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Snags, and their lichen flora in old Estonian peatland forests

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In this study, we (1) explored the lichen floras of snags and living trees of *Picea abies, Pinus sylvestris, Betula pubescens* and *Alnus glutinosa* in the Estonian peatland forests, distinguishing tree species, snags with bark (S1) and snags without bark (S2); (2) measured the availability and characteristics of snags. On average, 42–64 snags ha^{-1} were detected, but snag types differed in availability. Although S2 of *Betula*, *Alnus* and *Picea* were the rarest studied substrata, the highest numbers of lichen species were estimated to occur there. The lichen floras of S1 and S2 were distinct, with that of S1 resembling living trees. Tree species influenced the flora of living trees and S1 but not of S2; a similar pattern emerged in substratum acidity. 25% of the lichen species were unique to snags. Forest management activities should retain especially the naturally rare S2 of deciduous trees.

Key words: calicioid lichens and fungi, coarse woody debris, conservation, epiphytic lichens, epixylic lichens, snags

Introduction

In forest ecosystems, a variety of organisms inhabit different types and decay stages of coarse woody debris–snags (standing dead trees), logs (fallen trees), stumps, and large branches and pieces of roots (Harmon *et al*. 1986, Söderström 1988a, 1988b, Samuelsson *et al*. 1994, Renvall 1995, Esseen *et al*. 1997, McComb & Lindenmayer 1999). While the volume of dead trees may reach 30% of total stem volume in virgin forests (Linder *et al*. 1997), forest management tends to decrease the amount of dead wood (Green & Peterken 1997, Linder & Östlund 1998, Sippola *et al*. 1998). Today, the lack of coarse woody debris in managed forests is considered to be a major threat for many species (Berg *et al*. 1994, Samuelsson *et al*. 1994).

The importance of dead wood as lichen habitat has been recognised only recently. It has mostly been described in the conifer forests of Fennoscandia (Laaka 1995, Johansson 1997, Forsslund & Koffmann 1998, Holien 1998, Kuusinen & Siitonen 1998, Kruys *et al*. 1999), but also in Białowieża primeval forest in Poland (Chlebicki *et al*. 1996) and (only logs) in North Carolina, USA (McAlister 1997), and British Columbia, Canada (Qian *et al*. 1999). Among types of dead wood, snags are more favourable for lichens because they receive a higher amount of light and are drier than logs, which are favoured by bryophytes (Muhle & LeBlanc 1975, Chlebicki *et al*. 1996; *see also* Hong & Glime 1997, Pharo & Beattie 1997). Many species of crustose lichens (e.g. calicioid species) have been found only or mainly on snags (Holien 1996, Johansson 1997, Forsslund & Koffman 1998, Kuusinen & Siitonen 1998).

At present, there are several evident gaps in the knowledge concerning the lichen flora of snags. As mentioned above, the geographical scope of the studies has been extremely narrow. Consequently, only lichens of two common conifer snags (Scots pine *Pinus sylvestris* and Norway spruce *Picea abies*) have been studied, usually without separating the tree species (e.g. Johansson 1997, Forsslund & Koffman 1998), and no data on snags of deciduous trees exist. Moreover, there has been no separation between two different substrata — bark and wood of snags — or only wood has been studied (Chlebicki *et al*. 1996, Forsslund & Koffman 1998).

Species inhabiting temporary habitats (e.g. dead wood) should have a good dispersal ability to persist (Herben *et al*. 1991), but colonization also depends on the abundance and distribution of habitat patches. However, the relationship between the abundance of snags and lichen diversity has remained nearly unexplored (but *see* Forsslund & Koffman 1998 for differences between managed and unmanaged stands), and the role of snags in determining the diversity of forest lichens is not known. As a result, practical guidelines about snag retention in managed forests have been derived only from vertebrate studies (McComb & Lindenmayer 1999).

In this study, carried out in the peatland forests of east-central Estonia, we (1) explore the lichen floras of snags and living trees of four tree species, distinguishing tree species and snag types; (2) measure the availability, distribution and characteristics of snags; (3) evaluate the importance of snags for the forest lichen flora. In the light of the results, we review previously published reports and suggest some guidelines for snag retention.

Material and methods

Study area

The study was carried out in Alam-Pedja Nature Reserve (58°30´N, 26°10´E; east-central Estonia), which encompasses 26 000 ha of mainly forests and wetlands within the hemiboreal zone. The altitude of the area is between 30 and 40 m a.s.l. Forests (56% of the area) consist mostly of *Betula pubescens*, *Alnus glutinosa* and other deciduous trees (over 70% of forests) or *Pinus sylvestris* (ca. 25%). Of the forests, 66% can be classified as peatland forests, and about 30% as old (over 60 years deciduous or over 80 years coniferous stands). The lichen flora of the reserve, with its 216 species, is comparatively rich (P. Lõhmus unpubl.).

Sampling design

We studied the lichen flora of four tree species (*Picea abies*, *Pinus sylvestris*, *Betula pubescens*, *Alnus glutinosa*) and three types of trunks (living trees and snags with and without bark). All standing dead trees higher than 1.5 m and at least 10 cm in diameter at breast height were classified as snags. Snags with bark (S1) had over 80% of surface covered with bark, while snags without bark (S2) had less than 20% of bark surface. Lichens were not studied on snags with 20%–80% of bark surface, on the woody surface of S1, and on the bark surface of S2.

Sample plots were randomly selected from forestry databases at stand scale. All old (deciduous over 60 years, coniferous over 80 years) peatland forests with a minimum diameter over 30 m and any of the four studied tree species as main species were considered. For every tree

species, twenty main plots and some additional plots were selected. The mean age of the studied stands was 103 ± 14 years (mean ± S.D.) in *Picea* (n = 22), 117 ± 25 years in *Pinus* (n = 26), 83 ± 13 years in *Betula* (n = 25) and 75 ± 8 years in *Alnus* stands (n = 22).

The closest snag from the centre of plot, and the nearest living tree of the same species and the same age class, made up a description unit. The average distance between a snag and living tree was 3 ± 2 m (mean ± S.D.). All combinations of tree species and snag type were attempted to analyse in two replications in a plot, but in nineteen cases snags for the second replicate were not found in the field.

Field and laboratory work

During the fieldwork in 1999, the species composition and coverage of lichens on tree trunks, characteristics of the trunks, and snag density were measured. A total of 95 sample plots and 632 tree trunks were studied.

The lichen flora was described using a slightly modified method of Kuusinen (1996). The occurrence of lichen species at 0.2–2 m was recorded. For coverage estimates, a rectangle made of transparent plastic was placed on the northern side of each tree at 80 cm height. The 20 × 50-cm rectangle was divided into one hundred 2 × 5-cm subunits, and a single point was placed in the corners of the subunits (a total of 100 points). The number of points hit by each species was counted and these values were used as an estimate of the species' percentage cover on the trunk.

The nomenclature follows Randlane and Saag (1999). Fungi allied with lichens and lichenicolous species (mainly calicioids) are considered as lichens. *Lepraria* species were treated collectively. Specimens of difficult crustose species were collected and identified with a microscope and standard thin-layer chromatography. Voucher specimens were deposited at the lichenological herbaria of the Institute of Botany and Ecology of the University of Tartu (TU) and at the Botanical Museum of the University of Helsinki (H).

Bark or wood samples were collected from the trunks at 0.5–1.5 m and incubated in distilled water (1.5 ml g^{-1}) for 24 hours. The pH of the extract was measured with a standard pH meter. The snags were classified as decayed or not decayed, according to whether at least 1 cm of the wood could be easily penetrated with a knife or not.

In the centre of every sample plot all snags were counted, and their species and type were determined in a circular plot with a radius of 15 m. In contrast to the 20%-criteria in lichen analyses (*see above*), snag types were distinguished according to the substrate (bark or wood) covering most of the snag.

Data analysis

All analyses were performed with the STATISTICA 4.5 software. We characterised the distribution pattern of snags by dispersion coefficient (variance/mean), in which values < 1 indicate a regular and values > 1 indicate an aggregated pattern (Greig-Smith 1964). Differences in the lichen species composition of different tree species and types were explored with Ward's method of cluster analysis (Podani 1994), using only data from first replications.

Our limited samples certainly missed several lichen species of the studied substrata. To correct for the sample size, the species lists of the first replication were randomly explored to carry out regression analyses of cumulative "species-trunk curves" (the total number of lichen species found vs. the number of studied trunks) for all twelve substrata. As logarithmic functions fitted well to these curves (mean R^2 always exceeded 0.9), these were used to calculate the expected total number of species that would be found per 100 trunks. The same data was resampled ten times, changing the order of the trunks randomly to get the variance of the estimates. We also evaluated the estimates by comparison with the total number of species from both replications that were actually found.

The impact of tree species and type on the following characteristics of individual trunks was tested: (1) total number of all lichen species, calicioid lichens and fungi (*sensu* Tibell 1999), and rare species (the species known from

up to ten locations in Estonia, according to Randlane & Saag 1999). As three "rare" species — *Hypocenomyce sorophora*, *Lecidea nylanderi* and *Loxospora elatina* — were found frequently (in more than 50 samples), these were not considered rare in this study; (2) the cover of all lichens, calicioid species and rare species; (3) the diversity of lichens according to the Shannon-Wiener index (H'):

$$H' = -\sum_{i=1}^{s} p_i \ln p_i$$

where p_i is the proportion of the total cover of lichens contributed by the i:th species; (4) pH of bark or wood. In the tests, we used the average values of two replications to decrease the possible influence of unusual values. As ANOVA assumptions of normal distribution and homogeneous variances were usually violated, we performed the Mann-Whitney U-tests for pairwise comparisons. Two approaches were used to take into account the inflation of the overall level of significance, which resulted from multiple tests (n = 180). First, all significance levels were corrected using the Dunn-Šidák method (Sokal & Rohlf 1995). However, such corrections severely reduce the power of tests (Wright 1992), and our aim was rather to explore general patterns than individual differences. Therefore, we also considered other tests that initially resulted in $p < 0.01$, which roughly means that, on average, we could have included errors twice.

Results

Density, distribution, and characteristics of snags

Snags were distributed in a clumped pattern, with a mean density of 42–64 snags ha^{-1} (Table 1). One-way ANOVA showed no significant impact of dominating tree species on the total snag density (F = 1.32, p = 0.27). However, snags without bark were significantly more abundant in *Pinus* stands as compared with *Picea* (U = 106.5, Z = –3.17, p = 0.0015), *Betula* (U = 58.5, Z = –4.30, $p < 0.001$) as well as *Alnus* stands (U = 89.0, Z = –3.43, $p < 0.001$). Snags of five tree species were found, but there were great differences in the snag availability of different species and types, e.g. birch S1 was the most frequent and birch S2 the rarest combination (Fig. 1).

The bark of living coniferous trees was significantly more acid than that of deciduous trees (mean pH values 3.9–4.0 and 4.6–4.7, respectively); the difference was seen also in S1 (with the exception of spruce). pH values of wood (S2) were 4.2–4.4, with no significant difference between the tree species (Fig. 2 and Table 2). Within tree species, the acidity of bark and

Table 1. The average number (± S.D.) of snags ha^{-1} and the values of dispersion coefficient (DC) in different stands. DC < 1 indicates regular and DC > 1 clumped distribution of snags. Abbreviations: S1 = snag with bark, S2 = snag without bark.

Variable	Stand				
	Picea (n = 20)	*Pinus* (n = 23)	*Betula* (n = 21)	*Alnus* (n = 21)	Total (n = 85)
No. of S1	41 ± 33	26 ± 31	37 ± 32	43 ± 25	37 ± 30
No. of S2	12 ± 14	38 ± 30	5 ± 9	9 ± 15	16 ± 23
No. of S1 + S2	53 ± 35	64 ± 44	42 ± 33	51 ± 32	53 ± 37
DC of S1	1.61	2.38	1.73	1.16	1.72 ± 0.50
DC of S2	2.33	1.58	3.60	3.33	2.71 ± 0.93*
DC of S1 + S2	1.32	1.38	1.57	1.25	1.38 ± 0.14*

* according to the t-test, differs significantly ($p < 0.05$) from random distribution (DC = 1)

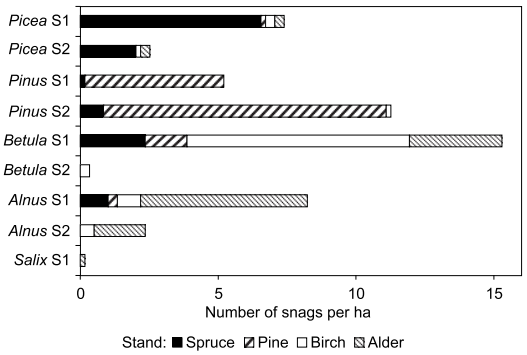

Fig. 1. Densities of detected snag types, and their distribution in different stands.

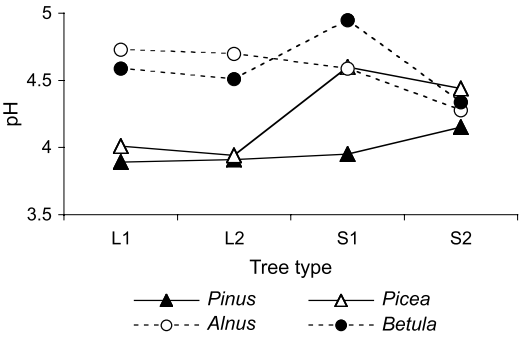

Fig. 2. Acidity (pH) of bark and wood of different tree species and types. Abbreviations: S1 = snag with bark; S2 = snag without bark; L1 and L2 = living trees near S1 and S2, respectively.

wood tended to differ in all species except *Pinus*, but the difference was highly significant only in *Alnus* (Table 3). The proportion of decayed snags was 43% in *Betula* (n = 72) and 35% in *Alnus* (n = 82), but only 8% in *Picea* (n = 77) and 15% in *Pinus* (n = 80). All pairwise comparisons of the proportions between a coniferous and a deciduous tree were significant (χ^2-test: $p < 0.01$, df = 1).

Table 2. Differences in the lichen flora and substratum pH of different tree species. Asterisks indicate significance levels of the Mann-Whitney *U*-tests: *$p < 0.01$, **$p < 0.001$, ***$p < 0.0003$ (i.e. significant after Dunn-Šidák correction for multiple tests). Abbreviations: L = living tree, S1 = snag with bark, S2 = snag without bark, H' = Shannon-Wiener diversity index.

Variable	Tree type	Comparisons between pairs of tree species					
		Picea–Pinus	*Picea–Betula*	*Picea–Alnus*	*Pinus–Betula*	*Pinus–Alnus*	*Betula–Alnus*
No. of lichen species	L	***	***	***		***	***
	S1	***	***	***			
	S2						
Total coverage of lichens	L	***	***	*		***	
	S1	***	***	*			
	S2		***		***		**
No. of calicioid species	L		***	***	***	***	*
	S1						
	S2						
Coverage of calicioid species	L		***	***	*	*	
	S1				*	*	
	S2	*	*		**		*
H'	L	*		***		*	**
	S1	***	*				
	S2		*				*
pH	L		***	***	***	***	
	S1	***			***	**	
	S2						

Species numbers and composition of the lichen flora

A total of 103 lichen species (incl. eight fungi allied with lichens and three lichenicolous species) were found (*see* Appendix); crustose species made up 69% of these. Snags were inhabited by 89 species, and living trees by 77 species (Table 4).

The mean estimates of species-richness for samples of one hundred trunks ranged from 20 to 51 species (Table 4), markedly depending on tree species (two-way ANOVA: $F = 150.2$, $p < 0.0001$), tree type ($F = 323.8$, $p < 0.0001$) as well as their interaction ($F = 40.6$, $p < 0.0001$). The estimated numbers of species were the highest in S2, intermediate in living trees, and lowest in S1. However, comparison with the actual numbers from two replications (sample sizes 74–82 in living trees, 34–46 in snags), shows that the absolute values of our estimates tended to be too low, and that at least living *Alnus* should be considered among the most species-rich substrata. Differently from living trees and S1, the estimates for S2 greatly exceeded the numbers actually found.

Contrarily to the large differences in species richness, the share of crustose lichens varied only slightly among substrata (55%–69%; Table 4), and the share of rare species did not differ between living trees and snags ($\chi^2 = 0.35$, df = 2, $p > 0.05$). Snags without bark (S2) had 15 unique species, while snags with bark had only three. Ten unique S2 species belonged to the calicioid species group (mainly genera *Calicium*, *Chaenotheca* and *Chaenothecopsis*), and seven species grew only on deciduous trees.

Table 3. Differences in the lichen flora and substratum pH of different tree types. Asterisks indicate significance levels of the Mann-Whitney *U*-tests: $*p < 0.01$, $**p < 0.001$, $***p < 0.0003$ (i.e. significant after Dunn-Šidák correction for multiple tests). Abbreviations: L = living tree, S1 = snag with bark, S2 = snag without bark, H' = Shannon-Wiener diversity index.

Variable	Tree species	Comparisons between pairs of tree types		
		L–S1	L–S2	S1–S2
No. of lichen species	*Picea*			**
	Pinus			
	Betula			
	Alnus			
Total coverage of lichens	*Picea*		**	**
	Pinus			
	Betula		***	***
	Alnus			
No of. calicioid species	*Picea*		*	***
	Pinus		***	***
	Betula		***	***
	Alnus	*	***	***
Coverage of calicioid species	*Picea*		*	*
	Pinus		***	***
	Betula		***	*
	Alnus		***	***
H'	*Picea*			
	Pinus			*
	Betula			**
	Alnus		*	
pH	*Picea*	**	**	
	Pinus			
	Betula			*
	Alnus		***	

According to the cluster analysis, the species composition of S1 resembled that of living trees, and differed from that of S2 (Fig. 3). The living trees, which were described near S1, were more similar to these snags than to the living trees near S2.

Analyses at trunk scale

The most remarkable patterns in the diversity and coverage of lichens on individual trunks were as follows (for a complete set of patterns and significance levels *see* Figs. 4–6 and Tables 2 and 3). Living and S1 trunks of *Picea* had fewer species and lower values of the Shannon-Wiener diversity index than the other substrata, but the total coverage of lichens was the highest there. The highest number of species per trunk and the highest values of the Shannon-Wiener diversity index were found on living *Alnus*, despite its lowest number of calicioid species. High numbers and great coverage of calicioid species were characteristic of S2, and coniferous trees tended to have more species and greater coverage of this group than deciduous trees. At the same time, the total coverage of lichens on S2 tended to be low compared to S1 and living trees (significant in *Picea* and *Betula*). Substrata did not differ significantly in respect to the total number and coverage of rare species.

To summarise, out of 180 pairwise comparisons between tree species or types, 66 were statistically significant. Tree species influenced the lichen flora of living trees more frequently (73% of comparisons significant, $n = 30$) than that of snags (32%, $n = 60$). Regarding tree type, living trees and S1 differed from S2 in 60% of comparisons ($n = 40$), but a difference between living trees and S1 was established only once (5%, $n = 20$). The average number of lichen species per trunk and the estimated total number of species (*see* Table 4) in the twelve substrata were not significantly correlated ($r_s = 0.32$, $t = 1.1$, $n = 12$, $p = 0.31$).

Table 4. Characteristics of the lichen flora of different tree species and types. Abbreviations: L = living tree, S1 = snag with bark, S2 = snag without bark. *See* Appendix for species list and sample sizes.

Tree type	Tree species	No. of species*			Microlichens (%)	Rare species (%)	No. of unique species
		Found	Estimated				
L	*Picea*	32	28 ± 2	F	66	16	3
L	*Pinus*	35	36 ± 1	DE	60	11	0
L	*Betula*	39	40 ± 2	D	56	8	1
L	*Alnus*	54	46 ± 1	C	67	7	8
L	Total	77			66	14	14
S1	*Picea*	21	20 ± 2	G	67	19	1
S1	*Pinus*	29	33 ± 2	E	55	10	0
S1	*Betula*	43	44 ± 2	C	60	14	1
S1	*Alnus*	42	40 ± 5	D	67	14	1
S1	Total	66			65	19	3
S2	*Picea*	35	49 ± 3	AB	69	6	1
S2	*Pinus*	35	45 ± 2	BC	69	14	1
S2	*Betula*	44	51 ± 2	A	55	7	3
S2	*Alnus*	43	50 ± 5	A	60	7	4
S2	Total	65			60	11	15
S1 + S2	Total	89			67	19	26

* The number of found species includes the species of both replications and can exceed the estimate, which is based on the first replication. The estimates (mean ± S.D.) were calculated from object–species curves for the sample of 100 trunks, and their variance estimated with resampling techniques. The letters after the values indicate the grouping of the substrata in descending order of species-richness from A to G (Tukey's HSD test at 5% significance level).

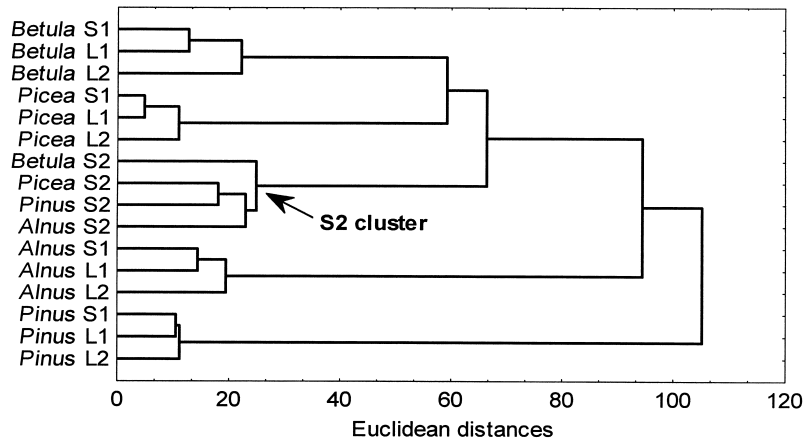

Fig. 3. Similarity of lichen species composition of different tree species and types according to cluster analysis (Ward's method). The data matrix reveals the abundance of lichen species in the first replication as presented in Table 2, except that two types of living trees have been considered. Abbreviations: S1 = snag with bark; S2 = snag without bark; L1 and L2 = living trees near S1 and S2, respectively.

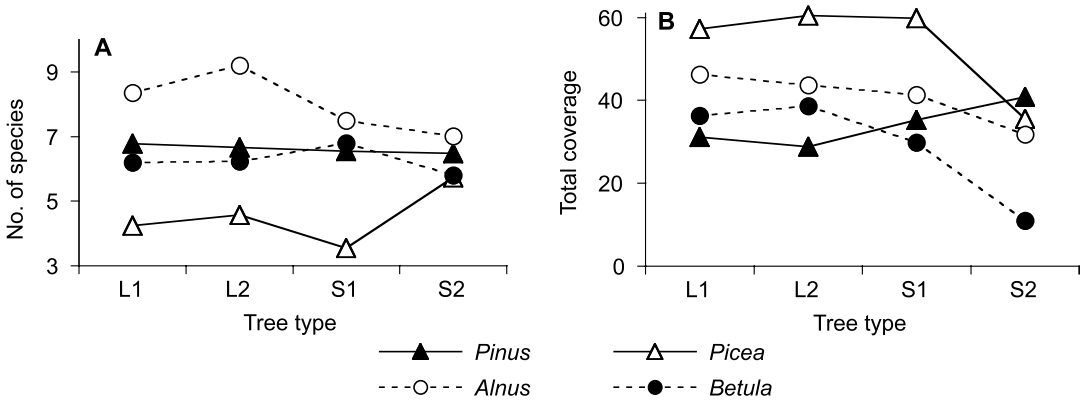

Fig. 4. Total number (**A**) and coverage (**B**) of lichen species per trunk on different tree species and types. Abbreviations: S1 = snag with bark; S2 = snag without bark; L1 and L2 = living trees near S1 and S2, respectively.

Discussion

Density and distribution of snags

The average density of snags in the studied forests (53 snags ha^{-1}) conforms with previously published values (Table 5). It is much lower than e.g. in the old *Pseudotsuga* or *Quercus–Carya* forests in North America (Cline *et al*. 1980, Spies & Franklin 1988), but exceeds the values in neotropical forests (Gibbs *et al*. 1993) or the boreal *Picea* stands in Sweden (Jonsson 2000). However, the data in Table 5 (which is not aimed to be comprehensive) show that snag densities may differ a lot even in geographically adjacent areas, in stands of similar composition and age. Our study also supported the findings of Cline *et al*. (1980) about clumped distribution of snags. This pattern is probably caused by spatial variation in tree death (*see* Franklin *et al*. 1987).

Tree mortality, decay and fall rates determine snag dynamics (Morrison & Raphael 1997), thus causing differences in the availability of

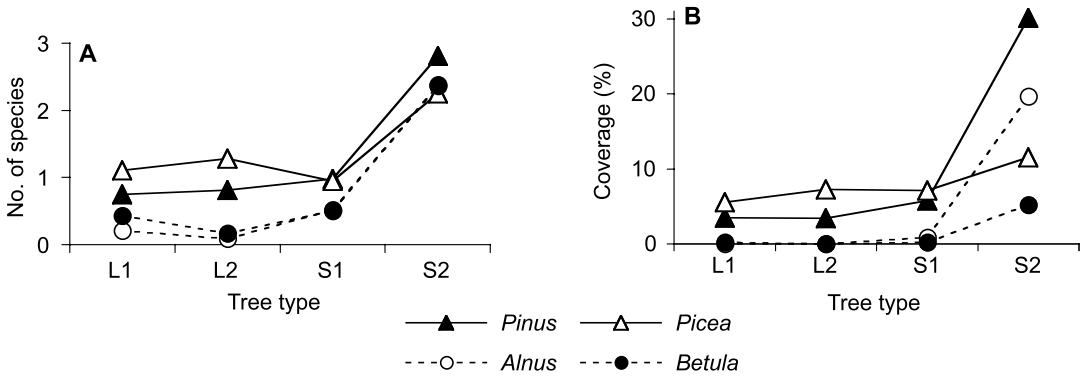

Fig. 5. Number (**A**) and coverage (**B**) of calicioid species per trunk on different tree species and types. Abbreviations: S1 = snag with bark; S2 = snag without bark; L1 and L2 = living trees near S1 and S2, respectively.

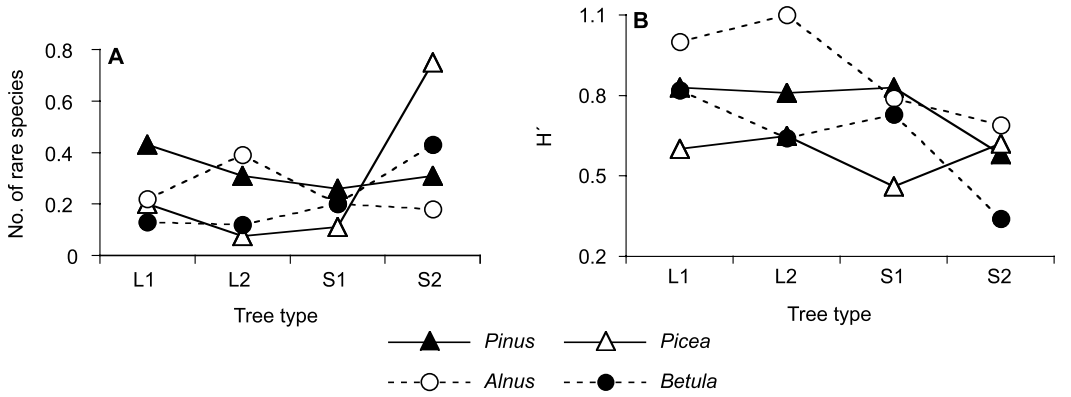

Fig. 6. Number of rare species (**A**) and the value of Shannon-Wiener diversity index (**B**) per trunk on different tree species and types. Abbreviations: S1 = snag with bark; S2 = snag without bark; L1 and L2 = living trees near S1 and S2, respectively.

different snag types. For example, in our study conifer snags were less decayed than those of deciduous trees, which is consistent with the difference in their decay rates (Harmon 1982, Harmon *et al*. 1986). The lower decay rates of conifers may explain why S2 of *Pinus* and *Picea* were more abundant than those of *Betula* and *Alnus*, and why S2 were most abundant in *Pinus* forests often consisting entirely of this species (*see also* Sippola *et al*. 1998). However, snag dynamics certainly change also during natural succession. On the one hand, it is likely that many secondary forests of the studied reserve will be replaced by mixed or coniferous ones, and only a small part of undrained deciduous forest will remain where periodical flooding destroys *Picea* undergrowth (fire does not influence these wet habitats). On the other hand, forests will be older, hence the remnant deciduous stands could have higher snag densities than currently found, and the individual snags could reach the S2 stage more often, as larger (older) dead trees persist longer (Keen 1955).

Lichen flora of snags and living trees

There are hardly any comparable published data about the species-richness of lichens on different tree species and types (Table 6). The main

Table 5. The average density of snags in old forests according to different studies.

Region	Forest type and/or dominating tree species	Stand age (yr.)	Snags ha^{-1}	Ref*
North America				
Virginia	*Quercus prinus* and *Quercus* spp.–*Carya* spp.	80–90	146	1
Oregon and	*Pseudotsuga menziesii*	65	171	2
Washington		121	121	
Oregon	*Pseudotsuga menziesii*	110	48	3
Montana	*Abies grandis*	?	69	4
Washington	subalpine forest	?	51	5
Alberta	boreal *Populus tremuloides*	50–65	73	6
	forest	> 120	66	
Europe				
Britain	broadleaved woodland	?	< 50	7
Komi Republic	boreal *Picea abies* forest	?	110	8
Sweden	boreal *Picea abies* forest	200–300	33	9
Estonia	hemiboreal peatland forest	88	53	10
New World	tropical and subtropical forest	?	4–21	11

*References: 1 = Rosenberg *et al*. 1988; 2 = Spies & Franklin 1988; 3 = Cline *et al*. 1980; 4 = Lesica *et al*. 1991; 5 = Flanagan *et al*. 1998; 6 = Lee *et al*. 1997; 7 = Kirby *et al*. 1998; 8 = Syrjänen *et al*. 1994; 9 = Jonsson 2000; 10 = this study; 11 = Gibbs *et al*. 1993.

Table 6. Species-richness of lichens on different tree types according to published studies. The numbers of studied trunks are given in superscript. Regarding living trees, only methodologically comparable studies from northern Europe have been considered.

Region	Forest type or tree species	Tree type			Ref*
		Living	Log	Snag	
Białowieża (Poland)	deciduous and mixed forest	147	72	55**	1
Carolina (USA)	pine-hardwood mixed forest		21^{131}		2
Sweden	coniferous forest		77^{86}**	85^{52}**	3
Estonia	peatland forest	77^{169}		90^{169}	4
E Finland	*Picea abies*	49^{20}			5
Estonia	*Picea abies*	32^{42}		43^{42}	5
Gotland (Sweden)	*Picea abies*	37^{27}	} 42^{32}	} 39^{16}	6
Gotland	*Pinus sylvestris*	45^{40}			6
Finland	*Picea abies*		} 39^{70}**		7
Finland	*Pinus sylvestris*				7
E Finland	*Pinus sylvestris*	41^{20}			5
Estonia	*Pinus sylvestris*	35^{41}		47^{41}	4
E Finland	*Betula pendula*	41^{20}			5
Estonia	*Betula pubescens*	39^{41}		62^{41}	4
Estonia	*Alnus glutinosa*	54^{45}		62^{45}	4
E Finland	*Alnus incana*	66^{20}			5
E Finland	*Salix caprea*	65^{20}			5
E Finland	*Populus tremula*	70^{190}			8

* References: 1 = Cieśliński *et al*. 1996, Chlebicki *et al*. 1996; 2 = McAlister 1997; 3 = Forsslund & Koffman 1998; 4 = this study; 5 = Kuusinen 1996; 6 = Johansson 1997; 7 = Laaka 1995; 8 = Kuusinen 1995.
** only species on wood included

problems are: (1) different substrata are seldom studied in the same areas and sample sizes are rarely similar (Kuusinen 1996 is an exception concerning living trees); (2) there are only few studies on coarse woody debris; (3) studies on coarse woody debris do not separate tree species, and hence represent an unknown number of different substrata. Only the lower species-richness of living *Picea* and *Pinus* in our study area as compared with that of Fennoscandian studies (Kuusinen 1996, Johansson 1997) could be stated more or less correctly.

In this study, species richness was not correlated between different scales (individual trunk vs. substratum), and the sample size strongly influenced the conclusions. Indeed, the rich biota of S2 was evident only if large samples were considered. This resulted from different object-species curves: continuous input of new species to S2 lists was observed in sample sizes, which included already most species on living trees and S1. Ecologically, this could mean that the higher species-richness in advanced decay stages is due to a greater number of rare species (*see* Høiland & Bendiksen 1997, for a similar conclusion about wood-inhabiting fungi in *Picea* logs). Why, then, the occurrence of rare lichens did not differ between substrata? Probably because many "rare lichens" (as defined by the number of known locations) where poorly studied. However, no better approach was available, since e.g. threat categories have only been determined for macrolichens in Estonia (Randlane 1998).

Two main patterns emerged from the analyses of the species richness, species composition and coverage of lichens: (1) the floras of S1 and S2 were distinct, with that of S1 resembling living trees; (2) tree species influenced the flora of living trees and S1 but not of S2. We interpret these patterns through the differences between bark and wood as habitats for epiphytic and epixylic organisms, respectively.

Epiphytic lichen communities depend mostly on the characteristics of bark (e.g. texture, water capacity, acidity), which differ significantly between tree species (Barkman 1958, Cieśliński *et al.* 1996, Kuusinen 1996). Differences in bark acidity of living trees were also detected by us, and the values were similar to those previously published (Barkman 1958, Kuusinen 1996). Moreover, bark acidity did not change after tree death (the exceptional result in *Picea* can be an error), which might explain the persistence of species-specific lichen floras in S1. Accordingly, the loss of interspecific differences in the lichen flora of S2 was accompanied with the lack of such differences in wood acidity.

Numerous unique species (those occurring only on one substratum) accounted for most differences in the species composition of S2 and living trees. Half of unique S2-species were wood specialists of the genera *Calicium*, *Chaenotheca* and *Chaenothecopsis* (i.e. calicioids). Other obligate wood species of *Cladonia*, *Hypocenomyce*, *Micarea*, *Trapeliopsis* and *Xylographa* (Ahti 1977, Forsslund & Koffman 1998) were not found, possibly because they prefer logs (Laaka 1995, Chlebicki *et al.* 1996, Forsslund & Koffman 1998). Indeed, some of these latter species occur on logs in the study area (P. Lõhmus pers. obs.).

The importance of snags as a habitat for calicioid lichens and fungi is widely accepted (Titov 1986, Holien 1996, 1998, Johansson 1997, Kuusinen & Siitonen 1998). In this study, both species-richness and coverage of calicioids were higher on S2 compared to living trees and S1. Most of the wood-inhabiting calicioids were non-lichenized saprobic fungi of *Chaenothecopsis*, *Mycocalicium* and *Microcalicium*, which are more specialised to substratum than the lichenized species (Titov 1986). Snags could be the only habitat available for these specialists, having low competitive abilities, since bryophytes and *Cladonia* spp. out-compete them from the wood of logs (Middelborg & Mattsson 1987, Holien 1996).

Generally, however, our results did not support the view of the special value of dead wood as a habitat for crustose lichens (Forsslund & Koffman 1998) because the share of these species varied only slightly among lichen floras of different substrata.

Snag availability and the diversity of forest lichens

Species unique to snags made up 25% of the total number of lichens on the studied tree trunks. Although this percentage should be treated cautiously (our definition of "uniqueness" depends on the sample size and may miss some specialist species, which only occasionally occurred elsewhere), it shows the importance of snags for the diversity of forest lichens.

Persistence of lichen populations on snags has clear parallels with metapopulation models: subpopulations frequently go extinct, and species persistence depends on the colonization of new snags. Large subpopulations have lower extinction probabilities, since large snags persist longer (Keen 1955). Due to clumped distribution, which reduces extinction probability in the clump, species persistence should increase (Adler & Nuernberger 1994).

Unfortunately, data to model the persistence of snag lichens in relation to snag availability (which could give important conservation implications) have yet to be collected. Also, no such empirical correlations have been established, but two results of this study should be emphasized. We estimated that the highest numbers of lichen species occurred on the S2 of *Betula*, *Alnus* and *Picea*, i.e. on the rarest studied substrata. This suggests lack of isolation effects in the natural conditions of our study area, and is consistent with the results of Kruys and Jonsson (1997). However, we got an indication of the isolation potential: the species composition of the living trees, which were described near S1, was more similar to these snags than to the living trees near S2. There were no apparent differences between the S1 and S2 sites, which were situated only some tens of metres from each other. We conclude that the lichen distribution was patchy within those superficially similar stands, but the patchiness did not decrease species richness on a larger scale.

The main conservation implication of this study is that, in addition to snag numbers and measurements, which are usually considered in snag retention techniques (Cline *et al*. 1980, Menasco 1983, McComb & Lindenmayer 1999), snag type is also important. Compared with S2, S1 added almost nothing to the lichen diversity of living trees, while foraging or breeding birds mostly use S1 (Scott & Oldemeyer 1983, Schreiber & deCalesta 1992). We propose to meet the different needs of biota by (1) retaining large snags, which more often reach both stages, (2) paying special attention to the rare existing S2 snags of deciduous trees.

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Appendix

The frequency (percentage of inhabited trees of the first replication) of lichen species on different tree species and types in the peatland forests of Alam-Pedja Nature Reserve. The taxa are arranged according to the total number of records. Symbols: L = living tree, S1 = snag with bark, S2 = snag without bark, # = lichenicolous fungus, * = fungus allied with lichens, + = found only in the second replication, – = not found.

Species	*Picea*			*Pinus*			*Betula*			*Alnus*			No. of records
	L	S1	S2	L	S1	S2	L	S1	S2	L	S1	S2	
n =	42	22	20	41	20	21	41	20	21	45	23	22	338
(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)	(13)	(14)
Hypogymnia physodes	93	95	85	85	95	95	98	95	48	84	78	77	293
Lepraria spp.	95	100	60	24	25	19	44	70	43	53	74	59	188
Cladonia digitata	10	9	15	56	40	33	44	50	19	53	39	36	120
Lecidea nylanderi	7	–	15	76	80	19	66	50	10	29	9	18	115
Parmeliopsis ambigua	17	9	10	85	80	24	44	50	+	9	4	9	102
Chaenotheca ferruginea	33	27	10	68	65	24	32	25	5	–	+	5	88
Phlyctis argena	–	+	25	5	+	5	5	20	10	91	87	36	85
Imshaugia aleurites	10	+	5	80	65	24	15	10	5	+	4	5	67
Pertusaria amara	2	+	–	–	+	–	29	30	–	71	65	+	66
Loxospora elatina	24	14	5	2	–	–	49	40	–	27	30	–	62
Parmelia sulcata	2	–	5	+	20	5	10	35	19	58	43	18	62
Cladonia coniocraea	2	–	10	5	10	–	29	55	24	33	35	5	59
Chaenotheca chrysocephala	57	45	10	7	25	33	–	5	–	2	13	9	58
Hypocenomyce sorophora	–	–	5	73	85	33	2	5	–	–	–	–	57
* *Mycocalicium subtile*	–	–	70	–	–	81	–	–	33	–	+	82	56
Platismatia glauca	2	+	+	2	+	–	27	20	10	53	30	9	52
Evernia prunastri	–	–	5	–	–	+	2	5	24	44	17	45	42
Chaenotheca xyloxena	–	–	30	–	–	24	–	–	67	–	9	64	41
Ramalina farinacea	–	–	5	–	–	10	–	5	10	38	26	41	38
Graphis scripta	–	–	–	–	–	–	7	25	–	47	26	–	35
Lecanora pulicaris	–	–	5	2	5	24	17	10	19	7	4	14	28
Vulpicida pinastri	2	5	25	2	10	10	7	5	5	2	–	14	21
Arthonia leucopellaea	26	23	–	–	–	–	2	5	–	+	4	–	19
Pseudevernia furfuracea	–	–	–	7	5	–	24	10	+	4	+	5	19
Usnea hirta	–	–	–	12	10	10	5	–	14	4	+	14	19
Calicium glaucellum	–	–	20	–	5	33	–	–	10	–	–	18	18
Chaenotheca stemonea	14	5	25	2	–	10	–	–	5	+	+	5	17
Lecanora norvegica	–	–	–	24	15	5	–	–	–	–	–	–	14
* *Chaenothecopsis pusiola*	–	–	5	–	–	19	–	–	38	–	–	–	13
Ochrolechia androgyna	–	–	–	–	–	5	+	–	–	16	22	–	13
Buellia griseovirens	–	–	–	–	–	–	20	–	–	4	–	9	12
Cladonia fimbriata	–	–	–	2	–	–	7	+	10	9	9	–	12
Chaenotheca trichialis	2	9	10	–	5	5	–	5	+	–	+	14	11
Biatora efflorescens	–	–	–	–	–	–	–	+	–	13	13	–	9
Chaenotheca brachypoda	–	–	5	–	–	–	–	–	33	–	–	5	9
Chaenotheca furfuracea	–	–	5	–	–	–	–	10	19	–	9	–	9
Micarea melaena	–	–	–	12	15	–	2	–	–	–	–	–	9
* *Chaenothecopsis pusilla*	2	–	–	2	–	10	–	–	14	–	–	9	9
Buellia disciformis	–	–	–	–	–	–	+	+	–	13	9	–	8
Cladonia cenotea	–	–	–	5	5	–	7	5	–	2	–	–	8
Lecanora expallens	2	–	15	2	–	–	–	–	5	4	–	–	8
Ochrolechia microstictoides	2	+	–	7	+	–	2	+	–	7	–	–	8
Calicium abietinum	+	–	5	–	–	14	–	5	5	–	–	5	7
Calicium parvum	–	–	–	7	20	–	–	–	–	–	–	–	7
Hypocenomyce scalaris	–	–	–	12	–	5	+	–	–	–	–	5	7
Chaenotheca brunneola	–	–	15	–	–	10	–	–	5	–	–	–	6
Chaenotheca chlorella	–	–	15	–	–	–	–	–	–	–	–	14	6
Arthonia vinosa	–	–	–	–	–	–	–	–	–	2	17	–	5
Fuscidea pusilla	–	–	–	–	–	–	2	5	–	7	+	–	5

Continued

Appendix. Continued.

Species	*Picea*			*Pinus*			*Betula*			*Alnus*			No. of records
	L	S1	S2	L	S1	S2	L	S1	S2	L	S1	S2	
n =	42	22	20	41	20	21	41	20	21	45	23	22	338
(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)	(13)	(14)
Lecidea turgidula	+	–	10	2	–	5	–	5	–	–	–	–	5
Melanelia fuliginosa	–	–	–	–	–	–	–	–	–	7	4	5	5
Micarea denigrata	–	–	–	5	–	+	+	5	–	–	–	9	5
Calicium trabinellum	–	–	–	–	–	14	–	–	5	–	–	–	4
* *Chaenothecopsis savonica*	–	–	+	–	–	10	–	–	5	–	–	5	4
Lecanora symmicta	–	–	–	–	–	5	–	–	10	–	–	5	4
Hypocenomyce friesii	5	5	–	–	–	+	–	–	–	–	–	–	3
Lecanora albella	–	–	–	2	+	–	2	5	–	+	+	–	3
Lecanora phaeostigma	–	–	–	5	5	–	–	–	–	–	–	–	3
Mycoblastus fucatus	–	–	–	–	–	–	7	+	–	–	+	–	3
Tuckermannopsis chlorophylla	+	–	5	+	5	–	–	–	5	+	–	–	3
Usnea subfloridana	–	–	–	–	–	–	+	–	–	7	–	–	3
Hypogymnia tubulosa	–	–	–	–	–	–	2	5	–	+	–	+	2
Lecanactis abietina	2	5	–	–	–	–	–	–	–	–	–	–	2
Lecanora chlarotera	–	–	–	–	–	–	–	5	–	–	–	5	2
Lecanora saligna	–	–	5	–	–	–	2	–	+	–	–	–	2
Melanelia exasperatula	–	–	–	–	–	–	–	–	5	2	–	–	2
Melanelia subaurifera	–	–	–	–	–	–	–	–	10	–	–	–	2
Menegazzia terebrata	–	–	–	–	–	–	–	–	–	2	4	–	2
Ochrolechia arborea	2	–	–	–	–	–	2	–	–	–	+	–	2
Parmelia saxatilis	–	–	–	–	–	–	2	–	–	2	–	–	2
Pertusaria coccodes	–	–	–	–	–	–	–	–	–	4	–	–	2
* *Sarea resinae*	2	5	–	–	–	–	–	–	–	–	–	–	2
Biatora helvola	–	–	–	–	–	–	–	–	–	2	–	–	1
Bryoria fuscescens	–	–	–	–	5	–	–	–	+	–	–	–	1
Calicium salicinum	–	–	–	–	–	–	–	–	–	–	–	5	1
Calicium viride	–	–	5	–	–	–	–	–	–	–	–	–	1
Chrysotrix candelaris	–	5	–	–	–	–	–	–	–	–	–	–	1
Cladonia chlorophaea	–	–	–	–	–	–	–	+	5	+	–	–	1
Dimerella pineti	–	–	–	–	–	–	–	–	–	2	–	–	1
Lecanora carpinea	–	–	–	–	–	–	–	–	–	+	4	–	1
Lopadium disciforme	+	+	–	–	–	–	–	–	–	–	4	–	1
Micarea peliocarpa	–	–	–	+	–	–	–	+	–	2	+	–	1
Micarea prasina	–	–	–	+	–	–	–	–	–	2	–	+	1
# *Microcalicium disseminatum*	+	–	–	–	–	–	–	–	–	–	+	5	1
* *Stenocybe pullatula*	–	–	–	–	–	–	–	–	–	2	–	–	1
Usnea filipendula	–	–	–	–	–	–	–	5	–	+	–	–	1
Xanthoria polycarpa	–	–	–	–	–	–	–	–	5	–	–	–	1
* *Chaenothecopsis haematopus*	–	–	–	–	–	–	–	–	+	–	–	5	1
Bryoria capillaris	+	–	–	–	–	–	–	–	–	–	–	–	+
Bryoria nadvornikiana	–	–	–	–	–	–	–	–	–	–	–	+	+
Chaenotheca hispidula	–	–	–	–	–	–	–	–	–	–	–	+	+
Chaenotheca subroscida	+	–	–	–	–	–	–	–	–	–	–	–	+
# *Chaenothecopsis consociata*	+	–	–	–	–	–	–	–	–	–	–	–	+
# *Chaenothecopsis epithallina*	–	–	–	–	–	–	–	–	–	–	+	–	+
Fuscidea praeruptorum	–	–	–	–	–	–	–	+	–	–	–	–	+
Haematomma ochroleucum	–	–	–	–	–	–	–	–	–	+	–	–	+
Lecanora argentata	–	–	–	–	–	–	–	–	–	+	–	–	+
Lecidella euphorea	–	–	–	–	–	–	–	–	–	+	–	–	+
Melanelia olivacea	–	–	–	–	–	–	–	–	–	–	–	+	+
* *Microcalicium ahlneri*	–	–	–	–	–	+	–	–	–	–	–	–	+
Opegrapha rufescens	–	–	–	–	–	–	–	–	–	+	–	–	+
Pyrrhospora quernea	–	–	–	–	–	–	+	–	–	–	–	–	+
Xanthoria parietina	–	–	–	–	–	–	–	+	+	–	–	–	+