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Factors determining plant and lichen
species diversity and composition in Estonian
Calamagrostis and *Hepatica* site type forests

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LIST OF ORIGINAL PUBLICATIONS

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

- I. Meier, E., Paal, J., Liira, J. & Jürriado, I. 2005. Influence of tree stand age and management on the species diversity in Estonian eutrophic alvar and boreo-nemoral *Pinus sylvestris* forests. Scandinavian Journal of Forest Research 20 (Suppl. 6): 135–144.
- II. Meier, E. & Paal, J. 2009. Cryptogams in Estonian alvar forests: species composition and their substrata in stands of different age and management intensity. Annales Botanici Fennici 46: 1–20.
- III. Rajandu, E., Kikas, K. & Paal, J. 2009. Bryophytes and decaying wood in *Hepatica* site-type boreo-nemoral *Pinus sylvestris* forests in Southern Estonia. Forest Ecology and Management 257 (3): 994–1003.
- IV. Paal, J., Rajandu, E. & Köster, T. 2010. Vegetation-environment relationship in Estonian *Hepatica* site type forests in the light of A. K. Cajander's forest site type approach. Baltic Forestry 16 (2): 194–208.

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Author's contribution to the papers (%):

	I	II	III	IV
Idea and design	10	90	90	50
Data collection	70	100	50	60
Data analysis	60	100	80	90
Manuscript preparation	60	90	80	40

I. INTRODUCTION

Preserving biodiversity is one of the basic ideas in contemporary sustainable nature management and protection. Numerous studies have confirmed that intensive management of boreal forests, usually forming a monodominant and even-aged tree layer, causes a remarkable decrease in their species number, especially of cryptogams (Rose 1976, Bazzaz 1983, Söderström 1988a, b, 1993, Gustafsson & Hallingbäck 1988, Jonsson & Esseen 1990, Tibell 1992, Selva 1994, Vellak & Paal 1999). At the same time, cryptogams, occupying various microhabitats and substrata, are an important part of the forest biodiversity (Kuusinen & Siitonen 1998, Lõhmus 2003).

Decline in species diversity is caused by different factors: intensively managed forests do not have such a multitude of microhabitats (snags, fallen and decaying stems, gaps with different microclimate, mixture of several tree species of various age, etc.) as less managed stands (Söderström 1981, 1988a, b, Gustafsson & Hallingbäck 1988, Jonsson & Esseen 1990, Samuelsson et al. 1994, Keddy & Drummond 1996, Esseen et al. 1997, Kuusinen & Siitonen 1998). As the intensively managed forests are after thinning more open, light reaching the ground vegetation can more easily increase herb layer species richness and change their composition – in these forests more graminoids, light-demanding and dry soil tolerant species can grow (Sepp & Liira 2009). Nevertheless, the gaps in subnatural stands can have similar effect on the species richness and composition. The effect of management depends on the forests' habitat conditions, i.e. to what site type the stands belong (Liira et al. 2007). It has been well proved by studies of management and age effect on the cryptogam species composition in forests of different types (Söderström 1988b, Lesica et al. 1991, Boudreault et al. 2002, Økland et al. 2003). Besides management intensity, forest age has considerable importance for biodiversity, as old, large stems offer the necessary substratum for many rare cryptogam species (Sõmermaa 1972, Rose 1976, Jonsson & Esseen 1990, Lesica et al. 1991, Hyvärinen et al. 1992, Goward 1994, Christensen & Emborg 1996, Crites & Dale 1998, Kuusinen & Siitonen 1998, Uliczka & Angelstam 1999). Moreover, differences in the substratum features are the main factors behind the phorophyte-dependent floristic variation in forest communities, although canopy structure and habitat preferences of the trees have also some influence (Sõmermaa 1972, Kuusinen 1996, Mežaka et al. 2005).

On plant communities level the differences in growth conditions are often characterized in terms of habitat site types (e.g. Pålsson 1998, Davies et al. 2004, Interpretation Manual of European Union Habitats 2007, Paal 2007). In numerous countries the forest site types are distinguished and delimited according to the concept developed mainly by A. K. Cajander (1909, 1926, 1930, 1949, Cajander & Ilvessalo 1921). The forest site type ordination scheme elaborated by Lõhmus (1974a,b, 2004) and accepted for several decades as an

official guideline of the Estonian forest inventory and management planning, is closely related to the same concept as well.

Cajander's forest site type approach proceeds from the presumption that between the habitat/site conditions, forest communities tree layer growth/productivity and ground vegetation species composition a rather strong correlation exists, whereas the tree layer composition may develop relatively independently, first of all due to the human interference or fires. In that way, the mapping of forest vegetation communities can also provide an overview or even map of forest soils (Cajander 1923, 1930, 1949, Kalela 1960). Still, as it has been demonstrated by several authors, the relationship between different components of forest communities' structure and habitat properties is often rather weak (e.g. Vasilevič and Konstantinova 1980). In different regions and in different communities correlation between the vegetation and habitat characteristics can have a various character. It has been established also that forming/dynamics of different components in the ecosystems is non-synchronous. According to Targuljan and Sokolov (1978) soil and vegetation have different 'characteristic time', i.e. a period in the course of which they will attain a state of relative equilibrium. This period can be different already for the particular soil properties. The relations between plant communities' components and environmental parameters can be substituted to some independent factors like soil parent material or climate not considered in analysis.

In the current study, forests of *Calamagrostis* site type and *Hepatica* site type were investigated. Selection of these types of forests was connected with the following considerations. Alvar forests represent a rarest forest type in Europe; their distribution is limited to limestone areas in western and northwestern Estonia (islands included) and southern Sweden (Laasimer 1965, Pettersson 1965, Engelmark & Hytteborn 1999). Therefore, from the viewpoint of protection of biological diversity, these forests are the responsibility communities for Estonia. Due to their peculiar content of flora and community structure, the alvar forests represent a most exciting vegetation type around the Baltic Sea (Sterner 1938, Laasimer 1975). To ensure their effective protection, thorough knowledge is needed about their components (species, synusia, micro-communities). *Hepatica* site type forests form an ecological as well as a typological continuum with *Calamagrostis* site type forests (e.g. Lõhmus 1984, Elterman 2001), and their parallel study offers possibilities for deeper understanding of forces shaping the biodiversity in forests of these types.

The aims of the current thesis were:

- (i) to find which factors determinate plant and lichen species richness and composition in *Calamagrostis* and *Hepatica* site type forests most essentially on stand level (**I, II, IV**);
- (ii) to evaluate the effect of several community structural and soil characteristics to the herb and moss layer species richness on the 1 m² quadrat scale (**I**);
- (iii) to discuss the variation of cryptogam species richness and composition on different substrata (**II, III**).

2. MATERIAL AND METHODS

2.1. Study area and experiment design

The fieldwork was carried out in Raplamaa district in north-western Estonia (**I, II, IV**), in Otepää Nature Park and in Karula National Park situated both in southern Estonia (**III, IV**; Fig. 1).

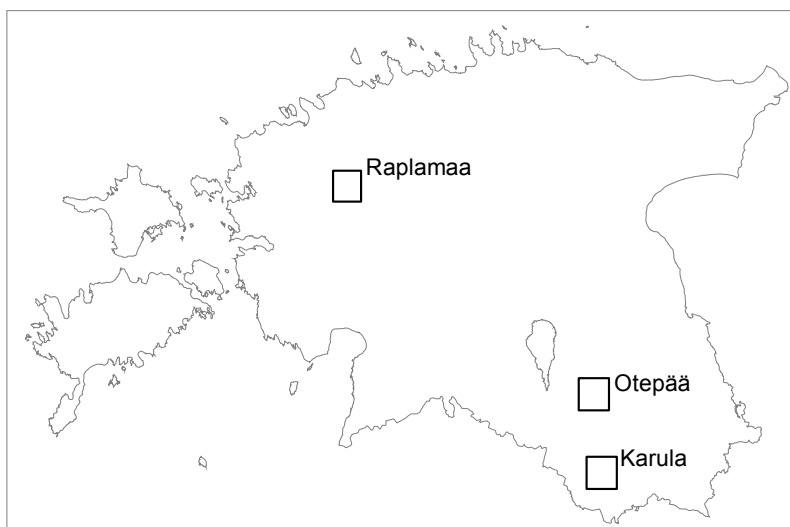


Figure 1. Location of study areas.

Topographically Raplamaa is a part of Harju Plateau where the landscape is dominated by limestone plains, locally also by tilly plains. Otepää Nature Park and Karula National Park are confined to the Otepää and Karula uplands, respectively. Otepää Upland has evolved during ice ages on bedrock upland made of sandstones, while Karula Upland has been formed as an edge formation between continental glaciers in the late glacial period on the same sandstone basement (Arold 2005).

Two forest types (*sensu* Paal 1997, 2002) were studied: eutrophic *Calamagrostis* site type alvar forest (**I, II**) and eutrophic boreo-nemoral *Hepatica* site type forest (**I, III, IV**). In *Hepatica* site type forests the tree layer is usually more diverse than in the forests of *Calamagrostis* site type. In alvar forests the tree layer density is often rather low and uneven, and the ground vegetation includes, besides common boreal forests species, a comparatively large number of grassland species (Laasimer 1945, Laasimer & Masing 1995). Alvar forests grow on shallow soils (thickness less than 30 cm) formed on limestone, gravel, grit or shingle. These soils are rich in carbonates but in

summer period they can often be very dry, containing some moisture only in microhollows (Lõhmus 2004). The *Hepatica* site type forests are considered as degraded remnants of nemoral mixed spruce forests from a warmer Atlantic climatic period (Laasimer 1965); they grow on the deep Rendzinas, Cambisols and Luvisols of moraine-rich areas, particularly on hillocks and undulating plains distributed throughout the Baltic region.

In studied forests the dominant species in the tree layer was *Pinus sylvestris*, while in the second tree layer *Picea abies* prevailed.

Forests in studies **I**, **II**, **IV** were represented with (i) intensively managed stands and, (ii) modestly managed subnatural stands. Management intensity was estimated according to the information about regular cuttings as typical management of Estonian forests means thinnings at 20-year intervals (Kaar 1986). Therefore, if the planned intermediate cuttings were not done, the stand was qualified as subnatural; if these cuttings were all done in time, i.e. there were stumps and openings of thinnings in the forests; the stand was interpreted as intensively managed. Stands without regular intermediate cuttings but with some cuttings because of windstorm impairment in 1967, were also included to the group of subnatural stands. Forests of every management class were presented by two groups: (i) younger forests about 40–80 years of age and (ii) forests older than 120 years.

In study **III** forests of three age classes were selected: (i) young forests with age of 40–55 years, (ii) mature forests with age of 65–70 years and, (iii) old forests with age of more than 120 years. All stands were divided into two classes according to the management index (MI; Liira et al. 2007). At each study site, visible signs of anthropogenic activities (e.g. cut stumps, forest tracks, trampling, ditches, trash, etc.) were recorded. Each indicator of anthropogenic activities got a score 1 or 2 that describes the proportional effect. The management intensity index is the sum of scores of indicators of anthropogenic disturbances, weighed by the distance class. The observation of any indicator within a radius of 0–25 m around the sample plot centre doubled the scores effect compared to the score effect within a radius of 25–60 m. The management intensity index is equal to zero if none of the anthropogenic activity indicators were present within a radius of 60 m. The maximum value of the MI-index for forestland fraction can reach the value of 30 in the case of a forest clear-cut area with soil damage, trash pollution, intersecting ditches and road, and surrounded by neighbouring arable fields or buildings. According to the value of management index all studied forests were divided into two classes: $MI < 4$ – unmanaged stands and $MI \geq 4$ – managed stands. Because of great importance of cutting activities in the case of our study we verified that all unmanaged stands were without regular cuttings. We also inspected critically the management effects in the forests with $MI \leq 4$.

2.2. Data collection

For data collection a circular sample plot with a radius of 25 meters (ca 0.2 ha) was analysed in each stand. If necessary, for remaining within the same community, the shape of sample plots was changed a little, maintaining the same surface area.

The tree stand parameters such as age (I–IV), site quality class (I–IV) and density of tree layer (I) were taken from forest taxation data. In nature, the basal area of every tree species at breast height (DBH) was measured in every sample plot 4–5 times and average values were used (I, IV) for further calculation of the Shannon index (McCune & Mefford 1999) of tree species diversity (I). In study I the bush layer was described by the number of bush species and in study IV by counting the number of stems of all bush species on five randomly placed subplots with a radius of 2 m. The average height of stems was also estimated. The value of stems' average height multiplied with the number of stems was used for analyses in paper IV. Young trees lower than 5 m and/or with a breast height diameter less than 5 cm were also considered belonging to the bush layer (I, IV).

Forest ground vegetation species were recorded on two scales: cover percentage of every ground vegetation species on 12 randomly placed 1 m² quadrates and the species number on the whole 25 m radius circular sample plot representing the whole forest community (I, IV).

Bryophyte and lichen species were recorded on: (i) bases (up to the height 0.7 m) of randomly selected ten dominating *Pinus sylvestris* and ten *Picea abies* trees, (ii) bases of other tree species if present in the stand (*Betula pendula* up to five trees, others up to some trees), (iii) fine woody debris (fallen branches), (iv) decaying wood (stems and stumps, coarse woody debris, $d \geq 0.1$ m), (v) windthrows, (vi) stones (erratic boulders and limestone rocks, up to five) and, (vii) ground (I, II). In study III bryophyte species were registered separately on logs and stumps. Tree remains not higher than 0.4 m were considered stumps. They were classified as natural and man-cut. Species abundance was evaluated by rank values from one to six according to the Braun-Blanquet' scale (II, III; Kreeb 1983). Specimens that were not identified in the field were collected for further laboratory investigation (I–IV). It was not possible to identify all the microlichens (sterile crustose species, e.g. *Lepraria* spp.) and we also did not identify epilithic species, due to the difficulties in collecting (I, II).

Nomenclature of vascular plant species (I, IV) follows Leht (1999, 2007), bryophytes (I–IV) Ingerpuu and Vellak (1998) and lichens (I, II) Randlane and Saag (1999). Lichenized fungus species are named 'lichen species'. Hemero-phobic species (I, II) were qualified according to Trass et al. (1999). To those belong species sensitive to various human activities, i.e. species growing on the border of their distribution area and being rare for that reason, or growing on substrata and/or in specific ecological conditions lacking in managed forests.

Red-listed species (**II**) are indicated according to the Red Data Book of Estonia (Ingerpuu 1998).

The soil morphology was described in the centre of every sample plot and the samples were taken for laboratory chemical analyses (**I**, **IV**). In every pit the deepness of occurrence of free carbonates was detected by 10% HCl. In the laboratory the following soil properties of the humus horizon and of the horizon under that were estimated: (i) $\text{pH}_{\text{H}_2\text{O}}$, (ii) pH_{KCl} , (iii) percentage of organic C content by oxidation of all organic matter with $\text{K}_2\text{Cr}_2\text{O}_7$ (Vorob'eva 1998); from this also the percentage of the humus content was calculated, (iv) percentage of total nitrogen by the Kjeldahl method (van Reeuwijk 1995), (v) soil specific surface area (m^2g^{-1}) by the water steam adsorption method (Klute 1986). All analyses were performed from the fine soil fraction with a diameter less than 2 mm. Soils were classified according to the morphological characteristics and texture class of the diagnostic horizons; if necessary, the properties estimated in the laboratory were taken into account. Nomenclature of soil types refers to the WRB (2006).

2.3. Data processing

To establish the best subset of factorial parameters for species richness estimates on the forest communities (stand) scale, General Linear Model (GLM) analysis (**I**, **IV**) with stepwise forward selection procedure for continuous variables was used (**I**, StatSoft 2001). Two categorical factors, 'Management' and 'Site type', were also kept in the model during the model building (**I**). In the models for bryophyte and lichen species growing on wood, the factor 'Site type' was replaced with 'Site quality class', as a more relevant factor and covering a more detailed range of various habitat conditions. To test which of the considered factors has a significant effect on the forest ground vegetation species richness on a 1 m^2 quadrat scale, the General Linear Mixed Model analysis (GLMM) was applied. The circular plot was defined as a random factor, grouping quadrats within each circle. A detailed list of variables used in models is given in Table 1, in study **I**.

Ecological indicator values of habitat lightness (**I**, **III**, **IV**), moisture (**I**, **III**, **IV**), acidity (**III**) and nitrogen content (**IV**) were calculated by means of calibration (Jongman et al. 1995), using the weighted averaging algorithm and indicator values of vascular plant (Ellenberg 1979) and bryophyte (Düll 1991) species.

The Multi-Response Permutation Procedure in the PC-ORD program package (MRPP test; McCune & Mefford 1999) was used to test the species composition differences between considered groups: the forests of different age and management groups (**II–IV**), species on different substrata (**II**), species on logs and stumps (**III**) and the forests of three study areas (**IV**). Cryptogams on

scarce substrata such as *Sorbus aucuparia* and *Salix caprea* were excluded from analyses (II).

The indicator values of the species in different groups (II, III) were calculated according to the Dufrêne and Legendre (1997) method included in the PC-ORD program package (McCune & Mefford 1999). Statistical significance of the obtained indicator values was evaluated with the Monte Carlo permutation test.

The variation in species composition in stands of different age and management intensity as well as on different substrata was explored using ordination techniques available in CANOCO program package (II; Ter Baak & Šmilauer 2002). First, the length of the species variation gradient was estimated using the Detrended Correspondence Analysis (DCA). Second, if the gradient length appeared to be relatively short (< 2 SD), the Principal Components Analysis (PCA) – a method based on a linear relationship between species abundances and ordination axes – was used (II). To establish forests ‘Age’, ‘Management’ and ‘Age x Management’ pure effects on the vegetation data (II), three separate partial Canonical Correspondence Analyses (CCA) were carried out, where one of the two categorical variables and their interaction, or both considered variables in the case of testing their interaction effect, were treated respectively together with substrata variables as covariables. After that only variables having a significant effect on the analysed data were treated as covariables of substrata and analyses were repeated to estimate the pure effect of substrata. Then the CCA analysis was repeated without covariables and the variance decomposition of the considered effects was evaluated.

For ranking of environmental variables according to their importance for determining the species data variation structure, the forward selection procedure available in the Redundancy Analysis (RDA) in case of short gradient, and CCA in case of longer gradient was used (II, IV). Significance of variables was evaluated by the Monte Carlo permutation test. Factors ‘Age’ and ‘Management’ interaction was removed from the analysis due to the high value (>20) of the variance inflation factor (IV), indicating multi-collinearity with some other environmental variables (Ter Baak and Šmilauer 2002).

Relationship between the forest’s age and their site index H100, referring to the dominant height (in meters) of the tree stand of a reference age of 100 years (Lahti 1995) was calculated by the Regression Analysis (IV). The site index H100 has been considered as a reliable indicator of site fertility (Kuusipalo 1985). For that analysis an independent sample of 800 stands for Raplamaa, 238 and 157 stands for Otepää and Karula Uplands were used. All these data were taken from the Estonian State Forest Inventory Database. The significance of differences between the H100 indices, timber volume, trees height and diameter in three study areas were tested by the One-Way Analysis of Variance. Pairwise multiple comparisons were performed by Tukey’s HSD test (StatSoft 2001).

3. RESULTS

3.1. Stand level

3.1.1. Species diversity in *Calamagrostis* and *Hepatica* site type forests

According to the GLM analysis the diversity of herb layer species is significantly affected by the habitat lightness (**I**, **IV**), nitrogen content and special surface area of soil humus horizon (Tables 1 and 2 in **I**). The factors ‘Management’ and ‘Site type’ are also almost significant (**I**). The increase in habitat lightness supports the number of vascular plant species (Fig. 1 in **I**, **IV**; Fig. 2). At the same time the increase in soil humus horizon nitrogen content enhances but increase of soil special surface area decreases the number of vascular plant species.

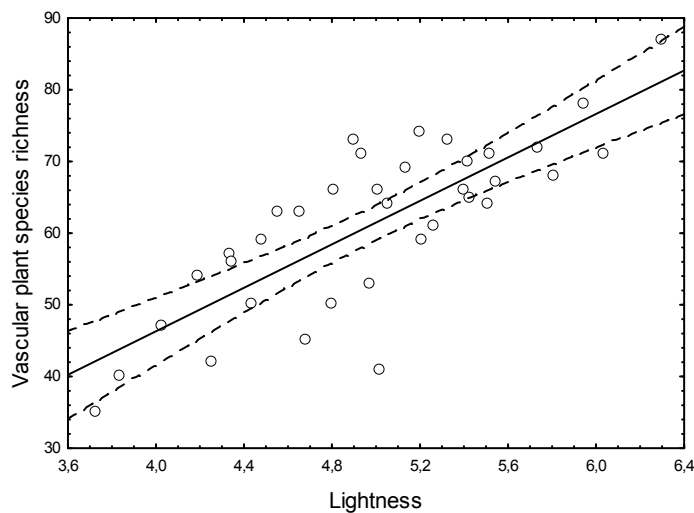


Figure 2. Relationship between the number of vascular plant species and habitat's lightness indicator value.

The diversity of bryophyte species growing on tree stem bases and decaying wood is significantly influenced by the factors ‘Management’ and ‘Site quality class’ (Tables 1 and 3 in **I**). In both forest site types the richness of bryophyte species is higher in subnatural stands and in sites of better quality (smaller rank values of the site quality class) (Fig. 3). The bryophyte species number increases linearly with the improvement in the forest site habitat quality (linear contrast $p = 0.0036$). Thirty-eight bryophyte species, among them 12 hepatics,

or altogether 10 hemerophobic forest species were recorded only in subnatural forests. For example *Anastrophyllum hellarianum*, *Barbilophozia hatcheri*, *Brachythecium erythrorrhizon*, *Fissidens bryoides*, *Hylocomium umbratum*, *Lophozia longidens*, *Metzgeria furcata*, *Riccardia palmata* belong to the latter species. Twelve species were presented only in managed forest (including four hemerophobic species, but no hepatics) (I).

The diversity of lichens growing on tree stem bases and decaying wood has a significant response to factor ‘Tree layer species diversity’ (Tables 1 and 4 in I); the diversity of lichens is promoted in forests with higher tree species diversity (Fig. 4).

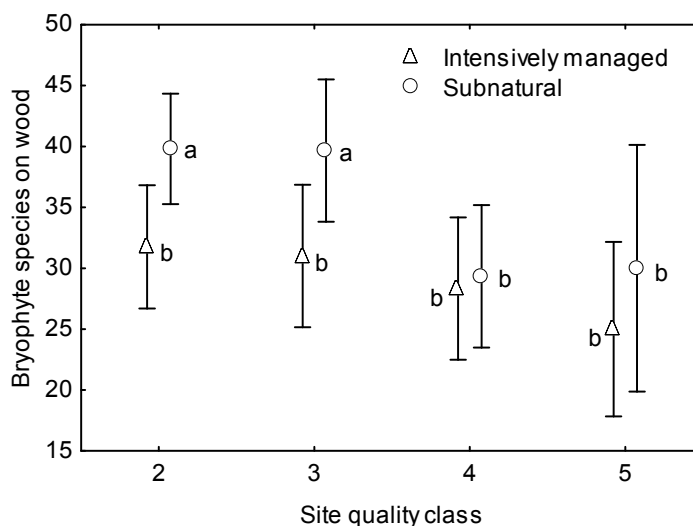


Figure 3. Number of bryophyte species growing on wood (on tree stem bases and decaying wood) in forests of different quality class and management intensity. a and b indicate homogeneity groups according to the Tukey's HSD test.

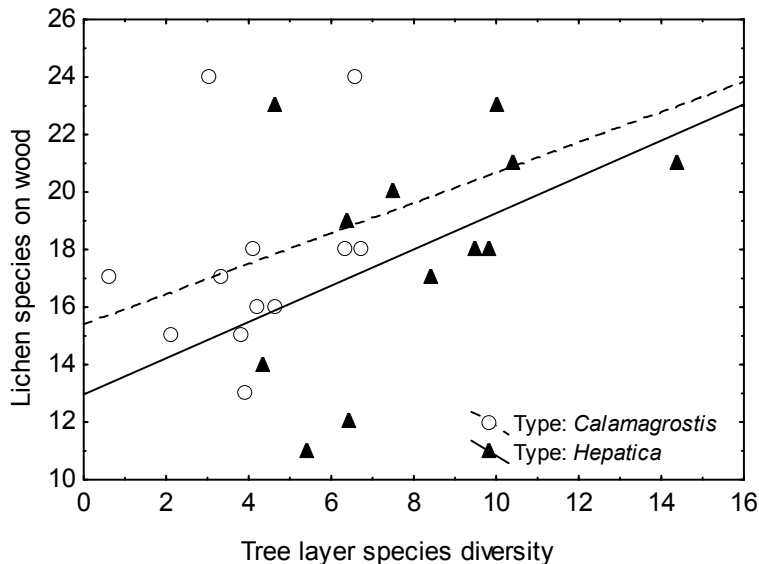


Figure 4. Relationship between the number of lichen species growing on tree stem bases and decaying wood and tree-layer species diversity.

3.1.2. Species composition in *Calamagrostis* and *Hepatica* site type forests

The difference between younger and older stands in the bryophyte species composition in *Calamagrostis* site type forests is significant (MRPP: $p = 0.013$), and the species composition differs considerably (MRPP: $p = 0.007$) also between all four groups of forests (Os, Om, Ys, Ym; Fig. 5), while in the species composition in subnatural and intensively managed forests no difference became evident (II). More hemerophobic, rare and threatened bryophyte species are bounded with older subnatural stands rather than with younger and well managed ones (Fig. 5). *Nowellia curvifolia* appeared to have a high indicator value for older forests and *Dicranum flagellare* for younger intensively managed ones. Species indicative for older subnatural stands are *Dicranum majus*, *Ptilidium pulcherrimum* and *Blepharostoma trichophyllum* (Table 1 in II). Species variance explained by factors 'Age' and 'Management' (in total 7%) was the same regardless of whether substratum variables were ignored or adjusted, indicating that there is no shared variance. Substratum variables explained 24% of the species total variance. 17% of total variance was connected with variables best explaining the species variance ('Ground', 'Stone' and 'Windthrow') (II).

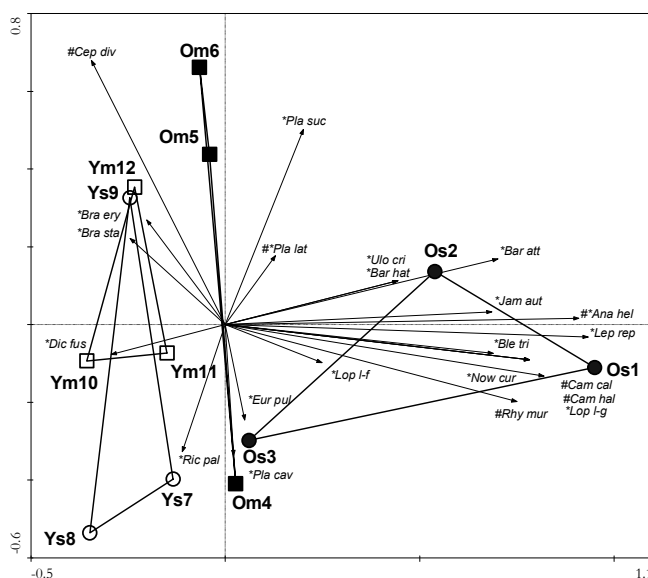


Figure 5. Ordination (PCA) of forest stands by bryophyte data. Only hemerophobic (*) and red-listed (#) species are presented. Notations for forest stands: Os – older subnatural, Om – older intensively managed, Ys – younger subnatural, Ym – younger intensively managed. For full names of species see Appendix 1 in II.

Lichen species composition in older and younger *Calamagrostis* site type forests is significantly different (MRPP: $p = 0.016$), while between subnatural and intensively managed forests and between all four forest groups (Os, Om, Ys, Ym) the differences are not significant (II). Species variance explained by factor ‘Age’ was 5% when ignoring substratum variables and 4% when adjusting them. In that way, the amount of shared variance is only 1%. Considering the effect of ‘Age’, substratum variables explained 37% of the total variance. The variables mainly determining lichen species variance are ‘Fine woody debris’, ‘Stone’ and stand ‘Age’, counting for 28% of the total variance. Most of the *Cladonia* and *Cladina* species were associated with younger forests. *Imshaugia aleurites* appears to be a good indicator for older forests and *Vulpicida pinastri* for younger ones (Table 2 in II)

The variable best and significantly explaining the *Hepatica* site type forests’ species composition of moss, herb, bush and tree layer is ‘Area’. With this categorical variable are bounded respectively 20, 10, 15 and 19 percents from total variance. According to the MRPP test, moss, bush and tree layer species composition in Raplamaa forests differs significantly from that in Otepää and Karula, while forests of both southern Estonian study areas are similar to each other. Ordination of bryophyte data (Fig. 6) illustrates these results explicitly – Raplamaa stands are obviously separated from others, whereas Otepää and

Karula forests occupy almost the same area on the ordination plot. The herb layer species composition of these three areas is different by the MRPP test but the difference is less expressed and not significant by pairwise comparison of Raplamaa and Otepää data (IV). Tree layer growth dynamics in all three regions is generally similar (Fig. 10 in IV) but in Raplamaa the average site quality class is 2.3, in Otepää and Karula 1.5 and according to that also height of trees, diameter of stems and timber volume are significantly lower than in Otepää and Karula uplands (Fig. 11 in IV). According to the GLM analysis (Table 2 in IV) pH, soil specific surface area, humus horizon depth and moisture differ between the study areas significantly but that result follows from the clear difference of Raplamaa forests soils, while in Otepää and Karula stands several soil properties are rather similar (Fig. 3 in IV).

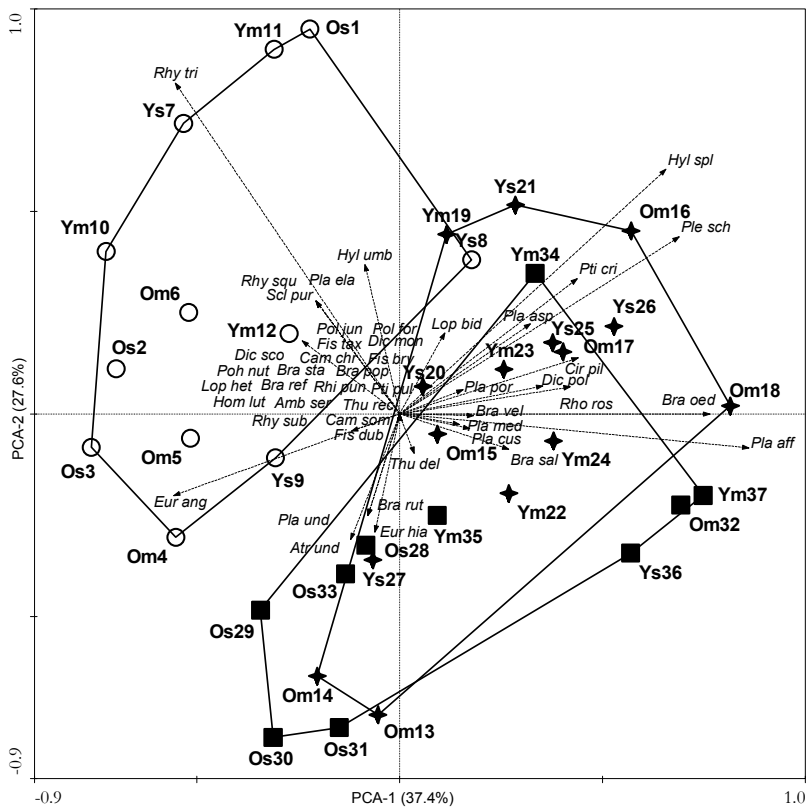


Figure 6. Ordination (PCA) of moss layer data. Forests of Raplamaa district are indicated with circles, forests of Otepää Nature Park with diamonds and forests in Karula National Park with squares. Os – old subnatural forest, Om – old intensively managed forest, Ys – young subnatural forest, Ym – young intensively managed forest. For abbreviations of species names see Fig. 6 in IV.

Other variables significantly explaining moss layer species composition in *Hepatica* site type forests are 'Herb layer cover' (15%), 'Bush layer species total abundance' (7%), 'pH_{KCl}' (6%), habitat 'Lightness' (5%), 'Basal area of deciduous trees' (4%) and 'Humus horizon depth' (3%). Herb layer species composition is also significantly explained by indicator values of nitrogen (7%) and lightness (4%), humus horizon depth (4%) and pH_{KCl} (4%). Other variables considerably affecting bush layer species composition are habitat 'Lightness' (14%), stand 'Age' (9%) and 'Humus horizon depth' (4%). For tree layer the important variable after 'Area' is 'Soil humus horizon special surface area' (6%) (IV).

3.2. Ground vegetation on the 1 m² quadrat scale (Paper I)

On the 1 m² quadrat scale the average species number of vascular plant species is higher in the *Calamagrostis* site type forests, while the *Hepatica* site type forests are a little richer in bryophyte species. The species richness of the herb and moss layer responds on this scale to several biotic and environmental conditions (Table 1 and 5 in I). However, the vascular plants and bryophytes react on all the considered factors differently. Three factors out of four (the traits of the tree layer and the soil pH) have more negative effects on species richness of the herb layer than on species richness of the moss layer. In particular, 'Tree-layer density' and 'Species diversity' have a significant negative effect on the herb-layer species richness, while the bryophyte species richness have a borderline significant positive correlation with the density of the tree layer ($p = 0.0607$; Table 5 in I). The factor 'Bush-layer species richness' is the only environmental factor that facilitates the diversity of the herb layer more positively than the moss layer.

3.3. Substratum level

3.3.1. Cryptogam species richness and composition on different substrata in *Calamagrostis* site type forests (Paper II)

Cryptogam species richness on different substrata has quite a striking variation (Fig. 7). Richness is the highest on decaying wood: 59% of the bryophyte species and 52% of the lichen species were recorded on this substratum. High species richness of bryophytes was also remarkable on windthrows and that of lichen species on different tree bases, especially on *Juniperus communis*, though the latter are growing only in 75% of the investigated stands. The bases

of the dominant *Pinus sylvestris* are comparatively poor in bryophytes. Decaying wood is especially species-rich in hepatics (15 of the 21 registered hepatic species).

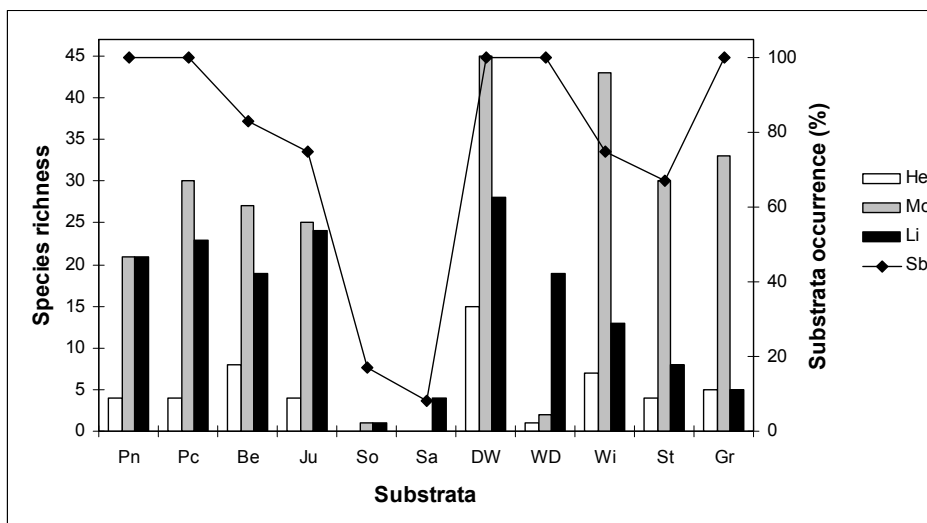


Figure 7. Species richness on different substrata. Notations: He – hepatics, Mo – mosses, Li – lichens, Sb – substrata occurrence (substrata availability in all studied stands). Pn – *Pinus sylvestris*, Pc – *Picea abies*, Be – *Betula pendula*, Ju – *Juniperus communis*, So – *Sorbus aucuparia*, Sa – *Salix caprea*, DW – decaying wood, WD – fine woody debris, Wi – windthrow, St – stone, Gr – ground.

Comparison of species composition on different substrata (MRPP test) shows that remarkably different bryophytes grow on bases of *Juniperus communis* as compared with those on the other trees. Bryophyte assemblages on *Picea abies* are significantly different ($p < 0.05$) from those growing on *Pinus sylvestris*, while the bryophytes growing on *Betula pendula* do not significantly differ from those on both *P. abies* and *P. sylvestris* (Table 3 in II).

Lichen species composition on the various tree species is dissimilar, except for *B. pendula* and *J. communis*, on which the species composition appears to be rather similar. On decaying wood, fine woody debris, windthrows, stones and ground the composition of both bryophytes and lichens are different; overlapping appears only for bryophytes growing on stones and windthrows, and for lichens recorded on stones and ground.

3.3.2. Bryophyte species diversity and composition on logs and stumps in *Hepatica* site type forests (Paper III)

Total number of species recorded on logs was 65 (inc. 16 hepatics) and on stumps 55 (inc. 10 hepatics). The largest part of species on both substrata belongs to generalists (Fig. 8); about a quarter of all species are epigeic ground flora species and approximately one fifth constitute epixylic species preferring decaying wood as a primary substratum. The proportion of epiphytes on logs is slightly higher than on stumps. The most frequent species on logs are *Hylocomium splendens* (total frequency of occurrence 100%), *Lophocolea heterophylla* (100%), *Dicranum scoparium* (96%), *Brachythecium oedipodium* (92%), *Hypnum cupressiforme* (92%) and *Sanionia uncinata* (92%). On stumps *Dicranum scoparium* (100%), *Lophocolea heterophylla* (96%), *Plagiothecium laetum* (92%), *Herzogiella seligeri* (88%), *Plagiomnium affine* (84%) and *Pleurozium schreberi* (84%) are common. According to the MRPP test, species composition on logs and stumps is significantly ($p < 0.001$) different. 18 species were recorded only on logs (e.g. *Orthotrichum speciosum* in 13 stands, *Climacium dendroides* in five stands and *Calypogeia suecica* in four stands) and six species only on stumps (e.g. *Fissidens adianthoides* in two stands). From species registered exclusively on logs, the largest part (about one third) are epiphytes, while among species found only on stumps, half are represented by generalists. The majority of hepatic species (14) grow on logs more frequently than on stumps.

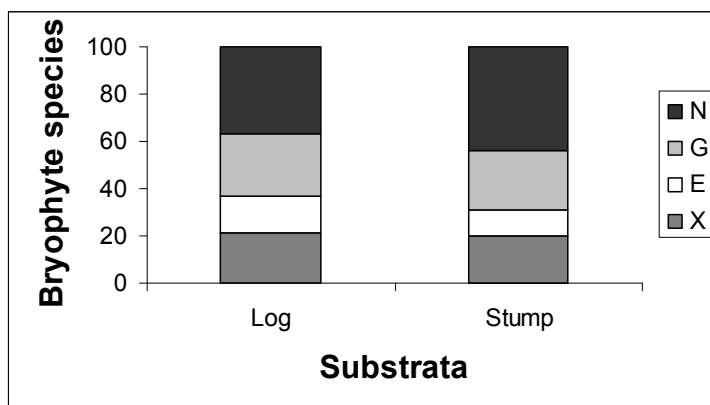


Figure 8. Bryophyte species richness on logs and stumps according to the ecological groups. Notations: X – epixylics, E – epiphytes, G – epigeics, N – generalists.

Species of logs having significant grouping indicator value ($p < 0.05$) are the following: *Hylocomium splendens*, *Hypnum cupressiforme*, *Lophocolea heterophylla*, *Nowellia curvifolia*, *Orthotrichum speciosum*, *Ptilidium pulcherrimum*, *Ptilium crista-castrensis*, *Rhytidiadelphus triquetrus* and *Sanionia uncinata*. In case of stumps three species, *Dicranum montanum*, *Plagiothecium laetum* and *Tetraphis pellucida*, had a reliable indicator value for grouping. According to the species ecological indicator values it appeared in addition that the logs are more humid and light microhabitats for bryophytes than stumps (Fig. 6 in **III**).

Stands 'Age' and 'Management' do not have any significant effect on bryophyte species richness on logs, but 'Management' has positive effect on species richness on stumps ($p < 0.05$). According to the MRPP test, significant ($p = 0.001$) difference was discovered between species composition on man-cut and naturally formed stumps. Species of man-cut stumps with significant indicator value are: *Brachythecium oedipodium*, *Brachythecium rutabulum*, *Dicranum polysetum*, *Hylocomium splendens*, *Plagiomnium affine* and *Plagiomnium cuspidatum*. There is no bryophyte species for natural stumps having a reliable grouping indicator value.

4. DISCUSSION

4.1. Species diversity and composition in *Calamagrostis* and *Hepatica* site type forests at the stand level

Several studies have confirmed the positive impact of light on vascular plant species diversity (**I**, **IV**) on half-open wooded meadows (Kull & Zobel 1991, Austad & Losvik 1998, Linusson et al. 1998, Einarsson & Milberg 1999) and also in old *Hepatica* and *Aegopodium* site type forests (Sepp & Liira 2009). The limiting ecological trait for forest understorey plants is often shade tolerance (Einarsson & Milberg 1999), and therefore the higher lightness explains the higher vascular species richness. However, species richness of different forests types is not always favoured by increasing quantity of light; therefore the positive relationship between species richness and habitats lightness in some forest communities is not valid for all stands (Härdtle et al. 2003).

Earlier experiments have shown an unimodal relationship between species richness and soil nitrogen content, i.e. the species richness is maximal by the medium level of nitrogen content (Grime 1979, Tilman & Pascala 1993). Still, a positive linear response is characteristic for species richness only if there is a deficit of nitrogen in the soil (Jentsch 2001); when the nitrogen content is surplus, it has a negative linear effect on species richness (Tilman 1993, Foster & Gross 1998, Dupré 2001).

Availability of soil nitrogen for plants is well expressed by the ratio of carbon to nitrogen; according to critical levels established for Estonian conditions by Kõlli and Lemetti (1999), 54% of sample areas in the study **I** have nitrogen deficit for optimal growth of plants and this explains well the positive response of species richness to the increase in soil nitrogen content (Rooma & Paal 2001). The negative influence of soil special surface area on vascular species richness (**I**) could be explained by the relatively high clay fraction content in the humus horizon, which causes impoverishment of herb-layer species diversity.

Bryophyte species richness appeared to be significantly higher in subnatural than in intensively managed forests (**I**). This result is in good accordance with former studies, confirming the negative impact of forest management on bryophyte species richness (Bazzaz 1983, Gustafsson & Hallingbäck 1988, Söderström 1988a, b, 1993, Jonsson & Esseen 1990, Andersson & Hytteborn 1991, Trass et al. 1999, Vellak & Paal 1999). The impact of forest management on hepatics is strikingly adverse (Söderström, 1988b, Vellak & Paal 1999), as also became evident in the results of study **I**. A typical substratum for hepatics is decaying wood (Lesica et al. 1991, Ingerpuu & Vellak 1998), which is more abundant in subnatural than in intensively managed forests. Hepatics strongly prefer shady and moist or at least fresh habitats (Ingerpuu & Vellak 1998), and

in particular the managed forests are subjected to drought more than subnatural stands (Lesica et al. 1991). Two species, *Anastrophyllum hellarianum* and *Lophozia longidens*, also found by Andersson and Hytteborn (1991) to be characteristic for unmanaged forests, were recorded in study **I** only in the subnatural forests. Thus, these species seem to be good indicators for subnatural boreo-nemoral forest communities in these two site types.

It was slightly surprising that according to the GLM analysis results (**I**) the effect of tree stand age appeared to be insignificant for both bryophyte and lichen species richness. This seems to be inconsistent with earlier results, confirming the importance of stand age on bryophyte (Söderström 1988b, Jonsson & Esseen 1990, Lesica et al. 1991, Vellak et al. 2003) and lichen diversity (Sömermaa 1972, Hyvärinen et al. 1992, Dettki & Esseen 1998, Glenn et al. 1998, Uliczka & Angelstam 1999, Jüriado et al. 2003). This negative result obtained in our study may be explained by the age limit of the studied forests, i.e. the lowest age limit of younger tree stands (60–80 years) included into the experiment was already high enough to enable the growth of the specific old growth forest cryptogams. In addition, these species could survive in younger stands on single old trees preserved for insemmination (plus-trees). However, there may be analytical bias in other studies, as forest age and silvicultural management effects were not analysed simultaneously. Nonsimultaneous analysis of both effects in the same model may transfer the management effect on species richness into terms of stand age or vice versa, as the impact of these two factors is frequently correlated.

Diversity of lichen species was significantly affected by the species richness of the tree layer (**I**). It is well known that the physical and chemical properties of tree bark influence the composition of lichen species on trees (Barkman 1958). The number and composition of lichen species are quite specific to certain tree species; in that way the diversity of lichen species in forests increases parallel to the diversity of tree species (Sömermaa 1972, Cieśliński et al. 1996, Kuusinen 1996, Jüriado et al. 2003).

In the study **II** the differences by cryptogam species composition in alvar forests between forest age groups appeared to be more striking than differences between their management groups, and the older stands became clearly discriminated from younger ones, as it has been established earlier for forests of other types (e.g. Lesica et al. 1991, Hyvärinen et al. 1992, Crites & Dale 1998, Boudreault et al. 2002). Low management effect on the species composition in alvar forests (**II**) can be explained by the removal of dead wood from subnatural stands at some period under the Soviet rule for the purpose of “protecting” these valuable communities. We got that information from the forestry officers after vegetation analyses. The studied subnatural stands have been under local protection since 1978 (Ehrpais & Ehrpais 1986). Anyway, the high number of hemerophobic bryophyte species in the unmanaged forests (**II**) indicates their quite good state of naturalness (Trass et al. 1999, Vellak & Paal 1999) in spite of inadequate protection measures. At the same time, a considerably large

number of hemerophobic lichen species in intensively managed alvar forests show that these forests form quite a natural habitat in spite of thinnings (II). Thinning effect is often associated with lower humidity and enhanced illumination of bottom layers (Söderström 1988b, Larsson 2001) but alvar forests are already naturally quite dry and open (Laasimer 1965) and this can be another explanation for the similar species composition in subnatural and intensively managed stands.

Several bryophyte species are sensitive to human impact and prefer older forests (Söderström 1988b, Andersson & Hytteborn 1991, Kuusinen 1996, Trass et al. 1999) and usually these species have a low abundance (Cooper-Ellis 1998). Hepatics are characteristic of old subnatural stands, mainly because there is more humidity on the level of undergrowth and presence of dead wood in different decay stages (Söderström 1988b, Samuelson et al. 1994). Among the bryophyte species having a significant indicator value for old subnatural stands (II), *Nowellia curvifolia* and *Blepharostoma trichophyllum* are also characteristic for old-growth natural forests (Trass et al. 1999), and *Ptilidium pulcherrimum* for old stands (Lesica et al. 1991). More bryophyte species (also red-listed, hemerophobic and/or hepatic species) were found in older, subnatural stands than in younger, intensively managed ones (II). The red-listed epixylic bryophyte *Anastrophyllum hellerianum* has also been found in earlier studies (Andersson & Hytteborn 1991, Söderström 1988b) only in subnatural forests, and according to Söderström (1988a) it prefers very large logs and can grow, therefore, in old forests as recorded also in study II. Species of the lichen genera *Cladonia* and *Cladina*, associated with younger forests (II), have been found to be more numerous and abundant in second-growth stands (Söderström 1988b, Lesica et al. 1991). In younger stands, the bottom layer gets more light, whereas humidity is comparatively low, i.e. the prevailing conditions are those to which the respective species are adapted (Söderström 1988b). The foliose lichen *Imshaugia aleurites*, recorded by us only in old forests (II), is considered a characteristic species of ecological continuity of native pinewoods in the British Isles as well (Coppins & Coppins 2002).

The species content in Raplamaa *Hepatica* site type forests differs considerably from that in South Estonian respective stands (IV). Sepp and Liira (2009) found also the influence of geographic location to the understory species composition being different in western and eastern part of Estonia. Distribution limits of numerous plant species in Estonia are conditioned by soils calcareousness. Soils in Raplamaa are remarkably more calcareous than in Otepää and Karula uplands, which follows from the closeness of limestone bedrock to the surface. Therefore several indicator species of Raplamaa forests (see study IV) are spread only or mainly in western Estonia, e.g. *Scleropodium purum* (Ingerpuu et al. 1994), *Carex ornithopoda*, *Carex flacca*, *Rubus caesius* and *Filipendula vulgaris* (Kukk and Kull 2005). In Otepää Nature Park and even more in Karula National Park the studied forests grow often on hilly landscape as fragmented patches surrounded by cultivated arable lands,

therefore in these stands beside many real indicator species rather large number of apophytic species (Kukk 1999) such as *Epilobium montanum*, *Geum urbanum*, *Stellaria media* and *Urtica dioica* was recorded. Environmental differences appeared also in humus horizon properties, e.g. the soil specific surface area is much higher in western than in southern Estonia. That is affirmed also by the ecological values of moisture, which are higher for Karula and Otepää forests than for Raplamaa.

The factors explaining species variance of different layers are diverse (IV). It confirms that every layer develops and forms its structure at least to some extent autonomously. Certain independence of layers in forest plant communities becomes evident also on the ground that species variance in every community layer has been determined usually with different environmental variables, i.e. for every layer its own system of relationships between the species as well between the species and environmental factors is characteristic (Šennikov 1964, Paal 1995). The relative autonomy of plant community layers is in good accordance with Cajander's theory of forest site types (Cajander 1930, Kalela 1960, Frey 1973). Still, some significant factors overlap for different layers, e.g. 'Habitat lightness' and 'Humus horizon depth' for moss, herb and bush layer. Bryophyte species composition is influenced by the other layers, especially by herb layer cover. Herb layer influence to the moss layer has been also demonstrated in earlier studies (Ingerpuu et al. 1998, Ingerpuu et al 2005). Herb layer species composition is determined more by soil characteristics than by other layers. In study IV we did not detect significant impact of either 'Management' or 'Age' factors on the species composition, except bush layer. In *Hepatica* site type forests the bush layer formed mainly by hazel is common and in older stands it often forms a dense canopy, being the reason why stand age appeared to be an important variable for bush layer. According to Sepp and Liira (2009), at least in the *Hepatica* site type old forests management affects the field layer species composition substantially. It seems that the only modest effect of 'Management' and 'Age' factors in the current study is overshadowed by the large variance connected with the categorical variable 'Area'.

4.2. Ground vegetation on the 1 m² quadrat scale (Paper I)

The small-scale species richness of the herb and moss layer on the 1 m² scale was clearly influenced by local environmental conditions, as shown by the results of the mixed model analysis (Table 5 in I). Moss and herb layers have layer-specific sensitivity to the variability in light and soil conditions, created by tree and bush layer diversity, tree-layer density and soil pH. The relative individuality of layers in Nordic forest communities is explained by the fact that each layer occupies its own clearly defined ecological niche and has its own

system of relationships between the species and between the species and environmental factors (Korčagin 1976, Paal 1995).

According to the results of our study, the number of vascular plants in the herb layer depends significantly on the conditions created by the tree layer, i.e. the forest openness promotes herb layer diversity, as several grassland species are able to grow in open microhabitats. The light availability for forest ground vegetation and tree-layer diversity depends on management intensity, as intensively managed forests are more open, with a lower number of tree species. It may be concluded that silvicultural management does, at least to some extent, favour vascular plant species richness. However, the moss layer diversity also depends on light conditions but the increase in light availability affects the moss layer significantly negatively. For grasslands, the relationship between the topsoil pH and the small-scale species richness of vascular plants is positive, as recognized in numerous publications (Grime 1979, Tyler 1997, Viiralt 1999). Most of the Estonian grassland species grow on soils where the humus horizon pH is between 5.0 and 7.5 (Viiralt 1999). As shown by the results of our study, on calcareous soils the forest herb layer species richness is determined mostly by the light conditions and not by the soil pH heterogeneity. The latter is connected with the limited variation in soil pH in the studied forests (Table 1 in I).

4.3. Cryptogam species diversity and composition on substratum level

A large proportion of organisms (incl. cryptogams) living in the forests are dependent on the presence of dead wood (Esseen et al. 1997, Jonsson & Jonsell 1999, Larsson 2001). High species diversity is evidently connected with large microsite heterogeneity constituted by decaying wood. That proceeds from several factors, e.g. from the size of wood fragments, bark and wood texture, nutrient composition, water-holding capacity and microclimatic conditions (Esseen et al. 1997). Therefore, as expected by comparison of different substrata (II), the cryptogam species richness is highest on decaying wood. Several studies confirm decaying wood being a very important substratum for lichens in quite dry pinewoods in contrast to humid spruce forests (cf. Humphrey et al. 2002).

A considerably high bryophyte species richness was recorded on windthrows (II). Jonsson and Esseen (1990) also emphasized the importance of windthrows as a substratum for bryophytes. Uprooting creates space for bryophyte colonization that is free from potential competitors. A number of various substrata (humus, mineral soil, stones and roots) are exposed on both the tip-up mounds and the pits, resulting together in high micro-habitat heterogeneity (Jonsson & Esseen 1990, Ulanova 2000). Windthrows are not scarce in alvar forests, where the soil is thin and tree roots can not entrench deep (Laasimer 1965).

It appeared that on *Juniperus communis* the lichen species richness is the highest among the studied trees though the number of these bushes or small trees was very low in comparison with that of the dominating trees (II). Up to now, little attention has been paid to *J. communis* as a cryptogam substratum, and the former studies carried out in Germany, Sweden and Finland (cf. Barkmann 1958) do not report high epiphytic species richness on it. Differences in bark characteristics, particularly in bark acidity, are the most prominent factors influencing the floristic differences of epiphytic species growing on various tree species. High pH of bark is usually considered to support the establishment of most epiphytic lichens and bryophytes (Kuusinen 1996). The bark of *J. communis* is less acid (pH > 5) than that of *Picea abies*, *Pinus sylvestris* or *Betula pendula*, being similar to that of deciduous trees (Barkmann 1958). This seems to be the reason why a larger number of species can grow on *J. communis* as compared with other coniferous trees.

The bryophyte species composition is similar on *Pinus sylvestris*, *Betula pendula* and *Picea abies* (II). These trees are quite poor in specialist species that are confined to a particular tree species (Kuusinen 1996). *Betula pendula* is an exception among the deciduous trees, having about the same epiphytic flora as conifers (Barkmann 1958, Kuusinen 1996). Bryophyte species composition on *Juniperus communis* differs from the other tree species (II), confirming once again the importance of this substratum in alvar forests. The composition of lichen species on *Juniperus communis* is most similar to that on *Betula pendula*, probably because the *B. pendula* bark is more alkaline than that of *P. sylvestris* and *P. abies* (Barkmann 1958).

Similarity of ground and stone lichens species composition (II) can be explained in two ways: (i) in forest stones are covered with a shallow layer of humus, which makes this substratum similar to ground and, (ii) the bedrock surface is frequently opened on alvar forest ground, making the latter similar to the stone substratum.

Our results demonstrated rather clearly the difference in bryophyte species composition on logs and stumps (III). That proceeds from the ecological conditions peculiar to these microhabitats: logs lying on ground are more saturated with moisture than stumps and this is one of the main factors determining the bryophyte species assemblages on both substrata (McCullough 1948, Jansová & Soldán 2006). The humid microhabitats are favourable first of all to the hepatics (Söderström 1988b, Rambo & Muir 1998, Jansová & Soldán 2006), therefore they are considerably more frequent on logs than on stumps (III). Hepatics grow usually on steep slopes on the sides of logs to avoid the humus layer, which accumulates easier on the flat upper parts of logs. Hepatics might thus also escape competition with faster expanding pleurocarpous mosses that usually occupy the upper parts of logs (Jansová & Soldán 2006).

The higher ecological indicator value of lightness for logs than for stumps (III) seems a bit confusing. This result accrued from the fact that several bryophytes actually growing on logs are remnants of the original epiphytic

bryophyte assemblages on living trees (Rambo & Muir 1998). Epiphytic species mainly associated with logs (III, e.g. *O. speciosum*, *P. pulcherrimum*) or found by us only on logs (III, other *Orthotrichum* species) have high light indicator value (7–8) (Düll 1991). But usually the *Orthotrichum* species grow higher on tree stems and larger branches (Dierßen 2001), where light conditions are better than in microhabitats closer to ground. In addition to that, several ground flora species (e.g. *R. triquetrus*, *H. splendens*) also having high light indicator value (6–7, Düll 1991) were more frequent on logs than on stumps (III). In that way the scoring indicator value of light conditions can be misleadingly high for logs. At the same time, *P. laetum* and *T. pellucida* recorded by us on stumps (III), prefer ordinarily shadow places (light indicator value 3–4; Düll 1991). *P. laetum* is especially common on bases of *P. abies*.

Bryophyte species identified by their grouping indicator value as bounded to logs (III), have various ecological behaviour (Andersson & Hytteborn, 1991). Among them epixylic specialists (e.g. *L. heterophylla*, *N. curvifolia*), epiphytes (*O. speciosum*, *P. pulcherrimum*), competitive epigeics (*H. splendens*, *P. cristacastrensis*, *R. triquetrus*) and opportunistic generalists (*H. cupressiforme*) are represented. Species content changes during the decaying process, being favoured by facultative epiphytes in early decay stages and by ground flora species in late decay period. Therefore variation in decay stages gives an opportunity of growing to species having different life strategy. Abundance of logs of various diameter classes (see paper III) is also important for bryophyte species diversity, because, e.g. late epixylic species use mostly only large logs, which will not become quickly overgrown by strong competitors from the forest floor bryophytes (Söderström 1988a, Rambo & Muir 1998). *T. pellucida*, being characteristic for stumps (III) was found by Söderström (1988b) on the stumps as the only member of the late epixylic group (*sensu* Söderström 1988a). This species can grow on different substrata but has perianth/sporophytes much more frequently on stumps than on logs or other substrata; stumps are, therefore, important substratum for persistence of this species, other substrata may be regarded as suboptimal (Söderström 1993).

A more numerous and diverse substratum of stumps in managed stands than in unmanaged forests (see paper III) increases the number of species growing there. From this follows that regular thinning will favour bryophyte species richness on stumps. Nevertheless, the characteristic species of man-cut stumps (e.g. *B. oedipodium*, *D. polysetum*, *H. splendens* and *P. affine*; III) are very common in boreal forests on several substrata and thereby the total bryophyte species richness often may not increase in these communities after loggings.

5. CONCLUSIONS

The influence of various factors on the species richness and composition in different scales, layers and site types has diverse character.

The direct management effect on the species diversity was essential for bryophyte species growing on wood; in both forest types the richness of bryophyte species is higher in subnatural than in intensively managed stands. Still, the number of bryophyte species growing on stumps in *Hepatica* site type forests is higher in managed forests than in the unmanaged ones. At the same time, the species having high indicator value for man-cut stumps are very common species in boreal forests and grow on other substrata as well.

Though the effect of tree stand age appeared to be insignificant for cryptogam species richness, it is essential for determining the bryophyte and lichen species composition in *Calamagrostis* site type forests. The stand age described also a considerable part of bryophyte species variance on logs and stumps in *Hepatica* site type forests. Nevertheless, availability of different substrata appeared even more essential for cryptogam diversity and species composition than forests age or management intensity. Decaying wood and *Juniperus communis* appeared to be important substrata for cryptogam species diversity in alvar forests. The bark of *J. communis* is less acid ($\text{pH} > 5$) than that of *Picea abies*, *Pinus sylvestris* or *Betula pendula*, being similar to that of deciduous trees. This seems to be the reason why a larger number of species can grow on *J. communis* as compared with other coniferous trees.

Bryophyte species composition differs between stumps and logs in *Hepatica* site type forests. That proceeds from the ecological conditions: logs are more humid microhabitats than stumps and suit better for growth of several hepatics.

On the 1 m² quadrat scale, diversity and density of tree layer, species richness of bush layer and soil pH have significant layer-specific effects on the ground layer species richness. Bryophyte diversity increases together with increasing shade in forest ground vegetation, while an increase of herb-layer diversity is connected with better lightness. Forest openness promotes also herb-layer diversity on stand level. In addition to lightness, the increase in soil humus horizon nitrogen content enhances vascular plant species richness, but increase of soil special surface area has an opposite effect.

The main factor on what the species composition of different layers in *Hepatica* site type forests depends is the geographic location of these stands: forests of north-western Estonia are significantly different from those in southern Estonia. Other factors which determine species composition varied in case of different layers as for every layer its own system of relationships between the species as well between the species and environmental factors is characteristic. Still, some significant factors overlap for different layers, e.g. habitat lightness and humus horizon depth for moss, herb and bush layer. Bryophyte species composition is influenced by the other layers, especially by herb layer cover. Herb layer species composition is determined more by soil characteristics than by other layers.

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SUMMARY IN ESTONIAN

Erinevate faktorite mõju taimede ja samblike liigirikkusele ning liigilisele koosseisule Eesti metskastiku ja sinilille kasvukohatüübi metsades

Bioloogilise mitmekesisuse kaitse pälvis kaasaegses säästlikus metsamajandamises ja looduskaitstes suurt tähelepanu. Kuigi paljud uurimused käsitlevad liigilise mitmekesisuse seost metsade majandamise ja vanusega, sõltub selle seose tugevus ja olemus paljuski keskkonnatingimustest, kusjuures puidul kasvavate sammalde ja samblike (krüptogaamide) varieeruvus oleneb suuresti erinevate substraatide esinemisest ja iseloomust. Ka liikide ja keskkonnapara-meetrite omavaheline seos võib olla erinevates kooslustes ja regioonides väga erinev.

Käesolevas töös uuriti metskastiku ja sinilille kasvukohatüübi metsi. Metskastiku kasvukohatüübi metsad kuuluvad loometsade hulka, mis on üheks haruldasemaks metsatüübiks Euroopas, olles esindatud üksnes lubjakivialadel Lääne- ja Loode-Eestis (sh saartel) ja Lõuna-Rootsis. Seega Euroopa looduse bioloogilise mitmekesisuse kaitse seisukohalt on loometsad meie n-õ vastutiskooslused. Et tagada efektiivne looduskaitse ja juhtnöörid mõistlikuks majandamiseks, peame me esmalt võimalikult täpselt teadma, millised on käsitletavate metsakoosluste komponendid. Sinilille kasvukohatüübi metsad on kastikuloo metsadele ökoloogiliselt ja tüpoloogiliselt küllalt lähedased, mistõttu nende paralleelne uurimine võimaldab paremini mõista bioloogilise mitmekesisuse olemust neis metsades.

Käesoleva töö eesmärgiks oli leida, millised faktorid mõjutavad taimede ja samblike liigirikkust ja liigilist koosseisu metskastiku ja sinilille kasvukohatüübi metsades, samuti kuidas see mõju avaldub koosluste erinevates rinnetes aga ka erinevates skaalades.

Kastikuloo metsi uuriti Raplamaal, sinilille kasvukohatüübi metsi Raplamaal, Otepää Looduspargis ja Karula Rahvuspargis. Koosluste tasandil analüüsiti keskkonnategurite mõju sambla-, rohu-, põõsa- ja puurindele. Samuti käsitleti krüptogaamide liigilist mitmekesisust mõjutavaid faktoreid. Erinevate tegurite mõju sambla- ja rohurindele uuriti ka 1 m² skaalas. Substraatide tasandil analüüsiti kastikuloo metsade sammalde ja samblike liigilist mitmekesisust ning Lõuna-Eesti sinilille kasvukohatüübi metsade samblaid kõdupuidu substraatidel – lamapuidul ja kändudel. Töös nimetatakse samblikuliikideks lihheniseerunud seente liike.

Töö tulemusena selgus, et puidul kasvavate sammalde liigirikkusele avaldab metsade majandamine vahetut mõju – nii metskastiku kui ka sinilille kasvukohatüübi vähemajandatud metsades kasvab erinevat liiki samblaid oluliselt rohkem kui intensiivselt majandatud metsades. Kuigi sinilille kasvukohatüübi majandatud metsades kasvab kändudel majandamata metsadega võrreldes rohkem liike, tuleb siinjuures silmas pida, et raiekändudele iseloomulikud

liigid on tavalised metsaliigid, mida kasvab enamasti ohtrasti ka teistel substraatidel, seega kogu koosluse liigirikkus raiekändudel esinevate liikide arvel ei suurene.

Ehkki puistu vanuse olulist mõju sammalde ja samblike liigirikkusele ei tuvastatud, osutus see kastikuloo metsades tähtsaks krüptogaamide liigilist koosseisu määravaks faktoriks. Vanus kirjeldas olulise osa ka sinilille kasvukohatüübi metsade sammalde liigilisest koosseisust kõdupuidul. Siiski, krüptogaamide mitmekesisus loometsades sõltub enam erinevate substraatide olemasolust kui puistu vanusest. Sammalde ja samblike liigilise mitmekesisuse seisukohalt on loometsades eriti olulisteks substraatideks kõdupuit ja kadakas. Kõdupuit on mikrokasvukohtade poolest väga mitmekesine – puiduosade suuruse, koore tekstuuri, toitainete sisalduse, niiskuse ja teiste kasvupinna omaduste suur varieerumine võimaldab seal kasvada väga erinevatel liikidel. Kadaka tähtsus seisneb eelkõige tema koore suuremas aluselisuses teiste puudega (mänd, kuusk ja kask) võrreldes, võimaldades seeläbi okasmetsade kooslustes kasvada ka lehtpuudele omastel epifüütsetel krüptogaamid. Palju sambalaliike kasvas ka tuuleheitel, mille puhul paljanduvad mullapind, kivid ja puude juured, mis pakuvad sammaldele ja samblikele mitmekesiseid kasvuvõimalusi. Tuuleheited on loometsades küllalt sagedased, kuna mullakiht on õhuke ja puude juured ei saa seetõttu väga sügavale tungida.

Ökoloogilised tingimused ja sellest tulenevalt ka sammalde liigiline koosseis on sinilille kasvukohatüübi metsades lamapuidul ja kändudel erinevad. Enamasti on lamapuidu niiskusesisaldus kändude omast suurem, sobides seetõttu paremini kasvupinnaks erinevatele helviksammaldele. Lamapuidul kasvas kändudega võrreldes rohkem valgusnõudlikke sambaliike, milledest osa on jäänud lamapuidule kasvama varasemast ajast, mil puu veel seisis püsti ja valgustingimused olid paremad.

Maapinna taimkatte analüüsimisel 1 m² suuruste prooviruutude põhjal selgus, et rohu- ja samblarinne käituvad uuritud keskkonnaparameetrite suhtes erinevalt. Samblarinde liigirikkus suureneb koos metsaaluse ulatuslikuma varjutatusega ülemiste rinnete poolt, samal ajal rohurinde liigirikkus seostub just paremate valgustingimustega.

Valguse oluline mõju rohurinde liigirikkusele ilmneb ka koosluste tasemel. Saadud tulemust kinnitavad varasemad uuringud nii sinilille kasvukohatüübi metsades kui ka puisniitudel, kuid sellest hoolimata pole see positiivne seos laiendatav kõikidele kooslustele. Lisaks valgusele suurendab soontaimede liigirikkust oluliselt mulla lämmastiksisalduse tõus, seevastu mulla suurema eripinna väärtusega kaasneb liigirikkuse vähenemine. Varasemad uurimused on näidanud eelkõige lämmastiku ja liigirikkuse unimodaalset seost, kuid lämmastiku defitsiidi korral on täheldatud ka positiivset seost. Ka käesolevas uurimuses täheldati enam kui pooltel uuritud aladest lämmastiku defitsiiti (I). Eripinna negatiivset mõju liigirikkusele võib seletada huumushorisondi küllalt kõrge savi sisaldusega.

Peamiseks faktoriks, millest sõltub sinilille kasvukohatüübi metsakoosluste erinevate rinnete liigiline koosseis, osutus analüüsitavate metsade geograafiline asukoht. Kuna käesolevas töös uuritud Loode-Eesti metsades on mulla lähtekivimiks karbonaatsed lubjakivid, Lõuna-Eestis aga märgatavalt happelisemad moreensed setted, tulenevad sellest suurel määral ka muud kasvukohtadele omased ökoloogilised tingimused, mistõttu Loode-Eesti metsad erinevad oluliselt Lõuna-Eesti metsadest. Loode-Eesti metsade liigilise koosseisu erinevust Lõuna-Eesti omadest mõjutab ka osa liikide levik, mis piirdub üksnes Põhja- ja Lääne-Eestiga. Teised liigilist koosseisu määravad faktorid varieeruvad eri rinetes, millest ilmneb iga rinde teatav eripära liikide ja keskkonnaparametrite vahelistes suhetes. Siiski esineb ka mitmeid keskkonnategureid, mis mõjutavad liigirikkust samaaegselt mitmes rindes, nt valgustingimused ja huumushorisoni sügavus sambla-, rohu- ja põõsarinde puhul. Samblarinde liigilist koosseisu mõjutavad suuresti teised rinded, eelkõige rohurinde katvus. Rohurinde liigiline koosseis sõltub eeskätt mulla omadustest, vähem teiste rinnete mõjust. Puurinde vanus osutus oluliseks liigilist koosseisu määravaks teguriks üksnes põõsarindele – sinilille kasvukohatüübi vanemates metsades moodustab põõsarinde sageli tihedalt kasvav sarapuu.

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PUBLICATIONS

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Main research interests

Biosciences and environment, ecology, biodiversity in forest, including different species groups: vascular plants, bryophytes and lichens and how different factors influence this.

Presentations

- 2008 Cryptogams in Estonian alvar forests: species composition and their substrata in stands of different age and management intensity. The Third ALTER-Net summer school 'Biodiversity and Ecosystem Services', Sept 2–14, Peyresq (Provence), France
- 2007 Cryptogams in Estonian alvar forests: species composition and their substrata in stands of different age and management intensity. EcoSummit 2007 'Ecological Complexity and Sustainability: Challenges and Opportunities for 21st Century's Ecology', May 22–27, Beijing, China
- 2006 The influence of different factors to forests species diversity. ISOBIS/GBIF PhD Summer School, 'Biodiversity Informatics', August 13–20, Sandbjerg, Denmark
- 2005 Eddy covariance method – applications in ecology. CBACCI Nordic Graduate School, Field Course on Micrometeorology, May 23–27, Hyytiälä, Finland
- 2004 The influence of stand age and management on species diversity in alvar and boreo-nemoral forests. International conference 'Natural Disturbances and Ecosystem Based Forest Management', May 27–28, Otepää, Estonia

Scholarships

- 2007 Kristjan Jaak's scholarship
- 2005, 2006, 2007 Doctoral School of Ecology and Environmental Sciences, graduate student scholarships
- 2002 Saaremaa Local Authorities Union, Johann von Luce scholarship
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Membership in organizations

- Estonian Seminatural Community Conservation Association (member since 2004)
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Publications

Articles indexed by ISI Web of Science

- Paal, J., **Rajandu, E.** & Köster, T. 2010. Vegetation-environment relationship in Estonian *Hepatica* site type forests in the light of A. K. Cajander's forest site type approach. *Baltic Forestry* 16 (2): 194–208.

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Other publications

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- 2008 Cryptogams in Estonian alvar forests: species composition and their substrata in stands of different age and management intensity. The Third ALTER-Net summer school 'Biodiversity and Ecosystem Services', 2.–14. september, Peyresq (Provence), Prantsusmaa
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- 2006 The influence of different factors to forests species diversity. ISOBIS/GBIF PhD Summer School, 'Biodiversity Informatics', 13.–20. august, Sandbjerg, Taani
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- 2004 The influence of stand age and management on species diversity in alvar and boreo-nemoral forests. International conference 'Natural Disturbances and Ecosystem Based Forest Management', 27.–28. mai, Otepää

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- Eesti Loodusuurijate Selts (liige 2000. aastast)

Publikatsioonide loetelu

Artiklid, mis on kajastatud ISI Web of Science and mebaasis

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