P. tenella	Phy_tene		33			7	
Placynthiella icmalea						7	
P. uliginosa						7	
Platismatia glauca	Pla_glau	60	100		33	100	
Pseudevernia furfuracea	Pse_furf	20	100			100	
Pycnora sorophora	Pyc_soro	7	7			80	B
Ramalina farinacea	Ram_fari		33			7	
Rinodina efflorescens			7				
Ropalospora viridis	Rop_viri	7	27			7	
Scoliciosporum chlorococcum	Sco_chlo	7	93			100	B
Trapeliopsis flexuosa	Tra_flex		7			60	B
Tuckermannopsis chlorophylla	Tuc_chlo	7	100			60	B
Usnea barbata	Usn_barb		27	B			
U. dasypoga	Usn_dasy	27	100			67	
U. fulvoreagens	Usn_fulv		27	B			
U. glabrescens	Usn_glab		40	B			
U. hirta	Usn_hirt	13	100			93	
U. lapponica	Usn_lapp		40	B			
U. subfloridana	Usn_subf	20	100	B		40	
U. substerilis			13				
U. wasmuthii	Usn_wasm		40	B			
Vulpicida pinastri	Vul_pina	7	67		13	33	
Xanthoria polycarpa	Xan_poly		27			7	

* Nomenclature follows Randlane *et al.* 2011

leprarioides, *Micarea nitschkeana*, and *Rinodina efflorescens*, are rather rare in Estonia (in up to 10 localities so far, according to local species databases eSamba and eElurikkus). Five species, *Evernia mesomorpha*, *Usnea barbata*, *U. fulvoreagens*, *U. substerilis*, and *U. wasmuthii*, are nationally red-listed (Randlane *et al.* 2008). All red-listed and three of the rather rare species (*F. subtilis*, *M. nitschkeana*, *R. efflorescens*) were recorded exclusively more than 2 m from the ground; most of these were growing on spruce branches.

https://doi.org/10.1017/S0024282912000564 Published online by Cambridge University Press

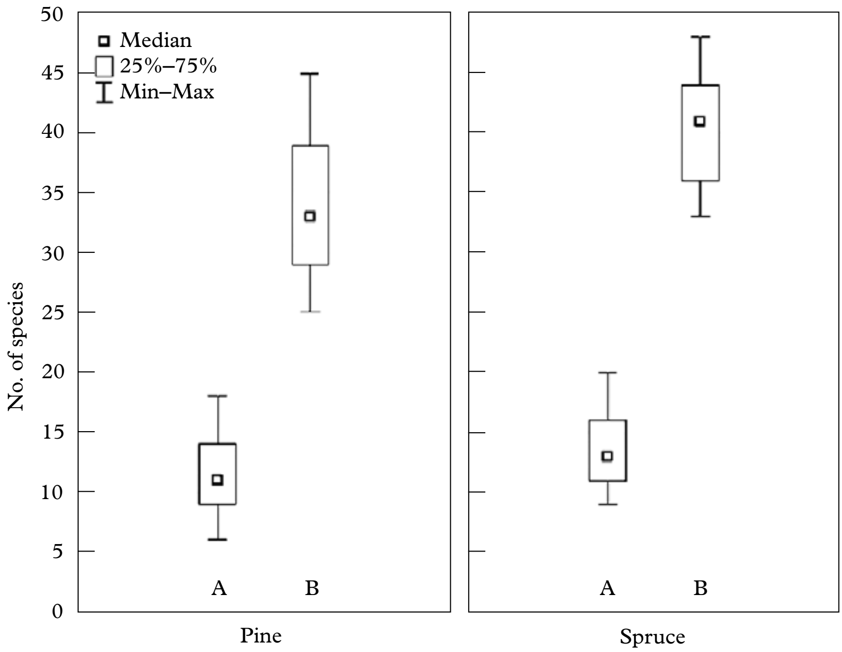

FIG. 2. Number of lichen species on the first 2 m from the ground (A) and the total number of lichen species (B) on pines ($t = -12{\cdot}8$; $n = 15$; $P \ll 0{\cdot}001$) and spruces ($t = -19{\cdot}7$; $n = 15$; $P \ll 0{\cdot}001$).

Discussion

In the present work we have recorded all lichen species on entire trees, allowing us to not only arrive at conclusions concerning the height preferences of individual species, but also the vertical changes in total lichen species richness. According to the results, the vertical trends in the number of lichen species recorded in a height range differ between tree trunk and branches, and also between the tree species. In the case of spruces, there were no significant vertical changes in the number of lichen species growing on the trunk; species richness on branches was highest in mid canopy (Fig. 3C & D). In pines, the number of lichen species on trunks was highest up to *c.* 10 m from the ground, and decreased significantly in upper parts of the trunk (Fig. 3A & B). This change can be associated with the changes in pine bark structure, as the smooth peeling bark in upper parts of the trunk provides no firm substratum for lichens. The number of lichen species on pine branches was highest in the upper canopy (Fig. 3); longer branches usually begin much higher in pines compared to spruces.

The comparison between the number of lichen species on the lowermost 2 m and on whole trees (Fig. 2) demonstrates that studying lichens only on the first 2 m of tree trunk and branches leads to a significant underestimation of total lichen species richness on trees. New lichen species that were not present in previous height ranges were added with height until the treetops (Fig. 7). On average, only about one third of the lichen species on a tree were present in the lowermost 2 m near the ground in the case of both spruces and pines, which means that if surveying only the lowest 2 m, two thirds of a tree's lichen species remain unrecorded. However, on the scale of a forest stand, an increase in the number of sample trees is likely to decrease the number of unrecorded species, whereas the frequency of many species still remains biased.

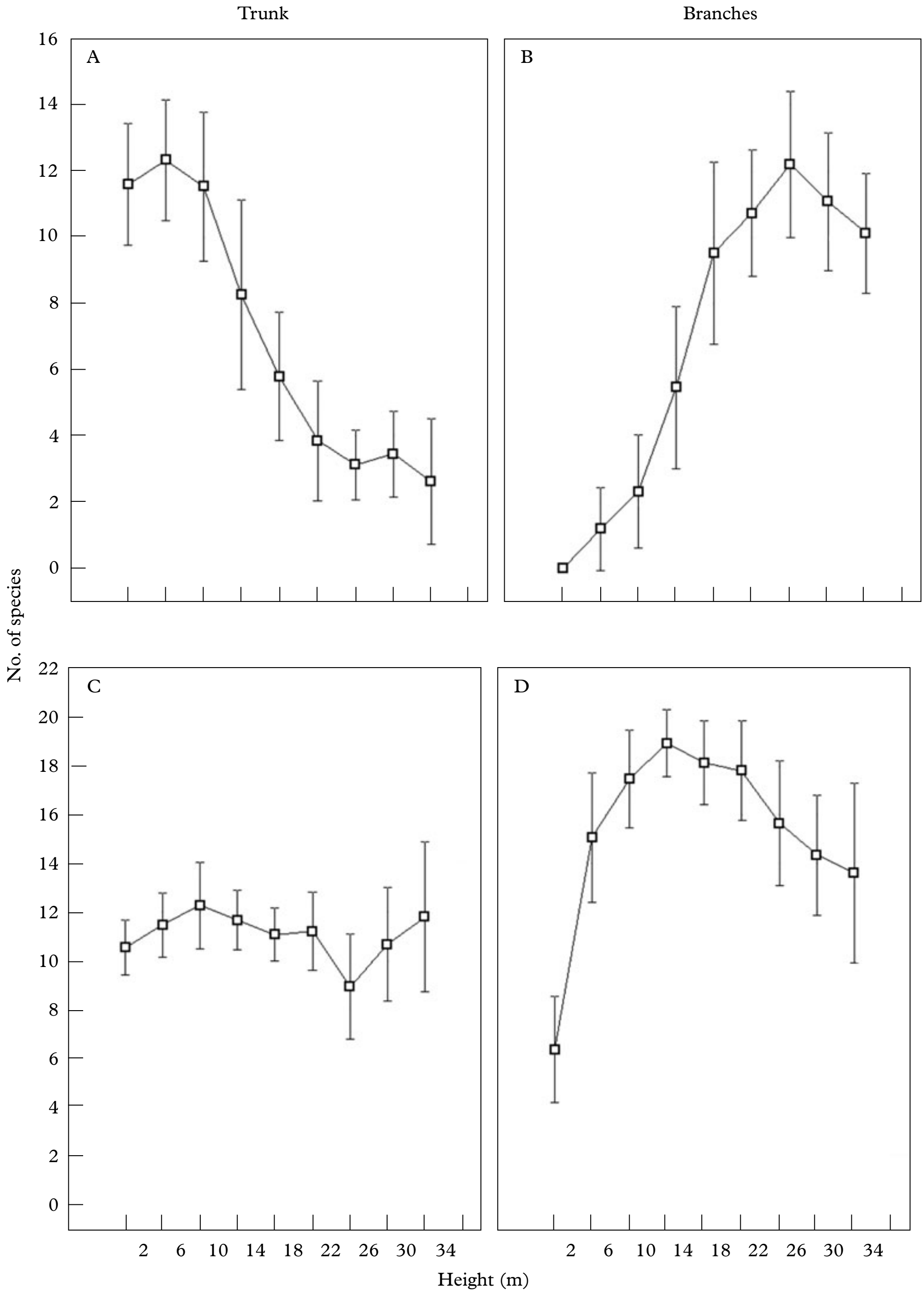

FIG. 3. The mean lichen species richness (±0·95 confidence interval) in the height ranges on trunks and branches. A & B, pine; C & D, spruce.

https://doi.org/10.1017/S0024282912000564 Published online by Cambridge University Press

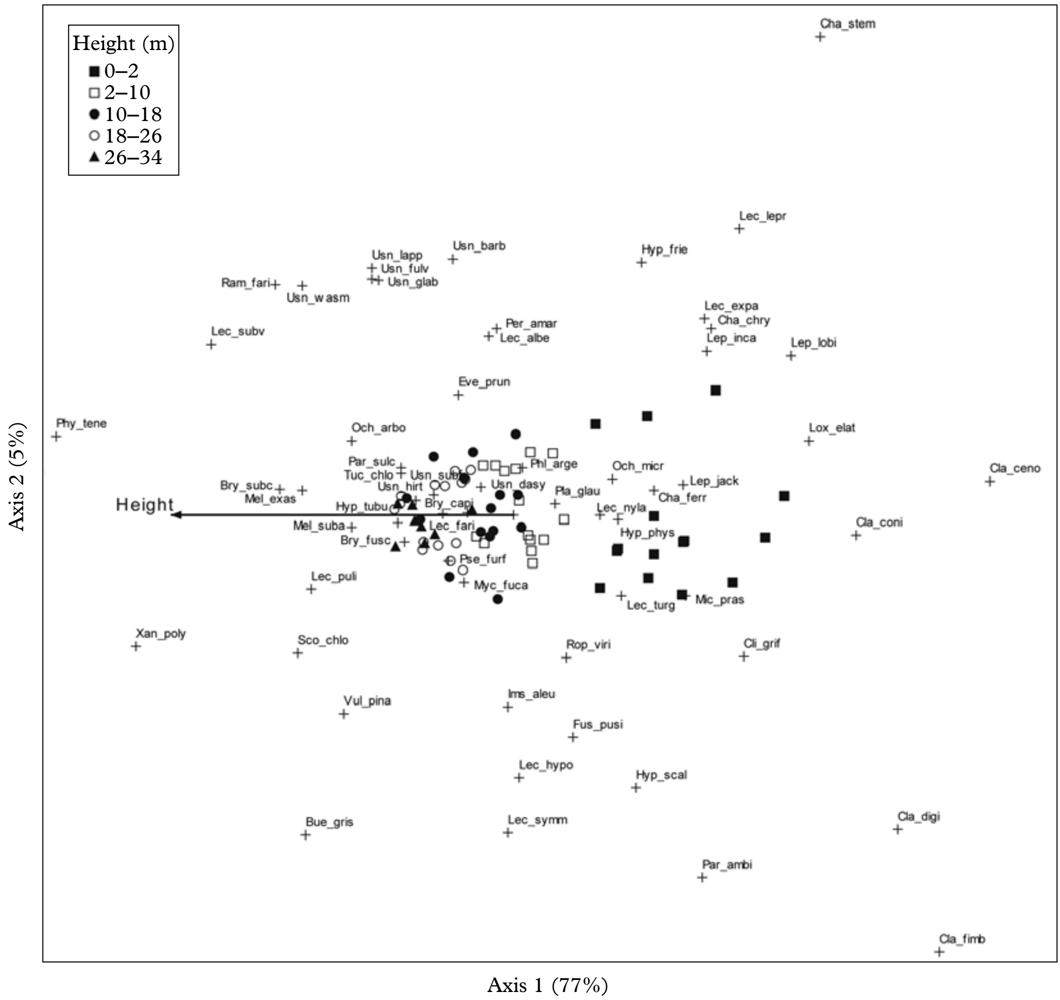

FIG. 4. DCA joint-plot of lichen species in the height ranges on spruces (correlation between axis 1 and height: $r^2 = 0{\cdot}73$). For abbreviations of lichen species names see Table 1.

In pines, the number of lichen species on the lowermost 2 m was strongly correlated with the number of lichen species on entire trees. Therefore, species richness on the lowest 2 m of trees could be used for finding the potentially most species-rich pine trees in a forest site. In the case of spruces, such a correlation was insignificant indicating that old spruces may support diverse lichen communities even if species richness on the first 2 m near the ground is not impressive. However, many lichen species that were absent in the lowest 2 m of spruces, including several species growing on branches, were already present in the next height range extending from 2 to 6 m; and on average 60% of the whole lichen species diversity on spruces was recorded in the height range from ground up to 6 m (Fig. 7). This means that climbing the trees or using adjusted equipment (e.g. blade on the top of a high stick or telescopic bar) to sample lichens in that relatively easy to reach height range could add much to the species list of spruces. In the

https://doi.org/10.1017/S0024282912000564 Published online by Cambridge University Press

FIG. 5. DCA joint-plot of lichen species in the height ranges on pines (correlation between axis 1 and height: $r^2 = 0{\cdot}90$). For abbreviations of lichen species names see Table 1.

case of pines, on average 51% of the lichen species recorded on trees was present already up to 6 m from the ground, whereas relatively more new species compared to spruces were added in the upper canopy (Fig. 7).

Earlier studies have proved that the occurrence of many lichen species changes vertically on trees and some species are mostly growing higher than 2 m (e.g. McCune *et al.* 2000; Rosso *et al.* 2000; Ellyson & Sillet 2003; Williams & Sillett 2007; Marmor *et al.* 2010). Lichen species composition also changed vertically according to our results, height from the ground being strongly correlated with DCA axis 1 in both tree species studied. The lowest height range did not overlap with other ranges in DCA joint-plots for either spruce or pine (Figs 4 & 5). The higher vertical zonation of lichen communities was more pronounced for pine than for spruce, however. This result corresponds with the findings of Jarman & Kantvilas (1995), who pointed out that there was only a small overlap in cryptogam communities

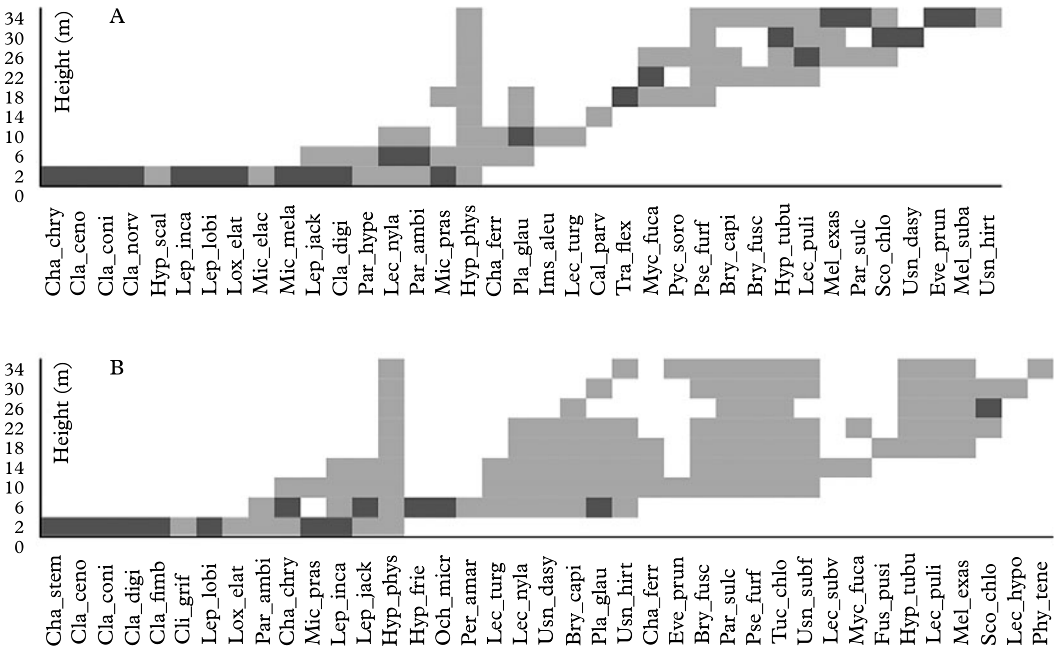

FIG. 6. The vertical changes in lichen species composition on pines (A) and spruces (B), according to the results of Indicator Species Analysis (statistically significant indicator values have been marked with dark grey, and other ≥10 indicator values with light grey). For abbreviations of lichen species names see Table 1.

between basal and canopy parts of Huon pine in Tasmania. Figure 6 demonstrates which relatively frequent lichen species could be associated with some specific height ranges on spruce and pine.

There were several species, for example *Chanotheca stemonea*, *Cladonia cenotea* and *C. norvegica*, which preferred to grow in the lowest height range. Some of these have also been associated with trunk bases by Holien (1997). Many lichens, such as *Bryoria fuscescens*, *Lecanora pulicaris*, *Melanohalea exasperatula* and *Tuckermannopsis chlorophylla*, that were not found or were infrequent on the first 2 m of our sampled trees, are generally very common in Estonia and can also be found in low height ranges. Some of them are already known from previous studies to be more common higher in spruce canopy. Kermit & Gauslaa (2001) have recorded a high frequency of *M. exasperatula* in spruce treetops in Norway; *Bryoria* spp. have been found by Gauslaa *et al.* (2008) to be more abundant at heights greater than 2 m.

Comparing our species list (Table 1) with previous data about lichens in Estonian coniferous forests (Jüriado *et al.* 2003; Marmor *et al.* 2011; eSamba), it became apparent that some species occurring rather frequently on spruce and/or pine higher than 2 m from the ground in the present study, have been rather rarely recorded on the lowest 2 m of these tree species in Estonia in general. These lichen species, such as *Fuscidea pusilla*, *Lecanora albellula*, *Micarea denigrata*, *Ochrolechia arborea*, and *Scoliciosporum chlorococcum*, seem to be more exclusively associated with higher height ranges in Estonian coniferous forests and are likely to remain systematically underrecorded if only the first 2 m are studied. At the same time, *F. pusilla* and *S. chlorococcum* are relatively frequent on spruce branches on the first 2 m in Norway (Lie *et al.* 2009).

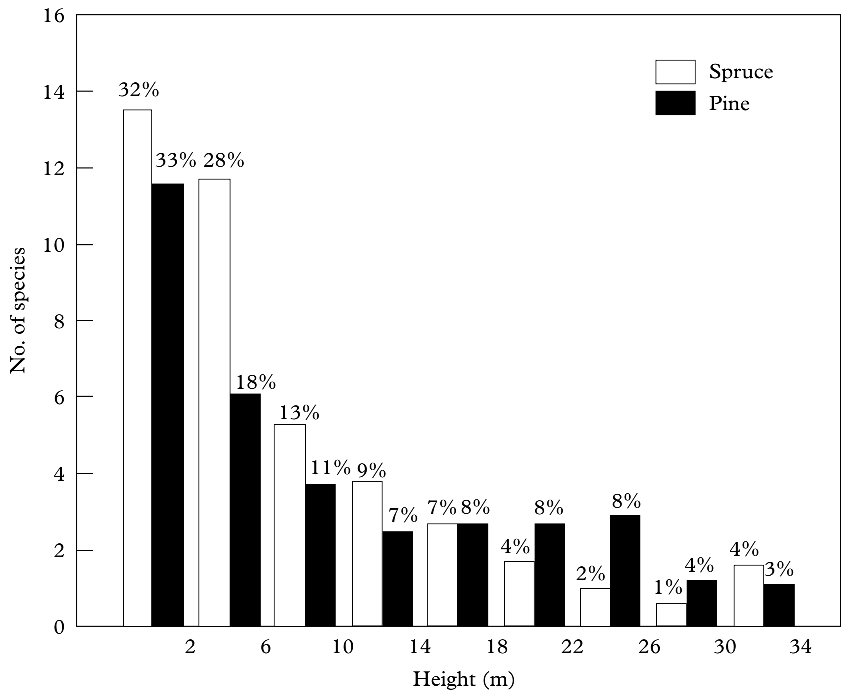

FIG. 7. The addition of new lichen species, absent in previous height ranges, with height from the ground: mean number of such species in every height range and percentage of mean species richness on whole trees.

The higher height ranges also provided some very interesting lichen records. One of the recorded species, *Lecanora farinaria*, is new for Estonia. It was found on the branches of six spruce trees. In addition, we registered five locally red-listed lichen species (*Evernia mesomorpha*, *Usnea barbata*, *U. fulvoreagens*, *U. substerilis*, and *U. wasmuthii*), growing on spruce branches higher than 2 m; and six nationally rare or rather rare species, three of them (*Fellhanera subtilis*, *Micarea nitschkeana*, *Rinodina efflorescens*) exclusively higher than 2 m. The results indicate that some rare lichen species and species of conservation concern may be associated with higher height ranges in old coniferous forests (all our sample plots were located in relatively old forests as the age of sample trees was ≥100 years). It is well known that many lichen species prefer older trees (e.g. Ranius *et al.* 2008; Fritz *et al.* 2009; Nascimbene *et al.* 2009) and old forests with long ecological continuity (e.g. Coppins & Coppins 2002; Josefsson *et al.* 2005; Fritz *et al.* 2008; Marmor *et al.* 2011), whereas there are only a few studies where such species have been looked for higher on the tree trunk and canopy. For example, Fritz (2009) found that several red-listed lichen species in Sweden are growing higher than 2 m on aspen trunks.

Different factors affect the vertical distribution of lichens in forest canopies (Sillett & Antoine 2004) and could be behind the absence or infrequency of some lichen species in the lowest 2 m of trees. Microclimatic variables change in forest canopies: light conditions improve, wind speed and amplitudes of temperature and humidity increase in the treetops (Gross 1993); as they were not directly measured in the present study, the possible effects on lichen communities will not be discussed. Substratum related changes are also one of the major drivers behind the vertical changes in lichen communities as substratum availability, quality and age change with height in the canopy.

As in previous studies (e.g. Holien 1997; Caruso & Thor 2007; Lie *et al.* 2009), many species were more frequent on branches (Table 1). For example, several *Usnea* species were recorded mainly on spruce branches; *Physcia tenella* was most frequent on spruce twigs in the upper canopy; *Trapeliopsis flexuosa* was associated with pine branches in mid canopy, growing mainly on deadwood branch stumps (*Placynthiella icmalea* and *P. uliginosa* were also found on deadwood). The presence of nitro/neutrophilic species, such as *Physcia adscendens*, *P. tenella*, and *Xanthoria polycarpa*, in treetops has been associated previously with the effects of air pollution (Marmor *et al.* 2010) and nutrients delivered by birds (McCune *et al.* 2000).

The Estonian State Forest Management Centre is gratefully acknowledged for permitting us to carry out the present study in state forests. Special thanks go to Martin Tõrra for cutting down the trees. Many thanks also to Inga Jüriado and Ave Suija for their help in identifying some exemplars, and to Martin Kukwa for confirming the identification of the nationally new species. Ants Kaasik is thanked for the comments on statistical analyses, and Andres Saag for general comments on the study. Financial support was received from the Norwegian Financial Mechanisms and EEA Financial Mechanisms (grant EMP9); the Estonian Science Foundation (grants no JD173 and 9109); the Estonian Ministry of Education and Research (targeted financing no 0153) and from the European Union through the European Regional Development Fund (Center of Excellence FIBIR).

References

Ahti, T., Hämet-Ahti, L. & Jalas, J. (1968) Vegetation zones and their sections in northwestern Europe. *Annales Botanici Fennici* **5:** 169–211.

Campbell, J. & Coxson, D. S. (2001) Canopy microclimate and arboreal lichen loading in subalpine spruce-fir forest. *Canadian Journal of Botany* **79:** 537–555.

Caruso, A. & Thor, G. (2007) Importance of different tree fractions for epiphytic lichen diversity on *Picea abies* and *Populus tremula* in mature managed boreonemoral Swedish forests. *Scandinavian Journal of Forest Research* **22:** 219–230.

Coppins, A. M. & Coppins, B. J. (2002) *Indices of Ecological Continuity for Woodland Epiphytic Lichen Habitats in the British Isles.* London: British Lichen Society.

eElurikkus (Database of Estonian Biodiversity). http://elurikkus.ut.ee.

Ellyson, W. J. T. & Sillet, S. C. (2003) Epiphyte communities on Sitka spruce in an old-growth redwood forest. *Bryology and Lichenology* **106:** 197–211.

EMHI (Estonian Meterological and Hydrological Institute). http://www.emhi.ee.

eSamba (Database of Estonian Lichens). http://www.eseis.ut.ee.

Fritz, Ö. (2009) Vertical distribution of epiphytic bryophytes and lichens emphasizes the importance of old beeches in conservation. *Biodiversity and Conservation* **18:** 289–304.

Fritz, Ö., Gustafsson, L. & Larsson, K. (2008) Does forest continuity matter in conservation? – A study of epiphytic lichens and bryophytes in beech forests of southern Sweden. *Biological Conservation* **141:** 655–668.

Fritz, Ö., Niklasson, M. & Churski, M. (2009) Tree age is a key factor for the conservation of epiphytic lichens and bryophytes in beech forests. *Applied Vegetation Science* **12:** 93–106.

Gauslaa, Y., Lie, M. & Ohlson, M. (2008) Epiphytic lichen biomass in a boreal Norway spruce forest. *Lichenologist* **40:** 257–266.

Gross, G. (1993) *Numerical Simulation of Canopy Flows.* Berlin: Springer.

Holien, H. (1997) The lichen flora on *Picea abies* in a suboceanic spruce forest area in Central Norway with emphasis on the relationship to site and stand parameters. *Nordic Journal of Botany* **17:** 55–76.

Jarman, S. J. & Kantvilas, G. (1995) Epiphytes on an old Huon pine tree (*Lagarostrobos franklinii*) in Tasmanian rainforest. *New Zealand Journal of Botany* **33:** 65–78.

Josefsson, T., Hellberg, E. & Östlund, L. (2005) Influence of habitat history on the distribution of *Usnea longissima* in boreal Scandinavia: a methodological case study. *Lichenologist* **37:** 555–567.

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

Kermit, T. & Gauslaa, Y. (2001) The vertical gradient of bark pH of twigs and macrolichens in a *Picea abies* canopy not affected by acid rain. *Lichenologist* **33:** 353–359.

Laasimer, L. & Masing, V. (1995). Taimestik ja taimkate [Flora and plant cover]. In *Eesti Loodus* [*Estonian Nature*] (A. Raukas, ed.): 364–401. Tallinn: Valgus & Eesti Entsüklopeediakirjastus.

Lie, M. H., Arup, U., Grytnes, J.-A. & Ohlson, M. (2009) The importance of host tree age, size and growth rate as determinants of epiphytic lichen diversity in boreal spruce forests. *Biodiversity and Conservation* **18:** 3579–3596.

Marmor, L., Tõrra, T. & Randlane, T. (2010) The vertical gradient of bark pH and epiphytic macrolichen biota in relation to alkaline air pollution. *Ecological Indicators* **6:** 1137–1143.

Marmor, L., Tõrra, T., Saag, L. & Randlane, T. (2011) Effects of forest continuity and tree age on epiphytic lichen biota in coniferous forests in Estonia. *Ecological Indicators* **11:** 1270–1276.

McCune, B. (1993) Gradients in epiphyte biomass in three *Pseudotsuga-Tsuga* forests of different ages in Western Oregon and Washington. *Bryologist* **96:** 405–411.

McCune, B., Rosentreter, R., Ponzetti, J. M. & Shaw, D. C. (2000) Epiphyte habitats in an old conifer forest in Western Washington, U.S.A. *Bryologist* **103:** 417–427.

Nascimbene, J., Marini, L., Motta, R. & Nimis, P. L. (2009) Influence of tree age, tree size and crown structure on lichen communities in mature Alpine spruce forests. *Biodiversity and Conservation* **18:** 1509–1522.

Orange, A., James, P. W. & White, F. J. (2001) *Microchemical Methods for the Identification of Lichens*. London: British Lichen Society.

Randlane, T., Jüriado, I., Suija, A., Lõhmus, P. & Leppik, E. (2008) Lichens in the new Red List of Estonia. *Folia Cryptogamica Estonica* **44:** 113–120.

Randlane, T., Saag, A. & Suija, A. (2011) Lichenized, lichenicolous and allied fungi of Estonia. Ver. November 1, 2011. http://esamba.bo.bg.ut.ee/checklist/est/home.php.

Ranius, T., Johansson, P., Berg, N. & Niklasson, M. (2008) The influence of tree age and microhabitat quality on the occurrence of crustose lichens associated with old oaks. *Journal of Vegetation Science* **19:** 653–662.

Rosso, A. L., McCune, B. & Rambo, T. R. (2000) Ecology and conservation of a rare, old-growth-associated canopy lichen in a silvicultural landscape. *Bryologist* **103:** 117–127.

Sillet, S. C. & Antoine, M. E. (2004) Lichens and bryophytes in forest canopies. In *Forest Canopies* (M. D. Lowman & H. B. Rinker, eds): 151–174. Amsterdam: Elsevier.

Williams, C. B. & Sillett, S. C. (2007) Epiphyte communities on redwood (*Sequoia sempervirens*) in northwestern California. *Bryologist* **110:** 420–452.