

**FOREST LICHENS AND
THEIR SUBSTRATA IN ESTONIA**

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LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following papers which are referred to in the text by the Roman numerals:

- I Lõhmus, P. 2003. Composition and substrata of forest lichens in Estonia: a meta-analysis. *Folia Cryptog. Estonica* **40**: 19–38.
- II Lõhmus, P. and Lõhmus, A. 2001. Snags, and their lichen flora in old Estonian peatland forests. *Ann. Bot. Fennici* **38**: 265–280.
- III Lõhmus, P., Saag, L. and Lõhmus, A. 2003. Is there merit in identifying leprarioid crusts to species in ecological studies? *Lichenologist* **35**: 187–190.
- IV Lõhmus, P., Rosenvald, R. and Lõhmus, A. Solitary retention trees on clear-cuts are life-boats for lichens but not for bryophytes. (submitted manuscript)
- V Lõhmus, A., Lõhmus, P., Remm, J. and Vellak, K. Old-growth structural elements in a strict reserve and commercial forest landscape in Estonia. *For. Ecol. Manage.* (in press)
- VI Lõhmus, A. and Lõhmus, P. Coarse woody debris in mid-aged stands: abandoned agricultural versus long-term forest land. *Can. J. For. Res.* (in press)

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The author participated in preparing the listed co-authored publications as follows:

paper II – collecting data (100%), analysing data and preparing the text (50%);
paper III – collecting data (50%), analysing data and preparing the text (70%);
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paper V – collecting data (70%), analysing data and preparing the text (30%);
paper VI – collecting data (100%).

1. INTRODUCTION

Forests are the major ecosystems of Eurasia and North America. They are biologically very diverse, due to stand-replacing disturbances, gap dynamics, post-fire succession, self-thinning and other natural processes that create specific structures (Peterken 1996, Esseen et al. 1997, Hunter 1999, Lindenmayer and Franklin 2002). For example, old coniferous and deciduous trees, hollow and fire-scarred trees, dead standing (snags) and downed trees (logs) in various sizes and stages of decomposition provide habitat for a wide array of organisms (e.g. Samuelsson et al. 1994, Esseen et al. 1997, McComb and Lindenmayer 1999, Siitonen 2001). The exact species richness and composition of boreal and temperate forest biota are unclear, particularly with regard to some diverse taxa (e.g. insects, fungi). In Estonia, which forms a part of the hemiboreal vegetation zone, 16–20 thousand multicellular species are likely to inhabit forests (Lõhmus and Soon 2004).

Lichens – symbiotic organisms consisting of a fungal and a photosynthetic partner – contribute significantly to the diversity and functioning of boreal and northern temperate forests. They participate notably in nitrogen fixation (cyanolichens) and cycling of other nutrients, and provide food or nest material for wildlife (Esseen et al. 1997, Will-Wolf et al. 2004 and references therein). Typical substrata for forest-dwelling lichens are bark and wood of trees, soil and dead organic matter, but their specific requirements for substrata or habitat are often narrow due to general (inability to regulate the uptake and loss of water; slow growth) and species characteristics (Will-Wolf et al. 2002, 2004).

In the last decades, conservationists have become increasingly concerned about the loss of lichen diversity and biomass during the commercial management of forests. Intensive forestry promotes compositional homogeneity (Kuuluvainen et al. 1996), disrupts the supply of mature trees and dead wood (e.g. Green and Peterken 1997, Linder and Östlund 1998, Bengtsson et al. 2001, Økland et al. 2003), and increases the isolation of forest tracts and the amount of edges (Saunders et al. 1991, Murcia 1995). Indeed, the impoverishment of lichen communities has been reported in managed second growth versus old-growth forests (e.g. Lesica et al. 1991, Esseen et al. 1996, Kuusinen and Siitonen 1998, Cameron 2002), and in forest edges compared with forest interior (Kivistö and Kuusinen 2000, Rheault et al. 2003). A major threat is the loss of lichen substrata below the threshold that is required for viable lichen populations. Hence, it is important to know the relationships between the abundance and quality of the substrata and the species richness and composition of lichens on them.

Old forests, which are under the most severe pressure of timber harvesting, have a continuous, abundant and diverse supply of microhabitats for specialized lichen species. Large old stems of many tree species have distinctive bark and canopy microsites for epiphytes (e.g. Barkman 1958, Kuusinen 1996b, Neitlich

and McCune 1997, McCune et al. 2000), while large decorticate snags, logs, dead branches and stumps (i.e. coarse woody debris – CWD) are crucial for epixylic species (e.g. Söderström 1988, Samuelsson et al. 1994, Holien 1996a, Esseen et al. 1997, Forsslund and Koffman 1998, Caruso 2004). The species, which require such specific structures of old-growth, tend to have limited dispersal abilities (e.g. Sillett et al. 2000, Hilmo and Sâstad 2002, Keon and Muir 2002) and are highly sensitive to desiccation and irradiance (e.g. Gauslaa and Solhaug 1996, Palmqvist and Sundberg 2000).

The influence of tree (phorophyte) species on the composition and diversity of epiphytic lichens has been frequently stressed (e.g. Barkman 1958, Sömermaa 1972, Lesica et al. 1991, Kuusinen 1996b, Boudreault et al. 2002, Juriado et al. 2003). For example, the aspen (*Populus tremula*) has been considered a key species for its rich and distinct lichen flora in European boreal forests (Kuusinen 1996a, Hedenås 2002). Also, several studies have confirmed the positive effect of phorophyte quality (tree age, size, bark texture and moisture holding capacity) on lichen diversity (e.g. Barkman 1958, Brodo 1968, Bates 1992, Holien 1996b, Dettki and Esseen 1998, Pipp et al. 2001, Cameron 2002, Johansson and Ehrlén 2003). In contrast, phorophyte abundance has been rarely related to epiphyte communities, and mostly at the presence-absence scale, e.g. Juriado et al. (2003) showed that the forests with aspen had, on average, five lichen species more than those without.

The importance of CWD as a habitat for lichens has been recognized rather recently. These studies have mainly explored only a few coniferous trees and macrolichens (a notable exception is the study by Forsslund and Koffman 1998, where also microlichens were considered), and have made no distinction between bark and wood microsites, and epiphytic and epixylic lichens. The main finding has been a higher species richness or more abundant red-listed species on well-decayed CWD (Crites and Dale 1998, Forsslund and Koffman 1998, Kruys et al. 1999, Berg et al. 2002, Humphrey et al. 2002), which is scarce in managed stands (e.g. Forsslund and Koffman 1998, Kruys et al. 1999). Size-effects of CWD are less clear – they may be absent in snags (Humphrey et al. 2002), but in case of equal surface, species richness on coarse and fine logs of *Picea abies* did not differ (Kruys and Jonsson 1999). The composition of lichen species on logs is also influenced by the presence of bark and tree species (McAlister 1997).

There are different possibilities to preserve the increasingly threatened biota of the substrata that are adversely affected by forestry (Berg et al. 1994). One is the protection of old-growth forests that support a continuous supply of substrata and favourable microclimatic conditions for threatened species (Esseen et al. 1997, Lindenmayer and Franklin 2002). However, the area of strict reserves is limited economically and socially. In Estonia, reserves cover 45–60% of the theoretical minimum need; the largest gaps are for mesic forests on fertile soils and swamp forests (Lõhmus et al. 2004). Therefore, more attention should be paid also to the ecologically sustainable management of

forests, which are not designated primarily for conservation of natural ecosystems, ecological processes, and biodiversity. According to this approach, forest structure, species composition, and the rate of ecological processes and functions with the bounds of normal disturbance regimes are perpetuated while continuing to provide wood and non-wood values (Lindenmayer and Franklin 2002). For example, retention of live trees may be a useful tool for the conservation of epiphytic lichens in timber harvesting areas (Hazell and Gustafsson 1999, Sillett and Goslin 1999), though the effect may differ among functional groups (Peck and McCune 1997). The Estonian Forest Act requires the retention of at least 5 m³ of live and dead trees per hectare of clear-cut, and this target has generally been met in state forests (Rosenvald and Lõhmus 2005). However, to assess whether such thresholds are sufficient for sustainable forestry, the abundance of old-growth features in commercial forests and the ability of reserves to sustain threatened species should be known.

This thesis consists of a review (I) and five case studies (II–VI) that focus on the gaps of knowledge related to the diversity and species composition of forest lichens, especially on snags, the impact of green-tree retention for epiphyte communities, and the abundance and characteristics of the substrata for old-growth lichens (remnant trees, large broad-leaved trees, snags, logs and windthrows) in hemiboreal forests. The main questions were: (1) what lichen species inhabit the Estonian forests, and what patterns characterise their frequency and substratum use (I); (2) do tree species and snag type influence the diversity, composition and cover of lichens on snags; how much do these communities differ from those on living trees, and contribute to the forest lichen flora (II); (3) are different species of *Lepraria* segregated by their substrata (snags, coniferous and deciduous trees), i.e. should such highly similar crusts be identified to species in ecological studies (III), (4) how viable are lichens and bryophytes on retention-trees in the short-term, does the viability depend on tree species and position, and which cryptogam species survive well (IV), (5) how much does the biological value of Estonian protected and commercial forests differ from natural hemiboreal forests; how are forest type and age, fragmentation and history related to the abundance of the structural elements of old-growth, and to what extent are these structures aggregated and co-occur on the landscapes (V–VI).

2. MATERIAL AND METHODS

2.1. The material and study areas

The studies were carried out in the forests of Estonia, northern Europe. Estonia is situated in the hemiboreal zone, which has an intermediate position between boreal coniferous and temperate deciduous forests (Ahti et al. 1968). *Forest* was defined as a vegetation type with trees as edificators (Masing 1992). During landscape-scale studies (IV–VI), early, temporary succession phases (clear-cuts, open burnt areas) were also analysed as parts of forest land.

In paper I, composition and substratum use of the Estonian forest lichens were reviewed according to 24 published and unpublished reports (13 of them quantitative). *Forest lichens* included lichenized fungi (true lichens), fungi that are systematically related to lichens, and lichenicolous fungi, which had been found in forests. To estimate species richness and composition of forest lichens, lists of confirmed and probable forest species were compiled. Confirmed forest lichens included the species that had been found in the forest studies, 1969–2000 (Table 1 in paper I), and all other epiphytic, epixylic, epigeic and epilithic species (Randlane and Saag 1999, Randlane et al. 2003) with at least one verified forest record in Estonia. The species found so far only in rural parks and wooded meadows, and the remaining species likely to inhabit bark, wood or ground in forests, made up the list of probable forest lichens. The species nomenclature followed Randlane et al. (2003).

The original studies V–VI were carried out in a 900-km² area in east-central Estonia (between 58°17–25'N and 26°9–50'E; altitude 30–40 m a.s.l., Fig. 1), that represents quite well the typical landscape characteristics and forest management regimes of Estonia, and has been used also for other strategical assessments (Lõhmus 2002, 2003, 2004). Forest land covered 49%, agricultural lands 36%, mires 8%, flood plains 2%, rivers and lakes 2%, and settlements 3% of the area. Fifty percent of forests grew on wet soils. Due to the long clear-cutting history, most forests had even-aged tree layer, consisting mostly of birch (*Betula sp.*), Scots pine (*Pinus sylvestris*) or Norway spruce (*Picea abies*). The area included many timber-harvesting units and 15% of it was covered by the Alam-Pedja Nature Reserve – one of the largest well-forested reserves in Estonia. The data of studies II–III were collected from the old peatland forests (>60 years for deciduous and >80 years for coniferous stands) of that reserve.

The epiphytes of retention trees (IV) were investigated on the clear-cuts of four state forest districts in central, eastern and southern Estonia (between 58–59°N and 25–27°E; altitude below 75 m a.s.l., Fig. 1). All studied districts comprised large extensively managed forest areas. On the clear-cuts, 31% of live trees (including seed trees) were birch, 20% Scots pine, 18% ash (*Fraxinus excelsior*), 14% aspen, and 13% other species (Rosenvald and Lõhmus 2005). Most trees had been retained solitarily.

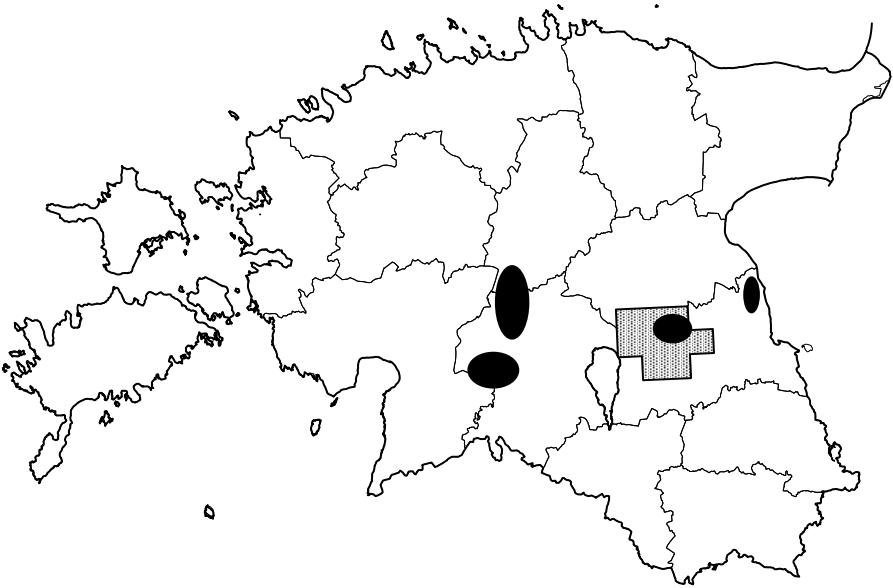


Figure 1. Locations of study areas. The 900-km² area of studies **II–III** and **V–VI** is shaded; black ovals indicate the four state forest districts where epiphytes of retention trees were studied (study **IV**).

2.2. Field data

Field data were collected between 1999 and 2004 using simple random or stratified random sampling of forest stands (**II–III**), clear-cuts (**IV**) and landscapes (**V–VI**). Epiphytic and epixylic lichens were investigated on Norway spruce, Scots pine, birch (**II–IV**), black alder (*Alnus glutinosa*) (**II–III**), aspen and ash (**IV**); additionally, two types of snags (with and without bark; **II**) and three locations on the landscape (the centre and the edge of the clear-cut, and the adjacent forest; **IV**) were distinguished.

Twenty forest stands (**II–III**) and 29–33 clear-cuts (**IV**) were selected per tree species. In the studies **II–III**, the snag of one type, which was most close to the centre of the stand, and the nearest living tree of the same species and the same age class made up a description unit (two replications per stand). In paper **IV**, one tree of each species was studied in the tree locations at each clear-cut.

Species composition, abundance (**II–IV**) and species-specific vitality (**IV**) of lichens were visually assessed for whole trunks between heights of 0.2–1.8 (2) m. More accurate numerical estimates (incl. coverage of lichen flora and vitality estimates for lichens and bryophytes in general) were obtained from 20x50 cm (**II–III**; slightly modified method of Kuusinen 1996b) or 20x20 cm plots (**IV**), which were placed at heights of 1.3 (**II–IV**) and 0.2 m (**IV**) on the

northern (II–IV) and southern sides (IV) of the tree trunks. Vitality estimates were based upon clearly visible changes in the colour and structure of thalli or shoots and were quantified as the share of the desiccated part of the total cover. Species-specific vitalities were coded according to Hedenås and Ericson (2003; slightly modified): 0, no change in colour and thus no desiccation damage; 1, few visible colour changes; 2, large patches with colour changes; 3, severe bleaching or thalli/shoots either dead or lost. All lichen and bryophyte specimens that could not be identified in the field (including all probable specimens of *Lepraria*) were collected and identified further in laboratory using microscopic characters and thin layer chromatography. Voucher specimens are stored at the lichenological herbaria of the University of Tartu (TU).

Acidity of the surface of different tree species was determined from bark or wood samples, which were incubated in distilled water (1.5 ml g^{-1}) for 24 hours; the pH of the extract was measured with a standard pH-meter (II).

Seven structural elements were mapped on thirty long, 100 m (for cavity trees) or 10 m (for other elements) wide, straight transects all over the forest land (V–VI). The elements were (1) cavity trees, (2) remnant trees (trees from the previous forest generation), (3) old broad-leaved trees (maple *Acer platanoides*, ash, oak *Quercus robur*, lime *Tilia cordata*, Wych elm *Ulmus glabra* and European white elm *U. laevis*) with diameter at breast height (dbh) $\geq 32 \text{ cm}$, incl. aspens with dbh $\geq 38 \text{ cm}$, (4–5) snags of two types (with and without bark) with dbh $\geq 10 \text{ cm}$ and over 1.5 m tall, (6) logs (diameter of the thickest end $\geq 20 \text{ cm}$, at least 50 cm long), and (7) windthrows ($\geq 30 \text{ cm}$ high). Three successional stages, four vegetation types, and edge and interior of the stand were distinguished according to the field and GIS-data (V). For each structural element, tree species and dbh (for standing trees) or diameter (for windthrows) were recorded. CWD was further characterized by its decay stage, height (snags) or, for logs, length and diameters of both ends (Dmax and Dmin) within the transect. Historical land cover of the transects was determined from digital GIS-linked images of topographic maps (prepared in 1937–1939; VI). In old peatland forests, snags were counted in circular plots with a radius of 15 m (one plot in each stand; II).

2.3. Data processing

In meta-analysis, the frequencies of forest lichens were expressed as the number of reviewed studies in which the species were identified, as well as the average and maximum frequencies among the species lists in the studies (only studies with more than ten species lists were included, totaling 12 studies for macro- and 8 for microlichens)(I).

To evaluate the impact of clear-cutting for epiphytes, exponential rate of vitality change of thalli (v) within two years on each tree was calculated as

$v = \ln (A_2(1-p_d)/A_1)$, where A_1 and A_2 are total coverages of lichens or bryophytes one and two years after the harvesting, respectively, and p_d is the damaged proportion of the total cover in the second year (IV). The volumes of individual snags and logs were computed as $V = h\pi(D/2)^2$, where h = height or length of the trunk within the transect, and D = average diameter of the trunk = $[(D_{\max} + D_{\min})/2]$ (V–VI). The dimensions and decay stages of CWD were summarized according to the concept of CWD profile (Stokland 2001).

To describe the extent of spatial aggregation of the structural elements, the transects were divided into 593 100-m sections (i.e. 1 ha for cavity trees and 0.1 ha for the other elements) and the density of each element in each section was calculated. The inclusion of each element (% of its total numbers) were assessed by the best 10% of sections (1) for each element individually, (2) for a single set of all elements (based on their total densities).

Conventional parametric statistics (t-tests for independent and paired samples V; ANOVA, IV, V; linear regression II, IV), or – if the assumptions of parametric tests were not met – non-parametric statistics (U-test, Wilcoxon's test, Kruskal-Wallis ANOVA, χ^2 -test, Spearman correlation; II–V) were used for hypothesis testing. Before using t-test or ANOVA, distributions of all variables were checked for normality (Kolmogorov-Smirnov test) and homogeneity of variances (Levene's test). The cover estimates (proportions) of epiphytes were arcsine-square-root transformed before analyses (IV). Similarities of substrata (I–II) or forest types (V) were identified with cluster analyses, based on Euclidean distances and Ward's method of linkage. Most analyses were performed with the Statistica 6.0 software (StatSoft, Inc. 1984–2001).

3. RESULTS

3.1. The lichen flora of Estonian forests

3.1.1. Composition, species richness and substrata of forest lichens

A total of 481 species of forest lichens were confirmed to inhabit Estonia. Additional 118 species inhabit substrata that occur in forests, but have not been confirmed there so far. Thus, the probable number of forest lichens reached 599 species (**I**).

Frequency estimates were computed for 70% of confirmed forest lichen species. The eight most frequent species were present in all but 1–2 studies (e.g. *Hypogymnia physodes*, *Parmelia sulcata*, *Chaenotheca ferruginea*), whereas 154 species (47%; mainly microlichens) occurred in only 1–2 studies. Among the studies with at least 10 species lists presented, the mean relative frequency exceeded 10% for 68 species, while it was below 5% for more than half (215) of the species considered. Ninety of these latter species have been classified as rather to very rare, and 83 species frequent to very frequent in Estonia (sensu Randlane and Saag 1999). However, some species with low average frequencies were locally quite common. For example, the macrolichen *Cetraria islandica* occurred on average in 8.4% of species lists, but it was present in 75% of the lists of one study.

Calicioid, cetrarioid, cladonioid, parmelioid, pendulous, sorediate crustose and lichenicolous and parasitic species totalled 46% of the forest lichen species, while some species rich genera (e.g. *Verrucaria*) were represented with only one species or were absent (Table 4 in **I**).

According to the species composition, there were five broad substratum types for the Estonian forest lichens – broad-leaved trees, common deciduous and coniferous trees, branches and undergrowth, windthrows, and other ground-level substrata (Fig. 2). The highest numbers of all and of unique species were recorded on living trees (**I**), particularly on aspen (**IV**). Ground and CWD (e.g. snags with exposed wood, **II**) were also found to host relatively high number of species, despite the low number of studies about these substrata.

Although the general species composition and substrata of forest lichens were assessed as relatively well known, groups with unclear taxonomy or difficult field identification are still insufficiently studied. For example, the occurrence of *Lepraria incana* and other highly similar *Lepraria* species differed significantly between substrata (χ^2 -test: $P < 0.01$) (**III**).

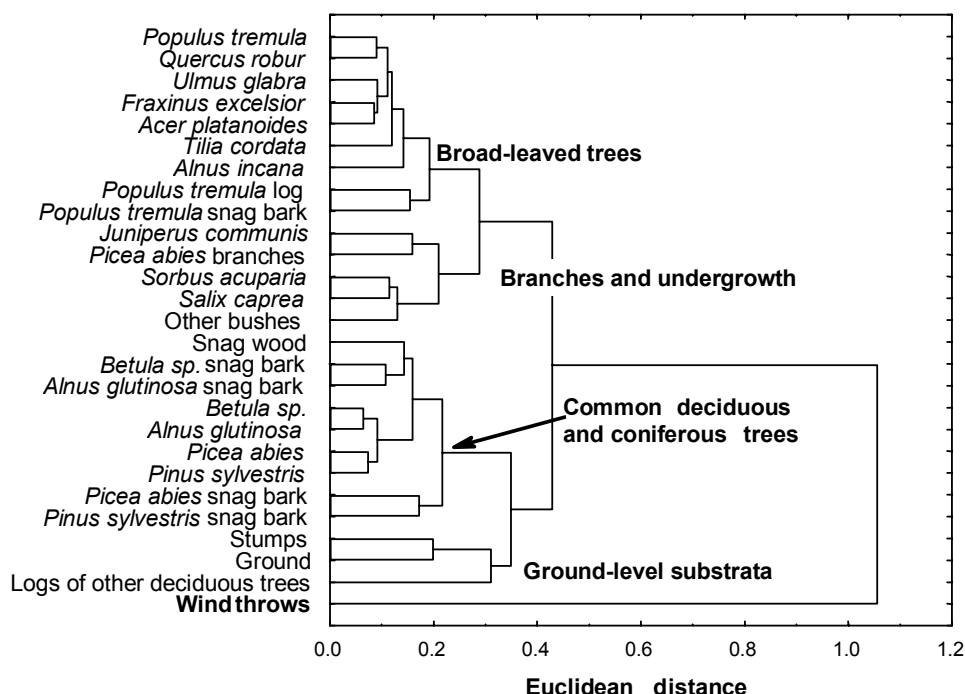


Figure 2. Similarity of lichen composition of different substrata in Estonian forests according to cluster analysis (Ward's method; I).

3.1.2. Lichen flora of snags

The lichen flora of snags without bark (S2) was distinct from that of snags with bark (S1) and live trees (Fig. 3 in II). Tree species influenced the number, total coverage and diversity of lichens on live trees and S1, but not on S2; a similar pattern emerged in substratum acidity (Fig. 3). The highest total numbers of lichen species per 100 trunks were estimated for S2 of birch, black alder and Norway spruce (Table 4 in II), which were relatively species poor substrata at the single trunk scale. Indeed, the average number of lichen species per trunk and the estimated total number of species of the twelve studied substrata were not significantly correlated ($r_s = 0.32$, $P = 0.31$). S2 had 15 unique species (ten of them calicioid species), while S1 had only three. In general, the species that were unique to snags made up 25% of the lichen species on the studied trunks (II). The estimates of relative species richness of different substrata were not influenced if leprarioid crusts were re-analysed and identified as six different species of *Lepraria* (III).

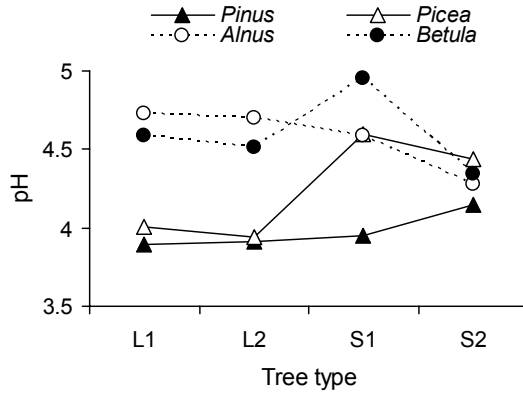


Figure 3. Acidity (pH) of bark and wood of different tree species and tree types (S1 = snag with bark, S2 = decorticate snag; L1 and L2 = live trees near S1 and S2, respectively). Live *Pinus* and *Picea* differed significantly from live *Betula* and *Alnus*, and S1 of *Pinus* from S1 of the other species (*U*-tests: $P < 0.001$).

3.1.3. Comparative vitality and diversity of lichens and bryophytes on retention trees

We explored general and species-specific vitality of lichens and bryophytes on live retention trees and adjacent forest tree trunks. The damages on retention trees were severe and independent of tree species for bryophytes throughout clear-cuts (Fig. 3 in IV), but weak for lichens, particularly at the edge of clear-cut, and on aspen and ash (Fig. 2 in IV). On average, 2% of lichen thalli, but 60% of bryophyte shoots became damaged in two years.

The retention trees and adjacent forest trees hosted similar total numbers of cryptogam species and mean numbers of lichen species per trunk. However, the average decrease of 1.1 bryophyte species per trunk on retention trees, compared with the forest trunks, was highly significant (paired *t*-test: $P < 0.001$).

Relationships between the average damage scores of the same species on retention trees and forests trees were different for lichens and bryophytes (Fig. 4). For lichens, the damages were mostly explained by the general sensitivity of certain species. Crustose lichens (e.g. *Loxospora elatina*, *Megalania grossa*, *Ropalospora viridis*) and some macrolichens with small foliose or podetial thalli (e.g. *Cladonia coniocræa*, *Vulpicida pinastri*) were in remarkably good condition. For bryophytes, the damages in clear-cuts greatly exceeded those in forests, particularly for the species that were relatively vital in forests (e.g. *Homalia trichomanoides*).

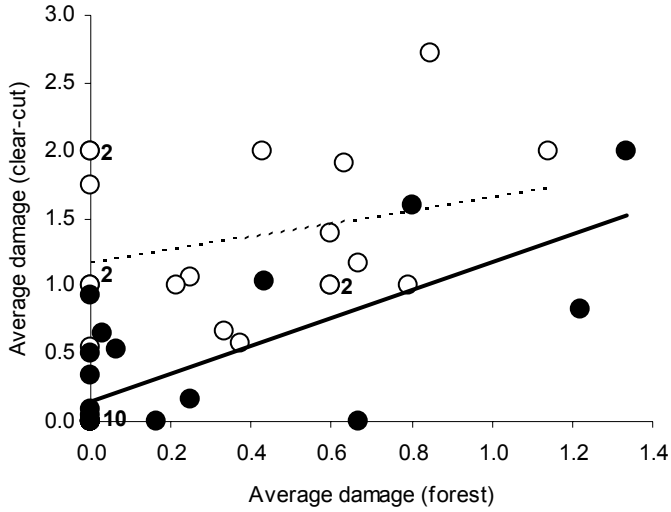


Figure 4. Linear regressions between the average damage scores on forest and retention trees of 19 bryophyte (circle dots, discontinuous line) and 24 lichen species (filled dots, solid line). For lichens: $P_{\text{intercept}} = 0.11$, $P_{\text{slope}} < 0.001$, $R^2 = 0.53$. For bryophytes: $P_{\text{intercept}} < 0.001$, $P_{\text{slope}} = 0.27$, $R^2 = 0.07$. Numeric labels indicate the number of species with similar values.

3.2. Density and distribution of the substrata of lichens

3.2.1. Abundance of the substrata at the landscape and stand scales

According to the data of 30 random transects, the abundance of structural elements was similar in the conserved and commercial forest land. Snags with exposed wood were more numerous in the reserve than in the surroundings, whilst the latter had more logs, windthrows, remnant trees and broad-leaved trees (Table 1). The mean volume of CWD did not differ between the studied reserve and the surrounding commercial landscape. However, though mature forest was as abundant in the managed forests (6.8%) as in the reserve (5.8%), there were important vegetation differences between two landscapes – nearly half of the commercial landscape, but less than one-fifth of the reserve, was covered with productive dry or mesic forests (Table 1 in V).

Only remnant trees were found to occur independently of any habitat characteristics, while the abundance of other structural elements depended on forest type and successional stage (Table 2 in V). Large broad-leaved trees were nearly a hundred times less abundant in regenerating areas than in mature

forests, and were concentrated to mesic mixed and deciduous forests. Windthrows tended to be less frequent on regenerating areas and in pine forests.

The average volumes of CWD (also of logs and snags separately) were 2–3 times higher in mature forests than in the other successional stages (Fig. 3A–C in V), the occurrence of snags and logs also depended on vegetation type (V). In old peatland forests, the dominating tree species had no significant effect on the total density of snags, though snags with exposed wood were significantly more abundant in *Pinus* stands, compared with *Picea*, *Betula* or *Alnus* stands (*U*-test: $P < 0.01$; II).

If the influences of vegetation types and successional stages were considered, comparison between habitats showed a slight and non-significant (on average 33%) recent loss of CWD in the commercial area (Table 3 in V). The scarcity of CWD was mostly attributed to long-term effects over the whole forest land (including the reserve): (1) in mixed and deciduous forests that were not forested in the 1930s, log volumes were about two times lower than in cutover sites; (2) at least fivefold losses were estimated to have occurred due to the long history of timber harvesting (VI).

Table 1. Densities of the structural elements of old-growth in commercial forests ($n = 20$ line transects) and the Alam-Pedja Nature Reserve ($n = 10$; V). For snags, densities in old peatland stands ($n = 85$) are also given (II).

Variable	Mean \pm 95% conf. interval	
	Commercial forest	Reserve
Structural elements		
Remnant trees ha ⁻¹	1 \pm 1	0 \pm 0
Broad-leaved trees (incl. aspen) ha ⁻¹ *	4 \pm 2	1 \pm 1
Snags with bark ha ⁻¹ *	22 \pm 7	24 \pm 10
<i>in old peatland forests</i>		37 \pm 6
Barkless snags ha ⁻¹ *	3 \pm 1	16 \pm 11
<i>in old peatland forests</i>		16 \pm 5
Logs ha ⁻¹ *	18 \pm 5	8 \pm 4
Windthrows ha ⁻¹	8 \pm 2	5 \pm 2
Cavity trees ha ⁻¹	1 \pm 0	1 \pm 0
CWD, m³ ha⁻¹	9 \pm 2	6 \pm 2
Snags with bark, m ³ ha ⁻¹ *	3 \pm 1	2 \pm 1
Barkless snags, m ³ ha ⁻¹ *	1 \pm 0	2 \pm 1
Logs, m ³ ha ⁻¹ *	6 \pm 2	2 \pm 1

*minimum dbh 38 cm for aspens, 32 cm for other broad-leaved trees, 10 cm for snags and 20 cm for logs.

3.2.2. CWD profiles

CWD comprised mostly trunks of Norway spruce, birch, grey alder or Scots pine (**II**, **V**). However, the general abundance did not always predict the occurrence of specific types; for example, among the snags of old peatland forests, birches with bark were the most frequent and birches with exposed wood were the rarest type (**II**). The average number of CWD substrata (type*decay stage) per transect did not differ between the protected and commercial forests (t -test: $P = 0.19$), also if tree species were taken into account (max 90 combinations, t -test: $P = 0.77$). However, large and well-decayed logs tended to be more abundant in commercial (**V**) and long-term forests (**VI**).

3.2.3. Spatial aggregation and co-occurrence of the substrata

According to the analyses of 100-m sections of the transects, most structural elements were highly aggregated within the forest landscapes. On average, 67% of the numbers of each element could be included in the best 10% of the sections (**V**; see also **II** for the clumping of snags). Yet, the generally best 10% of the sections included, on average, less than 30% of different elements (Table 4 in **V**). This was due to their weak ($r_s < 0.4$), though reliable ($P < 0.005$), spatial co-incidence. For example, there were more logs and snags with bark in sites having abundant windthrows, while the only clear spatial correlation for decorticate snags was their co-occurrence with the snags with bark.

4. DISCUSSION

I made one of the first quantitative assessments of the whole forest lichen flora of a large region (I) and of the importance of specific substrata for it (I–III). It appeared that a typical Estonian forest landscape (incl. a seemingly well-preserved reserve) had suffered a severe loss and degradation of such substrata, due to a long history of timber harvesting and only recent reforestation (V–VI). In their responses to clear-cutting, I documented a large variation between and among epiphytic lichens and bryophytes, between different tree species and tree positions on clear-cuts (IV). I also found that morphologically similar species of microlichens may differ ecologically and should be determined in biodiversity studies (III).

4.1. Estonian forest lichens and their substrata

Total number of lichen species in Estonia has increased from 930 to 1007 (Randlane et al. 2003, 2005) during the two years after the studies I–III, and several new species to Estonia have been found also from forests. Despite that, I suggest that the general patterns of lichen species composition, richness, and substrata, as presented in this thesis, are still valid.

Generally, the fraction of forest lichens among native lichen flora has been seldom quantified. In Estonia, forest lichens comprise between 52% (confirmed forest lichens) and 64% (probable forest lichens) (I) of the 930 known species of lichenized and lichenicolous fungi (Randlane et al. 2003). That is higher than the share in Sweden (34%; Hallingbäck 1995). The difference could be mainly due to the scarcity in Estonia of rocky outcrops, which are common and the most diverse habitats for lichens in Sweden (Hallingbäck 1995).

The most species-rich lichen taxa in the Estonian forests are generally well-known inhabitants of (hemi)boreal forests (Ahti 1977). The relatively large number of lichenicolous and parasitic fungi is obviously related to an increasing knowledge about these inconspicuous species (Suija 2005a, b). Of the 215 species that appeared on average in <5% of species lists, about half occur naturally at low frequencies (e.g. species of *Collema* and *Nephroma*; see also Vitikainen et al. 1997, Thor 1998, for Finland and Sweden). Some of them have narrow ecological niches and can be abundant where their habitat is found (e.g. ground-dwelling macrolichens in heath forests). Other “rare” forest species are likely to be common in Estonia, but their substrata have been seldom studied quantitatively (e.g. ground, stones, decaying wood, bark of deciduous trees)(I). By now, detailed studies have been initiated already about the lichen flora of broad-leaved trees in forests (by Inga Jüriado and Maarja Nõmm) and wooded-meadows (Ede Leppik), as well as about the lichens on forest floor, logs and windthrows (by the author).

The substrata of forest lichens have been unevenly studied everywhere – most attention has been paid to epiphytes (e.g. Barkman 1958, Rose 1976, Coppins 1984, Kuusinen 1996a,b, McCune et al. 2000), and less to the lichens on dead wood (e.g. Chlebicki et al. 1996, Holien 1996a, Forsslund and Koffman 1998, Humphrey et al. 2002). However, similarly to the results of the current work (II–IV), several of these studies have shown that broad-leaved trees (including aspen) and snags host the most diverse and unique lichen communities. Probably, bark characteristics of the broad-leaved trees (moderately acid to neutral reaction, rough texture in old trees) create favourable microsites for epiphytes (e.g. Kuusinen 1995, Johansson and Ehrlén 2003, Juriado et al. 2003). Surface acidity obviously influenced the diversity and composition of lichens also on snags with bark, but there were no significant differences between the structure of lichen communities on decorticate snags, accompanied with a lack of differences in wood acidity (II).

For epixylic lichens, snags are the superior habitat that receive more light and are drier than logs, which are favoured by bryophytes (Muhle and LeBlanc 1975, Chlebicki et al. 1996, Pharo and Beattie 1997). Calicioid lichens and fungi form a distinct group of snag specialists (Titov 1986, Holien 1996a, Johansson 1997, also paper II), adapted to high irradiance – their ascocarps are covered with crystallized lichen substances, shielding the reproductive structures from destructive UV-radiation (Rikkinen 1995). Snags could be the only habitat available for non-lichenized saprobic genera *Chaenothecopsis*, *Microcalicium* and *Mycocalicium*, which have narrower substratum requirements than the lichenized calicioid species (Titov 1986) and low competitive abilities on logs (Middelborg and Mattsson 1987, Holien 1996a). Overall, the species unique to snags (both with and without bark) made up 25% of the total number of tree-dwelling lichens in peatland forests (II).

In contrast to such well-adapted inhabitants of snags, the novel dry, sunny and windy conditions on retained live trees in clear-cuts (Chen et al. 1999) should depress the epiphytes, which grow mainly at medium levels of light and moisture under forest cover. However, while bryophytes were severely damaged on retained trees, epiphytic lichens showed remarkable resistance to desiccation (IV). This is probably due to the capability of lichens (1) to attain positive net photosynthesis using only air humidity, while bryophytes need more liquid water (Green and Lange 1995), and (2) to increase thallus thickness and/or concentration of sun-screen pigments (Rikkinen 1995, Gauslaa and Solhaug 2001, Hilmo 2002). However, the resistance differed among species. Vital species comprised several sorediate microlichens that grow higher on trunk, including some microlichens of conservation concern (e.g. *Acrocordia cavata*, *Mycoblastus sanguinarius*). The inhabitants of humid tree bases, such as bryophytes (IV) and species from lichen genera *Mycobilimbia* (Hedenås and Ericson 2003) showed severe damages.

Dynamics of lichen populations on snags (or logs) has clear parallels with metapopulation models: subpopulations frequently become extinct (because of

decomposition) and the species survival depends on the colonization of new snags. There are no field data to model the persistence of snag lichens in relation to snag availability, but our results (II) suggested the absence of significant isolation effects in the reserve, where the rarest substrata (decorticated snags of *Betula*, *Alnus* and *Picea*; Fig. 1 in II) hosted the highest number of lichen species. Species persistence could also be supported by the clumped distribution of snags (II, V), which should reduce extinction probability (Adler and Nuernberger 1994).

Forest history is well revealed in the profiles and amount of CWD: an abundant supply and a wide and even distribution of size classes and decay stages of dead wood are characteristic to natural forests, whilst the distributions of size classes and decay stages are narrow and uneven in managed forests (e.g. Lee et al. 1997, Kryus et al. 1999, McComb and Lindenmayer 1999, Jonsson 2000, Siitonen 2001, Stokland 2001). In east-central Estonia, the general supply of CWD both in the reserve and its surrounding was probably less than 10% of that of natural forests (e.g. Kasesalu 2001, Siitonen et al. 2000, Sippola et al. 2001). Such an impoverishment was probably due to the intensive human use of the whole area in the past, as indicated by CWD profiles (Fig. 5–6 in V). In addition, the Estonian forest cover has increased from c. 20% to over 50%, during the past 60 years, mostly on account of previous agricultural lands (Lõhmus et al. 2004), and the resulting first-generation forests are CWD-poor (VI, see also Ranius et al. 2003).

In Estonia, the major aim of strict forest reserves is to maintain viable populations of the species that do not survive in timber production areas. Our study showed similarly low abundance and quality of structural elements in the protected and commercial forests (V). The lack of large deciduous trees and logs was partly explained with the scarcity of fresh mixed and deciduous forests in the reserve (Table 1 in V) – such stands on productive soils contain more deciduous trees, the trees grow faster and CWD volumes are higher there (Carey 1983, Harmon et al. 1986, Sippola et al. 1998, Siitonen 2001, Uotila et al. 2001, Nilsson et al. 2002). However, the commercial landscape had abundant logs also on old clear-cuts, where large felled trunks had been left in the Soviet period (1945–1991).

4.2. Implications

Several results of this thesis are relevant for the biodiversity research and protection as well as forest management.

Future studies on the diversity of forest lichens should pay more attention to the insufficiently studied old broad-leaved trees, windthrows, burnt bark and wood, well-decayed large logs and boulders (I), to assess which species are threatened by the scarcity of these substrata in forest landscapes (V, VI). In

addition, leprarioid crusts should be determined to species in biodiversity studies, as *Lepraria* species showed preferences to different substrata (III). For conservation, it would be important to compile a list of obligate forest lichens, and to assess the potential of aspen as a surrogate of other broad-leaved trees in managed forests. This possibility was reflected by the similarity of the lichen communities of these trees (Jüriado et al. 2003; I) and the abundant supply of aspen in the Estonian forests (Kohava 2001). In addition, comparative studies of natural broad-leaved forests versus rural parks and wooded meadows should be carried out to assess the value of the latter habitats for lichens.

For forestry, the results implied that (1) in addition to snag density and size, which are usually considered in snag retention techniques (e.g. McComb and Lindenmayer 1999), snag type is also important, and the rare but species-rich decorticated snags of deciduous trees require special attention (II); (2) careful retention of live trees on clear-cuts can be a successful conservation tool for lichens, particularly for many microlichens on aspen and ash (IV); (3) green-tree retention and other close-to-nature management approaches in productive commercial forests and (4) restoration of old-growth features in reserves are essential to mitigate the biodiversity loss due to the present low quality of the Estonian reserves (V).

For reserve establishment, additional productive forests should be selected as sites where some old-growth structures can be more abundant (large deciduous trees) or develop more quickly (CWD)(V). Thereby, mid-aged first-generation forests should not be automatically excluded (VI), since the CWD-rich old-growth is almost absent already (Lõhmus 2002).

CONCLUSIONS

- (1) A meta-analysis of published and unpublished reports and herbarial data confirmed 481 species of lichenized, lichenicolous and systematically allied fungi in the Estonian forests, but their probable number may reach 599 species. The frequency distribution was characterised by a high share (47%) of rare species. Calicioid, cetrarioid, cladonioid, parmelioid, pendulous, sorediate crustose and lichenicolous and parasitic species totalled nearly half (46%) of the species. According to species composition, there were five broad substratum types – broad-leaved trees, common deciduous and coniferous trees, branches and undergrowth, windthrows, and other ground-level substrata.
- (2) Total cover and species diversity of lichens on snags with bark and live trees were similar and influenced by tree species and bark acidity, while such influences were weak in decorticate snags. The lichen flora of spruce, birch and black-alder snags without bark was distinct and most rich in species, although such snags were relatively rare and species-poor at the single trunk scale. Lichen species unique to snags contributed 25% of the lichen species on the studied trunks.
- (3) The common *Lepraria incana* tended to inhabit more coniferous trees while the five rare species of this genus preferred deciduous trees. Therefore, leprarioid crusts should be determined to the species in biodiversity studies.
- (4) Lichens were notably vital on retention trees, particularly at the edges of clear-cuts and on aspen and ash, while bryophytes were severely damaged independently of tree species all over the clear-cuts. On average, 2% of lichen thalli, but 60% of bryophyte shoots, became damaged in two years. The damages of lichens on aspen and birch were mostly explained by the general sensitivity of certain species (also influenced in forests). Aspen hosted many more species, including several of conservation concern, than birch.
- (5) The amount and quality of old-growth structures (large broad-leaved trees, cavity trees, dead wood, windthrows) were similarly low on randomly located transects in a protected and adjacent commercial forest area, mainly due to the scarcity of structurally rich mesic stands and past logging in the reserve. If variation in forest type and successional stage were taken into account, dead wood volumes were on average 33% lower in the timber-harvesting area. Historical logging was likely to have caused much larger (at least fivefold) reduction. The origin of forests had affected the supply of downed trees, which were about twice less abundant in mid-aged stands not forested in the 1930s than in similar cutover sites; the effect on snag volume depended on site type and was generally non-significant. Different structural elements were not aggregated to the same sites neither in commercial forests nor in the reserve, so that 10% of generally best sites contained less than 30% of the elements.

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KOKKUVÕTE

Metsasamblikud ja nende kasvupinnad Eestis

Borealse ja parasvöötme looduslikud metsad pakuvad elupaiku paljudele organismidele, sealhulgas samblikele. Tüüpilisteks kasvupindadeks (substraatideks) metsasamblikele on puude koor ja puit ning maapind, kuid tulenevalt samblike üldistest ja liigiomastest tunnustest on eri liikide kasvupinnad või elupaigad palju spetsiifilisemad. Metsaraie vähendab samblike liigirikkust ja biomassi, eriti just samblikele ainuomaste kasvupindade ja vanade puistute hävimise kaudu. Seetõttu tuleb selgitada samblike liigirikkuse ja koosseisu seoseid nende kasvupindade esinemise, ohtruse ja kvaliteediga. Käesoleva väitekirja raames viidi läbi ülevaateuuring ja viis originaaluuringut, et täiendada olemasolevaid vähesteid kvantitatiivseid teadmisi 1) metsasamblike liigilisest mitmekesisusest, koosseisust ja kasvupindade jaotusest, 2) tüügaspuude tähtsusest metsa lihheno-floora kujunemisel, 3) kasvupindade kasutusest morfoloogiliselt sarnaste lööve-sambliku (*Lepraria*) liikidel, 4) säilikuude, kui looduskaitsemeetodi tõhususest, arvestades eri puuliikide ja asukohtade mõju epifüütsetele samblikele ja sammaldele, ning 5) vana metsa struktuurielementide (jäänukpuude, suurte väärislehtpuude, tüügas- ja lamapuude ning tuuleheitejuurestike) tihedusest ja omadusest hemiboreaalses metsas.

Avaldatud ja avaldamata andmete põhjal esineb Eesti metsades 481 sambliku-, lihhenikoolse- ja süstemaatilisel neile lähedase seene liiki, kuid nende tõenäoline arv võib küündida 599 liigini. Esinemissagedusi iseloomustas suur (154 liiki, 47%) vaid 1–2 uurimuses esinevate liikide osakaal. Eesti metsasamblikest moodustavad ligi poole (46%) jalgsambliku-, käokõrva-, porosambliku- ja lapiksamblikulaadsed, rippuva tallusega suursamblikud, soredioossed koorik-samblikud ning lihhenikoolsed seened. Samblike liigilise koosseisu põhjal eristus viis suurt kasvupinna rühma: laialehised puud, tavalised leht- ja okaspuud, oksad ja põõsad, tuuleheited ning maapind koos seal asuvate teiste kasvupindadega. Suurim unikaalsete liikide arv registreeriti elusatel puudel, kuid kasvupindade kvantitatiivne uuritus on väga erinev ja suhteliselt palju liike on leitud ka maapinnalt ja jämedatelt surnud puudel (nt. tüügaspuudelt).

Alam-Pedja looduskaitseala soometsades viidi läbi võrdlev tüügaspuude ja elusate puude lihhenofloora uuring, kus eristati neli puuliiki (kask, sanglepp, kuusk, mänd) ja kaks tüügaspuu tüüpi (koorega või kooreta); lisaks hinnati ka tüügaspuude esinemist ja omadusi. Samblike liigiline koosseis elusatel puudel oli enam sarnane koorega tüügaste kui kooreta tüügaspuude omaga. Kui elusate puude ja koorega tüügaste liigirikkust mõjutasid oluliselt puu liik ja koore happelisus, siis paljandunud puiduga tüügaspuudel need faktorid mõju ei avaldanud. Kuuse, kase ja sanglepa kooreta tüügaspuude lihhenofloora oli liigirikkaim, hoolimata taoliste puude vähesusest ning samblike liigivaesusest ühe tüve piires. Kooreta tüügaspuudel leidis rohkem unikaalseid liike kui

koorega tüügaspuudel, neist suure osa moodustasid jalgsamblikulaadsed. Kokkuvõttes moodustasid üksnes tüügaspuudel kasvavad liigid 25% Alam-Pedja soometsades puutüvedel uuritud samblikuliikide arvust. Tulemust ei mõjutanud olulisel määral morfoloogiliselt sarnaste lõõvesamblike (*Lepraria*) liikide määramine ja täiendav analüüs nende jaotuse kohta eri substraatide vahel. Kõige sagedasemat lõõvesamblikku *Lepraria incana* leidis siiski enam okaspuude koorel, harvem esinenud liigid eelistasid aga oluliselt enam lehtpuude koort. Seega peaks edaspidi bioloogilist mitmekesisust käsitlevates töödes lõõvesamblikud liigini määrama.

Nelja säilikpuu liigi (haab, kask, mänd, saar) epifüütidest olid samblikud raiesmikel märkimisväärselt elujõulised, eriti langi servas ning haabadel ja saartel. Seevastu sammalde kahjustused olid suured kõigil puuliikidel, sõltumata nende asendist langil. Kahe aasta jooksul kahjustus samblike tallustest keskmiselt 2%, kuid sammalde võsudest 60%. Samblikuliikide kahjustuste ulatus seostus kindlate liikide tundlikkusega nii säilik- kui metsapuudel. Haabadel esines palju enam liike (sh. ka looduskaitsealiselt olulisi) kui kaskedel.

Vana metsa struktuurielementide hulk ja kvaliteet oli sarnane juhuslikult valitud transektidel Loode-Tartumaa kaitsealustes ja majandusmetsades. Kaitseala metsade vaesuse põhjusteks olid mitmekesise struktuuriga arumetsade vähesus ja endisaegsed raied. Kui arvestati metsa tüübist ja arengujärgust tulenevat varieeruvust, oli surnud puitu majandusmetsades keskmiselt 33% vähem. Minevikus toimunud metsaraied on põhjustanud surnud puidu mahu vähemalt viiekordse vähenemise. Lisaks mõjutas surnud puidu tagavara ka metsamaa päritolu: lamapuid oli keskealistes puistutes, mis polnud 1930-ndatel aastatel metsamaal, kaks korda vähem kui püsivalt metsastel aladel. Tüügaspuudele oli metsamaa päritolu mõju nõrk ning sõltus metsa tüübist. Eri struktuurielemendid ei koondunud kaitsealustes ja majandusmetsades samadesse kohtadesse – 10% parimatest aladest sisaldas <30% kogu ala struktuurielementidest.

Ökoloogiliselt looduslähedase metsamajanduse käigus peaks samblike jaoks eriti säilitama (1) jämedaid, looduslikult haruldasi lehtpuude kooreta tüügaspuid (nt. kask, sanglepp) ja (2) hoolikalt valitud säilikipuid (eriti suuri haabu ja saari), mis võivad olla elupaigaks ohustatud liikidele; lisaks tuleb toetada metsamajanduse suhtes tundlike liikide (s.h. samblike) elupaikade pidevust ja piisavust (3) taastades struktuurielemente kaitsealadel, ja (4) moodustades uusi kaitsealasid majandatavatesse arumetsadesse (s.h. ka hiljuti metsastunud aladele).

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SOLITARY RETENTION TREES ON CLEAR-CUTS ARE LIFE-BOATS FOR LICHENS BUT NOT FOR BRYOPHYTES

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ABSTRACT

Retention of live trees on clear-cuts is an attempt to mimics natural disturbances and to provide habitat for species that are generally absent in clear-cut stands, but its efficiency for sustaining biodiversity is poorly known. We studied (1) the cover and vitality of lichens and bryophytes on four common retention-tree species in three locations (centre and edge of clear-cut; adjacent forest), and (2) the composition and damage of different epiphytic species on aspens (*Populus tremula*) and birches (*Betula* spp.) during two post-harvesting years in Estonia. Bryophytes were severely damaged on all tree species throughout clear-cuts, but lichens were relatively vital, particularly at the edges of clear-cuts and on aspen and ash (*Fraxinus excelsior*). On average, 2% of lichen thalli, but 60% of bryophyte shoots became damaged in two years, and 1.1 bryophyte species per trunk were lost. For lichens, the damage levels were mostly explained by the general sensitivity of certain species (also influenced in forests). Among bryophytes, the species that suffered most on clear-cuts were those that were relatively vital in forests. Aspen hosted many more species, including those of conservation concern, than birch. We conclude that careful retention of live trees on clear-cuts can be a successful conservation tool for lichens, particularly for many microlichens on aspen and ash, but that solitary trees on clear-cuts cannot maintain bryophytes at least in the short term.

Keywords: Conservation; Epiphyte; Forest management; Green-tree retention; Hemiboreal forest.

INTRODUCTION

Green-tree retention – leaving large live trees during clear-cutting, instead of felling them all – has gained popularity in the management of boreal and temperal forests over the past decade (Angelstam and Pettersson, 1997; Lindenmayer and Franklin, 2002; Mielikäinen and Hynynen, 2002). Promoting late-successional characteristics in harvested stands mimics the influence of natural stand-replacing disturbances (storms, wildfires). Hence, retention trees are a part of the strategy to achieve ecologically sustainable management by adjusting forestry operations with natural disturbance regimes (Lindenmayer and Franklin, 2002).

An obvious aim of retention trees is to provide habitat for wildlife in managed forests. For example, although clear-cutting dramatically reduces the density and species richness of birds, the loss is smaller in sites where many trees have been left standing (e.g. Beese and Bryant, 1999; Tittler et al., 2001), particularly for bole- and canopy-feeding species (Johnson and Landers, 1981). Retention trees also help to sustain the diversity and abundance of small mammals (Sullivan and Sullivan, 2001) and macroarthropods (Siira-Pietikäinen et al., 2003). When the trees die, they may host numerous saproxylic insects adapted to large-scale disturbances (Kaila et al., 1997; Siitonen et al., 2000).

The epiphytes of old trees are distinct targets of green-tree retention. Several Fennoscandian and North-American studies have concluded that the trees where epiphytic lichens and bryophytes survive, may become centres of their recolonization in the next forest generation (Hazell and Gustafsson, 1999; Sillett and Goslin, 1999; Keon and Muir, 2002). This is especially important for those old-growth species whose populations are more limited by dispersal rather than by habitat availability or the ability to grow in young stands (Sillett et al., 2000; Hilmo and Sæstad, 2001; Rosso et al., 2001; Keon and Muir, 2002). However, the dry, sunny and windy conditions in clear-cuts (Chen et al., 1999) may limit this 'life-boating' function, since lichens and bryophytes cannot regulate water loss (Green and Lange, 1995) and have a high risk of desiccation. Probably, the risk depends on both epiphyte and tree species, given the strong phorophyte effects on epiphyte communities (e.g. Barkman, 1958). In Sweden, the transplants of two management-sensitive species – a bryophyte *Antitrichia curtipendula* and a lichen *Lobaria pulmonaria* – survived on retained aspens (*Populus tremula*) in clear-cuts after two years (Hazell and Gustafsson, 1999). In contrast, similar transplants of old-growth lichens *Lobaria oregana* and *Pseudocyphellaria rainierensis* on Douglas-fir (*Pseudotsuga menziesii*) had a low growth and a high mortality rate in Oregon, USA (Sillett and McCune, 1998). Clearly, additional comparative and quantitative studies are needed to assess the value of retention trees for epiphytes.

The aims of this study are i) to compare the vitality of lichens and bryophytes on trees of different species in the middle and at the edge of clear-cuts as well as in adjacent forests, ii) to compare the species diversity of lichens and bryophytes on the retention trees and on forest trees, and iii) to distinguish the species that survive well on retained trees in the short term. For that, we explore the abundance and vitality of bryophytes and lichens on four species of retention trees and adjacent forest trees in a hemiboreal area in Europe. In the light of the results, we discuss the efficiency and limitations of retention trees in cryptogam conservation.

METHODS AND MATERIALS

Study area

The study was carried out in four randomly selected state forest districts in central, eastern and southern Estonia, between 58–59°N and 25–27°E (Fig. 1). Estonia is situated in the hemiboreal vegetation zone (Ahti et al., 1968); forests cover *c.* 50% of the country. The terrain is flat. All studied districts comprise large but extensively managed forest areas below 75 m a.s.l. The dominating site types are dry boreal (mainly *Vaccinium myrtillus*-type) and meso-eutrophic (*Oxalis*- and *Hepatica*-types) in the western districts, and eutrophic boreo-nemoral and paludifying forests (mainly *Aegopodium*- and *Filipendula*-types) in the eastern districts.

Since 1999, the Estonian Forest Act requires the retention of at least 5 m³ of live and dead trees per clear-cut hectare. In state forests (38% of all forests), which have been granted an FSC Forest Management certification, this requirement has generally been fulfilled, though many of the live retention trees are young or vulnerable to windthrow. In the four districts studied by us, 31% of live trees on clear-cuts (including seed trees) were birch (*Betula* spp.), 20% were Scots pine (*Pinus sylvestris*), 18% were ash (*Fraxinus excelsior*), 14% were aspen, 7% were lime (*Tilia cordata*) and 6% were other species (Rosenvald and Lõhmus, 2005). Most trees are retained solitarily.

Study design and sampling

The sampling included three hierarchical steps: (1) screening of all clear-cuts to distinguish the tree species that should be included in the study; (2) random sampling of the four most common retention-tree species to record changes in the total cover and vitality of lichens and bryophytes between two years; (3) random sampling of two deciduous tree species (aspen and birch) with

contrasting patterns of cryptogam vitality to explore the species composition in detail. Step (1) included all 103 clear-cuts that had been harvested during 2001–2002 in the four forest districts. In spring 2002, all live trees and snags with a diameter at breast height >13 cm, were mapped, and the main characteristics of the trees as well as the sites were recorded. The mean size of the clear-cuts was 2.3 ha (range 0.2–6.6 ha) and there were on average 20 (2–57) live trees ha⁻¹. Most of the harvested stands had been of eutrophic boreo-nemoral ($N = 47$), dry boreal (22) and meso-eutrophic type (10).

For step (2) we selected randomly 33 clear-cuts for Scots pine, 31 for birch and aspen, and 29 for ash. In each clear-cut, three trees of the same species and size were selected at random, one each from: (1) the middle of the clear-cut (>25 m from forest edge), (2) the edge of the clear-cut (<15 m from forest edge), and (3) in the adjacent forest of the same type (>25 m from the clear-cut). Four of these trees fell over during the study and the total sample included 368 trees in 85 clear-cuts (on several clear-cuts, more than one species could be sampled). The average diameter at breast height of the sample trees was 33 cm (range 14–90).

It was not possible to determine cryptogam species on all trees. Therefore, in step (3), we studied composition of cryptogam species only on aspens and birches, which differed in several important patterns (cover of bryophytes, vitality of lichens; see Results). For both tree species, we explored 31 retention trees (mostly in the middle of clear-cuts) and 31 adjacent forest trees.

Field and laboratory work

The cover and vitality of lichens and bryophytes were measured visually in four 20 x 20 cm plots on each tree, at heights of 0.2 and 1.3 m on the northern and southern sides of the trunk. These microsites represent different growth conditions for cryptogams (e.g. Barkman, 1958; Hazell and Gustafsson, 1999; Hedenås and Ericson, 2003). The plots were surveyed twice (early summer 2003 and 2004); their exact location (upper corner) on trees was marked for the re-analysis. Up to 5% of the area, the cover was estimated at 1%-accuracy, larger cover area at 10%-accuracy. To quantify vitality, the share of the desiccated part of the total cover was estimated according to clearly visible changes in the colour and structure of thalli (in microlichens: including apothecia) or shoots.

In summer 2004, the occurrence of different cryptogam species was recorded on the trunks of aspens and birches. Small plots could not be used, since the individual species (particularly those of conservation concern) cover only minor and often loosely delineated parts of the trunk (e.g. the co-existing microlichens). Therefore, the occurrence and damages of each species were

visually assessed for the whole trunk between heights of 0.2–1.8 m. The damage was coded according to Hedenås and Ericson (2003; slightly modified): 0, no change in colour and thus no desiccation damage; 1, few visible colour changes; 2, large patches with colour changes; 3, severe bleaching or thalli/shoots either dead or lost. The species, which got average damage scores >1 are termed ‘sensitive species’ for the purposes of this study; it does not mean that they are generally threatened by forestry.

The nomenclature follows Ingerpuu and Vellak (1998) for bryophytes and Randlane et al. (2004) for lichens. Lichenicolous *Bispora* species were considered as lichens, *Lepraria* and *Ulotia* species were treated collectively and one specimen of *Mycomicrothelia* was identified only to the genera. We distinguished key-habitat indicator species (sensu Nitare, 2000) and rare species in Estonia (sensu Ingerpuu and Vellak, 1998; Randlane and Saag, 1999; Jüriado et al., 2000) as the species of conservation concern.

Data analyses

The cover of both bryophytes and lichens was strongly positively correlated between northern and southern sides of the trunk as well as between the two heights ($r_s = 0.41$ – 0.73 ; $N = 368$; $P < 0.001$). At both heights, their cover was higher on northern than on southern sides (Wilcoxon’s tests; $P < 0.001$). Both on northern and southern sides, bryophytes were more abundant at 0.2 m than at breast height (Wilcoxon test; $P < 0.001$); there was no such clear difference for lichens. Given that also Blomberg (2002) reported similar vitality of cyanolichens on the two sides of retention trees, we pooled the cover and vitality estimates for each trunk from different plots into one average value. We admit, however, that aspect may influence the vitality of more sensitive taxa (e.g. bryophyte *Antitrichia curtipendula* and lichen *Lobaria pulmonaria*, Hazell and Gustafsson, 1999), and it deserves separate study after these taxa have been distinguished.

Next, we calculated exponential rate of vitality change of thalli (shoots) (v) within two years on each tree: $v = \ln(A_2(1-p_d)/A_1)$, where A_1 and A_2 are total coverages of lichens or bryophytes one and two years after the harvesting, respectively. p_d is the damaged proportion of the total cover in the second year. v is analogous to the exponential rate of population increase that is widely used in population ecology (e.g. Caughley and Sinclair, 1994). The formula takes into account our inability to measure the cover prior to logging – we related the final live cover [$A_2(1-p_d)$] to the total cover in the first year (A_1) because some dead parts of thalli or shoots were likely to be broken and lost by the second year. However, we assumed that these parts were present (though desiccated) one year after the harvesting. Since desiccation might have also occurred in the

forest before the clear-cutting, the extra damage due to the logging should appear when comparisons are made with the adjacent forest trees. Note that v cannot be divided into annual amounts, because we have no actual measurements for the changes during the first post-logging year.

For testing the extent of damage, we omitted the trees with very few epiphytes and the species with very small samples in order to reduce random noise. Therefore: (1) for analyzing v with respect to tree location and tree species, we considered only the trees where the initial cover (A_1) of bryophytes and/or lichens exceeded 10%, and since only one Scots pine had such a high cover of bryophytes, we omitted all pines from bryophyte analyses; (2) for comparing the vitality of different cryptogam species, we considered the average damage values of each of the 24 lichen and 19 bryophyte species that occurred at least three times on both forest and retention trees. Note, that we use these latter average values only for comparisons between species; these should not be interpreted at an absolute scale, since the intervals between the classes are not equal.

We used conventional parametric statistics (t -tests for independent and paired samples; two-way ANOVA; linear regression) for hypothesis testing. In ANOVA, *post-hoc* comparisons were made using Tukey's honestly significant difference (HSD) tests. Prior to analyses, we checked the assumptions of normal distribution (Kolmogorov-Smirnov test) and the homogeneity of variances (Levene's test). Only the distributions of v deviated from normal (Kolmogorov-Smirnov test; $P < 0.01$) mostly because of their positive kurtosis (for bryophytes 2.6 ± 0.4 SE; for lichens 3.9 ± 0.3). Despite this, we used ANOVA for its better illustrative opportunities and the possibility to test for interactions, since the F -statistic is fairly robust to normality assumptions and positive kurtosis leads to smaller, not larger, F -values (and consequently, a more conservative test; Lindman, 1974). In this particular case, we also analyzed the main-effects with Kruskal-Wallis ANOVAs, which gave similar results to the parametric tests. For comparing the abundance of epiphytes on forest trees of different species, the cover values (proportions) were arcsine-square-root transformed, but we present descriptive statistics in their untransformed state for ease of interpretation. All confidence intervals (CI) given are at 95% probability.

RESULTS

General loss of cryptogam vitality on retention trees

Vitality change (v) of lichens on 325 trees depended on location ($F_{2,313} = 7.8$; $P < 0.001$), tree species ($F_{3,313} = 3.8$; $P = 0.010$), and their interaction ($F_{6,313} =$

2.6; $P = 0.018$; Fig. 2A). In general, vitality was lost at an increasing rate along the forest–clear-cut gradient (Fig. 2B), although we could not prove the difference between clear-cut edge and the other locations (Tukey’s test; $P = 0.11$ – 0.13), and the change was only due to birch and pine (Fig. 2A). Aspen (no loss) and birch (the strongest loss) were the most contrasting tree species in the middle of the clear-cuts (Tukey’s test; $P = 0.047$).

Vitality change of bryophytes on 182 deciduous trees was highly affected by tree location ($F_{2,173} = 14.7$; $P < 0.001$; Fig. 3A): clear-cut centre did not differ from the edge ($P = 0.44$) but in both of these locations the bryophytes were far less vital than in forest (Tukey’s test; $P < 0.001$; Fig. 3B). There was no interaction between tree location and tree species ($F_{4,173} = 0.8$; $P = 0.53$), and the main effect of tree species was only marginal ($F_{2,173} = 2.8$; $P = 0.064$) – bryophytes tended to be more suppressed on aspen than ash (Tukey’s test; $P = 0.069$) and birch ($P = 0.088$; Fig. 3A).

On 102 retention trees, the initial cover of both bryophytes and lichens exceeded 10%. A paired comparison indicated that the average exponential loss in the viability of bryophytes ($v = -0.94 \pm 0.21$; CI) was dramatically greater there than the loss of lichens ($v = -0.02 \pm 0.06$; paired t -test: $t_{101} = 8.2$; $P < 0.001$). Hence, on average, 2% of lichen thalli but 60% of bryophyte shoots had been lost two years after the logging – a 30-fold difference.

The live thalli or shoots of cryptogams did not decrease significantly on forest trees of any species (Fig. 2–3). There was even a tendency for lichen growth on birches during the two years ($v = 0.11 \pm 0.10$; CI). The mean cover of epiphytes on forest trees (Fig. 4) differed widely between tree species ($F_{3,238} = 18.1$; $P < 0.001$), and between lichens and bryophytes (main effect: $F_{1,328} = 80.2$; $P < 0.001$; interaction with tree species: $F_{3,328} = 56.9$; $P < 0.001$). The cover of lichens did not differ between the deciduous tree species, but pines had significantly more lichens than aspens (Tukey’s test; $P < 0.001$) and birches ($P = 0.016$). In contrast, pines had almost no bryophytes and birches had few, while aspen and ash were similarly bryophyte-rich (Fig. 4).

Species composition and species-specific vitality on aspen and birch

Altogether, 45 bryophyte and 74 lichen species (incl. one lichenicolous fungus) were recorded on the 62 aspens and 62 birches in 31 forests and 31 clear-cuts (Appendix). The forest trees and the retention trees hosted similar total numbers of cryptogam species (95 and 94, respectively) and mean numbers of lichen species per trunk (5.7 ± 0.7 and 5.6 ± 0.7 , CI; respectively). However, the retention trees had, on average, only 3.6 ± 0.6 (CI) bryophyte species per trunk compared to 4.7 ± 0.7 in the forest. This difference of 1.1 ± 0.6 bryophyte species per trunk was highly significant (paired t -test; $t_{61} = 3.6$, $P < 0.001$),

while the difference of 0.1 ± 0.9 lichen species was not (paired t -test; $t_{61} = 0.1$, $P = 0.88$).

The aspen was clearly more species-rich (73 species in forest; 72 in clear-cuts) than birch (47 and 41, respectively). The total cover of the 20 species that occurred on both tree species in forests did not differ significantly between them (paired t -test; $t_{19} = 0.97$, $P = 0.34$). Altogether, 66 species occurred only on aspens, including nine rare or indicator species (bryophytes *Frullania dilatata*, *Neckera pennata*, *Ulotia* spp.; lichens *Acrocordia cavata*, *A. gemmata*, *Leptogium saturninum*, *Leptogium teretiusculum*, *Megalaria grossa*, *Opegrapha rufescens*. Birch had 24 unique species, only two of them with indicator value (lichens *Arthonia leucopellaea*, *Mycoblastus sanguinarius*).

Relationships between the average damage scores of the same species on retention trees and forest trees were different for lichens and bryophytes (Fig. 5). For lichens, the damages in clear-cuts hardly differed from those in forests (intercept of the regression line: $P = 0.11$); instead, 53% of their variation was explained by the general sensitivity of the same species – the damage varied proportionately in both sites (slope: 1.03 ± 0.20 SE; $P < 0.001$). In bryophytes, the trend of general sensitivity of species was non-significant and non-proportional (slope: 0.47 ± 0.41 SE; $P = 0.27$), and the damage was significantly larger in clear-cuts than in forests, particularly for the species that were relatively vital in forests (intercept: 1.17 ± 0.21 SE; $P < 0.001$; Fig. 5).

Crustose lichens (e.g., *Buellia griseovirens*, *Loxospora elatina*, *Megalaria grossa*, *Ropalospora viridis*) and some macrolichens with small foliose (*Vulpicida pinastri*) or podethial thalli (*Cladonia coniocraea*) were remarkably vital. On the other hand, the mean damage score of 14 species was at least 1.0 in either forest or clear-cut (Fig. 5; see Appendix for the species list). The ten sensitive bryophytes were mainly mosses and hepatics that form distinct mats and wefts (e.g., *Homalia trichomanoides*, *Neckera pennata*, *Pylaisia polyantha*, *Radula complanata*). Three of the four sensitive lichens (*Lecanora allophana*, *Parmelia sulcata*, *Peltigera praetextata*) were damaged both in the forest and in clear-cuts, and their common features could not be analyzed.

DISCUSSION

We found that cryptogams suffered from additional mortality on retention trees, and although species richness on clear-cuts was not impoverished at the landscape scale, local extinctions took place within two years. Although we had no data about the pre-harvest situation, the total cover of epiphytes one year after logging seemed to be a suitable reference value, since we found no net loss of vitality in the adjacent forest trees. Hence, the average changes of

epiphyte vitality reported by us could more or less be directly attributed to clear-cutting.

For the first time, we documented a large variation in response to clear-cutting between and among lichens and bryophytes, at the centre and edge of clear-cuts and on different tree species. The negative impacts were severe and almost independent of tree species for bryophytes throughout clear-cuts, but were weaker for lichens, particularly in clear-cut edges and on aspen and ash. Such a variation may partly explain the controversial views about logging impacts on cryptogams. Several studies have reported decreased abundance, cover, growth, vitality or biomass of epiphytic cryptogams, even after partial cutting (e.g. Thomas et al., 2001; Coxson et al., 2003; Hedenås and Ericson, 2003) or near clear-cuts (Hilmo and Holien, 2002; Rheault et al., 2003). Yet, some transplantation experiments have demonstrated their high survival on retention trees in clear-cuts or in young forests (Hazell and Gustafsson, 1999; Gauslaa et al., 2001; Hilmo, 2002).

The resistance of lichens to desiccation could be explained by their ability (1) to attain positive net photosynthesis using only air humidity, while bryophytes need liquid water (Green and Lange, 1995), and (2) to recover from and adjust themselves to bright light by increasing thallus thickness and/or concentration of pigments, which act as sun-screens for photobiont cells against excessive UV radiation (Rikkinen, 1995; Gauslaa and Solhaug, 2001; Hilmo, 2002). Hence, many forest lichens obviously can survive on clear-cuts if suitable substrata are available, and the crucial question is – which species can and which cannot. The resistant species are likely to include cyanolichens, whose biomass is higher in regenerated stands with retained trees than in those without (Peck and McCune, 1997), the light-tolerant *Parmeliaceae*, and possibly also usneion species that experience a moderate level of photo-inhibition to intensive light (Gauslaa and Solhaug, 1996). Alectorioid and other green-algal lichens are probably much more stressed, though they can probably survive under some conditions. For example, the fruticose green-algal lichen *Sphaerophorus globosus* is most abundant near old remnant trees in forests (Sillett and Goslin, 1999). In our analysis, the few sensitive lichen species were not found to belong to distinct morphological or habitat types. Moreover, these species tended to be equally damaged both in the forest and on retention trees, i.e. they were affected mostly by processes other than logging. For example, apothecia of *Lecanora allophana* were frequently bleached or broken, apparently eaten by snails (personal observations; cf. Baur et al., 1994).

In contrast to lichens, epiphytic bryophytes were very sensitive to sudden changes in humidity and light conditions on retention-trees. Previously, also the rapid loss of understorey mosses in clear-cuts has been reported (Jalonen and Vanha-Majamaa, 2001). Generally, bryophytes' requirements for light and water are closely determined by their life-form (Mägdefrau, 1982): cushions predominate in open sites (such as on free-standing trees), whereas wefts and

fans are shade-lovers (e.g. on tree base). Indeed, the mat- and weft-forming mosses and hepatics were most sensitive in our study – they were vital in forests and heavily damaged on retention trees. Also Hazell and co-authors (1998) have pointed out the low tolerance of weft-forming *Pylaisia polyantha* and *Radula complanata* to low humidity, compared with cushion-forming *Orthotrichum speciosum* and *Nyholmiella obtusifolia*.

Although the structure of epiphyte communities is strongly influenced by the bark texture, chemistry, and moisture of the host tree species (e.g. Barkman, 1958), the vitality of epiphytes has not been compared on retention trees of different species before. We found high lichen vitality on retained aspen and ash, and low vitality on birch and pine. Probably the coarse bark provides better shade against desiccation, but aspens also have a distinct species composition (e.g. Kuusinen, 1996). For bryophytes, unsuitable moisture conditions at a larger (stand) scale could prevail over microclimatic or bark characteristics of a particular host species (e.g. Potzger, 1939; Frisvoll and Presto, 1997; Thomas et al., 2001). For example, the relative abundance of bryophytes on conifers is limited more by moisture than by bark pH (Hong and Glime, 1997).

Practical implications and conclusions

No study has covered the mortality of epiphytes within the 10–20 years following clear-cutting until the new stand starts providing enough shade. Hence, there is no conclusive answer to whether lichens really survive and whether bryophytes can adapt to these conditions and recover. The current success stories have explored only 1–2 post-logging years, which may be too short a time to detect the slow death of the transplants via decreased vitality or sustained photoinhibition on retention trees (see Hazell and Gustafsson, 1999; Gauslaa et al., 2001). Nevertheless, our results strongly suggest that careful retention of live trees on clear-cuts can be a successful conservation tool for lichens, particularly for many microlichens on aspen and ash. Although Tønsberg (1992) has considered the taxa with sorediate or granulous thalli to be prone to desiccation, this may perhaps pose more of a problem for the inhabitants of humid tree bases, such as *Mycobilimbia* (Hedenås and Ericson, 2003). The sorediate species growing higher on the trunk (e.g. *Biatora efflorescens*, *Loxospora elatina*, *Ropalospora viridis*) were vital in our study, similarly to several microlichens of conservation concern (*Acrocordia cavata*, *A. gemmata*, *Megalaria grossa*, *Mycoblastus sanguinarius*).

In principle, the omission of trees with less than 10% lichen cover from samples may have led to overly optimistic results. Gauslaa and Solhaug (1998) showed that larger thalli of folious cyanobacterial lichen *Degelia plumbea* had higher water-holding capacity than smaller thalli. In contrast, the propagules of

Lobaria pulmonaria were larger on clearcuts (four years after logging) than in young or old-growth stands (Sillett et al., 2000). Hence, foliose lichens may have survived less well on the sparsely inhabited trees (which we did not explore), though we did not observe this at the species level (species with small foliose or podethial thalli, such as *Vulpicida pinastri* and *Cladonia coniocraea*, had high vitality on retained trees). Thus, it could be important to retain, in particular, those trees that already have a well-developed cover of lichens. This often coincides with the retention of old trees, which can also host desiccation-sensitive and threatened epiphytes (e.g. *Leptogium teretiusculum* and *Ulotia* spp.; see also McGee and Kimmerer, 2002) and can probably catch their spores more effectively (Hazell et al., 1998).

Tree species and their epiphyte communities vary geographically and exact recommendations for tree-retention should be elaborated at a regional scale. Among the species studied by us in Estonia, the retention of aspen and ash produced the best results: they had relatively high cover of cryptogams, and lichens certainly survived best on these tree species. The diverse and unique communities on aspen are well documented in boreal forests (e.g. Kuusinen, 1996; Hedenås, 2000; Jüriado et al., 2003). We recorded several unique and rare species on aspen, too. On the other hand, since ash survives better on the clear-cuts (Rosenvald and Lõhmus, 2005) and its lichen flora resembles that of aspen (Lõhmus, 2003), this species may be more preferable in the long term. However, it is important to study what proportion of (threatened) forest lichens could be protected using these two tree species.

Single-tree retention clearly does not provide sufficient protection for bryophytes, notably weft-, fan- or mat-forming species that have a high risk of dessication on clear-cuts. Retaining trees near the edges (current study), as groups (Hazell and Gustafsson, 1999) or using shelterwood cutting (Hannerz and Hånell, 1997) might be more acceptable logging techniques for them, but further research is needed. Group-retention also has technical advantages over single-tree retention (Hazell and Gustafsson, 1999), so the principal question is the sufficient size of the groups to moderate microhabitat (Fenton and Frego, 2004), resist windfall (Esseen, 1994) and meet the requirements of other taxa (Beese and Bryant, 1999). In Estonia, for example, the current clear-cuts are too small (on average, 2.3 ha in our study districts) for large patches to be retained. Whether such a fine-grained landscape mosaic may eventually lead to the extinction of forest interior species, including bryophytes, is not known.

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Appendix. Number of occurrences of bryophyte and lichen species (V – completely vital, D – at least partly damaged) on aspens and birches in forest and clear-cuts, and share of damages (%) of all inhabited trees. Among the species that occurred on at least three forest and three retention trees, sensitive (*) and insensitive (#) species have been indicated.

Species	Forest				Clear-cut				Total dama- ge %
	Aspen		Birch		Aspen		Birch		
	(N = 31)		(N = 31)		(N = 31)		(N = 31)		
	V	D	V	D	V	D	V	D	
Bryophytes									
<i>Amblystegium serpens</i>	3	0	—	—	0	2	—	—	40
* <i>Amblystegium subtile</i>	5	3	1	1	1	6	—	—	59
<i>Brachythecium populeum</i>	—	—	—	—	1	0	—	—	0
<i>Brachythecium reflexum</i>	1	0	—	—	—	—	—	—	0
* <i>Brachythecium rutabulum</i>	4	0	—	—	1	1	0	1	29
<i>Brachythecium salebrosum</i>	1	0	—	—	2	2	—	—	40
* <i>Brachythecium velutinum</i>	3	0	—	—	1	5	—	—	56
<i>Calypogeia integristipula</i>	—	—	—	—	—	—	0	1	100
<i>Campylium sommerfeltii</i>	1	0	—	—	2	1	—	—	25
<i>Cirriphyllum piliferum</i>	4	0	—	—	2	0	—	—	0
<i>Climacium dendroides</i>	4	0	—	—	0	1	—	—	20
# <i>Dicranum montanum</i>	7	0	15	0	3	0	11	8	18
* <i>Dicranum scoparium</i>	5	0	20	0	1	0	4	11	27
# <i>Eurhynchium angustirete</i>	2	1	—	—	2	1	—	—	33
# <i>Eurhynchium hians</i>	6	2	1	0	4	3	—	—	31
<i>Eurhynchium pulchellum</i>	2	0	—	—	0	1	—	—	33
<i>Fissidens adianthoides</i>	3	0	—	—	2	0	—	—	0
<i>Frullania dilatata</i>	—	—	—	—	1	0	—	—	0

<i>Herzogiella seligeri</i>	—	—	—	—	—	—	1	0	0
* <i>Homalia trichomanoides</i>	4	0	—	—	0	7	—	—	64
* <i>Hylocomium splendens</i>	3	2	—	—	1	3	—	—	56
* <i>Hypnum cupressiforme</i>	8	7	4	2	2	8	1	1	55
<i>Hypnum pallescens</i>	1	0	—	—	—	—	—	—	0
<i>Jamesoniella autumnalis</i>	—	—	1	0	—	—	—	—	0
<i>Lepidozia reptans</i>	—	—	2	1	—	—	—	—	33
<i>Lophocolea heterophylla</i>	1	0	4	1	—	—	0	1	29
* <i>Neckera pennata</i>	6	1	—	—	1	8	—	—	56
<i>Orthotrichum gymnostomum</i>	—	—	—	—	1	0	—	—	0
* <i>Orthotrichum speciosum</i>	14	2	—	—	5	9	—	—	37
* <i>Plagiomnium cuspidatum</i>	4	3	1	1	4	2	1	1	41
<i>Plagiothecium curvifolium</i>	—	—	0	1	—	—	—	—	100
<i>Plagiothecium laetum</i>	—	—	3	1	—	—	1	0	20
* <i>Pleurozium schreberi</i>	—	—	5	0	—	—	2	6	46
<i>Pseudeleskeella nervosa</i>	—	—	—	—	0	1	—	—	100
* <i>Ptilidium pulcherrimum</i>	2	3	13	7	—	—	8	7	43
<i>Ptilium crista-castrensis</i>	1	0	—	—	—	—	—	—	0
* <i>Pylaisia polyantha</i>	11	7	2	1	4	12	0	2	56
* <i>Radula complanata</i>	10	15	1	0	0	24	0	1	78
<i>Rhodobryum roseum</i>	3	1	—	—	—	—	—	—	25
* <i>Rhytidiadelphus triquetrus</i>	7	2	0	1	1	3	—	—	43
* <i>Sanionia uncinata</i>	12	2	1	0	3	4	1	0	26
<i>Tetraphis pellucida</i>	—	—	1	0	—	—	—	—	0
<i>Thuidium delicatulum</i>	2	0	—	—	—	—	—	—	0
<i>Thuidium philibertii</i>	3	1	—	—	0	2	—	—	50
<i>Ulota</i> spp.	—	—	—	—	1	0	—	—	0
Lichens									
<i>Acrocordia cavata</i>	2	0	—	—	1	0	—	—	0
<i>Acrocordia gemmata</i>	—	—	—	—	2	0	—	—	0
<i>Anaptychia ciliaris</i>	0	3	—	—	1	0	—	—	75
<i>Arthonia leucopellaea</i>	—	—	—	—	—	—	1	0	0
<i>Arthonia spadicea</i>	1	0	—	—	—	—	—	—	0
<i>Arthopyrenia punctiformis</i>	—	—	—	—	1	0	—	—	0
<i>Arthothelium ruanum</i>	1	0	—	—	—	—	—	—	0
<i>Bacidia arceutina</i>	3	0	—	—	2	0	—	—	0
<i>Bacidia fraxinea</i>	—	—	—	—	1	0	—	—	0
<i>Bacidia rubella</i>	1	0	—	—	—	—	—	—	0
<i>Bacidia subincompta</i>	—	—	—	—	4	0	—	—	0
# <i>Biatora efflorescens</i>	1	0	3	0	—	—	4	0	0

<i>Bispora</i> sp.	—	—	—	—	1	0	—	—	0
# <i>Buellia griseovirens</i>	3	0	14	0	1	0	11	0	0
<i>Caloplaca cerina</i>	—	—	—	—	1	0	—	—	0
# <i>Caloplaca flavo-rubescens</i>	7	1	—	—	10	2	—	—	15
<i>Chaenotheca trichialis</i>	—	—	1	0	—	—	—	—	0
# <i>Cladonia cenotea</i>	—	—	3	0	—	—	5	1	11
<i>Cladonia chlorophaea</i>	1	0	1	0	—	—	—	—	0
# <i>Cladonia coniocraea</i>	7	0	22	2	3	0	16	11	21
* <i>Cladonia digitata</i>	—	—	4	0	—	—	7	7	39
# <i>Cladonia fimbriata</i>	6	0	6	0	4	0	5	0	0
<i>Cladonia ochrochlora</i>	—	—	—	—	—	—	1	0	0
<i>Cladonia</i> sp. (only <i>prothalli</i>)	1	0	1	0	—	—	1	0	0
<i>Dimerella pineti</i>	1	0	2	0	—	—	—	—	0
<i>Graphis scripta</i>	—	—	1	0	1	1	2	0	20
* <i>Hypogymnia physodes</i>	—	—	16	7	0	2	7	16	52
<i>Imshaugia aleurites</i>	—	—	1	0	—	—	—	—	0
<i>Lecania cyrtella</i>	—	—	—	—	1	0	—	—	0
* <i>Lecanora allophana</i>	3	6	—	—	5	7	—	—	62
<i>Lecanora argentata</i>	2	2	1	0	0	1	0	1	57
<i>Lecanora expallens</i>	1	0	—	—	1	0	1	0	0
# <i>Lecanora pulicaris</i>	—	—	6	0	—	—	6	0	0
# <i>Lecanora rugosella</i>	4	0	—	—	2	1	—	—	14
# <i>Lecidea nylanderii</i>	—	—	22	0	—	—	24	1	2
<i>Lecidella elaeochroma</i>	2	0	—	—	1	0	—	—	0
<i>Lecidella euphorea</i>	6	1	—	—	2	0	—	—	11
# <i>Lepraria</i> sp.	16	1	19	0	5	8	14	1	16
<i>Leptogium saturninum</i>	0	1	—	—	1	0	—	—	50
<i>Leptogium teretiusculum</i>	—	—	—	—	1	0	—	—	0
<i>Loxospora elatina</i>	—	—	11	0	—	—	11	1	4
# <i>Megalaria grossa</i>	4	0	—	—	4	0	—	—	0
<i>Melanelia exasperatula</i>	0	1	—	—	2	0	—	—	33
<i>Melanelia subaurifera</i>	—	—	—	—	0	1	—	—	100
<i>Micarea prasina</i>	2	0	4	0	—	—	—	—	0
<i>Mycobilimbia carneoalbida</i>	3	0	—	—	—	—	—	—	0
<i>Mycobilimbia epixanthoides</i>	2	0	—	—	2	0	—	—	0
<i>Mycobilimbia sabuletorum</i>	1	0	—	—	—	—	—	—	0
<i>Mycobilimbia tetramera</i>	—	—	—	—	1	0	—	—	0
# <i>Mycoblastus fucatus</i>	—	—	3	0	1	0	5	0	0
<i>Mycoblastus sanguinarius</i>	—	—	1	0	—	—	1	0	0
<i>Mycocomrothelia wallrothii</i>	—	—	—	—	—	—	1	0	0

<i>Mycomicrothelia</i> sp.	—	—	—	—	2	0	—	—	0
<i>Ochrolechia microstictoides</i>	—	—	1	0	—	—	—	—	0
<i>Opegrapha rufescens</i>	1	0	—	—	1	1	—	—	33
<i>Parmelia saxatilis</i>	—	—	—	—	—	—	1	0	0
* <i>Parmelia sulcata</i>	—	—	1	5	0	2	0	1	89
# <i>Parmeliopsis ambigua</i>	—	—	5	0	—	—	13	0	0
<i>Peltigera canina</i>	0	1	—	—	—	—	—	—	100
<i>Peltigera membranacea</i>	1	0	—	—	—	—	—	—	0
* <i>Peltigera praetextata</i>	2	3	—	—	1	4	—	—	70
# <i>Pertusaria amara</i>	3	0	2	1	5	0	—	—	9
<i>Pertusaria coccodes</i>	—	—	—	—	1	0	—	—	0
<i>Pertusaria leioplaca</i>	0	1	—	—	—	—	—	—	100
# <i>Phlyctis argena</i>	27	0	4	0	23	0	—	—	0
<i>Physcia stellaris</i>	1	0	—	—	—	—	—	—	0
<i>Physcia tenella</i>	1	1	—	—	1	0	—	—	33
<i>Physconia distorta</i>	0	6	—	—	—	—	—	—	100
<i>Platismatia glauca</i>	—	—	1	1	—	—	0	2	75
# <i>Ramalina farinacea</i>	2	1	—	—	8	0	—	—	9
# <i>Ropalospora viridis</i>	3	0	15	0	1	0	10	0	0
<i>Usnea hirta</i>	—	—	—	—	—	—	1	0	0
# <i>Vulpicida pinastri</i>	—	—	11	0	—	—	16	0	0
<i>Xanthoria parietina</i>	0	1	0	0	2	0	—	—	33



Fig. 1. Location of the study areas.

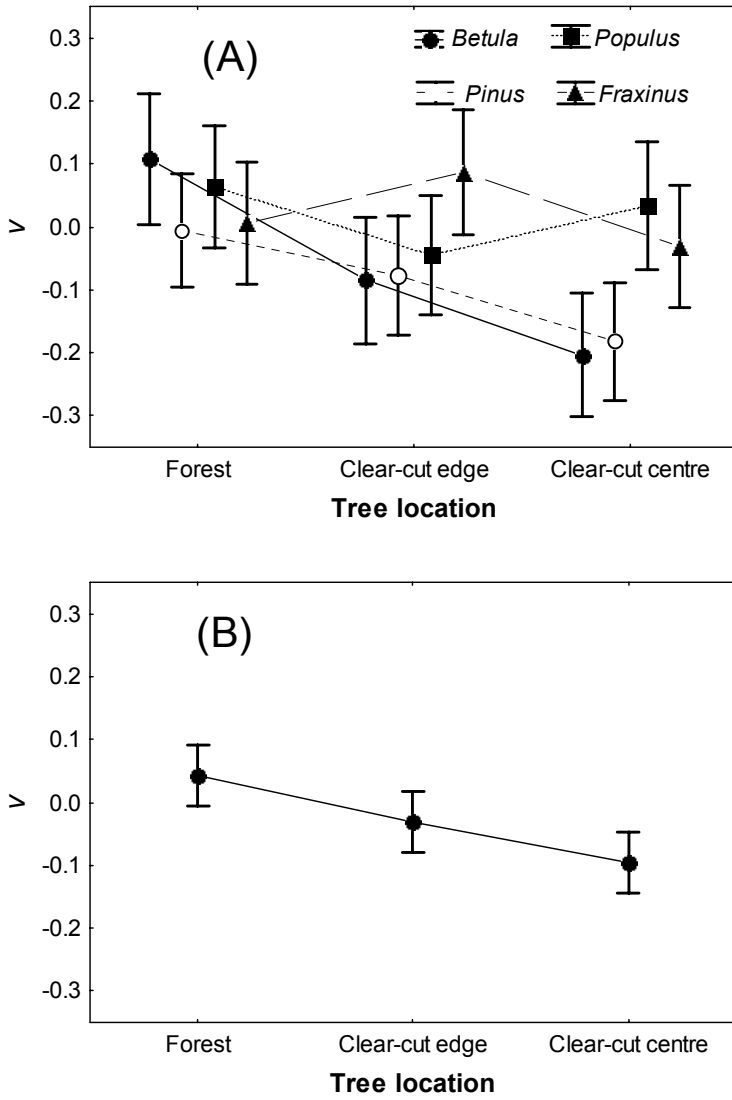


Fig. 2. Mean exponential rate of vitality change (v ; \pm 95% CI) of lichens according to the tree species (A) and position (B).

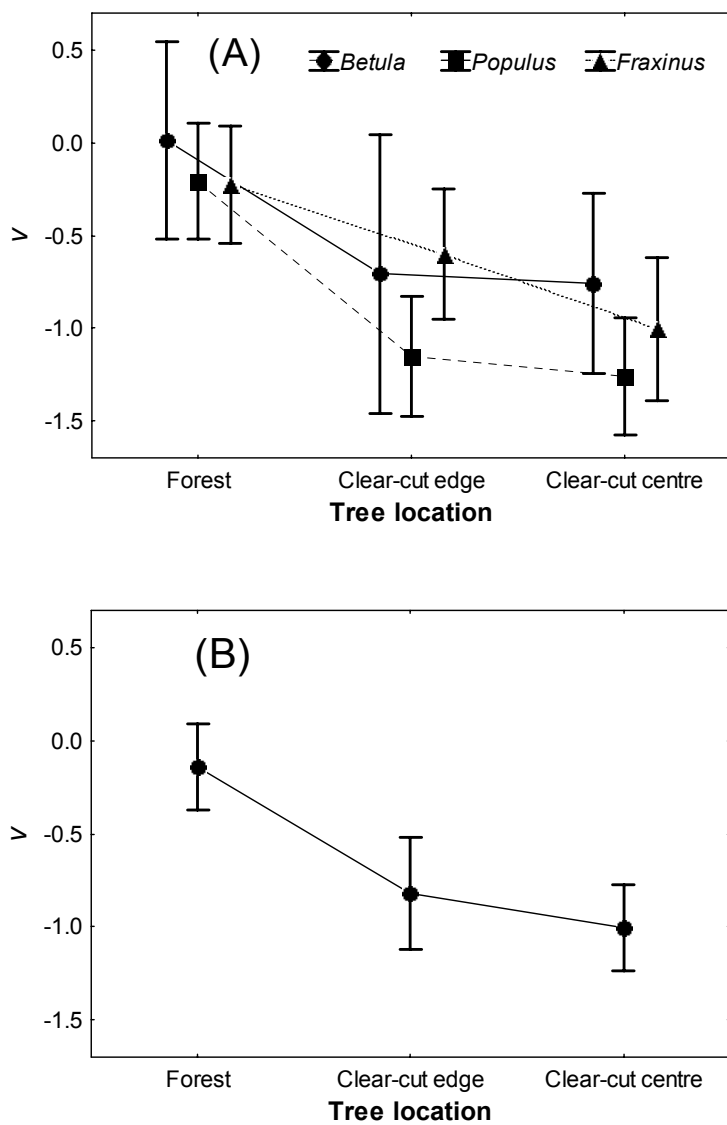


Fig. 3. Mean exponential rate of vitality change (v ; \pm 95% CI) of bryophytes according to the tree species (A) and position (B).

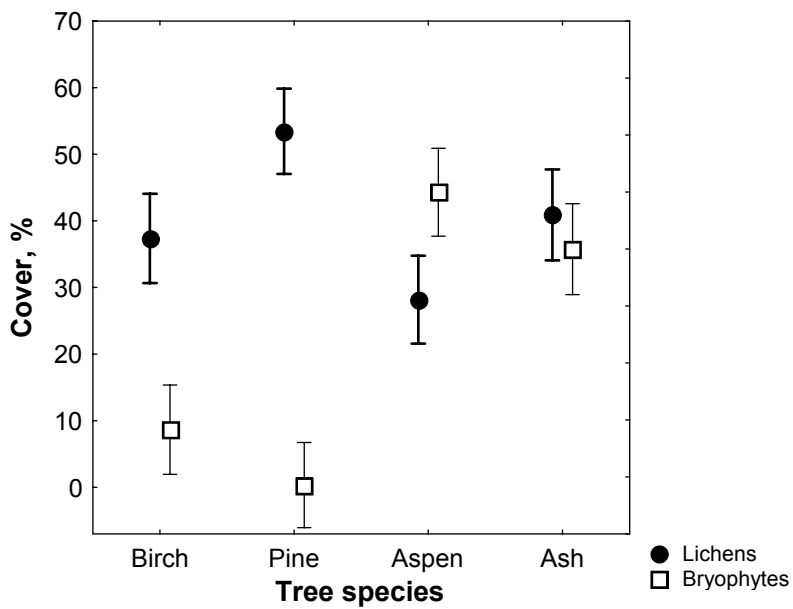


Fig. 4. The mean (\pm 95% CI) cover of lichens and bryophytes on forest trees of different species. The sample includes 31 birches, 33 Scots pines, 31 aspens and 29 ashes.

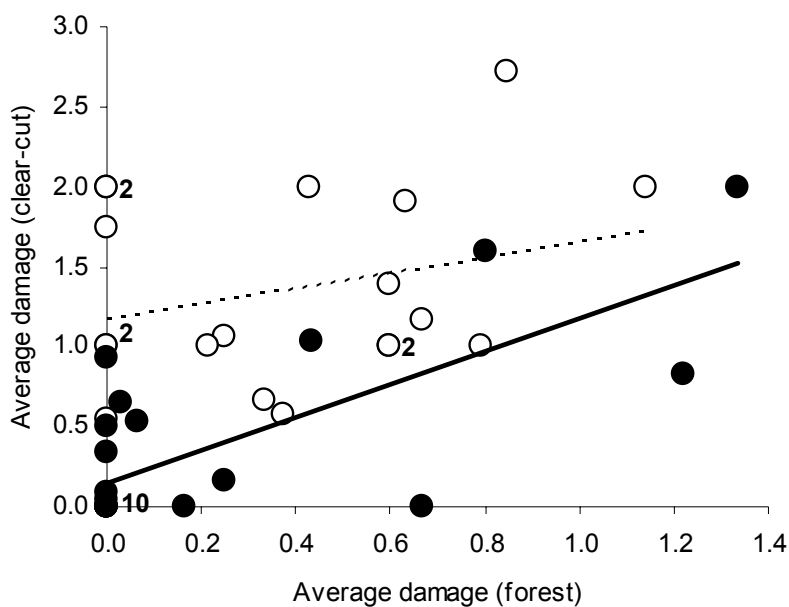


Fig. 5. Linear regressions between the average damage scores on forest and retention trees of 19 bryophyte (circle dots, discontinuous line) and 24 lichen species (filled dots, solid line). Numeric labels indicate the number of species with similar values.

OLD-GROWTH STRUCTURAL ELEMENTS IN A STRICT RESERVE AND COMMERCIAL FOREST LANDSCAPE IN ESTONIA

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ABSTRACT

Although 7% of forest land is strictly protected in Estonia, it is unknown whether the reserves and the surrounding timber-production areas provide enough habitat for viable populations of threatened species. We mapped large broad-leaved trees, remnant trees, cavity-trees, coarse woody debris (CWD; i.e., logs and snags) and windthrows on randomly located transects in a typical protected and adjacent commercial forest area. As generally in Estonia, the reserve lacked structurally rich mesic forests, had been at least once clear-cut within 200 yr and, as a result, only snags with exposed wood were more numerous there (on average, 16.2 ± 10.5 snags ha^{-1}) than in the managed landscape (3.4 ± 1.1). The latter had more logs (17.6 ± 5.0 ha^{-1}), including those large and well-decayed, and broad-leaved trees (3.6 ± 2.1 ha^{-1}) than the reserve (7.8 ± 4.1 and 0.6 ± 0.5 , respectively). The average volumes of CWD were 6.2 ± 2.2 m^3 ha^{-1} in the reserve and 9.0 ± 2.4 in the commercial area. When forest age and type were taken into account, CWD volumes were on average 33% and the density of cavity-trees 42% lower in the timber-harvesting area, but the reduction was statistically non-significant. In either landscape, different structural elements were not aggregated to the same sites, so that 10% of generally best sites contained less than 30% of the elements. We conclude that the present quality of Estonian forest reserves is low because they lack structurally rich old mesic stands and have been protected for too short time. Restoration of reserve forests, protection of additional productive forests, and close-to-nature management approaches in commercial areas are the major challenges for the preservation of forest biodiversity in Estonia.

Keywords: coarse woody debris; conservation planning; forest structure; hemiboreal forest; tree cavities.

INTRODUCTION

Many species are specialized to live in old forests, where they occupy the continuous and abundant supply of specific microhabitats – coarse woody debris (CWD), large old trees and tree cavities (Esseen et al., 1997; Hunter, 1999; Lindenmayer and Franklin, 2002). CWD (large snags, logs, dead branches and stumps) hosts numerous saproxylic macrofungi, bryophytes, lichens, insects and vertebrates (Maser and Trappe, 1984; Samuelsson et al., 1994; Siitonen, 2001). Old living trees provide nest sites for several large bird species (Tucker and Evans, 1997) and distinctive bark and canopy habitats for epiphytes and invertebrates (Schowalter, 1989; Pettersson et al., 1995; Neitlich and McCune, 1997; Holien, 1997; Hazell et al., 1998; Sillett and Matthew, 1999). Tree cavities are essential for many vertebrates and insects (Lindenmayer and Franklin, 2002).

These structures of old-growth have dramatically declined in boreal and temperate forest landscapes (e.g. Green and Peterken, 1997; Linder and Östlund, 1998), mainly because of intensive forestry and fire protection (Ohlson et al., 1997; Sippola et al., 1998; Crites and Dale, 1998; Duvall and Grigal, 1999). An urgent question is how to preserve the large number of increasingly threatened species inhabiting these substrata (e.g. Berg et al., 1994). Given that the area of strict reserves is limited economically and socially, old-growth features should be retained and restored also in managed forests (Frelich and Puettmann, 1999; Lindenmayer and Franklin, 2002).

To set regional targets for sustainable forestry and forest protection, the abundance and distribution of old-growth structures in forest landscapes should be assessed. In northern Europe, the Fennoscandian timber-harvesting areas are structurally poor and the reserves are small and scattered (Esseen et al., 1997; Anon., 2000). Due to a less intensive economy and a higher share of strictly protected forests (7% of the 2.25 million ha of forest land; Lõhmus et al., 2004), old-growth species could have more viable populations in the adjacent Estonia. Yet, Estonian forestry also uses mostly clear-felling systems with rotation ages not exceeding 100 yr. Recently, volumes of felling have sharply increased (2.4 million m³ in 1993, 10.8 million m³ in 2000; Kuuba, 2001) and the area of old-growth outside reserves has decreased to only 1–2% of forest land – a nearly Fennoscandian level (Lõhmus, 2002). Obviously, forest conservation strategies and tools should be urgently re-assessed in Estonia, but this is complicated because (1) the ability of reserves to sustain threatened species and (2) the abundance of remaining old-growth features in commercial forests are not known.

We studied the occurrence of large trees, cavity trees, snags, logs and windthrows (hereafter: structural elements) in a large reserve and adjacent commercial forests in east-central Estonia. It was not possible to replicate the landscape-scale analysis, but this is a common situation at large scales and its consequences depend on the particular problem (Oksanen, 2001). Our well-

studied area represents the general Estonian situation well and has been used for strategical assessments also before (Lõhmus, 2002, 2003, 2004). We asked (1) how much the density and volume of structural elements differ between protected and commercial forests to show what are their relative values for biodiversity, (2) how forest type and age, edge effects and management explain variation in the abundance of structural elements. This could help to predict the effects of new reserves, which have been proposed to improve the representativity of the current network (Viilma et al., 2001; Lõhmus, 2004; Lõhmus et al., 2004); (3) to what extent the structural elements are aggregated and co-occur in the landscape, i.e. whether management-sensitive species can be effectively protected in small 'key-sites' (see Lindenmayer and Franklin, 2002, pp. 123–125). To answer these questions, we mapped and described the structural elements on random transects and analysed the data at the landscape and habitat type scales.

MATERIAL AND METHODS

Study area and sampling design

The study was carried out in a 900-km² area with random (UTM-grid) borders in east-central Estonia (Fig. 1). Forest land covers 49%, agricultural lands 36%, mires 8%, flood-plains 2%, rivers and lakes 2%, and settlements 3% of the area. Fifty percent of forests grow on wet soils. Due to a long clear-cutting history, most forests have one even-aged tree layer, consisting on average of 46% birch (*Betula* spp.), 17% Scots pine (*Pinus sylvestris*), 15% Norway spruce (*Picea abies*), 9% aspen (*Populus tremula*), 7% grey alder (*Alnus incana*), 6% black alder (*Alnus glutinosa*) and 1% other tree species. The area includes many timber-harvesting units (four state forest districts, a large number of private owners) and 15% of the territory (23% of forest land) is covered by the Alam-Pedja Nature Reserve, which is one of the largest well-forested reserves in Estonia. The landscape composition is very similar to the Estonian average, although the forests contain more birch and fewer coniferous trees. The share of old-growth forest in the commercial landscape (1.2%) is similar to the Estonian average (1.5%), but higher in the Alam-Pedja Reserve (6.4%) than in most other Estonian reserves (3.5%; see Lõhmus, 2002 and Discussion for further details).

The structural elements were mapped on 30 north-south transects on forest land (forest and clear-cuts; Fig. 1). Each transect started from a randomly selected point. More transects (20) were established in managed forests to better represent their larger area. Initially, each transect was 2 km long but in the field (particularly in mires), some parts were reclassified as non-forest lands due to their less than 30% canopy closure (the official criterion for forest definition in Estonia). The actual average length of transects was 1.95 km (minimum 1.76,

total 39.22 km) in managed areas and 1.82 km (minimum 1.34, total 18.12 km) in the reserve.

Fieldwork

The structural elements and vegetation types were mapped on the transects between September 2002 and January 2004. Among vegetation types, four successional stages were distinguished: clear-cut (without tree-layer), scrub (15–20-yr-old thicket), young or middle-aged forest (less than 80 yr), and mature forest (>80 yr). Young, middle-aged and mature forest areas were further delineated according to their type (nine types; see Appendix 1 and Lõhmus, 2004 for details) and location within edge zone (up to 30 m from forest edge to an opening). The baseline for wet forests was at least 30 cm thick peat layer (Paal, 1997); mixed forests were those where neither coniferous nor deciduous trees reached 80% of stand composition.

The following types of structural elements were mapped: (1) cavity trees, (2) remnant trees (trees from the previous forest generation), (3) large broad-leaved trees, which support rich biota or are naturally rare in Estonia (hereafter: broad-leaved trees) – maple (*Acer platanoides*), ash (*Fraxinus excelsior*), oak (*Quercus robur*), lime (*Tilia cordata*), elm (*Ulmus glabra*) and water elm (*U. laevis*) with diameter at breast height (dbh) ≥ 32 cm, and aspen with dbh ≥ 38 cm, (4) snags with dbh ≥ 10 cm and height >1.5 m, divided into those with bark (over 20% of surface covered with bark) and without (Lõhmus and Lõhmus, 2001), (5) logs (diameter of the thickest end ≥ 20 cm; ≥ 50 cm long), and (6) windthrows (≥ 30 cm high). The scarce cavity trees were mapped on 100 m wide belts by J.R. (the total studied area 563 ha), the other elements were studied on 10-m belts by P.L. and K.V. (57 ha). Tree cavities are difficult to detect, and were searched from the ground twice in each transect and once more in selected cavity-rich sites. In the latter areas, no more than 30% additional cavities were found compared to the results of two mappings. J.R. had a five-year field experience in an area where all cavities were also climbed, so most true cavities (suitable for animals) were probably distinguished from unsuitable holes (Wesolowski, 2001). Therefore, we suggest that at least 75% of cavity trees were detected on the transects.

For each element, the tree species and (for standing trees) dbh were recorded. Snags were further characterized by their height and decay stage (1 – hard wood, knife penetrates less than 1 cm into bark, 2 – fairly hard wood, knife penetrates 1–3 cm into the wood, 3 – soft wood, knife penetrates over 3 cm into the wood; Lõhmus and Lõhmus 2001). For logs, their length and diameters of both ends (D_{\max} and D_{\min}) within the transect as well as decay stage (according to Renvall, 1995; five classes ranging from freshly downed logs to those with soft wood) were recorded. Cavities were classified as woodpecker-excavated and other natural cavities, and their minimum entrance size estimated as small

(1–4 cm; incl. those made by *Dendrocopos minor*), medium (>4–6.5 cm; incl. those of medium-sized woodpeckers such as *D. major*), large (>6.5–11; incl. those of *Dryocopos martius*) or very large (>11 cm).

Data analysis

The volumes of individual snags and logs were computed as $V = h\pi(D/2)^2$, where h = height or length of the trunk within the transect, and D = average diameter of the trunk = $[(D_{\max} + D_{\min})/2]$. To calculate D_{\max} and D_{\min} of snags, we used their dbh and height as well as a coefficient describing the average reduction of diameter per height unit. The latter was calculated using the measurements of 782 logs. There were no differences in this coefficient between seven most common tree species (ANOVA: $F_{6, 767} = 0.6$; $P = 0.74$) and we used 1.78 cm diameter change per m of trunk for all snags. We used the concept of CWD profile sensu Stokland (2001) to describe the composition of CWD according to dimensions and decay classes.

The sample unit was one transect. To explore differences between forest types, successional stages or forest interior vs. edge, all patches of the same type were pooled within a transect (as not fully independent observations). Yet, since each transect contained only some of these type*stage*edge combinations (or in too small areas for reasonable density estimates), we were not able to pool these factors into one multivariate model. Instead, we used a two-step procedure by analysing first their univariate effects, and then including significant factors into a reduced set of combinations to test for their pairwise differences between the reserve and the commercial area.

Conventional parametric (t -tests for independent and paired samples; ANOVA) or – if the assumptions of parametric tests were not met – non-parametric statistics (U -test; Kruskal-Wallis ANOVA; χ^2 -test) were used for hypothesis-testing. Before using parametric tests, distributions of all variables were checked for normality (Kolmogorov-Smirnov test) and homogeneity of variances (Levene's test). We did not *a priori* adjust Type I error levels due to multiple tests because these corrections severely reduce test power (Wright, 1992). However, we kept in mind that at $\alpha = 0.05$, given the approximately 80 independent tests, we could have rejected true null-hypothesis in a few cases. Similarities of forest types were identified with a cluster analysis, based on Euclidean distances and Ward's method of linkage. The calculations were performed with Statistica 6.0 software (StatSoft, 1984–2001).

To describe the extent of spatial aggregation of the structural elements, the transects were divided into 100-m sections and the density of each element in each section was calculated. We assessed the inclusion of each element (% of its total numbers) by 10% of best sections (1) for each element individually, (2) for a single set of all elements (based on their total densities). The 10%-level was chosen for illustrative purposes, considering that at least 10% of forest land

warrants strict protection in Estonia (Anon., 2003a; Lõhmus et al., 2004). The co-occurrence of the elements was explored using pairwise non-parametric correlations.

RESULTS

Abundance of the structural elements at the landscape scale

The mean total volume of CWD (logs and snags), density and volume of snags with bark, and the density of cavity trees did not differ between the reserve and the managed landscape (Table 1). Snags with exposed wood were more numerous in the reserve than managed forests, whilst the latter had more logs, windthrows, remnant trees and broad-leaved trees than the reserve. There were also large differences in the vegetation of the two landscapes (Table 1). Nearly half of the commercial landscape, but less than one-fifth of the reserve, was covered with productive dry or mesic forests. Although 21% of the managed area was clear-cut, mature forest was as abundant there (6.8%) as in the reserve (5.8%). Hence, the commercial area generally had no fewer structural elements of old-growth than the reserve, but the effects of timber harvesting and different vegetation were not separable at the landscape scale.

The effects of vegetation type, successional stage, edge and management

Appendix 1 lists the densities of the structural elements in different vegetation types. Given our limited sample sizes, we pooled structurally similar vegetation types for the statistical exploration of vegetation and management effects. The cluster analysis (Fig. 2) brought out four forest types: (1) spruce forests (incl. also coniferous forests of spruce and pine); (2) pine forests (both on mineral and peat soils); (3) mesic mixed and deciduous forests; (4) wet mixed and deciduous forests. The cluster analysis also supported the pooling of clear-cuts and scrub to one regeneration phase, which reduced the number of successional stages to three. Edge area formed 27.6 % of the total area of mesic mixed and deciduous forests, 23.3% of spruce, 17.0% of pine, and 11.7% of wet mixed and deciduous forests.

One-way ANOVAs showed that the abundance of most structural elements differed significantly between successional stages and forest types, but not between forest edge and interior (Table 2). Only remnant trees were found independently of any habitat characteristics and their higher density in commercial forests (Table 1) can be directly attributed to recent green-tree retention strategies. Windthrows tended to be less frequent on regenerating

areas and in pine forests (Appendix), but these differences were statistically not significant (Table 2).

Large broad-leaved trees were nearly a hundred times less abundant in regenerating areas (on average, 0.1 ± 0.3 S.D. ha^{-1}) than in mature forests (9.0 ± 10.4), and were expectably concentrated to mesic mixed and deciduous forests, typical to commercial landscapes (Appendix; Table 1). The mean density of cavity trees in mature forests (1.68 ± 1.33 S.D. ha^{-1}) exceeded the density in regenerating areas by 25 times (0.07 ± 0.15) and the density in young or middle-aged forests (0.54 ± 0.37) by three times (Fig. 3D). Cavity trees tended to be most frequent in mixed and deciduous forests (both mesic and wet) but forest type was statistically significant only if all mixed and deciduous forests were compared to all coniferous forests ($t_{55} = -2.26$, $P = 0.028$).

The mean total volume of CWD was similar in regenerating areas and young or middle-aged forests (Fig. 3C), although there tended to be fewer snags and more logs on regenerating areas (Fig. 3A–B). The amount of CWD in mature forests (19.4 ± 6.9 S.D. $\text{m}^3 \text{ha}^{-1}$) was 2–3 times higher than in the other successional stages; this was true also for snags and logs taken separately (Fig. 3A–C). The occurrence of snags and logs also depended on forest type. Snags with bark were most numerous in mesic and wet mixed and deciduous forests (Appendix), though this difference was not significant for volumes (Table 2). In contrast, decorticate snags occurred typically in pine forests (Fig. 4A). Logs were significantly more abundant in mesic mixed and deciduous than wet forests and pine groves (Fig. 4B).

Considering these effects, we re-established the difference between the reserve and commercial forests for CWD and cavity-trees. Between-habitat comparisons showed large (though statistically not significant) differences in the expected direction – CWD volumes were on average 33% and the density of cavity-trees 42% lower in the managed area (Table 3).

Co-occurrence and spatial aggregation of the structural elements

In 593 100-m sections of the transects, densities of different structural elements correlated weakly ($r_s < 0.4$), though reliably ($P < 0.005$), with each other. Notably, the densities of logs, snags with bark, large broad-leaved trees and cavity-trees were all interdependent ($r_s = 0.15\text{--}0.39$, $P < 0.001$, except for logs vs. cavity-trees, where $r_s = 0.12$, $P < 0.005$). There were also more logs and snags with bark in sites having abundant windthrows ($r_s = 0.39$, $P < 0.001$, and $r_s = 0.27$, $P < 0.001$, respectively). The significant co-occurrence of the two types of snags ($r_s = 0.21$, $P < 0.001$) was the only clear spatial correlation for decorticate snags. There were no such spatial correlations between remnant trees and the other elements.

Most structural elements were also highly aggregated, and there was no difference in the aggregation extent between the reserve and commercial forests. On average, 67% of the numbers of each element could be included in the best 10% of the transect area (the upper half of Table 4). The captured share was <50% only for the most common structural elements – logs and snags with bark. Yet, the generally best 10% of area (based on the total density) included only 12–48% of different elements (mean 27–29%; the lower half of Table 4).

Characteristics of coarse woody debris and tree cavities

CWD was comprised of nine tree species, 78% of the 2564 trunks were Norway spruce, birch, grey alder or Scots pine. Sixty-one percent of all logs and snags were deciduous trees. The CWD profiles of both areas included most decay stages and size classes, but large and well-decayed logs were more abundant in commercial forests (Fig. 5–6). Logs contributed 40% of the total volume of CWD in the reserve and 65% in the managed landscape. The average number of CWD substrata (type*decay stage; up to three stages of both snags with and without bark as well as five stages of logs) per transect did not differ among the reserve and managed forests ($t_{28} = 1.1$, $P = 0.19$), also if tree species were taken into account (max 90 combinations, $t_{28} = -0.29$, $P = 0.77$).

In the managed landscape, cavities were found slightly more often in snags (56% of cavity trees; $n = 201$) than in the reserve (49%; $n = 108$), though the difference was not significant ($\chi^2_1 = 1.3$, $P = 0.26$). On average, each cavity tree had 1.4 (max. 9) cavities. Among all cavities, woodpecker cavities were relatively more frequent in commercial forests (75%; $n = 265$ cavities) than in the reserve (52%; $n = 141$; $\chi^2_1 = 23.5$, $P < 0.001$). In both areas, medium-sized cavities were the most frequent. The main difference between the landscapes was the much lower (4.4 times) density of large natural cavities in commercial forests (Fig. 7).

DISCUSSION

We found that the abundance and quality of structural elements was similar in the commercial and the protected forest landscape, or even lower in the latter. Obviously, larger areas of structurally rich mesic stands concealed the negative effect of timber harvesting in commercial forests (the effect appeared when forest age and type were taken into account in the comparison). Below, we discuss, (1) how much the studied forests differed structurally from natural hemiboreal forests, (2) what consequences the underrepresentation of some forest types in the reserves may have for old-growth biota, (3) what could be the

urgent actions to sustain management-sensitive species in the Estonian forest landscapes.

Landscape-scale comparison with natural forests

The cover of unmanaged old-growth stands in the forest landscapes studied by us (6.4% in the reserve, 1.2% in the commercial landscape; Lõhmus, 2002) is much lower than simulation modelling has estimated for naturally dynamic forest landscapes of Estonia (32–42% of >100-yr-old stands; Lõhmus et al., 2004). Hence, abundance of the structural elements of old-growth in the modern landscape has to be reduced but – to what extent, and what are the consequences to biota? The areas of mature forest did not differ between the reserve and managed landscape (though most such stands had been recently thinned in the latter). Thus the magnitude of the reduction mostly depends on how well the structural features of old-growth have survived outside old-growth stands.

The abundance, size and decay stage of CWD are reliable characters of natural forest, where many species use large and well-decayed dead trees (e.g. Gustafsson and Hallingbäck, 1988; Berg et al., 1994; Hoiland and Bendiksen, 1996; McComb and Lindenmayer, 1999; Siitonen, 2001). The mean volume of CWD in the reserve was 9–20 times less than in Estonian old-growth forests: 98 ± 39 (max. 227) m^3 of total CWD ha^{-1} in Järvselja, eastern Estonia (Kasesalu, 2001), and 110 (max. 200) m^3 of logs ha^{-1} near Muraka bog, north-eastern Estonia (I. Sell, pers. comm.). On average, 41 cavities ha^{-1} have been found in mixed and deciduous old-growth stands in hemiboreal Sweden (Sandström, 1992), i.e. at least 40 times more than in our study landscape (0.5–0.6 cavity trees ha^{-1} having on average 1.4 cavities per cavity-tree, about 30% underestimation). Indeed, the latter resembled rather the cavity-poor north-boreal forests in Lapland (0.5 trees ha^{-1} ; Pulliainen and Saari, 2002). In an old-growth stand in Sweden, 76% of cavities were formed at injuries of old deciduous trees (Carlson et al., 1998), while most of the scarce tree-holes in our area had been excavated by woodpeckers [mostly by *Dendrocopos major* as judged by cavity sizes and bird census data]. Total density of these cavity-nesters in our area (1.5–1.9 pairs km^{-2} of forest land) corresponded to the Estonian average (1.4–1.9; Lõhmus et al., 2000; Lõhmus, 2004). Also the large (dbh >41 cm) broad-leaved trees are drastically more abundant in Swedish reserves (15–120 ha^{-1} ; Götmark and Thorell, 2003) than in the Estonian reserve and managed forests (0.6 and 3.6 trees having dbh ≥ 32 cm ha^{-1} , respectively). The lack of such trees may prevent the occurrence of specialized epiphytes and insects, and partly explains the scarcity of cavities.

To summarize, the general supply of studied substrata for management-sensitive species in the reserve and its surroundings was probably less than 10% of that of natural forests. CWD profiles (Fig. 5–6) indicated that this was due to intensive human use of the whole area in the past. Up to two-fold reduction of

average CWD volumes can be attributed to recent afforestation (Lõhmus and Lõhmus, 2005), which has occurred in our study area as well as other large reserves and their surroundings (Aaviksoo, 2002). Most of the impoverishment, however, has to be attributed to long-term intensive forest management: the first forest reserve was established only in 1924, and most of the Estonian forests, including the current Alam-Pedja Nature Reserve, have been clear-cut at least once within 200 yr (Valk and Eilart, 1974).

Commercial vs. protected forest

The major aim of strict forest reserves in Estonia is to maintain viable populations of the species that do not survive in timber production areas. The focus is on old-forest species, since a natural Estonian landscape would have had much more old stands than the current commercial forests (Lõhmus et al., 2004). It might seem odd that the timber-harvesting area was not more impoverished than the reserve, and one may even ask whether additional reserves, or even those already established, are needed at all for the preservation of old-growth dependent species. But, we argue that the recent harvesting effects in the commercial landscape were concealed by (1) a larger share of structurally rich forest types, and (2) extensive rather than intensive management practices in the recent past.

In boreal and temperate regions, the stands on productive soils contain more deciduous trees; the trees grow faster, provide more cavities and higher CWD volumes (Carey, 1983; Harmon et al., 1986; Sippola et al., 1998; Siitonen, 2001; Uotila et al., 2001; Nilsson et al., 2002). Due to conflicting interests with forestry, such productive areas are usually under-represented in reserves (e.g. Stokland, 1997). In Estonia, the most productive forest types (*Aegopodium*, *Dryopteris*, *Oxalis* and *Hepatica* types; Lõhmus, 1984; Kõlli, 2002) cover only 10% of strictly protected forests but 28% of all forests, while the least productive types (bog, oligotrophic paludifying and heath forests) cover 35% and 7%, respectively (Anon., 2003b; K. Viilma, pers. comm.). This scarcity of mesic mixed and deciduous forests obviously caused the near-absence of large broad-leaved trees in the studied reserve, which in turn was also likely to negatively influence the density of tree cavities.

Logs were also more abundant in the mesic forests as well as on clear-cuts, which are generally very poor of old-growth features, unless these are purposefully retained (e.g. Sturtevant et al., 1997; Sippola et al., 1998; Pedlar et al., 2002). In the Soviet period (1945–1991), large felled trunks were often left on clear-cuts in Estonia; similar clear-cut practices are still used in Russia (Tarasov and Birdsey, 2001). These old clear-cuts provided the large and well-decayed logs of the managed forests, and explain why the mean volume of CWD in the commercial landscape (9.0 m³/ha) exceeded that of the Fennoscandian hemiboreal and south-boreal managed forests (1.2–3.5 m³/ha;

Siitonen, 2001). Our results (Fig. 3) recall the “U-shaped” abundance trend of logs, and a general increase of snags, found within 100 yr after clear-cut disturbance in boreal Newfoundland (Sturtevant et al., 1997). Some increase of logs in the managed area could be also attributed to their accumulation in forest edges, which was nearly significant in our data (Table 2) and has been shown also in other studies (Mills, 1995; Snäll and Jonsson, 2001). Though the areas of edge-zones did not differ between the reserve and the commercial landscape, the latter had more sharp (e.g., forest-field) and recent (forest-clearcut) edges (Löhmus, 2002) where trees relatively more often die and fall (Snäll and Jonsson, 2001).

When forest type and successional stage were taken into account, CWD volumes were on average 33% and the density of cavity-trees 42% lower in the timber-harvesting area. A high variation among our small samples reduced the power to detect statistically significant differences, but such timber-harvesting effects on CWD have been convincingly shown for dry boreal forests of Estonia (Kohv, 2003). The lack of large cavities and snags has been also demonstrated in the commercial forests of our study area, and linked to low numbers and productivity of a large cavity-nesting bird, the Ural owl (*Strix uralensis*) (Löhmus, 2003). Thus, there is little doubt that recent thinnings and sanitary cuttings are affecting the old-growth structures negatively, but this far their effect seems to be smaller than the confounding effects of different vegetation and previous clear-cutting techniques. For example, the harvest-induced reduction of tree-cavity abundance may be concealed by their aggregation to mature forests and broad-leaved trees, which were either similarly represented (mature forests) or more frequent (large broad-leaved trees) in the commercial area.

Management implications

In Estonia, the extant fragments of old-growth still host high numbers of hemerophobic species (Trass et al., 1999; Vellak and Paal, 1999; Parmasto et al., 2004) but 5% of such stands are being lost annually (Kurlavicius et al., 2004). As discussed above, our sample area represented all the major processes which are typical for Estonian forest landscapes. In fact, the reserve had even an above-average share of old-growth among the Estonian reserves, and also a relatively rich biota (see Methods; Löhmus and Löhmus, 2001; Parmasto et al., 2004). Yet, it contained as few substrata for old-growth species as the surrounding timber-harvesting area. Based on this model system, we distinguish three major challenges for biodiversity protection in Estonian forests.

(1) Restoration of old-growth features in the extensive, but poor-quality reserves. The Estonian Forestry Development Programme aims to strictly protect at least 10% of forest land by year 2010 (Anon., 2003a). While this has been an important step towards representative reserve network, an area itself

does not sustain management-sensitive species, unless the quality of the reserves also meets acceptable levels. For example, breeding specialist woodpecker species need at least 4–5 times higher volumes of snags in the long term (see Angelstam et al., 2003) than we found both in the reserve ($3.9 \text{ m}^3 \text{ ha}^{-1}$) and in the commercial forest ($3.2 \text{ m}^3 \text{ ha}^{-1}$). Currently, mean CWD volumes $28\text{--}49 \text{ m}^3 \text{ ha}^{-1}$ have been found in the core areas of strict reserves that have been unmanaged over 30 years (Köster et al., 2003).

(2) Protecting additional productive (dry and mesic) forests, not only to conserve their type-specific biota (Lõhmus et al., 2004) but also to add sites where some old-growth structures can be more abundant (large deciduous trees, tree cavities) or develop more quickly (CWD).

(3) Close-to-nature approaches in commercial forests, because areas not devoted primarily to nature conservation will always stay important for biodiversity conservation (Lindenmayer and Franklin, 2002). Moreover, given that different structural elements were concentrated in separate sites, small additional reserves would not effectively increase the protected supply of old-growth features in the studied landscape. Our results suggest that in Estonia, the quality of commercial forests may be critical during some next decades, until sufficient amounts of specific habitats for old-growth species will be developed or restored in the reserves. The relevant techniques to manage commercial forests include (a) retaining small patches with old-growth characteristics in thinning areas to increase the average amount and continuity of CWD within a stand (e.g. Ranius et al., 2003); (b) retention of cavity-trees and CWD at thinnings (Siitonen et al. 2000; Bebbber et al., 2005); (c) additional tree retention on clear-cuts. Clear-cuts during the Soviet era held a relatively large amount of CWD but they are nowadays cleaned more carefully. The mean volumes of CWD in our study were already much lower than in the adjacent western Russia ($14\text{--}20 \text{ m}^3/\text{ha}$; Krankina et al., 2002), and one can expect a negative trend to continue and important habitats for threatened saproxylic species (Kaila et al., 1997) to be lost.

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Table 1. Vegetation characteristics and densities of the structural elements of old-growth in commercial forests ($n = 20$ line transects) and the Alam-Pedja Nature Reserve ($n = 10$)

Variable	Mean \pm 95% conf. interval		Difference	
	Commercial forest	Reserve	Statistic	<i>P</i>
Vegetation characteristics (%)				
Clearcuts	20.6 \pm 6.3	0.1 \pm 0.2	$U = 0$	< 0.001
Dry and mesic forests	48.8 \pm 11.8	18.3 \pm 14.3	$U = 37$	0.005
Mature forests	6.8 \pm 5.2	5.8 \pm 4.8	$t = 0.24$	0.812
Forest edge (30 m from opening)	17.9 \pm 5.3	15.9 \pm 6.1	$t = 0.45$	0.656
Structural elements (no. ha⁻¹)				
Remnant trees,	1.10 \pm 0.53	0.16 \pm 0.23	$U = 39$	0.006
Broad-leaved trees (incl. aspen),	3.62 \pm 2.12	0.57 \pm 0.53	$U = 57$	0.051
Snags with bark*	21.92 \pm 6.88	24.12 \pm 9.98	$t = -0.4$	0.722
Barkless snags*	3.37 \pm 1.10	16.21 \pm 10.49	$U = 42$	0.011
Logs*	17.65 \pm 4.95	7.80 \pm 4.10	$t = 2.5$	0.017
Windthrows	8.12 \pm 1.92	4.50 \pm 2.44	$t = 2.2$	0.036
Cavity trees	0.50 \pm 0.14	0.60 \pm 0.22	$t = -0.7$	0.475
CWD (m³ ha⁻¹)	8.99 \pm 2.36	6.24 \pm 2.17	$t = 1.5$	0.156
Snags with bark*	2.61 \pm 0.78	2.20 \pm 1.06	$t = 0.6$	0.557
Barkless snags*	0.56 \pm 0.34	1.68 \pm 1.29	$U = 50$	0.028
Logs*	5.82 \pm 1.88	2.36 \pm 1.22	$U = 45$	0.016

*minimum dbh 38 cm for aspens, 32 cm for other broad-leaved trees, 10 cm for snags and 20 cm for logs

Table 2. Differences between three successional stages, four forest types, and forest edge and interior in the abundance of the structural elements (one-way ANOVA or Kruskal-Wallis ANOVA). See Fig. 3–4 for details about significant effects

Structural element	Effects on density or volume					
	Successional stage		Forest type		Forest edge	
	Statistic	<i>P</i>	Statistic	<i>P</i>	Statistic	<i>P</i>
Density (no. ha⁻¹)						
Broad-leaved trees	H = 12.8	0.002	F = 8.2	<0.001	H = 0.1	0.816
Remnant trees	F = 0.4	0.651	H = 4.4	0.219	H = 0.5	0.826
Snags with bark	F = 5.8	0.006	F = 5.4	0.003	F = 0.8	0.373
Barkless snags	F = 4.3	0.018	H = 20.8	0.000	F = 0.5	0.501
Snags total	<i>F</i> = 7.5	<i>0.001</i>	<i>F</i> = 2.6	<i>0.059</i>	<i>F</i> = 0.2	<i>0.640</i>
Logs	F = 0.4	0.069	H = 18.5	<0.001	H = 3.5	0.063
Windthrows	F = 3.1	0.056	F = 2.5	0.070	H = 2.7	0.100
Cavity trees	H = 32.2	<0.001	F = 1.8	0.157	H = 0.9	0.332
Volume (m³ ha⁻¹)						
Snags with bark	F = 3.4	0.041	F = 1.8	0.155	H = 0.5	0.479
Barkless snags	F = 8.7	0.001	F = 14.7	<0.001	F = 0.8	0.372
Snags total	<i>F</i> = 8.3	<i>0.001</i>	<i>F</i> = 0.9	<i>0.456</i>	<i>F</i> = 0.8	<i>0.388</i>
Logs	F = 7.9	0.001	F = 7.0	<0.001	F = 2.2	0.148
CWD total	<i>F</i> = 10.9	<i><0.001</i>	<i>F</i> = 2.3	<i>0.087</i>	<i>F</i> = 1.8	<i>0.192</i>
No. of patches*	53		57		51	

* for cavity trees *n* = 52, 57 and 37, respectively

Table 3. Volume of coarse woody debris and density of cavity trees in different forest habitats of the reserve (A) and commercial landscape (B). Total numbers (based on summed areas) are presented due to small and unequally distributed samples. Forestry effects were tested between habitats (paired *t*-tests), using those habitats with at least 0.25 (CWD) or 2.50 (cavities) ha of total studied area in both landscapes

Vegetation type and age*	CWD volume, m ³ ha ⁻¹		No. of cavity trees ha ⁻¹	
	A	B	A	B
Spruce forest (M)	36.4	9.4		
Pine forest (M)	16.3	12.5	1.22	0.90
Pine forest (Y)	3.4	5.6	0.18	0.33
Mesic mixed and deciduous forest (M)	9.3	21.9		
Mesic mixed and deciduous forest (Y)	9.8	10.8	0.97	0.57
Wet mixed and deciduous forest (M)	38.8	17.8	4.35	2.15
Wet mixed and deciduous forest (Y)	4.5	6.3	0.61	0.64
Regenerating area	19.5	7.7	0.57	0.03
Mean difference	5.7		0.55	
Significance of the effect	$t_7 = -1.22,$ $P = 0.26$		$t_5 = -1.57,$ $P = 0.18$	

* M – mature; Y – young or middle-aged forest

Table 4. Share of structural elements in the best 10% of area in commercial forests and the Alam-Pedja Nature Reserve

Structural element*	% of elements in the best sites	
	Commercial forests	Reserve
Sites selected for each element		
Broad-leaved trees (incl. aspen)	92	100
Remnant trees	100	(100)
Snags with bark	46	38
Barkless snags	73	60
Logs	46	58
Windthrows	54	60
Cavity trees	56	56
Average for all elements	67	67
Sites selected for the total set of elements		
Broad-leaved trees (incl. aspen)	48	45
Remnant trees	15	(0)
Snags with bark	36	27
Barkless snags	23	28
Logs	34	40
Windthrows	31	35
Cavity trees	16	12
Average for all elements	29	27

* sample sizes in commercial forest + reserve: 143+11 large broad-leaved trees, 41+3 remnant trees, 865+454 snags with bark, 134+262 barkless snags, 698+151 logs, 322+88 windthrows, 198+108 cavity trees

Appendix. Summary statistics of different vegetation types on the 30 random line transects in east-central Estonia. Densities and volumes of structural elements have been calculated for the total area of each vegetation type to represent the landscape scale

Variable	Forest type							Scrub	Clear-cut
	Mesic spruce	Dry pine	Mesic coniferous	Mesic mixed	Mesic deciduous	Wet pine	Wet mixed	Wet deciduous	Wet birch
Abbreviation:	<i>MSP</i>	<i>DPN</i>	<i>MCO</i>	<i>MMX</i>	<i>MDE</i>	<i>WPN</i>	<i>WMX</i>	<i>WDE</i>	<i>WBR</i>
General characteristics									
Area in 10-m (100-m) belt, ha	2.7 (26.0)	1.0 (9.9)	0.7 (8.4)	6.8 (65.6)	11.5 (113.3)	7.1 (68.9)	4.1 (40.9)	7.7 (76.2)	5.7 (57.2)
% of total area	5	2	1	12	20	12	7	14	10
Age, yr	30–50	55–110	40–110	35–85	40–80	40–130	30–90	30–70	20–80
Structural elements, no. ha ⁻¹									
Broad-leaved trees*	1.10	–	–	5.78	9.01	–	0.24	0.77	0.18
Remnant trees**	1.46	–	2.67	1.33	1.13	0.28	0.49	0.26	0.53
Snags with bark*	15.74	14.72	14.71	29.63	35.71	9.79	24.47	34.86	23.52
Barkless snags*	0.73	15.70	2.67	2.96	3.29	29.78	10.28	3.49	1.93
Logs*	12.81	4.91	16.04	21.33	22.10	2.27	9.30	9.04	5.97
Windthrows	13.18	3.93	10.70	11.41	8.41	1.13	9.05	7.62	5.97
Cavity trees	0.38	0.20	0.48	1.07	0.65	0.45	1.04	0.66	0.35
Volume of CWD, m ³ ha ⁻¹									
CWD total	7.83	6.56	8.14	11.75	11.53	5.02	7.72	6.52	3.85
snags with bark*	3.57	1.57	1.37	3.55	3.66	1.17	2.48	3.19	2.29
barkless snags*	0.04	2.34	0.35	0.33	0.32	2.94	1.82	0.41	0.11
logs*	4.22	2.65	6.43	7.86	7.56	0.91	3.41	2.92	1.46

*minimum dbh >30 cm for broad-leaved trees (incl. aspen), 20 cm for logs, and 10 cm for snags

**trees from the previous forest generation, excl. broad-leaved trees

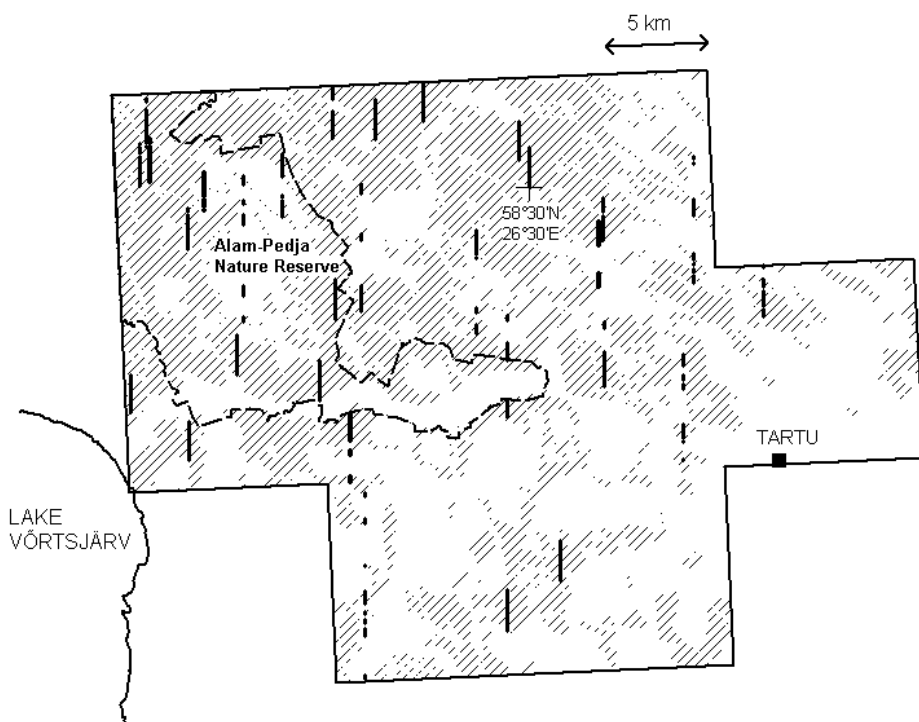


Fig. 1. Location of the study area and the survey transects (straight N-S lines). Forest land is dashed and the border of the Alam-Pedja Nature Reserve is marked with the broken line.

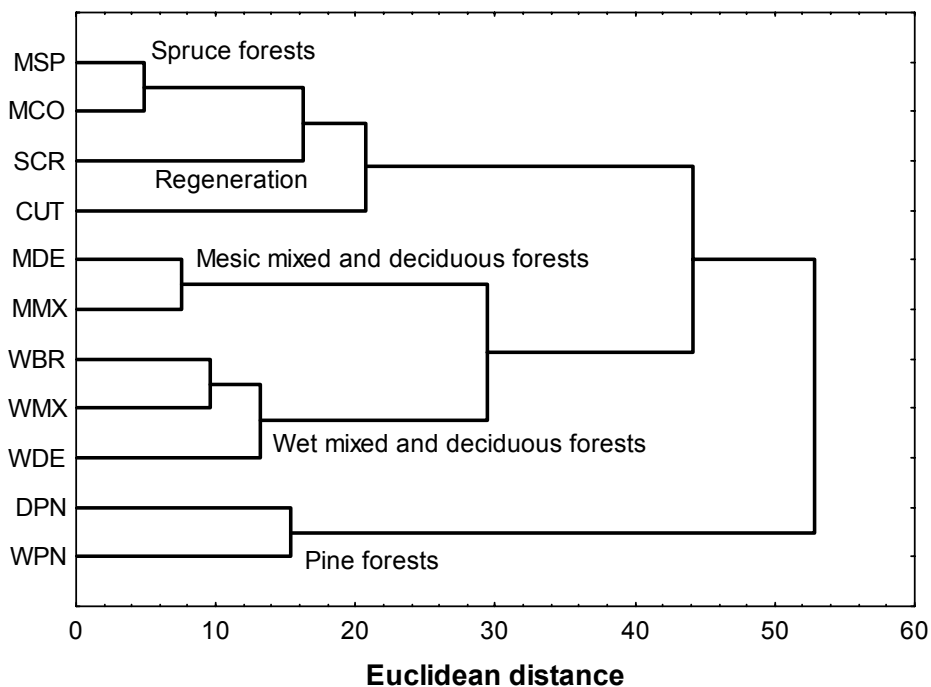


Fig. 2. Similarity of nine forest types, clearcuts and scrub according to their densities of structural elements of old-growth. Ward's method was used for clustering. The main clusters, which were used in further analyses, are indicated with labels. See Appendix for raw data and the abbreviations of vegetation types.

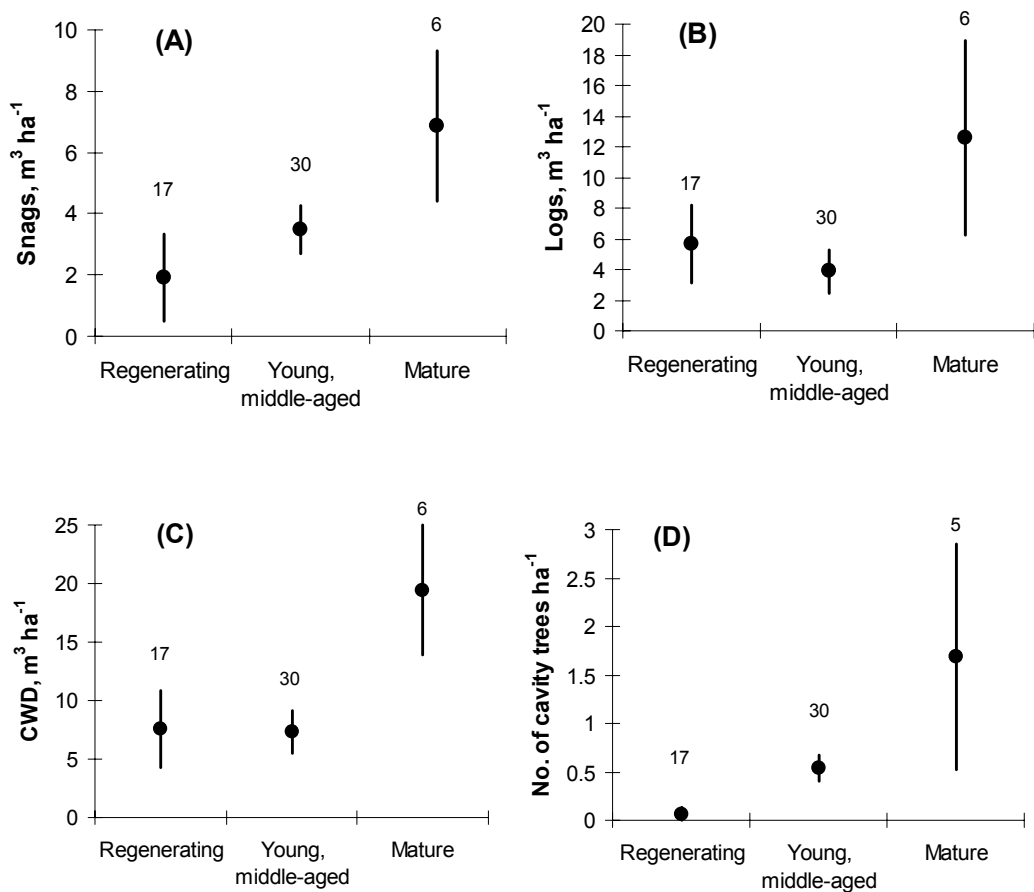


Fig. 3. Average (± 95% confidence intervals) amounts of structural elements (A – snags, B – logs, C – total CWD, D – cavity trees) in relation to successional stage. Sample sizes are indicated with numbers. See Table 2 for statistical tests.

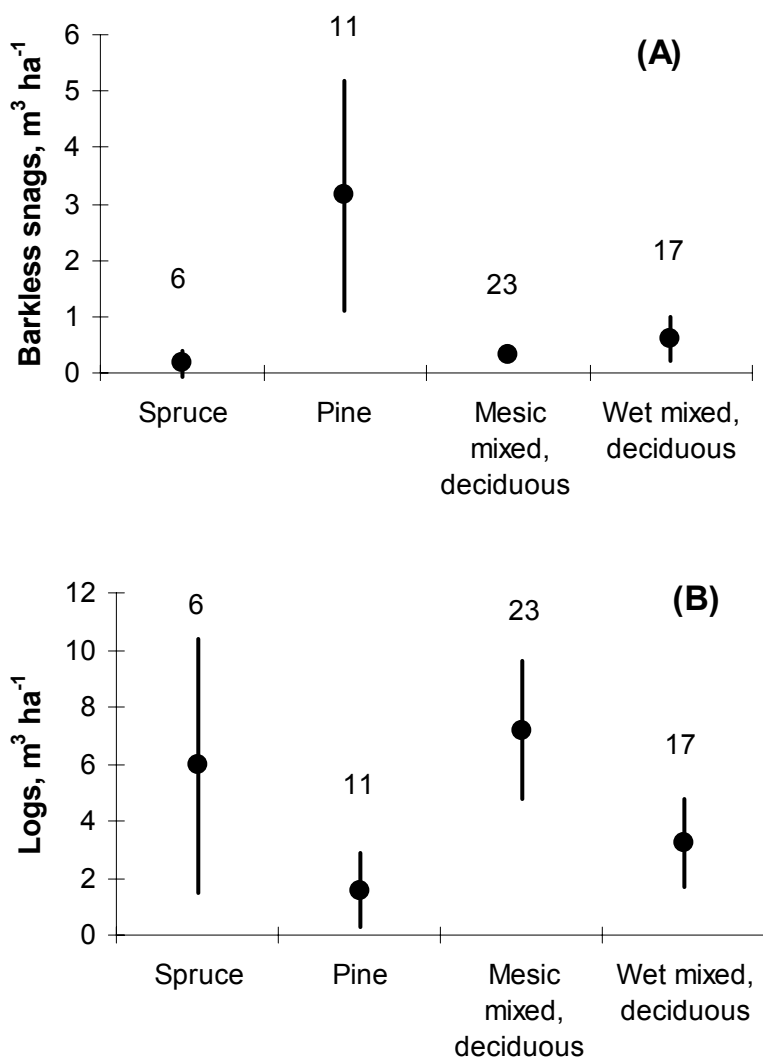


Fig. 4. Average (\pm 95% confidence intervals) amounts of structural elements (A – snags with exposed wood; B – logs) in relation to forest type. Sample sizes are indicated with numbers. See Table 2 for statistical tests.

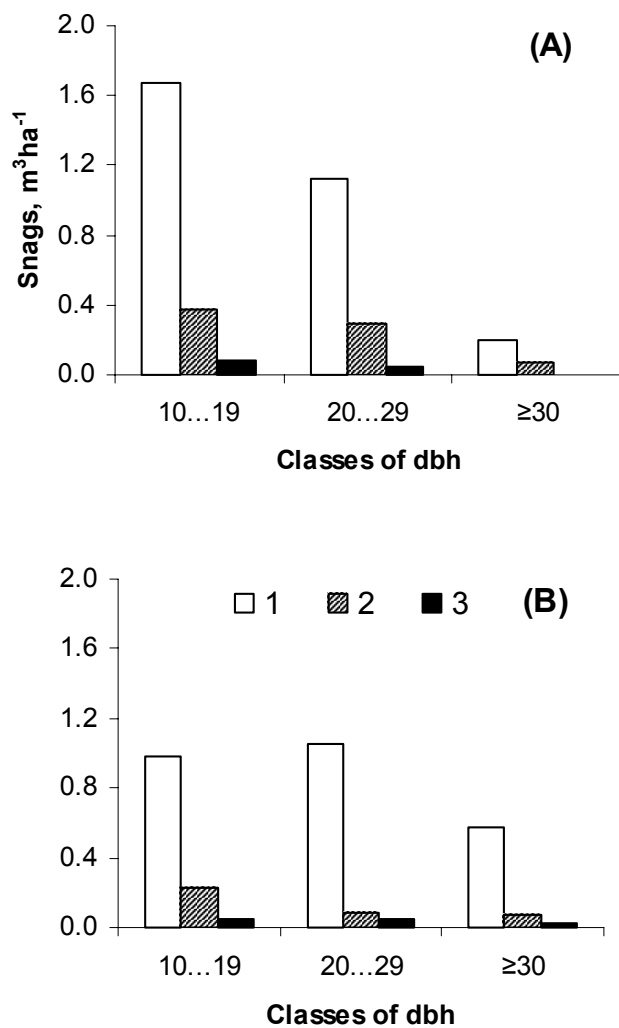


Fig. 5. The average volume of snags in the reserve (A) and managed forest (B) according to three diameter classes and three decay stages (wood: 1, hard; 2, fairly soft; 3, soft).

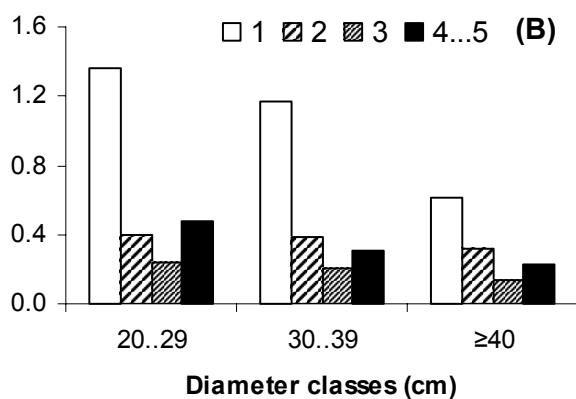
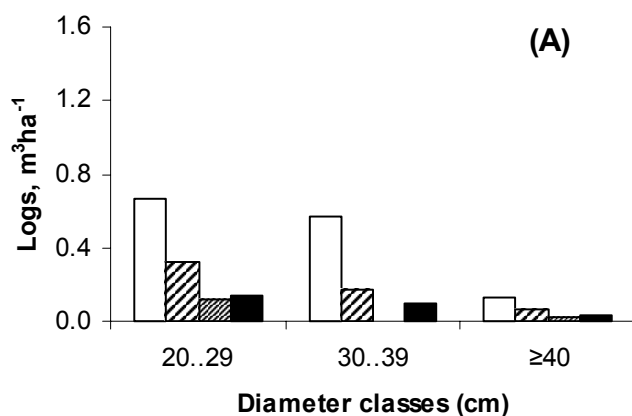


Fig. 6. The average volume of logs in the reserve (A) and managed forests (B) according to three diameter classes and four decay stages (1, wood hard, bark ± intact, freshly downed logs; 2, wood fairly hard, small patches of bark left; 3, wood fairly soft, trunks decorticated; 4–5 wood soft to very soft, trunks extensively to almost completely decomposed).

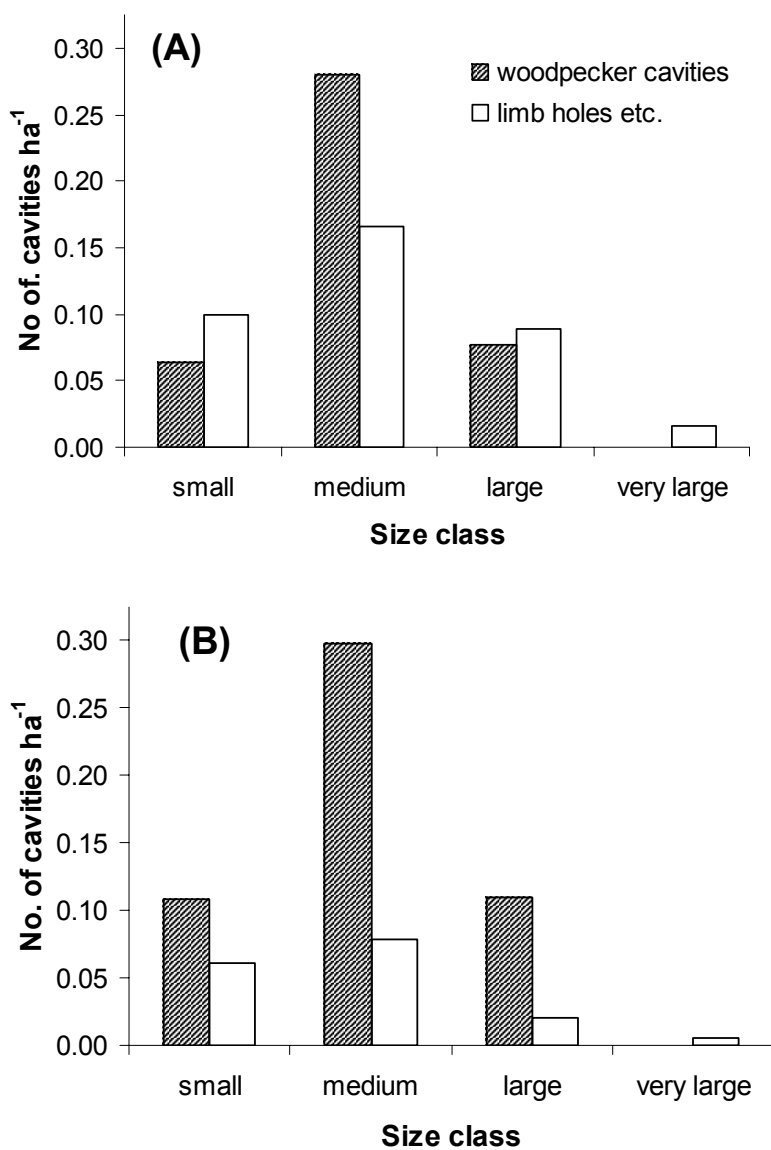


Fig. 7. Average density of woodpecker-cavities and other natural cavities in the reserve (A) and managed forest (B).

COARSE WOODY DEBRIS IN MID-AGED STANDS: ABANDONED AGRICULTURAL VERSUS LONG- TERM FOREST LAND

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ABSTRACT

During the 20th century, large agricultural areas in Eastern Europe have become forested after their abandonment. To explore the value of these new forests for biota, we assessed volumes of coarse woody debris (CWD) on random transects in mid-aged (40–75 yr) stands. In mixed and deciduous forests that were not forested in the 1930s, downed tree (log) volumes were about two times lower than in cutover sites. The effect on snag volume depended on site type and was generally non-significant. Large-diameter CWD comprised similar proportions in the long-term and new forest areas, but large well-decayed trunks tended to be less frequent in the latter. No reduction of dead wood volume was found in new pine stands, 98% of which had previously been classified as mires (bogs). Hence the origin of mid-aged successional forests had affected their CWD-supply (particularly logs) to some extent, but the general scarcity of CWD all over the forest land indicated much larger (at least five-fold) losses due to timber-harvesting. We conclude that naturally reforested areas should not be automatically excluded from reserve establishment or other CWD-related conservation programmes.

INTRODUCTION

In forest ecosystems, coarse woody debris (CWD, incl. standing and downed dead trees, dead branches and stumps) plays an important role in nutrient and energy flows as well as for biodiversity (Harmon et al. 1986, Samuelsson et al. 1994, Jonsson and Kruys 2001). Hence, for the planning of ecologically sustainable forest management, it is crucial to know the factors that affect the amount, types and continuity of CWD (Harmon 2001, Lindenmayer and Franklin 2002). Since the basic processes are slow (tree growth and decomposition) or rare (tree death, particularly from large-scale disturbances), the supply of CWD in an area is largely determined by its past (e.g. Storaunet et al. 2000, Stokland 2001, Krankina et al. 2002, Ramovs and Roberts 2003).

While timber-harvesting effects on CWD are obvious and have been extensively studied (McComb and Lindenmayer 1999, Siitonen 2001), other human influences are far less documented. Notably, the CWD-supply in recently forested areas could be largely determined by their non-forest history; for example, in Europe where vast new woodlands have appeared during the 20th century after millennia of deforestation. This reforestation (currently c. 11 000 km² per year) is mainly taking place in those countries that have implemented special programmes through planting or by allowing open lands to be converted to forest (European Environment Agency 2003). The biodiversity value and the need for ecological restoration of reforested areas are important areas of research worldwide (Frelich and Puettmann 1999).

In theory, long-term forests should have more CWD than new forests of similar composition and age, because the latter have no residual CWD from previous tree generations (Harmon 2001). This implies a relatively low biodiversity value of the reforested areas, as these are likely to provide fewer habitats for saproxylic or epixylic species, which in northern forests, for example, comprise 20–25% of all and the majority of threatened forest-dwelling species (Berg et al. 1994, Siitonen 2001). Indeed, the scarcity of CWD and low conservation value are obvious in intensive forest plantations (Fleming and Freedman 1998), such as those used for afforestation in West- and South-Europe. In Eastern Europe, however, large abandoned agricultural areas and grasslands have reforested naturally and most have been unmanaged for decades (Tucker and Evans 1997, Mander and Palang 1999). Such areas may have more potential for sustaining threatened forest species and improving reserve networks, particularly if traditional forest lands are impoverished due to long-term intensive forestry (Löhmus 2004, Löhmus et al. 2004). Their value, however, has not been explicitly evaluated so far.

In this paper, we explore whether long-term forests have more CWD than new stands on previous agricultural lands, and discuss how large this effect is compared to that of timber-harvesting. We compare stands of similar age and composition with different previous land use in Estonia, where the forest cover has increased from about 20% to over 50% during the last 60 years (Lõhmus et al. 2004). We focus on deciduous and mixed mid-aged stands, which cover the largest areas of new forest land and are characteristic of natural regeneration on the moderately fertile soils of abandoned farmland. Between 1958 and 2000, deciduous stands comprised 68% of the 0.84 mln ha increase in the Estonian forest area (calculated from Viilup 2000). We expect that the history has mostly influenced downed dead trees (logs), not the standing ones (snags), since few dead trees stand for decades (e.g., the mean 'life expectancy' of large hollow snags is below 10 yr in Estonia; Lõhmus 2003). As a reference process, we analyse the afforestation of drained (wooded) mires, which is not a primary succession in the strictest sense.

MATERIALS AND METHODS

The study was carried out in a 900-km² area with UTM-grid (10*10 km) borders in east-central Estonia. Forest land covered 49%, agricultural lands 36%, mires 8%, flood-plains 2%, rivers and lakes 2%, and settlements 3% of the area. Due to a long clear-cutting history, most forests had one even-aged tree layer, consisting on average of 46% birch *Betula* sp., 17% Scots pine *Pinus sylvestris*, 15% Norway spruce *Picea abies*, 9% aspen *Populus tremula*, 7% grey alder *Alnus incana*, 6% black alder *Alnus glutinosa* and 1% other tree species. The landscape composition was similar to the Estonian average, though the forests contained more birch and fewer coniferous trees.

For sampling, thirty long (2 km), straight and narrow (10 m) transects were randomly delineated on forest land (forest and clear-cuts). The total considered area was 57.3 ha, since some sites were reclassified as non-forest land in the field. Mid-aged (40–75 yr) stands comprised 67% of the transect area, followed by clear-cuts (14%), young (20–35 yr) stands (10%), mature (at least 80 yr) stands (6%) and scrub (3%). According to cluster analysis of stand structure (Lõhmus et al., in review), four main forest types were distinguished: fresh mixed and deciduous forests (mostly *Aegopodium* and *Filipendula* types; hereafter FRESH), fresh spruce forests (at least 80% of Norway spruce in the tree layer; SPRUCE), wet mixed and deciduous forests (swamp, mixotrophic bog and drained peatland forests; WET), and pine forests (at least 80% of Scots pine; either *Vaccinium*-type or bog forests; PINE). Further details about the area, transects, habitats and the general amounts of CWD across the forest

landscape are available elsewhere (Löhmus 2002, 2004; Löhmus et al., in review).

We determined historical land cover (forest land, agricultural land or mire) of the transects from digital GIS-linked images of topographic maps (1:50 000; prepared in 1937–1939). The comparison of long-term and new forest land was possible for mid-aged FRESH (a total of 15.0 ha), WET (15.0 ha) and PINE (7.1 ha), which covered sufficiently large areas for statistical treatment. SPRUCE covered only 3.0 ha (44% of this new forest), and was structurally too different to be pooled with the other types. The intensity of recent management did not differ significantly between the forests with different previous land use: recent (10–15 yr old) signs of thinnings or sanitary cuttings were found in 17% of state forests (mostly long-term forest land) and 21% of private forests (the main area of reforestation) (A. Löhmus, unpubl. analysis; see Löhmus 2002 for methods).

Between September 2002 and January 2004, snags (diameter at breast height, DBH ≥ 10 cm; over 1.5 m tall) and logs (diameter of the thickest end ≥ 20 cm; ≥ 50 cm long) were mapped on the transects. Snags were characterized by their height and decay stage (1 – hard wood, knife penetrates less than 1 cm into bark, 2 – fairly hard wood, knife penetrates 1–3 cm into the wood, 3 – soft wood, knife penetrates over 3 cm into the wood; Löhmus and Löhmus 2001). For logs, their length and diameters of both ends (D_{\max} and D_{\min}) within transect as well as decay stage were recorded (Renvall, 1995: five classes ranging from freshly downed logs to those with soft wood). The volumes of individual snags and logs were computed as $V = h\pi(D/2)^2$, where h = height or length of the trunk within the transect, and D = average diameter of the trunk = $[(D_{\max} + D_{\min})/2]$. To calculate D_{\max} and D_{\min} of snags, we combined their DBH and height with a coefficient describing the average reduction of diameter per height unit. Considering the measurements of 782 logs, we found no differences in this coefficient between the seven most common tree species (ANOVA: $F_{6, 767} = 0.6$; $P = 0.74$) and we used 1.78 cm diameter change per every m of trunk for all snags.

In analyses, the sample unit was a transect, so that all patches of the same type were pooled within a transect (as not fully independent observations). Before using t -test or ANOVA, distributions of all variables were checked for normality (Kolmogorov-Smirnov test) and homogeneity of variances (Levene's test). The tests of historical effects on CWD volumes were one-tailed, since there was no reason to expect more CWD in new than long-term forest areas.

RESULTS

The three types of new forests had different origins. Ninety-eight percent of the new PINE area (a total of 4.0 ha) had been mires in the 1930s; this share was 59.0% for WET (8.6 ha), but only 22.4% for FRESH forests (6.0 ha). The historical maps we used did not distinguish mire types, but landscape characteristics and the present situation indicated that most of the mires under PINE had been bogs, while most of the mires under WET and FRESH stands had been fens. The share of previous agricultural lands ranged from 2.0% (PINE) and 13.8% (WET) to 51.1% (FRESH). In addition, significant deciduous and mixed forest areas had developed from flood-plain meadows (25.5% of FRESH, 24.2% of WET).

As expected, logs were more abundant in the long-term than in new mixed and deciduous forests (Table 1); the differences between means being 1.8-fold for FRESH and 2.5-fold for WET stands (Fig. 1). For snags, a similar 2.4-fold difference was observed in WET, but not in FRESH, sites; this dependence of the effect on forest type was statistically near-significant ($P < 0.1$), and the main effect of origin was non-significant (Table 1). The total average volumes ($\pm 95\%$ confidence intervals) of CWD in new and long-term forests were 8.5 ± 4.2 ($n = 12$) and 10.9 ± 4.4 ($n = 18$) in FRESH, and 4.2 ± 2.1 ($n = 12$) and 10.1 ± 9.1 ($n = 12$) in WET stands, respectively. CWD was not more abundant in long-term than new PINE areas ($t_{10} = -0.71$, $P = 0.75$, and $t_{10} = -1.32$, $P = 0.89$, for logs and snags, respectively).

Large logs ($D_{\max} \geq 30$ cm) and snags ($DBH \geq 25$ cm) comprised similar fractions of all items in FRESH and WET stands of different previous land use, but large well-decayed items (stages 4–5 of logs, stage 3 of snags) tended to be less frequent in the new forests. Large logs formed 29% of all logs both in the long-term ($n = 332$) and new forests ($n = 86$); the proportions for large snags were 8% ($n = 713$) and 7% ($n = 358$), respectively. Among large logs, well-decayed ones comprised 10% in long-term forests ($n = 97$) and 4% in new forests ($n = 25$), these proportions were 7% ($n = 60$) and 4% ($n = 24$) for large snags. Yet, with our small sample sizes, we were not able to prove the role of history in the share of well-decayed items even when large logs and snags were pooled ($\chi^2_1 = 1.2$, $P = 0.27$).

DISCUSSION

We found that in mid-aged forests in east-central Estonia, log volumes were about two times lower in first-generation deciduous and mixed stands than in those regenerated after clear-cutting; there was no such clear pattern for snags

in these stands; and CWD reduction was not observed in pine groves. The differences between forest types were expected given their different histories – most of the “new” pine stands were not true first-generation forests, but originated from wooded bogs, overgrown after drainage or reclassified as forest due to changed criteria. In contrast, most of the new deciduous and mixed forests had been previously used as pastures (e.g. fens), for hay-making (e.g. flood-plain meadows; Laasimer 1965) or for agricultural crops. Namely such productive or swampy forest lands are currently in the heart of the conservation debate in many countries including Estonia, since they have been extensively drained, cleared for agriculture or intensively managed for timber production, and they are dramatically under-represented in reserves (Lindenmayer and Franklin 2002: 89–90; Lõhmus et al. 2004).

The accumulation of logs through forest history is theoretically sound (Harmon 2001) and documented also on previous agricultural lands (Currie and Nadelhoffer 2000), but the near-significant dependence of snag accumulation on forest type (the interaction term in Table 1) requires some interpretation. It can be a random error, given the relatively low confidence ($P < 0.1$), our limited samples, and the number of statistical tests performed. CWD is often very unequally distributed across landscapes, which makes the sampling rather laborious (Jonsson and Kruys 2001) and causes large variation among measurements (see the wide confidence intervals in Fig. 1). We hypothesize, however, that the interaction term may also reveal different tree growth rates, when new large snags appear and/or old ones decay more slowly in wet than fresh forests. Such differences in turnover rates may explain the existence or absence of the old snag cohort in mid-aged stands (see e.g. Harmon et al. 1986), and suggest that management or disturbance effects may be more long-term in wet than fresh forests.

Our numerical results provide insight into two major issues of East European forestry: (1) human-induced loss of CWD, and (2) the conservation value of reforested areas. The conclusions may also apply in other boreal or temperate areas that have reforested naturally after the Second World War, but not in recently afforested regions where the young new stands differ drastically from cutover sites.

(1) The average CWD-volumes on the Estonian forest land are approximately ten times lower than expected under natural disturbances (Lõhmus et al., in review). Our study suggests that rapid reforestation can explain only a minority of this reduction, since the differences between mid-aged forests with different previous land use, if present at all, were just two-fold. Most of the historical forest land had probably had several forest generations, since our land-use data represents the most forest-poor period in Estonia (Lõhmus et al. 2004). Therefore, long-term intensive forestry is probably the

major cause of CWD-scarcity in Estonia – the clear-cutting system has skewed the age distribution of stands, and the removal of dead or dying trees in sanitary cuttings and thinnings as well as extensive firewood collecting up to the middle of the 20th century (Valk and Eilart 1974), have obviously reduced the actual and potential CWD within stands. By now, CWD-rich old-growth is almost absent (Lõhmus 2002), and mid-aged stands that often have the lowest amounts of CWD (Sturtevant et al. 1997, Carmona et al. 2002) are over-abundant compared to the natural situation in Estonia (Lõhmus et al. 2004). On our random transects, mid-aged stands formed 67% of the forest land.

(2) Hence, the conservation value of the first-generation mid-aged forests can be interpreted in two ways. On an absolute scale, the stands studied by us were CWD-poor, and hardly provided superior habitat for epixylic or saproxylic organisms. However, in relative terms (compared with the available second-growth), the new forests were only slightly more impoverished. In addition to the forestry effects discussed above, one reason for the small difference may be that most of the historical grasslands in Estonia have been wooded meadows (Kukk and Kull 1997). The trees from such meadows may have added some CWD (and particularly the large and well-decayed stems found by us) to the reforested areas.

Our conclusion is that mid-aged first-generation forests, such as those in Eastern Europe, should not be automatically excluded from reserve establishment or other CWD-related conservation programmes. We admit, however, that the quality of these areas may be further reduced for slowly dispersing organisms, which are not able to occupy the sites within a few decades (e.g. Peterken and Game 1984, Dzwonko 1993; but see also Koerner et al. 1997 for the absence of such an effect). This problem should be explored in detail by comparing the biota of logs and snags of similar size and decay stage on long-term and new forest lands.

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Table 1. Two-way ANOVAs of the mean volumes of logs and snags in mid-aged mixed and deciduous stands of different previous land use (forest and non-forest) and type (fresh and wet forests). See also Fig. 1.

Source of variation	Mean square	<i>df</i>	<i>F</i>	<i>P</i> *
Logs, m³ ha⁻¹				
Origin	127.1	1	2.9	0.046
Type	52.7	1	1.2	0.276
Origin * Type	<0.1	1	<0.1	0.993
Error	43.4	50		
Snags, m³ ha⁻¹				
Origin	14.4	1	1.1	0.150
Type	4.1	1	0.3	0.581
Origin * Type	40.1	1	3.0	0.088
Error	13.2	50		

* One-sided probabilities for Origin; two-sided for other tests.

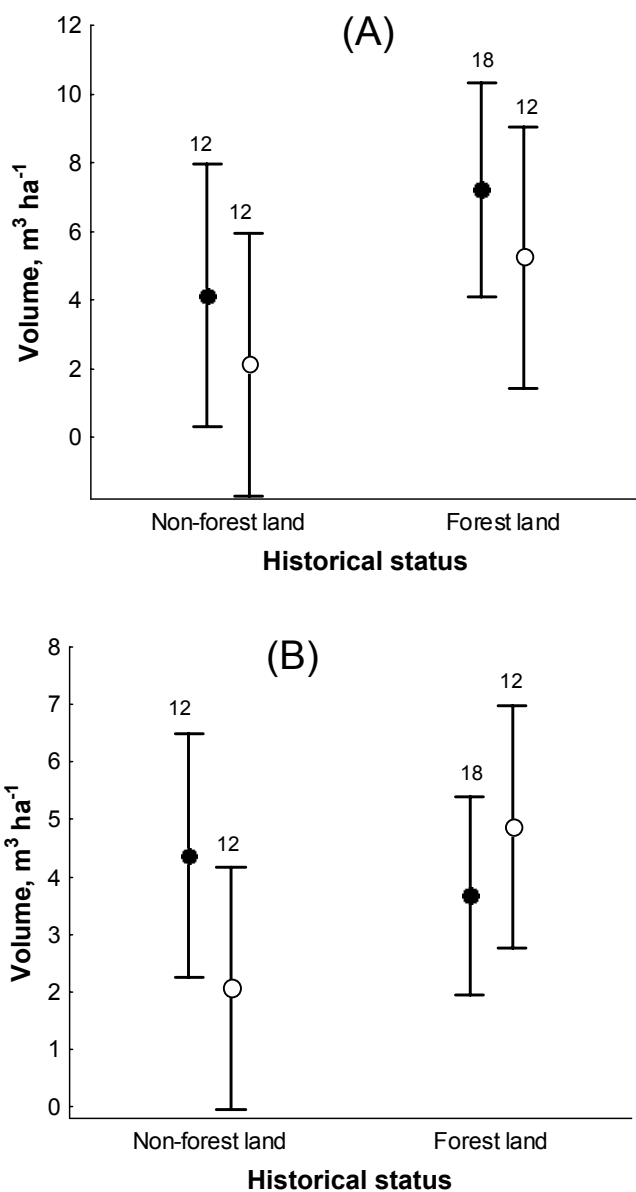


Fig. 1. Mean (\pm 95% confidence intervals) volumes of logs (A) and snags (B) in mid-aged fresh (spots) and wet (circles) deciduous and mixed forests. The labels are sample sizes; see Table 1 for statistical tests.

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Teaduspublikatsioonid

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