

Floristical and ecological properties for identifying of primeval forests in Estonia

Hans Trass, Kai Vellak & Nele Ingerpuu

Trass, H. & Vellak, K., Institute of Botany & Ecology, University of Tartu, 40 Lai str., 51005 Tartu, Estonia

Ingerpuu, N., Institute of Zoology & Botany, Estonian Agricultural University, 181 Riia str., 51014 Tartu, Estonia

Received 25 March 1998, accepted 3 February 1999

Trass, H., Vellak, K. & Ingerpuu, N. 1999: Floristical and ecological properties for identifying of primeval forests in Estonia. — *Ann. Bot. Fennici* 36: 67–80.

True primeval forests in Estonia generally occur as isolated small patches while only a few larger forest stands still remain, mainly in some protected areas. All the surviving primeval forests have many characteristics in common, e.g., the abundance of hemerophobic vascular plant, lichen, bryophyte and fungus species, the high diversity of the biota in general, and the abundance of coarse woody debris. In 1994 we started to study primeval forests of Estonia and developed a ten point scale to estimate the status of a forest to decide whether it can be classified as a primeval forest or rather as another category of forest stand. Of the surviving primeval forests all the larger stands and some of the smaller ones must be protected if they still support sufficiently large numbers of rare species and hemerophobic species specific to primeval forests.

Key words: criteria for identifying primeval forest, Estonia, hemerophobic species

INTRODUCTION

Primeval forests have become rare and fragmented in the whole of Europe (Harris 1984, Saunders *et al.* 1991, Noss & Csuti 1994, Kellman 1996). They are biotopes that contain the maximum forest biodiversity characteristics for the geographical region and forest type (Magurran 1988, Groombridge 1992, Ledig 1993, Ricklefs & Schuster 1993, Huston 1994, Samuelsson *et al.* 1994, Heywood & Watson 1995, Rosenzweig 1995) and are refugia for many vulnerable and rare species

and those sensitive to human influence.

The area of woodland in Estonia was 2.015 million ha in 1996. Forests form 46.2% of the whole territory (Meikas 1997). Several reforms have been carried out in Estonian forestry in recent years (a reduction in the number of forestry districts and the number of people working in forestry, the growth of private forestry, rearrangements in forest research, etc.). They have caused a rise in timber production and simultaneously weakened controls over it. That is why some forest types have been put under strong economic

pressure. There is a need for forest classification according to the intensity and duration of human impact. Several classifications of forest site types in Estonia have been implemented (Karu & Muiste 1958, Masing 1969, Lõhmus 1984, Paal 1997), but a classification and criteria for distinguishing primeval forests from forests with different rates of human impact is still missing.

In a modern environment, the primeval forests are characterized by a fragmentation into small-areal forest pieces. When we look at the floristic descriptions and associations distinguished in SW Estonia 70 years ago (Lippmaa 1931), we can see that there were large untouched primeval forests, which, together with fens, transitional mires and bogs, formed varied complexes. The mapping of Estonian plant cover (under the leadership of T. Lippmaa and later, L. Laasimer) began in the 1930s and finished in the 1950s. Descriptions of the mapping units show that primeval forests were quite widespread even at the end of the 1950s (Laasimer 1965). Since then forest management has been intensified enormously. As a result of this, the total area of primeval forests has decreased, the former large forests have been split into smaller parts, and their structure and species composition have been altered and impoverished. The fragmentation is characteristic of all forests at present time, but the primeval forests are more vulnerable to it. The rate and extent of changes in different types of primeval forests under different kinds of human influence is still insufficiently researched.

The term "primeval forest" has been used differently by different authors. The aim of this paper is to give a definition of primeval forests and criteria for identifying them.

DEFINITION OF PRIMEVAL FORESTS

Several authors have used the terms corresponding to primeval forest (old forest, undisturbed f., virgin f., primary f., natural f., ancient f., pristine f.), but unfortunately, the literature has not contained an advanced and specific definition for primeval forests. As a rule, the definitions given include only some characters, usually the age and rate of human impact. For example, Finnish forest researchers (*Atlas of Finland*) have said: "pri-

meval forests are generally ancient forests untouched by the axe which are protected against all forms of forestry". An exception is the 10-step scale for identifying and defining nemoral forests by Keddy and Drummond (1996), that partly resembles our 10-step criteria for identifying primeval forests. The selected identification properties of eastern North American nemoral forests by Keddy and Drummond are: (1) basal area of trees per hectare, (2) tree canopy composition, (3) occurrence of coarse woody debris in the forest, (4) herbaceous layer, (5) corticolous bryophytes, (6) wild-life trees, (7) macrofungi, (8) avian communities, (9) large carnivores, (10) forest area. We think that not all properties used by those authors are suitable for delimiting primeval forests in Estonia.

We define: (1) primeval forest is ecoenergetically a relatively stable old-growth natural woodland, (2) the development of its stands, habitat parameters, community structure and species composition has taken place in an area that has not significantly been touched by human activity during at least the last one-two forest generations, (3) the stands contain a great number of old trees and logs of different age and rate of decay, (4) presence of numerous hemerophobic species is characteristic. Its stability should be understood as a dynamic balance that enables the system to persist as a more or less stable type in spite of minor changes in ecological conditions, species composition and community structure.

CRITERIA FOR IDENTIFYING PRIMEVAL FORESTS

To identify primeval forests we have defined 10 criteria that have each been divided into 3 grades (scoring 1–3). The maximum sum of points is 30, which would correspond to an "ultimate primeval forest". However, a few species-poor forest types (e.g., heath forest, oligotrophic bog forest) have very little chance of scoring the maximum sum of points due to a very small numbers of hemerophobic species in some forest biodiversity groups, even if the stand has not been affected by any human activities. Our studies have shown that if a forest scores 25 or more points, it has to be classified as a primeval forest, if it scores 20–

24 points, the final decision should be made after careful analysis of the criteria which have reduced the sum (some of the criteria have more weight than others); if a forest scores less than 20 points, then it cannot be classified as primeval.

Criteria concerning the tree layer and human impact (A)

- I. The landscape surrounding the forest.
 1. The forest forms an islet in a landscape that has been strongly altered by human activity.
 2. The surrounding landscape has been altered by intermediate human activity.
 3. The forest is surrounded by a natural landscape little disturbed by human activity, the width of the surrounding zone must be at least 0.5 km.
- II. The age of individual trees.
 1. Young forest (max 40 years).
 2. Middle-aged forest, main tree species are more or less of similar age (40–80 years).
 3. Old forest with forest gaps, main tree species belonging to at least three age classes, the age of the oldest class being more than 80 years for deciduous trees and more than 100 years for coniferous trees.
- III. The number of logs and windfall ($\varnothing > 20$ cm).
 1. Absent or cleared away.
 2. Few (on the average 2–5 per 400 m²).
 3. Many (6 or more per 400 m²).
- IV. The degree of decaying of larger logs ($\varnothing > 20$ cm) and their coverage with bryophytes.
 1. The majority of logs are quite fresh, bryophyte coverage is absent or low (small, young patches).
 2. At least half of the logs are moderately decayed, bryophyte coverage up to 50%.
 3. At least one third of the logs are strongly decayed, bryophyte coverage on them 50%–100%.
- V. Latest intensive cutting.
 1. Less than 10 years ago.
 2. 10–40 years ago.
 3. More than 40 years ago or never cut.

- VI. Other human impact.
 1. Clearly visible (intensive cutting, trampling that has strongly damaged the ground layer, heavy vehicle tracks, fresh ditches, etc.).
 2. Intermediate (moderate cutting, tracks or trampling, old ditches, etc.).
 3. No clearly visible damage, may belong to the limitation zone or reservate of a nature reserve.

Forest biodiversity criteria (B)

- VII. Occurrence of hemerophobic vascular plant species.
 1. Hemerophobic species absent, only hemeradiophobic, many apophytic and some anthropohoric species present.
 2. Few hemerophobic species present.
 3. Many hemerophobic species occurring (sometimes up to 10% of the forest vascular plant flora).
- VIII. Occurrence of hemerophobic bryophyte species.
 1. Absent.
 2. Few species present, less than 10% of the whole forest bryoflora.
 3. More than 10% of the whole forest bryoflora.
- IX. Occurrence of hemerophobic lichen species.
 1. Absent.
 2. Few species present.
 3. More than 10% of the whole forest lichen flora.
- X. Occurrence of hemerophobic macrofungal wood-rotting species.
 1. Absent, only common nonhemerophobic wood-rotting fungi on trunks and logs.
 2. 1–10 species.
 3. More than 10 species.

The A-criteria can be used by all forest owners and managers. If the sum of scores of the A-criteria is 13–18, the forest should also be evaluated by specialists on the basis of B-criteria for final evaluation. As an example we have compared three primeval forests (Table 1): in Uriissaare (South-western Estonia), in Kaukvere (North-eastern Estonia) and in Järvelja (eastern Estonia).

HEMEROPHOBIC SPECIES OF ESTONIAN PRIMEVAL FORESTS

We mainly follow the treatment of hemerophoby of Linkola (1916). Species are divided into 4 groups according to their sensitivity to human activities: hemerophobic (species sensitive to various hu-

man activities), hemeradiaphoric (sensitive species which are tolerant to weak or moderate influence of human activities), apophytic (species which prefer sites moderately changed by man) and anthropohoric (species which are regularly disseminated by man, e.g., weeds and cultivated plants).

Table 1. Comparison of Järvselja*, Kaukvere** and Urissaare*** primeval forests.

Criteria	Järvselja	Points	Kaukvere	Points	Urissaare	Points
I. Landscape surrounding the forest	natural, partly little disturbed by human activity	3	natural, partly little disturbed by human activity	3	natural, partly little disturbed by human activity	3
II. Age of the individual trees	110–130 yr	3	90–120 yr	3	80–140 yr	3
III. Amount of logs and windfall	10	3	12	3	2	2
IV. Degree of decaying of logs and their coverage with bryophytes	At least half of logs strongly decayed, 1/3 moderately decayed, bryophyte coverage 50%–100%	3	1/3 strongly and 1/3 moderately decayed, bryophyte coverage 50%–80%	3	1/3 strongly, 1/3 moderately and 1/3 slightly decayed, bryophyte coverage 30%–80%	3
V. Last cutting	more than 60 years ago	3	40–50 years ago	3	At least 20 years ago	2
VI. Other human impact	old ditches	2	old ditches	2	old ditches	2
VII. Occurrence of hemerophobic vascular plant species	56	3	31	3	30	3
VIII. Occurrence of hemerophobic bryophyte species	16	3	16	3	24	3
IX. Occurrence of hemerophobic lichen species	18	3	25	3	24	3
X. Occurrence of hemerophobic macrofungal wood-rotting species	19	3	no special studies	–	at least 10 species	3
Total		29		26		27

*Järvselja primeval forest reserve, founded in 1923, ca. 20 ha, 100% forested; partly on mineral (27%), partly on peat soils (73%); forests belong to the meso-oligotrophic boggy forests, drained peatland forests, mobile-water swampy forests, coniferous subtaiga forests, deciduous broad-leaved forests (small patches).

** Kaukvere primeval forest, part of Muraka nature reserve founded in 1997, ca. 30 ha; mobile-water swampy forests, meso-oligotrophic boggy forests, coniferous subtaiga forests.

*** Urissaare primeval forest, part of Nigula nature reserve founded in 1957; ca. 30 ha; predominantly mobile-water swampy forests.

Lists of hemerphobic species have been compiled considering the distribution, habitat requirements and sensibility of species only in Estonian forests. Data from these lists can not be automatically transferred for the evaluation of hemerphobic species in neighbouring regions, since these species behave differently according to their location within the distribution area.

Vascular plants

The Estonian indigenous flora contains 1 675 species (Trass 1994), and the Estonian forest flora more than 450 species. About one third are obligatory forest species (those that occur preferably in forest ecosystems, very rarely elsewhere). There are 90 hemerophobic species in the whole forest flora (Table 2). By compiling the list we have taken into account also the manuscript of L. Enari "Cultural influences on the flora of Estonia" and "The list of Estonian vascular plants" by T. Kukk (unpubl.). The indicator value of hemerophobic forest species is considerable and they can be used as a basis for assessment of forest environmental properties. Indeed, several other researchers have also done this (e.g., Wulf 1997).

Bryophytes

Estonian bryoflora contains 520 species (Ingerpuu *et al.* 1994, Kannukene *et al.* 1997). The majority of them can to a greater or lesser extent inhabit forests, but we have defined 96 species as obligatory forest species. The list of hemerophobic forest species contains 79 bryophytes (Table 3), about one third of which are facultative forest species. We treat as hemerophobic: (1) species that are rare in Estonian forests (being near the border of their distribution area and therefore sensitive to human influence), (2) species inhabiting large logs, which usually are absent from managed forests and (3) species inhabiting trunks and stones and demanding special shade and moisture conditions that may be destroyed by cutting or draining.

Bryophytes have often been used as indicators of ecological conditions in forest ecosystems,

especially in primeval forests (McCullough 1948, Davis 1964, La Roi & Stringer 1976, Söderström 1981, 1988, Gustafsson & Hallingbäck 1988, Gustafsson *et al.* 1992, Hallingbäck 1992, Frisvoll & Prestø 1997).

Lichens

About 800 species belong to the lichen flora of Estonia. Approximately 300 are more or less associated with forests. Only macrolichens (332 species; Trass & Randle 1994) have been studied sufficiently to divide them into obligatory and facultative forest species groups. The list of more significant hemerophobic forest lichens is given in Table 4, which contains 88 species.

Several authors have used the frequency, coverage, vitality and other characters of forest lichens as indicators for the condition of forest ecosystems (Sömermaa 1972, Rose 1976, 1985, 1992, Esseen 1981, Lesica *et al.* 1991, Wolseley 1991, Galloway 1992, Hyvärinen *et al.* 1992, Tibell 1992, McCune 1993, Goward 1994, Hilmo 1994, Kuusinen 1994a, 1994b, 1995, 1996a, 1996b, Selva 1994, Rosentreter 1995, Scheidegger *et al.* 1995, Alstrup 1996, Esseen *et al.* 1996, Pfeifferkorn 1996).

The informative value of hemerophobic species may be reduced under some circumstances: (1) if they occur very rarely (frequency index 1), (2) if a change in certain ecological factors tends to suppress some hemerophobic species (for example good lichen indicators such as *Usnea*-species may be eliminated from the forest community if the canopy coverage is 0.7 or more).

Fungi

Parmasto and Parmasto (1997) have compiled a list of wood-rotting fungi as a result of their study in the old forests of central Estonia. This list has been amended and several species added in 1998 (Table 5). Some of these species are extremely sensitive. If the habitats for such species (different types of decaying wood) have once been destroyed, the return of the species is very slow or almost impossible after the re-establishment of these habitats.

Table 2. Hemerophob forest vascular plant species of Estonia. Abbreviations of forest type groups: AL = alluvial forest (f.), AR = alvar f., BG = meso-oligotrophic boggy f., BO = oligotrophic bog f., DE = deciduous broad-leaved f., DP = drained peatland f., FE = eutrophic fen f., HE = heath f., ME = mesotrophic boggy f., MW = mobile-water swampy f., SC = slightly calciphilous herb-rich f., SH = semiheath f., ST = coniferous subtaiga f., WS = wet herb-rich secondary f. Frequency (1 ... 5) is given for species occurrence in studied primeval forests. Nomenclature follows Lid (1987).

Species	AL	AR	BG	BO	DE	DP	FE	HE	ME	MW	SC	SH	ST	WS	Freq.
<i>Actaea spicata</i>	X				X										4
<i>Adoxa moschatellina</i>	X									X					3
<i>Allium ursinum</i>					X										2
<i>Alnus glutinosa</i>	X				X		X			X					5
<i>Anemone ranunculoides</i>					X							X	X		4
<i>Asarum europaeum</i>	X				X							X			3
<i>Athyrium filix-femina</i>					X					X		X			5
<i>Botrychium virginianum</i>					X										2
<i>Brachypodium sylvaticum</i>					X							X			2
<i>Bromus benekenii</i>					X					X					3
<i>Campanula latifolia</i>					X					X					3
<i>Carex digitata</i>								X				X			4
<i>Carex disperma</i>										X		X			3
<i>Carex elongata</i>									X	X				X	4
<i>Carex globularis</i>				X						X					3
<i>Carex heleonastes</i>			X						X	X					3
<i>Carex loliacea</i>						X			X	X		X	X		3
<i>Carex pauciflora</i>			X	X					X						3
<i>Carex remota</i>									X	X				X	3
<i>Carex rhynchophysa</i>		X													2
<i>Carex sylvatica</i>							X			X		X			3
<i>Carex vaginata</i>												X			4
<i>Chimaphila umbellata</i>												X	X		3
<i>Cinna latifolia</i>					X					X					2
<i>Circaea alpina</i>	X									X		X			2
<i>Corallorhiza trifida</i>			X				X		X						3
<i>Cotoneaster niger</i>		X									X				2
<i>Crataegus rhipidophylla</i>		X			X						X				2
<i>Cypripedium calceolus</i>					X					X					2
<i>Daphne mezereum</i>												X	X		3
<i>Diphasiastrum complanatum</i>								X				X			3
<i>Dryopteris carthusiana</i>					X							X	X		4
<i>Dryopteris expansa</i>					X							X	X		3
<i>Dryopteris filix-mas</i>							X		X	X		X	X	X	4
<i>Epipactis atrorubens</i>								X				X			3
<i>Epipactis helleborine</i>					X							X			3
<i>Epipogium aphyllum</i>												X	X		2
<i>Festuca altissima</i>					X										2
<i>Festuca gigantea</i>					X					X					2
<i>Galeobdolon luteum</i>	X				X					X	X	X			3
<i>Galium odoratum</i>					X					X		X			3
<i>Glyceria lithuanica</i>	X									X					3

Continued

Table 2. Continued.

Species	AL	AR	BG	BO	DE	DP	FE	HE	ME	MW	SC	SH	ST	WS	Freq.
<i>Goodyera repens</i>												X	X		3
<i>Gymnocarpium dryopteris</i>					X							X	X		4
<i>Huperzia selago</i>												X	X		2
<i>Impatiens noli-tangere</i>	X									X					3
<i>Lathraea squamaria</i>					X					X					3
<i>Lathyrus niger</i>					X						X				2
<i>Lathyrus pisiformis</i>					X						X				3
<i>Lathyrus sylvestris</i>					X								X		3
<i>Lathyrus vernus</i>					X								X		4
<i>Linnaea borealis</i>												X	X		3
<i>Listera cordata</i>													X		2
<i>Lonicera caerulea</i>					X								X		3
<i>Lunaria rediviva</i>					X					X					2
<i>Lycopodium annotinum</i>						X						X	X		5
<i>Lycopodium clavatum</i>						X		X				X	X		4
<i>Maianthemum bifolium</i>					X							X	X		4
<i>Matteuccia struthiopteris</i>	X									X			X		4
<i>Mercurialis perennis</i>	X				X					X			X		4
<i>Moehringia lateriflora</i>					X					X					1
<i>Moneses uniflora</i>												X	X		3
<i>Monotropa hypopitys</i>								X				X			3
<i>Mycelis muralis</i>	X									X			X		4
<i>Neottia nidus-avis</i>													X		3
<i>Orthilia secunda</i>											X	X	X		4
<i>Oxalis acetosella</i>											X	X	X		5
<i>Paris quadrifolia</i>					X						X		X		4
<i>Phyteuma spicatum</i>	X				X								X		2
<i>Poa remota</i>	X						X			X				X	3
<i>Pulmonaria officinalis</i>					X					X	X				4
<i>Pyrola chlorantha</i>												X	X		2
<i>Pyrola media</i>												X	X		2
<i>Pyrola minor</i>			X			X						X	X		3
<i>Ranunculus lanuginosus</i>					X										2
<i>Ranunculus nemorosus</i>					X								X		2
<i>Sanicula europaea</i>					X					X	X				3
<i>Sorbus rupicola</i>		X									X				2
<i>Stachys sylvatica</i>	X				X					X			X		4
<i>Stellaria holostea</i>					X								X		4
<i>Stellaria longifolia</i>					X								X		4
<i>Stellaria nemorum</i>	X									X					4
<i>Taxus baccata</i>			X							X			X		1
<i>Thelypteris phegopteris</i>			X			X				X					3
<i>Trientalis europaea</i>												X	X		5
<i>Ulmus glabra</i>					X					X	X				3
<i>Ulmus laevis</i>					X					X	X				3
<i>Vicia sylvatica</i>					X					X			X		3
<i>Viola hirta</i>											X	X	X		2
<i>Viola riviniana</i>					X								X		4

Table 3. Hemerophobc forest bryophyte species of Estonia. Abbreviations of forest type groups and frequency as in Table 2. Nomenclature follows Ingerpuu *et al.* (1994) and Kannukene *et al.* (1997).

Species	AL	AR	BG	BO	DE	DP	FE	HE	ME	MW	SC	SH	ST	WS	Freq.
<i>Anastrophyllum hellerianum</i>	X	X		X											2
<i>Anomodon attenuatus</i>	X				X										3
<i>Anomodon longifolius</i>		X			X						X				4
<i>Anomodon viticulosus</i>		X			X										3
<i>Aulacomnium androgynum</i>		X											X		1
<i>Barbilophozia attenuata</i>			X		X							X			1
<i>Barbilophozia hatcheri</i>		X		X								X			1
<i>Barbilophozia floerkei</i>												X			1
<i>Barbilophozia lycopodioides</i>	X										X		X		1
<i>Bazzania trilobata</i>				X								X		X	1
<i>Blepharostoma trichophyllum</i>	X	X	X	X		X		X			X			X	4
<i>Brachythecium campestre</i>					X										1
<i>Brachythecium erythrorrhizon</i>						X							X		1
<i>Brachythecium starkei</i>					X							X	X		2
<i>Buxbaumia viridis</i>					X										1
<i>Callicladium haldanianum</i>					X					X					2
<i>Calyptogeia suecica</i>		X	X											X	3
<i>Cynodontium strumiferum</i>												X			1
<i>Dichelyma capillaceum</i>					X										1
<i>Dichelyma falcatum</i>					X										1
<i>Dicranum drummondii</i>												X			1
<i>Dicranum flexicaule</i>												X		X	1
<i>Dicranum fuscescens</i>		X						X				X			2
<i>Dicranum spurium</i>		X						X				X			2
<i>Dicranum viride</i>					X						X				1
<i>Eurhynchium pulchellum</i>		X			X									X	2
<i>Fissidens bryoides</i>					X							X		X	1
<i>Fissidens exilis</i>		X			X										1
<i>Frullania dilatata</i>	X				X										4
<i>Helodium blandowii</i>			X			X			X						3
<i>Hylocomium umbratum</i>					X										1
<i>Isopterygiopsis pulchella</i>														X	1
<i>Isothecium alopecuroides</i>		X			X							X			1
<i>Isothecium myosuroides</i>		X										X			1
<i>Jamesoniella autumnalis</i>		X	X		X		X		X	X			X		2
<i>Jungermannia leiantha</i>		X			X				X	X		X	X		2
<i>Lejeunea cavifolia</i>					X										3
<i>Lepidozia reptans</i>	X	X	X		X		X			X		X	X	X	4
<i>Leskea polycarpa</i>		X			X							X			3
<i>Leucobryum glaucum</i>		X	X												2
<i>Lophozia incisa</i>			X		X					X		X			1
<i>Lophozia longidens</i>		X	X									X			1
<i>Lophozia longiflora</i>		X	X		X	X			X			X			1
<i>Lophozia opacifolia</i>					X							X			1
<i>Lophozia ventricosa</i>	X	X	X	X	X		X					X			2
<i>Metzgeria conjugata</i>					X										1
<i>Metzgeria furcata</i>	X	X			X										4
<i>Mnium hornum</i>	X				X					X					3
<i>Mnium stellare</i>		X			X									X	2
<i>Neckera complanata</i>		X			X					X					1
<i>Neckera pennata</i>	X	X			X								X		3
<i>Nowellia curvifolia</i>		X	X		X				X	X		X	X	X	3

Continued

Table 3. Continued.

Species	AL	AR	BG	BO	DE	DP	FE	HE	ME	MW	SC	SH	ST	WS	Freq.
<i>Plagiothecium cavifolium</i>		X			X									X	1
<i>Plagiothecium latebricola</i>	X				X									X	1
<i>Plagiothecium nemorale</i>					X							X			1
<i>Plagiothecium ruthei</i>									X			X			1
<i>Plagiothecium succulentum</i>					X							X			2
<i>Plagiothecium undulatum</i>													X	X	1
<i>Platygyrium repens</i>	X				X		X			X					2
<i>Pohlia cruda</i>					X						X				2
<i>Polytrichum formosum</i>												X			4
<i>Porella platyphylla</i>		X			X										1
<i>Pseudobryum cinclidioides</i>			X				X		X	X					3
<i>Riccardia latifrons</i>	X		X	X	X		X					X	X		4
<i>Riccardia palmata</i>	X		X	X	X		X						X	X	3
<i>Scapania apiculata</i>		X			X									X	2
<i>Scapania umbrosa</i>			X	X											1
<i>Scapania undulata</i>					X					X				X	1
<i>Schistostega pennata</i>					X							X			2
<i>Thamnobryum alopecurum</i>					X										1
<i>Thuidium tamariscinum</i>			X					X	X				X		2
<i>Timmia bavarica</i>					X										1
<i>Timmia megapolitana</i>					X										1
<i>Trichocolea tomentella</i>			X		X			X	X				X		2
<i>Tritomaria exsectiformis</i>			X	X								X			1
<i>Tritomaria quinquedentata</i>		X										X			1
<i>Ulota bruchii</i>	X				X					X	X		X	X	1
<i>Ulota crispa</i>	X				X					X	X		X	X	3
<i>Zygodon viridissimus</i>					X		X								1

Occurrence of hemerophobic species in different forest site type groups

To ascertain the relationships between forest site type groups and hemerophobic vascular plant, bryophyte and lichen species, the data from the studied forests as well as data from herbaria and literature was used. The frequency index (1–5) is based on the studies in primeval forests (Tables 2–4). The results are influenced by distribution frequency and the rate of investigation of different forest site type groups.

The diversity of hemerophobic species in forest site type groups is different (Table 6). As we can see from these lists the forest type groups richest in hemerophobic species of vascular plants are coniferous subtaiga forests (51 species), deciduous forests (44) and mobile-water swampy forests (37), of bryophytes are deciduous forests (53), semiheath forests (31) and alvar forests (31) and of lichens are coniferous subtaiga forests (55),

deciduous forests (34) and mobile-water swampy forests (26). This does not mean that these forest type groups are most primeval, but that the ecological conditions for hemerophobic species are most suitable in these forests and that hemerophobic-poor forests, especially strongly paludified and extremely dry (heath-) forests, are as a rule species-poor. There is a great similarity between vascular plants and lichens — the five most hemerophobic-rich groups overlap. The sequence of forest site type groups according to hemerophobic bryophyte species richness is different. The reason for this could be the different ecological demands of bryophytes and the differences in investigation rates in various forest sites.

CONCLUSIONS

Primeval forests with their rich and differentiated species compositions and complicated commu-

Table 4. Hemerophobic forest lichen species of Estonia. Abbreviations of forest type groups and frequency as in Table 2. Nomenclature follows Trass and Randlane (1996) and Santesson (1993).

Species	AL	AR	BG	BO	DE	DP	FE	HE	ME	MW	SC	SH	ST	WS	Freq.
<i>Arthonia leucopellaea</i>					X					X					1
<i>Arthothelium ruanum</i>	X				X										1
<i>Bacidia arceutina</i>					X										1
<i>Bactrospora dryina</i>					X										2
<i>Biatora efflorescens</i>			X		X								X		2
<i>Biatora helvola</i>	X					X	X						X		3
<i>Bryoria capillaris</i>			X	X								X	X		3
<i>Bryoria fuscescens</i>									X			X	X		4
<i>Bryoria implexa</i>												X	X		2
<i>Bryoria nadvornikiana</i>						X		X				X			3
<i>Bryoria subcana</i>					X	x	X						X		3
<i>Buellia erubescens</i>					X										3
<i>Buellia griseovirens</i>		X			X					X			X		4
<i>Buellia schaererii</i>					X										2
<i>Calicium adpersum</i>					X								X		2
<i>Calicium claucellum</i>					X	X							X		4
<i>Calicium viride</i>		X				X						X	X		5
<i>Cetraria sepincola</i>		X					X		X				X	X	4
<i>Cetrelia cetrarioides</i>										X					1
<i>Chaenotheca chlorella</i>								X			X				2
<i>Chaenotheca chrysocephala</i>										X			X		4
<i>Chaenotheca furfuracea</i>						X				X			X		4
<i>Chaenotheca trichialis</i>										X			X		4
<i>Chaenothecopsis consociata</i>									X				X		2
<i>Chrysothrix candelaris</i>		X			X						X				3
<i>Dimerella lutea</i>		X										X	X		2
<i>Evernia divaricata</i>			X	X									X		2
<i>Evernia mesomorpha</i>			X										X		2
<i>Gualecta ulmi</i>					X	X									2
<i>Hypogymnia farinacea</i>												X	X		3
<i>Hypogymnia tubulosa</i>								X				X	X		3
<i>Hypogymnia vittata</i>													X		2
<i>Lecanactis abietina</i>										X			X		3
<i>Lecanora albella</i>					X										3
<i>Lecanora piniperda</i>			X	X				X	X			X			3
<i>Lecanora populicola</i>	X													X	4
<i>Lecidea turgidula</i>													X		2
<i>Leptogium cyanescens</i>					X					X					1
<i>Leptogium saturninum</i>					X					X			X		3
<i>Lobaria pulmonaria</i>	X				X					X					3
<i>Lobaria scrobiculata</i>	X														1
<i>Loxospora elatina</i>											X	X	X		2
<i>Megalaria grossa</i>					X										1

Continued

Table 4. Continued.

Species	AL	AR	BG	BO	DE	DP	FE	HE	ME	MW	SC	SH	ST	WS	Freq.
<i>Melanelia glabra</i>					X										2
<i>Melanelia glabratula</i>	X									X			X		4
<i>Melanelia septentrionalis</i>							X		X					X	2
<i>Menegazzia terebrata</i>						X				X			X		3
<i>Mycoblastus fucatus</i>													X		2
<i>Mycoblastus sanguinarius</i>			X			X						X	X		3
<i>Nephroma bellum</i>					X								X		1
<i>Nephroma helveticum</i>					X								X		2
<i>Nephroma laevigatum</i>					X								X		2
<i>Nephroma resupinatum</i>	X												X		2
<i>Ochrolechia androgyna</i>	X						X		X	X		X	X		4
<i>Ochrolechia arborea</i>												X	X		2
<i>Ochrolechia pallescens</i>	X				X						X				2
<i>Opegrapha atra</i>	X				X										3
<i>Opegrapha rufescens</i>					X					X					3
<i>Opegrapha varia</i>	X				X										3
<i>Opegrapha vulgata</i>						X			X				X		4
<i>Pannaria pezizoides</i>										X					1
<i>Parmeliella triptophylla</i>										X			X		2
<i>Parmeliopsis hyperopta</i>			X	X				X				X	X		4
<i>Peltigera collina</i>	X		X										X		2
<i>Peltigera degenii</i>										X			X		2
<i>Peltigera horizontalis</i>					X					X			X		4
<i>Peltigera membranacea</i>											X	X	X		2
<i>Peltigera neopolydactyla</i>										X			X		1
<i>Peltigera polydactyla</i>		X										X	X		4
<i>Pertusaria flavida</i>	X				X										3
<i>Pertusaria hemisphaerica</i>					X								X		2
<i>Pertusaria leioplaca</i>					X						X				2
<i>Pertusaria pertusa</i>	X				X					X					3
<i>Physcia semipinnata</i>					X					X					2
<i>Psilolechia lucida</i>						X							X		2
<i>Pyrenula coryli</i>	X				X					X					4
<i>Pyrrhospora querneae</i>										X			X		2
<i>Ramalina dilacerata</i>			X										X		2
<i>Ramalina thraucta</i>										X			X		2
<i>Rinodina exigua</i>					X					X					2
<i>Thelotrema lepadinum</i>	X									X			X		3
<i>Tuckermannopsis chlorophylla</i>		X	X	X						X					4
<i>Usnea filipendula</i>						X	X						X	X	4
<i>Usnea fluvoreagens</i>								X	X						3
<i>Usnea glabrata</i>							X	X					X		2
<i>Usnea glabrescens</i>						X	X	X				X	X		4
<i>Usnea lapponica</i>						X							X		3
<i>Usnea scabrata</i>						X						X	X		4
<i>Varicellaria rhodocarpa</i>												X	X		2

nity structure have as a result of human activities become rare and fragmented in Estonia today. The remnants of primeval forests have already an impoverished species composition and they are ex-

tremely vulnerable. They serve as refugia for a great number of rare and specialized species that are sensitive to human impact. Now is our final chance to register and give protection to the for-

Table 5. Hemerophobic old forest fungi indicator species of Estonia. Nomenclature follows Hansen and Knudsen (1997) and Ryvarden and Gilbertson (1993–1994).

<i>Amylocorticium subincarnatum</i>	<i>Junghuhnia separabilima</i>
<i>Amylocystis lapponica</i>	<i>Leptoporus mollis</i>
<i>Anomoporia bombycina</i>	<i>Multiclavula mucida</i>
<i>Antrodia crassa</i>	<i>Oligoporus guttulatus</i>
<i>Asterodon ferruginosus</i>	<i>Oxyporus philadelphi</i>
<i>Boletopsis leucomelaena</i>	<i>Oxyporus placentus</i>
<i>Byssocorticium atrovirens</i>	<i>Perenniporia medulla-planis</i>
<i>Ceriporia excelsa</i>	<i>Perenniporia subacida</i>
<i>Ceriporia subreticulata</i>	<i>Phaeolus schweinitzii</i>
<i>Ceriporiopsis aneirina</i>	<i>Phellinus ferrugineofuscus</i>
<i>Ceriporiopsis myceliosa</i>	<i>Phellinus nigrolimitatus</i>
<i>Ceriporiopsis resinascens</i>	<i>Phlebia centrifuga</i>
<i>Dentipellis fragilis</i>	<i>Physisporinus sanguinolentus</i>
<i>Diplomitoporus flavescens</i>	<i>Physisporinus vitreus</i>
<i>Fomitopsis rosea</i>	<i>Pseudomerulius aureus</i>
<i>Ganoderma lucidum</i>	<i>Punctularia strigosozonata</i>
<i>Gloiodon strigosus</i>	<i>Pycnoporellus fulgens</i>
<i>Grifola frondosa</i>	<i>Rigidoporus crocatus</i>
<i>Hapalopilus croceus</i>	<i>Serpula himantioides</i>
<i>Hapalopilus salmonicolor</i>	<i>Sistotrema raduloides</i>
<i>Haplotrichum aureum</i>	<i>Skeletocutis odora</i>
<i>Hericium coralloides</i>	<i>Skeletocutis stellae</i>
<i>Inonotopsis subicolosus</i>	<i>Skeletocutis vulgaris</i>
<i>Junghuhnia collabens</i>	<i>Steccherinum robustius</i>
<i>Junghuhnia luteoalba</i>	<i>Tomentella crinalis</i>
<i>Junghuhnia pseudozilingiana</i>	

Table 6. The number of hemerophobic vascular plant, bryophyte and lichen species in different forest type groups in Estonia.

Forest type groups	Vascular plants	Bryophytes	Lichens
Coniferous subtaiga f. ST	51	15	55
Deciduous broad-leaved f. DE	44	53	34
Mobile-water swampy f. MW	37	15	26
Semiheath f. SH	23	31	19
Alluvial f. AL	15	13	16
Slightly calciphilous herb-rich f. SC	14	6	7
Mesotrophic boggy f. ME	7	9	8
Meso-oligotrophic boggy f. BG	6	20	10
Eutrophic fen f. FE	6	7	10
Wet herb-rich secondary f. WS	6	19	5
Heath f. HE	5	3	8
Alvar f. AR	4	31	7
Drained peatland f. DP	4	4	13
Oligotrophic bog f. BO	2	7	4

est communities that still satisfy the criteria for primeval forests.

We have compiled a 10-step system for identifying primeval forests. The 6-step A-criteria of this system can easily be used by every forest inspector. With minor changes it can be applied to neighbouring countries, too.

As an appendix to the B-criteria lists of hemerophobic vascular plant, bryophyte, lichen and fungi species have been compiled. These lists are specific to Estonia and can not be used without revision in neighboring countries.

Acknowledgements: The investigations were supported by the Estonian Science Foundation. We are thankful to A. Roosma and E. Leibak for useful comments on the manuscript and for helping us to find suitable primeval forests and to V. Masing, M. Toom and M. Leis for the help during the field works. Many thanks to T. Kukk and E. Parmasto for the kind permission to use their unpublished data.

REFERENCES

- Alstrup, V. 1996: Natural forests and endangered lichens in Denmark. — *IAL 3: Progress and problems in lichenology in the nineties*. Abstracts: 43. Salzburg.
- Atlas of Finland* 1988. Appendix 141–143. — Helsinki.
- Davis, R. B. 1964: Bryophytes and lichens of the spruce-fir forests of the coast of Maine, I. The ground cover. — *Bryologist* 7: 189–196.
- Esseen, P.-A. 1981: Host specificity and ecology of epiphytic macrolichens in some central Swedish spruce forests. — *Wahlenbergia* 7: 73–80.
- Esseen, P.-A., Renholm, K.-E. & Pettersson, R. B. 1996: Epiphytic lichen biomass in managed and old-growth boreal forests; effect of branch quality. — *Ecol. Appl.* 6: 228–238.
- Frisvoll, A. A. & Prestø, T. 1997: Spruce forest bryophytes in central Norway and their relationship to environmental factors including modern forestry. — *Ecography* 20: 3–18.
- Galloway, D. J. 1992: Biodiversity: a lichenological perspective. — *Biodiv. Conserv.* 1: 312–323.
- Goward, T. 1994: Notes on oldgrowth-dependent epiphytic macrolichens in inland British Columbia, Canada. — *Acta Bot. Fennica* 150: 31–38.
- Groombridge, B. (ed.) 1992: *Global biodiversity: Status of the Earth's living resources*. — Chapman & Hall, London. 586 pp.
- Gustafson, L. & Hallingbäck, T. 1988: Bryophyte flora and vegetation of managed and virgin coniferous forest in South-West Sweden. — *Biol. Conserv.* 44: 283–300.
- Gustafsson, L., Fiskesjö, A., Pettersson, B., Hallingbäck, T. & Ingelög, T. 1992: SeminatURAL deciduous broad-leaved woods in southern Sweden — habitat factors of importance to some bryophyte species. — *Biol. Conserv.* 59: 175–181.
- Hallingbäck, T. 1992: The effect of air pollution on mosses in Southern Sweden. — *Biol. Conserv.* 59: 163–170.
- Hansen, L. & Knudsen, H. (eds.) 1997: *Nordic macromycetes*. Vol. 3. — Nordsvamp, Copenhagen. 444 pp.
- Harris, L. D. 1984: *The fragmented forest*. — Univ. Chicago Press, Chicago. 211 pp.
- Heywood, V. H. & Watson, R. T. 1995: *Global biodiversity assessment*. — Cambridge Univ. Press, Cambridge. 1140 pp.
- Hilmo, O. 1994: Distribution and succession of epiphytic lichens on *Picea abies* branches on a boreal forest, Central Norway. — *Lichenologist* 26: 149–169.
- Huston, M. A. 1994: *Biological diversity*. — Cambridge Univ. Press, Cambridge. 681 pp.
- Hyvärinen, M., Halonen, P. & Kauppi, M. 1992: Influence of stand age and structure on the epiphytic lichen vegetation in the middle-boreal forest of Finland. — *Lichenologist* 24: 165–180.
- Ingerpuu, N., Kalda, A., Kannukene, L., Krall, H., Leis, M. & Vellak, K. 1994: List of Estonian Bryophytes. — *The Naturalist's Noteb.* 94: 1–176.
- Kannukene, L., Ingerpuu, N., Vellak, K. & Leis, M. 1997: Additions and amendments to the list of Estonian bryophytes. — *Folia Cryptog. Estonica* 31: 1–7.
- Karu, A. & Muiste, L. 1958: *Eesti metsakasvukohatiübid*. — ERK, Tallinn. 36 pp.
- Keddy, P. A. & Drummond, C. G. 1996: Ecological properties for the evaluation, management, and restoration of temperate deciduous forest ecosystems. — *Ecol. Appl.* 6: 748–762.
- Kellman, M. 1996: Redefining roles: plant community reorganization and species preservation in fragmented systems. — *Global Ecol. Biogeogr. Lett.* 5: 111–116.
- Kuusinen, M. 1994a: Epiphytic lichen flora and diversity on *Populus tremula* in old-growth and managed forests of southern and middle boreal Finland. — *Ann. Bot. Fennici* 31: 245–260.
- Kuusinen, M. 1994b: Epiphytic lichen diversity on *Salix caprea* old-growth southern and middle boreal forests of Finland. — *Ann. Bot. Fennici* 31: 77–92.
- Kuusinen, M. 1995: Cyanobacterial macrolichens on *Populus tremula* as indicators of forest continuity in Finland. — *Biol. Conserv.* 75: 43–49.
- Kuusinen, M. 1996a: Epiphytic lichen flora and diversity in old-growth boreal forest of Finland. — *Publ. Bot. Univ. Helsinki* 23: 1–29.
- Kuusinen, M. 1996b: Importance of spruce swamp-forests for epiphyte diversity and flora on *Picea abies* in southern and middle boreal Finland. — *Ecography* 19: 41–51.
- Laasimer, L. 1965: *Eesti NSV taimkate* [Vegetation of the Estonian S.S.R.]. — Valgus, Tallinn. 398 pp. [In Estonian with English summary].
- La Roi, G. H. & Stringer M. H. L. 1976: Ecological studies in the boreal spruce-fir forests of the North American taiga, II. Analysis of the bryophyte flora. — *Canadian*

- J. Bot.* 54: 619–643.
- Ledig, F. T. 1993: Secret extinction: the loss of genetic diversity in forest ecosystems. — In: Fenger, M. A., Miller, E. H., Johnson, J. F. & Williams, E. J. R. (eds.), *Our living legacy. Proceedings of a symposium on biological diversity*: 127–140. Royal British Columbia Mus.
- Lesica, P., McCune, B., Cooper, S. V. & Hong, W. S. 1991: Differences in lichen and bryophyte communities between old-growth and managed second-growth forests in the Swan Valley, Montana. — *Canadian J. Bot.* 69: 1745–1755.
- Lid, J. 1987: *Norsk, svensk, finsk flora*. — Det Norske Samlaget, Oslo. 837 pp.
- Linkola, K. 1916: Studien über den Einfluss der Kultur auf die Flora in den Gegenden nördlich vom Ladogasee. I. — *Acta Soc. Fauna Fl. Fennica* 45(1): 1–432.
- Lippmaa, T. 1931: Beiträge zur Kenntnis der Flora und Vegetation Südwest-Estlands. — *Archiv Naturk. Estlands*. 2. Ser. 13(3): 95–347.
- Lõhmus, E. 1984: *Eesti metsakasvukohatiübid*. — ENSV Agrotööstuskoondise Info- ja Juurutusvalitsus, Tallinn. 88 pp.
- Magurran, A. E. 1988: *Ecological diversity and its measurement*. — Princeton Univ. Press, Princeton. 179 pp.
- Masing, V. 1969: Metsatüpoloogia probleemid. — *Looduseuurijate Seltsi Aastaraamat* 59: 150–168.
- McCullough, H. A. 1948: Plant succession on fallen logs in a virgin spruce-fir forest. — *Ecology* 29: 508–513.
- McCune, B. 1993: Gradients in epiphyte biomass in three *Pseudotsuga-Tsuga* forests of different age in western Oregon and Washington. — *Bryologist* 96: 405–411.
- Meikas, E. (ed.) 1997: *Estonian environment 1996*. — Min. Env. Estonia, Tallinn. 96 pp.
- Noss, R. F. & Csuti, B. 1994: Habitat fragmentation. — In: Meffe, G. K. & Carroll, C. R. (eds.), *Principles of conservation biology*: 327–364. Sinauer, Sunderland.
- Paal, J. 1997: *Eesti taimkatte kasvukohatiüptide klassifikatsioon*. — Keskkonnaministeeriumi Info- ja Tehnokeskus, Tallinn. 297 pp.
- Parmasto, E. & Parmasto, I. 1997: Lichenicolous Aphyllporales of old and primeval forests in Estonia. 1. The forests of northern Central Estonia with a preliminary list of indicator species. — *Folia Cryptog. Estonica* 31: 38–45.
- Pfeifferkorn, V. 1996: Epiphytische Flechtenvereine in Voralberg/Österreich und besonderer Berücksichtigung der Hemerobia von Waldökosystem. — *Voralberger Naturschau. Forschen u. Entdecken* 1: 9–152.
- Ricklefs, R. E. & Schuster, D. 1993: Species diversity: regional and historical influence. — In: Ricklefs, R. E. & Schuster, D. (eds.), *Species diversity in ecological communities*: 350–363. Univ. Chicago Press, Chicago.
- Rose, F. 1976: Lichenological indicators of age and environmental continuity in woodlands. — In: Brown, D. H., Hawksworth, D. L., Bayley, R. H. (eds.), *Lichenology: Progress and problems*: 279–307. Acad. Press, London, New York & San Francisco.
- Rose, F. 1985: The old forests of western Europe and their epiphytic lichens. — *British Lichen Soc. Bull.* 56: 1–8.
- Rose, F. 1992: Temperate forest management: its effects on bryophyte and lichen flora and habitats. — In: Bates, J. W. & Farmer, A. M. (eds.), *Bryophytes and lichens in a changing environment*: 211–233. Clarendon Press, Oxford.
- Rosenzweig, M. L. 1995: *Species diversity in space and time*. — Cambridge Univ. Press, Cambridge. 436 pp.
- Rosentreter, R. 1995: Lichen diversity in managed forests of the Pacific Northwest, USA. — *Mitt. Eidgenöss. Forsch. Anst. Wald Schnee Landsch.* 70: 103–124.
- Ryvarden, L. & Gilbertson, R. 1993–1994: *European Poly-pores*. Part I-II. — Fungiflora, Oslo. 743 pp.
- Samuelsson, J., Gustafsson, L. & Ingelög, T. 1994: *Dying and dead trees — a review of their importance for biodiversity*. — Swedish Threatened Species Unit, Uppsala. 109 pp.
- Santesson, R. 1993: *The lichens and lichenicolous fungi of Sweden and Norway*. — SBT-förlaget, Lund. 240 pp.
- Saunders, D. A., Hobbs, R. J. & Margules, C. H. 1991: Biological consequences of ecosystem fragmentation: a review. — *Conserv. Biol.* 5: 18–32.
- Scheidegger, C., Wolseley, P. A. & Thor, G. (eds.) 1995: Conservation biology of lichenized fungi. — *Mitt. Eidgenöss. Forsch. Anst. Wald Schnee Landsch.* 70(1): 1–173.
- Selva, S. B. 1994: Lichen diversity and stand continuity in the northern hardwood and spruce-fir forests of northern New England and western New Brunswick. — *Bryologist* 97: 424–429.
- Sõmermaa, A. 1972: Ecology of epiphyte lichens in main Estonian forest types. — *Scripta Mycologica* 4: 1–117.
- Söderström, L. 1981: Distribution of bryophytes in spruce forests on hill slopes in central Sweden. — *Wahlenbergia* 7: 141–153.
- Söderström, L. 1988: The occurrence of epixylic bryophyte and lichen species in an old natural and managed forest stand in Northeast Sweden. — *Biol. Conserv.* 45: 169–178.
- Tibell, L. 1992: Crustose lichens as indicators of forest continuity in boreal coniferous forests. — *Nordic J. Bot.* 12: 427–450.
- Trass, H. 1994: Liigirohke elustik on Eestimaa rikkus [Biodiversity of the Estonian flora and fauna constitutes the wealth of our country]. — *Eesti Loodus* 2: 34–36. [In Estonian with English summary].
- Trass, H. & Randlane, T. (eds.) 1994: *Eesti suursamblikud [Macrolichens of Estonia]*. — Greif, Tartu. 400 pp. [In Estonian with English summary].
- Wolseley, P. A. 1991: Observations on the composition and distribution of the 'Lobarion' in forests of South East Asia. — In: Galloway, D. J. (ed.), *Tropical lichens: Their systematics, conservation and ecology*: 217–243. Clarendon Press, Oxford.
- Wulf, M. 1997: Plant species as indicators of ancient woodland in northwestern Germany — *J. Veg. Sci.* 8: 635–642.