

ORIGINAL ARTICLE

Influence of tree stand age and management on the species diversity in Estonian eutrophic alvar and boreo-nemoral *Pinus sylvestris* forests

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Abstract

The influence of tree stand age, silvicultural management and several habitat variables on species diversity was analysed in *Calamagrostis* site type alvar forests and *Hepatica* site type boreo-nemoral forests. On the community scale, the herb-layer species richness appeared to be determined mostly by forest soil and light conditions. However, the number of bryophyte species growing on tree stem bases and on decaying wood was dependent on management intensity and forest site quality class. On the same substrate types the number of lichen species was promoted only by tree species diversity. 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 species richness. Bryophyte diversity increases together with increasing shade and moisture in forest ground vegetation, while an increase of herb-layer diversity is connected with lightness. Therefore, maintenance of the small-scale species richness of forest ground vegetation cannot be achieved by uniform management practice.

Keywords: *Bryophytes, decaying wood, general linear model analysis, lichens, small-scale diversity, subnatural forests, substrates, vascular plants.*

Introduction

Preserving biodiversity is one of the basic ideas for contemporary nature 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, 1988*a, b*, 1993; Gustafsson & Hallingbäck, 1988; Jonsson & Esseen, 1990; Tibell, 1992; Selva, 1994; Vellak & Paal, 1999). 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, 1988*a, b*; Gustafsson & Hallingbäck, 1988; Jonsson & Esseen, 1990; Samuelsson et al., 1994; Keddy & Drummond, 1996; Esseen et al., 1997; Kuusinen & Siitonen, 1998). Besides the management intensity, forest age also has considerable importance for biodiversity, as old, large

stems offer the necessary substrate for many rare cryptogam species (Sömermaa, 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). Although the amount of publications dealing with the problems of forest species diversity change is remarkable, the environmental conditions and species content in every site type and/or geographical region have certain original features and the respective studies can never be exhaustive.

In the current study, forests of *Calamagrostis* (alvar) site type and *Hepatica* site type were investigated. Selection of these types of forests was connected with the following considerations. Alvar forests represent one of the rarest forest types in Europe; their distribution is limited to limestone areas in Estonia and southern Sweden (Laasimer, 1965; Pettersson, 1965). From the viewpoint of protection of biological diversity, for Estonia these forests are the responsibility communities, i.e. communities that can grow in some region over a

comparatively large area, but are, nevertheless, lacking elsewhere. To ensure their effective protection, thorough knowledge is needed about their components (species, synusia, microcommunities). Although the forests of *Hepatica* site type are distributed all over Estonia, their detailed peculiarities on localities confined to soils on limestone parent material are unknown. Finally, the *Calamagrostis* and *Hepatica* site type forests form an ecological as well as a typological continuum (e.g. Lõhmus, 1984; Elterman, 2001), and parallel study offers possibilities for deeper understanding about forces shaping the biodiversity in forests of these types.

In the current study the following null hypotheses were tested: (1) the diversity of forest herb-layer species does not depend on stand age, management intensity and site type; (2) the diversity of forest bryophyte-layer species does not depend on stand age, management intensity and site type; and (3) the diversity of cryptogams growing on tree stem bases and on decaying wood does not depend on stand age, forest management intensity and forest site type. In addition, the effect of several community structural and soil characteristics on the ground vegetation (herb and moss layer) and cryptogams diversity was evaluated.

Materials and methods

Study area and experimental design

The study was carried out in Vardi forestry (Rapla-maa district, north-western Estonia) in 2002–2003. Two forest types (*sensu* Paal, 2002) were studied: eutrophic *Calamagrostis* site type alvar pine forest and eutrophic boreo-nemoral *Hepatica* site type pine forest. *Hepatica* site type forests have an average site quality class 1.5–2.0 degrees lower than for *Calamagrostis* site type (Table I), and therefore have better conditions for tree growth. Site quality class 1 means that a 100-year-old coniferous stand is over 27 m high, a stand of class 2 has a height of 24–26 m, class 3 stand 20–23 m, class 4 stand 16–19 m and a class 5 stand ≤ 15 m (Krigul, 1971). In *Hepatica* site type forests the tree layer is usually more diverse than in the *Calamagrostis* site type. In alvar forests the tree-layer density is usually rather low and uneven, and the ground vegetation includes, besides all common boreal forests species, a comparatively large number of grassland species (Laasimer, 1945; Laasimer & Masing, 1995). The *Hepatica* site type forests are considered as degraded remnants of nemoral mixed spruce forests from a warmer Atlantic climatic period (Laasimer, 1965).

The study area was located on undulating limestone plain, where the height differences are no more than 1 m. The alvar forests grow on shallow or moderately thick (up to 30 cm) humus-rich Rendzic leptosols; soils of boreo-nemoral forests belong to the thicker Rendzic Leptosols or Eutric Cambisols (World Reference, 1998) that contain less humus and carbonates but more moisture (Table I).

Both forest types were represented by both intensively managed stands and modestly managed sub-natural stands. Forests of every management class were divided into two groups: younger forests about 60–80 years of age, and forests older than 125 years. Management intensity was estimated according to the inscriptions in the forests management plans: if in the past 20–30 years the planned intermediate cuttings were not done, the stand was qualified as weakly managed (subnatural); if the planned intermediate cuttings were all done in time, i.e. in the forest there were stumps and openings of these thinnings, the stand was interpreted as intensively managed. Each forest category (experiment variant) was replicated three times.

Data collection

Circular sample plots with a radius of 25 m were used for data collection.

The tree stand parameters (age, site quality class, density of tree layer) were taken from forest taxation data of 1999. In nature, the basal area of every tree species at breast height [diameter at breast height (dbh)] was measured in every sample plot repeatedly four or five times and average values were used for further calculation of the Shannon index (McCune & Mefford, 1999) of tree species diversity.

The bush layer was described by the number of bush species. Trees lower than 5 m and/or dbh less than 5 cm were also considered to belong to the bush layer.

Forest ground vegetation species were recorded on two scales: on 12 randomly placed 1 m² quadrats and on the whole 25 m radius circular sample plot representing the whole forest community. In addition to these data, bryophytes and lichens were registered from bases of 10 randomly selected dominating pine and spruce trees (up to the height of 70 cm), from bases of other tree species as they were presented in the stand, from fine woody debris (branches), from decaying stems and stumps, from pit-mounds of windthrown trees and from stones.

The soil morphology was described in the centre of every sample plot and the samples were taken for laboratory chemical analyses.

Nomenclature of vascular plant species follows Leht (1999), bryophytes Ingerpuu and Vellak (1998) and lichens Randle and Saag (1999).

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 with stepwise selection procedure for continuous variables was used (StatSoft, 2001). Habitat lightness and soil moisture were evaluated by means of calibration (Jongman et al., 1995), using the weighted averaging algorithm and indicator values of herb-layer plant species (Ellenberg, 1979). These mean values were exploited in GLM analyses as the factors Habitat lightness and Soil moisture. Two categorical factors, Management and Site type, were also kept in the model during the model building. 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 have a significant effect on the forest ground vegetation species richness on a 1 m² 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 I.

Results

Altogether 179 vascular plant species were recorded in the studied forests. Among them nine species represent the Estonian Red Data Book (Lilleleht, 1998) taxa: *Cypripedium calceolus*, *Daphne mezereum*, *Epipactis atrorubens*, *E. helleborine*, *Gymnadenia conopsea*, *Listera ovata*, *Neottia nidus-avis*, *Platanthera chlorantha* and *Pulsatilla patens*. The total species number found in *Calamagrostis* site type forests (153) was higher than in *Hepatica* site type stands (135). Usually, the frequency of common hemerophobic forest species (Trass et al., 1999) (e.g. *Daphne mezereum*, *Dryopteris carthusiana*, *Gymnocarpium dryopteris*, *Mycelis muralis*, *Orthilia secunda*, *Carex ornithopoda*) was remarkably higher in old stands than in younger ones. Species such as *Agrimonia eupatoria*, *Filipendula vulgaris* and *Galium album* were more restricted to younger forests.

The total list of identified bryophytes included 128 species, 27 of them hepatics. 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 presented only in managed forest (including four hemerophobic species, but no hepatics).

A relatively high number (12) of rare (Ingerpuu & Vellak, 1998) and threatened bryophytes (Lilleleht, 1998) was discovered: *Amblystegium saxatile*, *Campylium halleri*, *Hylocomium umbratum*, *Seligeria campylopoda*, *Trichostomum crispulum* var. *brevifolium*, *Anastrophyllum hellarianum*, *Campylium calcarum*, *Cephaloziella divaricata*, *Fissidens pusillus*, *Geocalyx graveolens*, *Plagiothecium latebricola* and *Rhynchostegium murale*. The first five of these have been found not more than five times in Estonia before. Nine of these rare and threatened species were recorded in old and subnatural forests. It is characteristic that the diversity of rare bryophyte species growing on tree stems bases and decaying wood was lower in more intensively managed forests and all rare bryophytes growing on decaying wood were found in weakly managed subnatural forests. Rare bryophyte species in intensively managed forests (e.g. *Fissidens pusillus*, *Rhynchostegium murale*, *Trichostomum crispulum* var. *brevifolium*) were almost all growing on stones.

The total number of identified lichen species was 59; however, this figure is not final because it was not possible to identify all of the microlichens (sterile crustose species, e.g. *Lepraria* spp.).

Eleven lichen species were found only in old stands, for example *Imshaugia aleurites* and *Arthonia vinosa*. Species such as *Chaenotheca chrysocephala*, *C. ferruginea*, *Hypocenomyce scalaris* and *Parmeliopsis hyperopta* were discovered more frequently in old forests than in younger ones. Foliose lichen *Vulpicida pinastri* as well as *Cladina* spp. and *Cladonia* spp. were more abundant in younger and intensively managed forests than in older subnatural stands.

There were more microlichen species in old forests, but the species number of macrolichens (mainly foliose and squamulose ones) was higher in younger stands.

In *Calamagrostis* site type forests three very rare lichen species (found not more than five times in Estonia before; Randle & Saag, 1999) were registered: *Arthonia didyma*, *Melaspilea* spp. and *Strangospora moriformis*.

According to the GLM analysis, large-scale (i.e. community-scale) diversity of herb-layer species was significantly affected by the habitat lightness, nitrogen content and special surface area of the soil humus horizon (Table I, model 1; Table II). The factors Management and Site type were also almost

Table II. Effect of the environmental factors on the diversity of vascular plant species by general linear model analysis

Factor	df	F	p	Slope	SE
Intercept	1,18	23.00	0.0001		
Site type	1,18	3.07	0.0966		
Management	1,18	3.57	0.0752		
N% in soil humus horizon	1,18	6.56	0.0197	81.026	31.641
Soil humus horizon special surface area	1,18	5.18	0.0353	-0.226	0.100
Habitat lightness	1,18	63.18	0.0001	30.514	3.839

Note: df = degrees of freedom; F = F-criterion value; p = significance level; slope = slope of the regression line; SE = standard error; N = nitrogen.

significant. The increase in habitat lightness and soil humus horizon nitrogen content enhanced, and the increase in soil special surface area decreased the number of species of vascular plants (Figure 1).

The diversity of bryophyte species growing on tree stem bases and decaying wood was significantly influenced by the factors Management and Site quality class (Table I, model 3; Table III). In both forest types the richness of bryophyte species was higher in subnatural stands and in sites of better quality (smaller rank values of the site quality class) (Figure 2). The bryophyte species number increased linearly with the improvement in the forest site habitat quality (linear contrast $p = 0.0036$).

The diversity of lichens growing on tree stem bases and decaying wood had a significant response to the factor Tree-layer species diversity (Table I, model 3; Table IV); the diversity of lichens is promoted in forests with higher tree species diversity (Figure 3).

On the 1 m² quadrat scale the average species number of vascular plant species was higher in the *Calamagrostis* site type forests, while the *Hepatica* site type forests were a little richer in bryophyte species. The species richness of the herb and moss layer responded to several biotic and environmental conditions on this scale (Table I, model 2; Table V). However, the vascular plants (herb layer) and bryophytes (moss layer) reacted differently on all

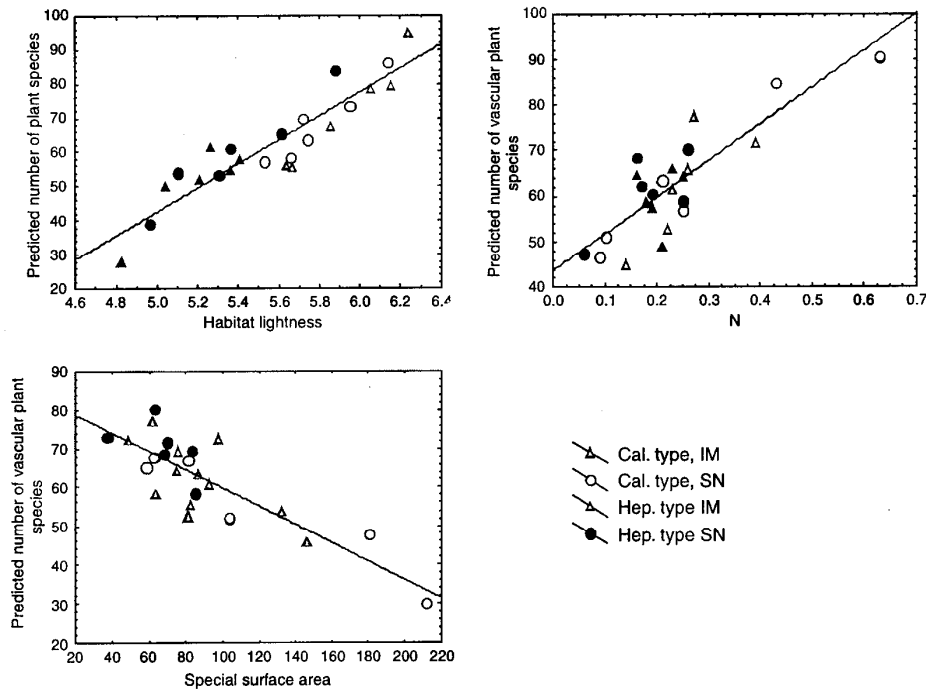


Figure 1. Predicted number of vascular plant species in forests stand according to the general linear model (GLM) model (see Table II). Scatter of observations is based on model residuals. Hep. = *Hepatica* site type; Cal. = *Calamagrostis* site type; IM = intensively managed stands; SN: subnatural stands.

Table III. Effect of the environmental factors on the diversity of bryophyte species growing on tree stem bases and decaying wood by general linear model analysis

Factor	df	F	p
Intercept	1,19	938.12	0.0001
Management	1,19	9.72	0.0057
Site quality class	3,19	4.39	0.0165

Note: df = degrees of freedom; F = F -criterion value; p = significance level.

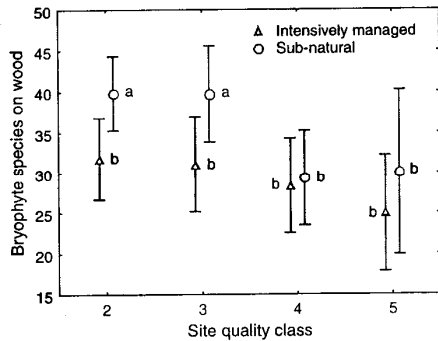


Figure 2. Number of bryophyte species growing on wood (on tree stem bases and decaying wood) in forests of different quality class and management intensity. a and b indicate homogeneity groups according to the Tukey test.

the considered factors. Three factors out of four (the traits of the tree layer and the soil pH) had more negative effects on species richness of the herb layer than on species richness of the moss layer. In particular, Tree-layer species diversity and Density of tree layer had a significant negative effect on the herb-layer species richness, while the bryophyte species richness showed a borderline significant positive correlation to the Density of the tree layer ($p = 0.0607$; Table V). 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.

Discussion

Several studies have confirmed the positive impact of light on vascular plant species diversity on half-open wooded meadows (Kull & Zobel, 1991; Austad & Losvik, 1998; Linusson et al., 1998; Einarsson & Milberg, 1999). In the Estonian alvar forests the tree-layer density is low in comparison with other forest types (Laasimer, 1986). 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 in *Calamagrostis* site type forests.

Earlier experiments have shown a 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). However, 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 to 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 present study 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 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. 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 the current study. A typical substrate 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 the current study only in the subnatural forests. Thus, these species seem to be good indicators for subnatural boreo-nemoral forest communities in these two site types.

The high diversity of bryophyte species in the studied forests, as well as a comparatively high fraction of rare species, is due to the fact that they mostly prefer to grow in shady places on calcareous soil and limestone (Ingerpuu & Vellak, 1998; Lilleht, 1998).

Table IV. Effect of the environmental factors on the diversity of lichen species growing on tree stem bases and decaying wood by general linear model analysis

Factor	df	F	p	Slope	SE
Intercept	1,18	67.76	0.0001		
Management	1,18	0.12	0.7480		
Site quality class	3,18	1.72	0.1986		
Tree-layer species diversity	1,18	6.34	0.0215	0.721	0.286

Note: df = degrees of freedom; F = F -criterion value; p = significance level; slope = slope of the regression line; SE = standard error.

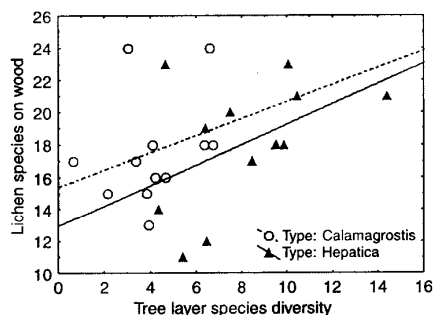


Figure 3. Relationship between the number of lichen species growing on wood (on tree stem bases and decaying wood) and tree-layer species diversity.

It was slightly surprising that according to the GLM analysis results the effect of tree stand age per se appeared to be insignificant for both bryophyte and lichen species richness. This seems to be inconsistent with earlier results from this group (Jürjado et al., 2003; Vellak et al., 2003) as well as with the results of other authors, confirming the importance of stand age on bryophyte (Söderström, 1988b; Jonsson & Esseen, 1990; Lesica et al., 1991) and lichen diversity (Sömermaa, 1972; Hyvärinen et al., 1992; Dettki & Esseen, 1998; Glenn et al., 1998; Uliczka & Angelstam, 1999). This 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 insemination (plus-trees). However, there may be analytical bias in other studies, as forest age and silvicultural management effects were not analysed simultaneously, as they were here. Non-simultaneous analysis of both effects in the same model may cause the transfer of the management effect on species richness into terms of stand age or vice versa, as the two factors are frequently correlated.

The foliose lichen *Imshaugia aleurites*, recorded only in old forests, is a characteristic species of ecological continuity of native pinewoods in the

British Isles (Coppins & Coppins, 2002). The crustose lichen *Arthonia vinosa*, recorded only in old *Calamagrostis* site type forests, is considered to be a characteristic species for old growth stands (Rose, 1992; Tibell, 1992). According to Trass et al. (1999), *Chaenotheca chrysocephala* and *Parmeliopsis hyperopta*, frequently recorded by the present authors in old forests, are characteristic of old subnatural stands. Regarding *Cladonia* spp. and *Cladonia* spp., which grew more frequently in younger forests, Söderström (1988b) and Lesica et al. (1991) also showed that these species are predominant in second growth managed stands. In agreement with recent results, Glenn et al. (1998) found that foliose and fruticose macrolichens had higher cover and richness in younger forests, while the fertile crustose lichens had significantly higher cover and species richness in the old growth stands. Diversity of lichen species was significantly affected by the species richness of the tree layer. 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, so the diversity of lichen species in forests increases parallel to the diversity of tree species (Sömermaa, 1972; Cieslinski et al., 1996; Kuusinen, 1996; Jürjado et al., 2003).

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 (Table V). Moss and herb layers had 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 (Korchagin, 1976; Paal, 1995). According to the results, 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

Table V. Effect of the considered factors on the number of undergrowth species on 1 m² quadrat scale according to general linear mixed model analysis

Factor	df	F	p	Layer	Slope	SE	p
Site type	1,545	0.92	0.3380				
Layer	1,545	36.4	0.0001				
Site type × Layer	1,545	2.74	0.0982				
Tree-layer species diversity	1,545	7.65	0.0059				
Tree-layer species diversity × Layer	1,545	32.94	0.0001	Herb	-0.7362	0.142	0.0001
				Moss	0.0440	0.142	0.7574
Bush-layer species richness	1,545	0.01	0.9211				
Bush-layer species richness × Layer	1,545	6.84	0.0091	Herb	0.1644	0.142	0.2460
				Moss	-0.1891	0.142	0.1822
Density of tree layer	1,545	0.06	0.8021				
Density of tree layer × Layer	1,545	19.35	0.0001	Herb	-0.0739	0.032	0.0207
				Moss	0.0598	0.032	0.0607
pH of soil humus horizon	1,545	0.01	0.9059				
pH of soil humus horizon × Layer	1,545	4.41	0.0363	Herb	-0.4428	0.493	0.3697
				Moss	0.5453	0.493	0.2694

Note: df = degrees of freedom; *F* = *F*-criterion value; *p* = significance level; slope = slope of the regression line; SE = standard error; Layer = ground vegetation layer.

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 more 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 the analyses in the forest herb layer on calcareous soils, the vascular plant 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 I).

Conclusions

The results of the analyses indicate that the herb layer and lichen species large-scale diversity in an old growth forest is affected primarily by the stand structure and environmental conditions of the habitat. Nevertheless, silvicultural management also has indirect effects on the species content in a forest stand, as several structural and environmental parameters are management dependent. The results suggest that the continuity of a forest is important; for example, several species that are known to be

sensitive to forest management were present in forests that had not been managed during the past few decades. The most sensitive to forest management appeared to be the bryophytes on tree stem bases and on decaying wood, several species of which could be used as indicators of a forest's natural status.

The small-scale species richness of vascular plants and bryophytes was also influenced by the structural changes in forest stands, which are caused by management activities. However, species richness in both these layers had varying trends along the forest stand structural changes, according to the microclimatic environmental requirements of the species. Bryophyte diversity increases with the general increase in shade and moisture, while vascular plant diversity increases with light availability. Consequently, for the maintenance of and increase in small-scale species richness of forest ground vegetation on calcareous soils, silvicultural management should include various management practices that will create heterogeneous microconditions and ensure the historical continuity of the forest.

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