

Diversity and Distribution Pattern of Bryophytes and Vascular Plants in a Boreal Spruce Forest

Kai Vellak, Jaanus Paal and Jaan Liira

Vellak, K., Paal, J. & Liira, J. 2003. Diversity and distribution pattern of bryophytes and vascular plants in a boreal spruce forest. *Silva Fennica* 37(1): 3–13.

Small scale pattern of bryophyte communities is one of the remarkable sources of diversity in species-poor boreal forests. By means of correlation and general linear model approaches, the relationships between bryophyte vegetation and upper layers, as well as the response of ground and field layer species to several environmental factors, was analyzed in a boreal spruce forest in South-East Estonia. Of the studied factors, the strongest influence on the diversity and spatial distribution of ground and field layer species was found for ‘distance from nearest tree’. Species from different layers react differently to the proximity of trees. Species richness of bryophytes is higher further from trees, whereas more vascular plant species prefer to grow in the vicinity of tree trunks. For bryophyte species richness, the pH of the decay horizon is also important; fewer bryophyte species occur in more acid conditions.

Keywords boreal forests, general linear models, correlation, Estonia, field layer, ground layer, spatial patterns

Authors’ addresses *Vellak*: Institute of Zoology and Botany, Estonian Agricultural University, 181 Riia str., 51014 Tartu, Estonia; *Vellak, Paal & Liira*: Institute of Botany and Ecology, University of Tartu, 40 Lai Str., 51005 Tartu, Estonia

E-mail kvellak@zbi.ee

Received 10 July 2000 **Accepted** 16 December 2002

1 Introduction

According to numerous authors (e.g. Greig-Smith 1979, Pielou 1984, Legendre & Fortin 1989), organisms are distributed in nature neither uniformly nor randomly. As a rule they are aggregated as patches or are distributed continuously, depending on habitat conditions. Due to the universal character of this phenomenon, investigation of the heterogeneity of populations and

communities on various spatio-temporal scales is one of the central questions in plant ecology and plays a crucial role in many ecological theories (Legendre et al. 1985, Addicott et al. 1987) and in the maintenance of species diversity (Mladenoff 1994, Frisvoll and Prestø 1997 etc.).

In boreal forests, bryophytes are important structural components of ground vegetation as well as of the whole community (Lai Roi and Stringer 1976, Longton 1984, Økland 1994,

Esseen et al. 1996). It has been demonstrated that the spatial aggregation of species in communities represents habitat partitioning corresponding to microhabitat heterogeneity (Whittaker and Levin 1977, Greig-Smith 1979, 1983, Beatty 1984, Legendre and Fortin, 1989, Slack 1990, Frego and Carleton 1995, Gillet and Gallandat 1996). Several authors have affirmed that in forests, besides the factors of the abiotic environment, the composition and structure of the undergrowth vegetation depends mainly on the tree layer above it, which determines directly or indirectly the conditions for the field and ground layers (Abolin 1974, Kotov 1983, Beatty 1984, Hytteborn et al. 1987, Gustafsson and Hallinbäck 1988, During and Verschuren 1988, Jonsson and Esseen 1990, Saetre 1999). As already stated by Cajander (1926), trees modify to a great extent the light conditions and water and nutrient availability for the understorey, and affect the composition, abundance and spatial distribution of species in the forest understorey. In that way, the plants of the ground and field layers are influenced by the same microenvironment conditions, but, as argued by Scott (1971), Herben (1987), and Slack (1990), due to their specific anatomy, bryophytes react to changes of the microenvironment more rapidly than vascular plants. Studies in grassland communities, where big trees are sparse or missing, have also shown that vascular plants and bryophytes react differently to changes in habitat conditions (Herben 1987, Ingerpuu et al. 1998). How bryophytes and vascular plants share the space in forests, has been discussed only briefly (e.g. Aude and Lawesson 1998, Saetre 1999).

In studies of plant-environment relationships, or mutual dependency between different layers of the plant community, it is very important to consider also the spatial scale used for data collection, since the character of these relations may change crucially at different scales (Stowe and Wade 1979, Greig-Smith 1979, McCune and Antos 1981, Hanski 1983, Maslov 1989, Reed et al. 1993). In the current study we analyse the relationships between field and ground layer species and the environment on a decimeter scale.

In the current study our basic object of investigation is the bryophyte vegetation in a typical boreal forest and its relationship with the upper layers and some other environmental factors. The

study is addressed at the two main questions: 1) how are bryophytes and vascular plants correlated in forest floor vegetation and, 2) how does ground and field layer structure react to different environmental factors, particularly to the spatial pattern of trees in the same forest community.

2 Material and Methods

2.1 Study Area

The study was carried out in the southeastern part of Estonia, in the landscape reserve of the Ahja river valley, near the village of Valgemetsa (58°08'N, 26°59'E). Phytogeographically this area belongs to the East-Baltic subprovince, where moderately humid boreal forest is typical. Mean annual temperature in winter is -7.0°C and in summer 17.5°C ; there are about 200 rainy days per year, most of them occur in the springtime (Laasimer 1965). According to Moen (1999) the area is located in the indifferent oceanic-continental section of the boreonemoral vegetation zone.

An *Oxalis-Vaccinium myrtillus* site type spruce forest (Paal 1997), representing a species-poor community with simple structure and abundant ground layer, was chosen for the analysis. The dominating trees of *Picea abies* are about 100 years old. Some trees of *Pinus sylvestris* also occur in the tree layer; composition of the tree layer is 9 parts *Picea abies* and 1 part *Pinus sylvestris*. The diameter at breast height of all trees occurring in the studied forest was at least 24 cm. The canopy coverage is approximately 70%. Natural regeneration is scattered, consisting only of *Picea abies*. The shrub layer is represented by very sparsely growing *Sorbus aucuparia*, *Frangula alnus* and *Salix cinerea*.

2.2 Data Collection and Analyses

The data was collected in September 1996. To avoid the biasing of data due to topographical heterogeneity, a homogenous area without obvious variation in microtopography was chosen. A rectangular grid for 500 plots of 20×20 cm was placed down on the ground. In every plot the total

cover of bryophytes and vascular plants, and then the cover of each species, was estimated according to the scale 0.1, 1, 2, 3, 5, 7, 10, 15, 20, 25, 30, ..., 100 % (Suominen 1969). The tree juveniles, that occurred in plots were included in the field layer. The nanotopographical form (height interval up to 1 dm) was visually evaluated and classified as a concavity, plain, or a hump. The distance from the centre of every plot to the nearest tree trunk was measured in centimetres. From the centre of each plot, the thickness of the decay horizon was measured. Samples of the decay horizon were taken for the estimation of pH in the laboratory. All samples were air-dried and weighed. Before measuring, the soil samples were mixed with 2.5 times their own weight of distilled water, according to Økland and Eilertsen (1996). pH was measured with the pH/C^o-meter E6121A.

Since field and ground layer species form and modify the environment in their surrounding, some plant-related factors such as the number of vascular plant and bryophyte species in a sample plot, and the total cover of vascular plants and bryophytes in a sample plot were treated as additional environmental factors in data processing.

The frequency and mean cover for all species registered in studied plots were calculated. Correlation between cover values of bryophyte and vascular plant species was evaluated on the basis of Spearman's rank correlation coefficients. The general linear model (GLM) was used for analyzing the significance of the environmental factors on the ground and field layer species-richness and on the cover values of the dominant species. In that model, only plots with total cover values greater than zero and species with a relative frequency greater than 20% were included. To describe the effect of environmental factors on species-richness in both considered layers, cover values of the dominant species of the corresponding layer were also included. To approximate distribution to the normal, the cover values were square root transformed before analysis. The nanotopography was treated as a categorical factor with three levels: 1) a concavity, 2) a plain and 3) a hump. When nanotopography had a significant effect on the cover values, the Tukey HSD test was used to determine significant differences between group means. The distance from

nearest tree trunk, thickness of decay horizon, and pH of decay horizon were treated as continuous factors in the model. All statistical analyses were performed using the statistical package Statistica 6.0 (StatSoft, Inc. 2001).

Nomenclature for bryophytes follows Ingerpuu et al. (1998), for vascular plants Leht et al. (1999).

3 Results

In total, twelve bryophyte and thirteen vascular plant species occurred in the ground and field layers of the studied forest. Only one vascular species (*Vaccinium myrtillus*) and three bryophyte species (*Hylocomium splendens*, *Pleurozium schreberi* and *Ptilium crista-castrensis*) had a frequency of occurrence more than 70% (Table 1). Four bryophyte and four vascular plant species occurred in less than five plots and were treated as occasional species for this community.

Not one of bryophyte species cover values had a significant correlation with the cover of the dominating vascular plant species *Vaccinium myrtillus* (Table 2). The cover of *Pleurozium schreberi* had a weak but significant positive correlation with the cover of *Maianthemum bifolium* and *Oxalis acetosella* and a negative correlation with the cover of *Vaccinium vitis-idaea*, while the cover of *Hylocomium splendens* and *Ptilium crista-castrensis* had just the opposite relation with the cover of these vascular plant species. The cover of *Ptilium crista-castrensis*, *Aulacomnium palustre* and *Brachythecium oedipodium* was weakly positively correlated with the cover of young regrowth of *Picea abies*. The latter species tended also to prefer the neighbourhood of *Vaccinium vitis-idaea*.

According to the general linear model, distance from the nearest tree trunks had significant effect both on the ground and field layer species-richness (Table 3). Bryophyte species number increased with distance from the tree trunks (Fig. 1), whereas the species number for vascular plants was higher close to the trees (Fig. 2). Species-richnesses of different layers also had opposite regression parameter signs for the increase of total cover of the corresponding layer – the number of

Table 1. Relative frequency (Freq) of ground and field layer species and their mean cover values (Cov) in studied plots.

Species	Abbreviation	Freq (%)	Cov (%)
BRYOPHYTES			
Aulacomnium palustre	Aul pal	1.4	0.01
Brachythecium oedipodium	Bra oed	5.2	0.01
Dicranum polysetum	Dic pol	41.0	0.6
Dicranum scoparium	Dic sco	8.0	0.2
Hypnum cupressiforme	Hyp cup	0.2	0.0
Hylocomium splendens	Hyl spl	95.8	27.9
Lophocolea heterophylla	Lop het	0.4	0.01
Pleurozium schreberi	Ple sch	92.0	14.6
Ptilium crista-castrensis	Pti cri	74.8	21.4
Rhizomnium punctatum	Rhi pun	0.4	0.01
Rhytidiadelphus triquetrus	Rhy tri	1.2	0.01
Tetraphis pellucida	Tet pal	0.6	0.01
Total cover			64.2
VASCULAR PLANTS			
Deschampsia flexuosa	Des fle	4.6	0.01
Luzula pilosa	Luz pil	30.8	2.3
Maianthemum bifolium	Mai bif	29.2	1.6
Melampyrum pratense	Mel pra	28.6	0.7
Oxalis acetosella	Oxa ace	19.8	0.6
Picea abies	Pic abi	12.8	2.6
Pteridium aquilinum	Pte aqu	0.2	1.3
Rubus saxatilis	Rub sax	0.2	0.2
Salix cinerea	Sal cin	0.2	0.01
Sorbus aucuparia	Sor auc	0.2	0.01
Trientalis europaea	Tri eur	11.0	0.3
Vaccinium myrtillus	Vac myr	76.4	14.8
Vaccinium vitis-idaea	Vac vit	38.0	2.3
Total cover			19.6

Table 3. Influence of environmental factors to the field and ground layer species richness according to general linear model. E- model parameter estimates; F – F-criterion. Notations for environmental factors: pH – pH of decay horizon; Distance – distance to the nearest tree; Nanotopography – nanotopography with three levels: concavity, plain, and hump; Thickness – thickness of decay horizon; Vas cover – total cover of vascular plants in plot; Vas no – number of vascular plant species in plot; Bry cover – total cover of bryophytes in plot; Bry no – no of bryophyte species in plot. Abbreviations of species included into model are given in Table 1. The values marked by * are considered significant at the level $p \leq 0.01$.

Environmental factor	Species richness			
	Field layer Est	F	Ground layer Est	F
pH	0.07	0.55	0.23	11.2*
Distance	-0.005	110.6*	0.004	22.4*
Thickness	0.02	0.76	0.01	0.42
Nanotopography		8.55*	2.94	0.06
concavity	3.33		1.39	
plain	3.41		1.41	
hump	3.25		1.33	
Vas cover	0.01	8.74*		
Bry cover			-0.29	27.4*
Vac myr	-0.02	0.45		
Ple sch			0.18	33.7*
Hyl spl			0.21	54.5*
Pti cri			0.21	34.7*

Table 2. Spearman’s rank correlation coefficients between the cover values of bryophyte and vascular plant species. Species’ name abbreviations as in Table 1. With * marked correlation coefficients are significant at $p \leq 0.01$.

Bryophyte species	Vascular plant species								
	Des fle	Mai bif	Mel pra	Luz pil	Oxa ace	Pic abi	Tri eur	Vac myr	Vac vit
Aul pal	-0.02	-0.07	-0.07	-0.00	-0.05	0.20*	-0.04	-0.05	0.08
Bra oed	-0.05	-0.11	-0.04	-0.07	-0.07	0.15*	-0.05	0.08	0.15*
Dic pol	-0.06	-0.04	0.00	-0.01	-0.02	-0.03	0.02	0.00	0.03
Dic sco	-0.06	0.03	0.05	-0.05	-0.03	0.00	0.03	0.09	-0.00
Hyl spl	-0.01	-0.12*	0.02	-0.05	-0.12*	0.02	-0.05	-0.01	0.12*
Ple sch	0.06	0.18*	0.00	0.05	0.14*	-0.01	0.10	-0.07	-0.16*
Pti cri	-0.02	-0.65*	0.09	-0.01	-0.50*	0.16*	-0.41*	-0.01	0.30*
Rhy tri	-0.02	-0.07	-0.02	-0.03	-0.00	0.06	-0.03	0.01	0.10

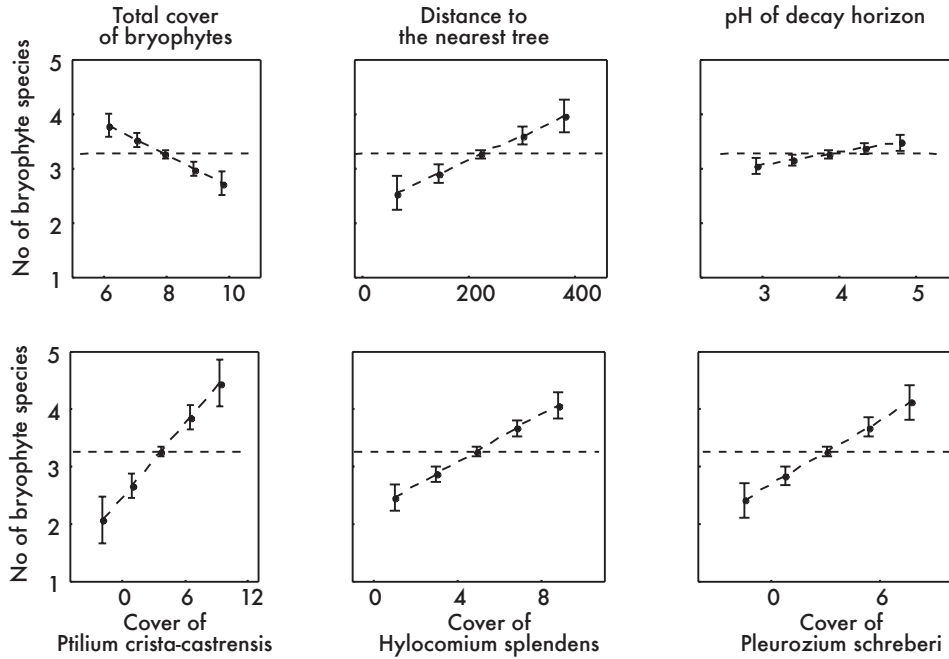


Fig. 1. Effect of significant environmental factors on the predicted values of ground layer species richness.

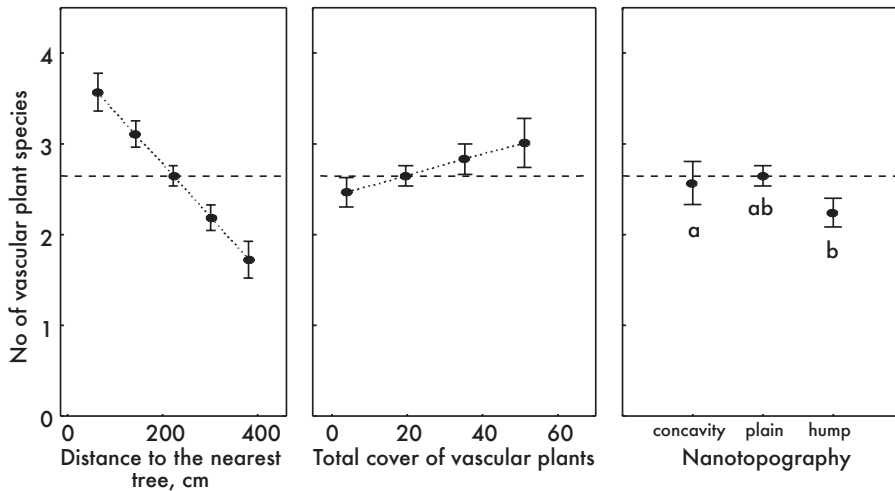


Fig. 2. Effect of significant environmental factors on the predicted values of field layer species richness.

vascular plants increased, but the species number of bryophytes decreased. In the same model the cover values of dominant bryophyte species had a positive effect on bryophyte species-richness. More bryophyte species occurred in plots where the decay horizon had a higher pH value. The pH of the decay horizon had no significant effect

on the vascular plant species-richness. Vascular plants species richness was higher in the nanotopographically lower parts (Fig. 2). The same tendency could be observed for bryophytes, but for them the topographical effect was not significant.

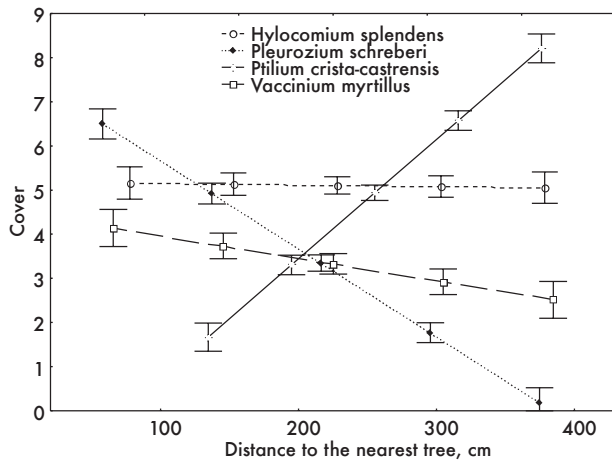


Fig. 3. Influence of the distance to the nearest tree trunk on the expected values of dominant ground and field layer species cover.

Table 4. The effect of environmental factors to the cover values of dominant ground layer species according to general linear model. Notations and abbreviations for species names, environmental factors are given in Table 1 and 3 respectively. Abbreviations for model parameter estimate and F-criterion as in Table 3. The values marked by * are considered significant at the level $p \leq 0.01$.

Environmental factor	Hyl spl		Bryophyte species				Dic pol	
	Est	F	Est	Ple sch	Est	Pti cri	Est	F
pH	0.05	0.10	0.04	0.06	-0.24	2.65	0.09	1.67
Distance	-0.001	0.12	-0.01	484.1*	0.03	558.1*	-0.001	16.9*
Thickness	-0.08	3.57	-0.06	2.05	0.13	13.47*	0.02	1.53
Vas cover	-0.01	2.01	-0.02	14.7*	-0.01	3.72	-0.001	0.25
Nanotop		7.72*		2.12		0.24		0.06
concavity	4.69		7.41		-1.49		1.12	
plain	5.34		7.75		-1.57		1.10	
hump	5.24		7.69		-1.58		1.11	

Additional GLM modelling by species revealed that distance from nearest tree had a significant effect on the cover values of almost all dominant ground (Table 4) and field layer species (Table 5). Cover of *Ptilium crista-castrensis* was higher at a greater distance from trees, while cover of *Pleurozium schreberi* and *Dicranum polysetum* increased near tree trunks (Fig. 3). Cover of *Hylocomium splendens* did not have a significant relationship with the distance from trees. *Ptilium crista-castrensis* grew better in plots with a thicker decay horizon. At the same time, pH of the decay horizon had no influence on the cover of the considered bryophyte species. Of bryophytes, only *Hylocomium splendens* was dependent on

nanotopography. According to the Tukey HSD test, *Hylocomium splendens* was more abundant on little humps compared to concavities.

Of vascular plants, the distance to the nearest tree trunks had a significant negative effect on the cover values of *Vaccinium myrtillus* and a positive effect on the cover values of *Luzula pilosa* (Table 5). Cover of *Vaccinium myrtillus* depends significantly also on nanotopography, having a higher value on humps. The Tukey HSD test recorded a significant difference in the cover value in concavities and on humps.

Table 5. The results of the effect of different environmental factors to the cover values of dominant field layer species according to general linear model. Notations and abbreviations for species names and environmental factors are given in Table 1 and 3 respectively. Abbreviations for model parameter estimate and F-criterion as in Table 3. The values marked by * are considered significant at the level $p \leq 0.01$.

Environmental factor	Vac myr		Vac vit		Vascular plant species Mai bif		Mel pra		Luz pil	
	Est	F	Est	F	Est	F	Est	F	Est	F
pH	-0.32	2.91	0.06	0.19	-0.17	1.41	-0.11	1.41	0.15	1.12
Distance	-0.005	20.77*	0.001	0.78	-0.001	0.10	-0.001	5.22	0.002	10.32*
Thickness	-0.02	0.20	0.03	0.77	-0.01	0.12	0.05	6.39	0.01	0.07
Nanotop		7.10*		0.03		0.32		0.20		0.95
concavity	6.09		1.74		2.90		1.99		0.28	
plain	5.81		1.70		3.00		1.95		0.27	
hump	6.16		1.72		2.99		1.95		0.34	

4 Discussion

The structure of vegetation is determined by the synergetic effect of several biotic and abiotic factors. The most evident result of the current analysis is that, among the studied environmental parameters, the tree layer has the strongest influence on the distribution of field and ground layer species. This is in good accordance with the well-known theory of 'single-tree influence circles' (Zinke 1962) or 'phytogenic field' (Uranov 1965, 1968), according to which all plant specimens, particularly big and dominating trees, affect their closest surroundings and change the environmental conditions there. Every tree has an influence circle approximately proportional to the size of the crown projection on the soil surface; outside the crown projection the influence decreases rather quickly. It has been shown that under the crowns of trees amount and chemical composition of throughfall, temperature, frost heaving, light flux, and several soil chemical properties (Beatty 1984, Boettcher and Kalisz 1990), as well as soil microbial biomass and activity (Saetre 1999) can be rather different in comparison to gap areas. Therefore, in boreal forests the influence circles of trees may be superimposed on the environmental pattern, and they can have privilege in the forming of the understory vegetation structure (Abolin 1974, Korchagin 1976, Beatty 1984, Boettcher and Kalisz 1990). Obviously, this is true only in the case of comparatively homogeneous microtopography. If the latter is more heterogeneous, rather remarkable differences can be discovered

between the ecological conditions of different microsites, and these factors may prove to be decisive for the formation of the horizontal pattern of the undergrowth (e.g. Kuusipalo 1984, Økland and Bendiksen 1985, Maslov 1989, Økland 1994, Frego and Carleton 1995).

Our results indicate a rather strong influence of the tree canopy on ground layer vegetation, which is in good accordance with other related investigations (e.g. Havas and Kubin 1983, Økland et al. 1999 etc.). Both the species-richness and cover values of dominant species of the ground and field layers are influenced by the vicinity of trees. The number of vascular plant species is higher near tree trunks, whereas more bryophyte species occur farther from trees. The cover of the majority of dominant bryophyte species is negatively affected by the vicinity of trees. Of vascular plants, only the cover of *Vaccinium myrtillus* is significantly affected by trees. Phanerogams are in general larger and better adapted to microenvironment variation, whereas bryophytes, due to the absence of roots, a well developed vascular system and cuticle, are more sensitive to environment alternations (Lee and La Roi 1979, Herben 1987). As shown in previous studies, the throughfall of precipitation is the most important source of moisture for bryophytes (Tamm 1953, Beier et al, 1993, Weibull, 2000). Since the throughfall of precipitation is higher near the crown perimeter, this explains the higher cover values of bryophytes at a greater distance from tree trunks.

Kotov (1982, 1983) has asserted that if the structure of the tree layer essentially affects the

spatial distribution of lower layers, the components of those layers should be correlated. In other words, if vascular plants and bryophytes respond linearly to the same ecological factors, then species of both groups are structured similarly and are mutually well correlated (Herben 1987). As it appears from our results, the correlation between the cover of bryophyte and vascular plant species is rather weak on a species level. Only *Ptilium crista-castrensis* has a stronger relationship with field layer species, while the absolute value of correlation coefficients between other bryophytes and vascular plants remains under 0.2 (Table 2). Thus, we can conclude that on the decimetre scale the patterns of the field- and bryophyte layers do not coincide. The modest negative effect of the total cover of vascular plants on dominant bryophyte species can be explained by the sharing of growth space. Competition between vascular plants and bryophytes is considered less important (Carleton 1990, Økland and Eilertsen 1996). For example, McCune and Antos (1981) and Diekmann (1994) have shown that the different layers of vegetation exploit, at least to some extent, different complexes of ecological factors, which can result in the observed unrelated pattern of two layers. Qian et al. (1998) have argued that the smaller size of bryophytes allows them access to microhabitats which are not available to vascular plants. Still, on a community scale, forest stand classification based on bryophytes could be in good concordance with the classification established on the basis of vascular species (La Roi 1967, La Roi and Stringer 1976).

Besides the effect of trees and total cover of lower layers, the pH and thickness of the decay horizon, or nanotopography could be important in the formation of the richness and spatial pattern of ground and field layer species. Although Cox and Larson (1993) have argued that, due to the narrow range of changes within a habitat, pH does not have a significant effect on the vegetation composition on a community level, many authors have considered soil reaction to be one of the most important ecological factor influencing the distribution of vascular and bryophyte species (Robinson et al. 1989, Pärtel 2000, Virtanen et al. 2000). Our results show that the pH of the decay horizon at the decimeter scale has a significant effect on the bryophyte species richness: higher

pH increases the species number.

The contrasting effect of total cover of the bryophyte layer and cover values of dominating species on bryophyte species-richness became evident from our results. Contrary to expectations, bryophyte species-richness is negatively influenced by the total cover of bryophytes, and positively, by cover of single dominant species. Treating the cover of bryophytes as an indicator of biomass, then, analogously to the biomass–species-richness ‘hump-back’ curve relation (Grime 1979), we could expect the decrease of bryophyte species-richness with an increase in the total cover of the ground layer. The cover of any single species was not found to constitute as much as half of the total cover (Table 1), and probably the increase in abundance of a single species promotes the species diversity of the layer. It has been shown that different factors may cause lower species-richness at higher cover levels, competition between species could be one of them (Grime 1979). Still, competition among bryophytes has been considered unimportant (Økland 1994) and it has been connected more with space than with resources (e.g. During 1990). If the role of competition is considered to be important in the formation of the species-richness pattern, we can speculate that, at a higher level of total cover, competition between bryophytes may reduce ground layer species richness. But, in order to verify this statement, detailed investigation of bryophyte competition is needed.

In conclusion, although distance to nearest tree has a remarkable effect on the distribution of ground and field layer species, others environmental factors are also significant predictors of the structure of the lower layers. Our results showed that there are different rules for the formation of spatial patterns and structure in different understorey layers in boreal forest. To maintain also small-scale species-richness on the forest floor, both plant-related, as well as different environmental factors should be considered in forest planning and management.

Acknowledgements

We are grateful to Mare Leis, who helped us during the fieldwork. Prof. Martin Zobel and McS Nele Ingerpuu made valuable comments on the early version of this manuscript. Ilmar Part revised the English. This study was financially supported by the Estonian Science Foundation (grants no 0619 and 0552).

References

- Abolin, A.A. 1974. [Change of the structure of the moss cover in relation to the distribution of precipitation under the forest canopy]. *Ekologia* 3: 51–56. (in Russian)
- Addicott, J.F., Aho, J.M., Antolin, M.F., Padilla, D.K., Richardson, J.S. & Soluk, D.A. 1987. Ecological neighbourhoods: scaling environmental patterns. *Oikos* 49: 340–346.
- Aude, E. & Lawesson, J. E. 1998. Vegetation in Danish beech forests: the importance of soil, microclimate and management factors, evaluated by variation partitioning. *Plant Ecology* 134: 53–65.
- Beatty, S.W. 1984. Influence of microtopography and canopy species on spatial patterns of forest understorey plants. *Ecology* 65(5): 1406–1419.
- Beier, C., Hansen, K. & Gundersen, P. 1993. Spatial variability of throughfall fluxes in spruce forest. *Environmental Pollution* 81: 257–267.
- Boettcher, S.E. & Kalisz, P.J. 1990. Single-tree influence on soil properties in the mountains of eastern Kentucky. *Ecology* 71: 1365–1372.
- Cajander, A.K. 1926. The theory of forest types. *Acta Forestalia Fennica* 29(3). 108 p.
- Carleton, T.J. 1990. Variation in terricolous bryophyte and macrolichen vegetation along primary gradients in Canadian boreal forests. *Journal of Vegetation Science* 1(5): 585–594.
- Cox, J.E. & Larson, D.W. 1993. Environmental relations of the bryophytic and vascular components of a talus slope plant community. *Journal of Vegetation Science* 4: 553–560.
- Diekmann, M. 1994. Deciduous forest vegetation in Boreo-nemoral Scandinavia. *Acta Phytogeographica Suecica* 80: 3–116.
- During, H.J. & Verschuren, G.A.C.M. 1988. Influence of the tree canopy on terrestrial bryophyte communities: microclimate and chemistry of throughfall. In: Barkman, J.J. & Sykora, K.V. (eds.), *Dependent plant communities*. SPB Academic Publishing, The Hague. p. 99–109.
- Esseen, P.A., Ehnström, B., Ericson, L. & Sjöberg, K. 1996. Boreal forests – the focal habitats of Fennoscandia. In: Hansson, L. (ed.), *Ecological principles of nature conservation*. Elsevier Applied Science, London. p. 252–325.
- Frego, K.A. & Carleton, T.J. 1995. Microsite conditions and spatial pattern in a boreal bryophyte community. *Canadian Journal of Botany* 73: 544–551.
- Frisvoll, A.A. & Prestø, T. 1997. Spruce forest bryophytes in central Norway and their relationship to environmental factors including modern forestry. *Ecography* 20: 3–18.
- Gillet, F. & Gallandat, J.D. 1996. Integrated synusial phytosociology: some notes on a new, multiscalar approach to vegetation analysis. *Journal of Vegetation Science* 7: 13–18.
- Greig-Smith, P. 1979. Pattern in vegetation. *Journal of Ecology* 67(3): 755–779.
- 1983. *Quantitative plant ecology*. Blackwell Scientific Publications, Oxford, London, Edinburgh. 354 p.
- Grime, J.P. 1979. *Plant strategies and vegetation processes*. John Wiley & Sons, Chichester.
- Gustafsson, L. & Hallingbäck, T. 1988. Bryophyte flora and vegetation of managed and virgin coniferous forests in South-West Sweden. *Biological Conservation* 44: 283–300.
- Hanski, I. 1983. Coexistence of competitors in patchy environment. *Ecology* 64(3): 493–500.
- Havas, P. & Kubin, E. 1983. Structure, growth and organic matter content in the vegetation cover an old spruce forest in Northern Finland. *Annales Botanici Fennici* 20: 115–149.
- Herben, T. 1987. Bryophytes in grassland vegetation sample plots: what is their correlation with vascular plants. *Folia Geobotanica et Phytotaxonomica* 22: 35–41.
- Hytteborn, H., Cramer, W., Packham, J.R. & Verwijst, T. 1987. Three different types of forest dynamics. In: Yang Hanxi, Wang Zhan, Jeffers, J.N.R. & Ward, P.A. (eds.), *The temperate forest ecosystem (ITE symposium No. 20)*. Institute of terrestrial Ecology, Abbots Ribton. p. 32–39.
- Ingerpuu, N. (ed.), Kalda, A., Kannukene, L., Krall, H., Leis, M. & Vellak, K. (ed.) 1998. *Eesti sammalde*

- määräja. Eesti Loodusfoto, Tartu. 239 p. [Key-book of Estonian bryophytes]
- Jonsson, B.G. & Esseen, P.A. 1990. Treefall disturbance maintains high bryophyte diversity in a boreal spruce forest. *Journal of Ecology* 78: 924–936.
- Korchagin, A.A. 1976. [Structure of plant communities]. In: Lavrenko, E.M. & Korchagin, A.A. (eds.), [Field geobotany, 5]. Leningrad, Nauka. p. 7–320. (in Russian)
- Kotov, S.F. 1982. [A method of the quantitative evaluation of the edificative role of the species]. *Botanicheskii Zhurnal* 67: 235–240. (in Russian)
- 1983. [The quantitative estimate of edificative role of woody species]. *Botanicheskii Zhurnal* 68: 39–48. (in Russian)
- Kuusipalo, J. 1984. Diversity pattern of the forest understorey vegetation in relation to some site characteristics. *Silva Fennica* 18(2): 121–131.
- Laasimer, L. 1965. Eesti NSV taimkate. Valgus, Tallinn. 396 p. [Vegetation of the Estonian S.S.R.]
- Lai Roi, G.H. 1967. Ecological studies in the boreal spruce-fir forests in the North American taiga. I. Analysis of the vascular flora. *Ecol. Monogr.* 37: 229–253.
- & Stringer, M.H.L. 1976. Ecological studies in the boreal-fir forests of the North-American taiga, II. Analysis of the bryophyte flora. *Canadian Journal of Botany* 54: 619–643.
- Legendre, P., Dallot, S. & Legendre L. 1985. Succession of species within a community: cronological clustering, with applications to marine and freshwater zooplankton. *The American Naturalist* 125: 257–288.
- & Fortin, M.J. 1989. Spatial pattern and ecological analysis. *Vegetatio*, 80: 107–138.
- Lee, D.T. & La Roi, G.H. 1979. Bryophyte and understorey vascular plant beta diversity in relation to moisture and elevation gradients. *Vegetatio* 40(1): 29–38.
- Leht, M. (ed.) 1999. Eesti taimede määräja. EPMÜ ZBI, Eesti Loodusfoto, Tartu. 447 p. [Key-book of Estonian plants]
- Longton, R.E. 1984. The role of bryophytes in terrestrial ecosystems. *Journal of Hattory Botanical Laboratory*: 55: 147–163.
- Maslov, A.A. 1989. Small-scale patterns of forest plants and environmental heterogeneity. *Vegetatio* 84: 1–7.
- McCune, B. & Antos, J.A. 1981. Correlation between forest layers in the Swan Valley, Montana. *Ecology* 62(5): 1196–1204.
- Mladenoff, D.J. 1994. Spatial analysis of forest landscape pattern. In: Haila, I., Niemelä, J. & Kouki, J. (eds.), Effects of management on the ecological diversity of boreal forests. *Metsäntutkimuslaitoksen tiedonantoja 482* (The Finnish Forest Research Institute, Research Papers): 33–39.
- Moen, A. 1999. Atlas of Norway: Vegetation. Norwegian Mapping Authority, Hønefoss. 200 p.
- Økland, R.H. 1994. Bryophyte and lichen persistence patterns in a Norwegian boreal coniferous forest. *Lindbergia* 19: 50–62.
- & Bendiksen, E. 1985. The vegetation of the forest-alpine transition in the Grunningsdalen area, Telemark, SE Norway. *Sommerfeltia* 2: 1–224.
- & Eilertsen O. 1994. Canonical correspondence analysis with variation partitioning: some comments and an application. *Journal of Vegetation Science* 5: 117–126.
- & Eilertsen O. 1996. Dynamic of understorey vegetation in an old-growth boreal coniferous forest 1988–1993. *Journal of Vegetation Science* 7: 747–762.
- , Rydgren, G. & Økland, T. 1999. Single-tree influence on understorey vegetation in a Norwegian boreal spruce forest. *Oikos* 87: 488–498.
- Paal, J. 1997. Eesti taimkate kasvukohatüüpide klassifikatsioon. Keskkonna Info- ja Tehnokeskus, Tallinn, 297 p. [Classification of Estonian vegetation site types.]
- Pielou, E.C. 1984. The interpretation of ecological data. A primer on classification and ordination. John Wiley & Sons, New York. 263 p.
- Pärtel, M. 2000. Species richness of vascular plant species and soil pH. In: Joint Meeting of the British Ecological Society and the Ecological Society of America, April 10–13, Orlando, Florida, USA, p. 36. Ecological Society of America, Washington.
- Qian, H., Klinka, K. & Kayahara, G. J. 1998. Longitudinal patterns of plant diversity in the North American boreal forest. *Plant Ecology* 138: 161–178.
- Reed, R.A., Peet, R.K., Palmer, M.W. & White, P.S. 1993. Scale dependence of vegetation-environment correlations: a case study of a North Carolina Piedmont Woodland. *Journal of Vegetation Science* 4: 329–340.
- Robinson, A.L., Vitt, D.H. & Timoney, K.P. 1989. Patterns of community structure and morphology of bryophytes and lichens relative to edaphic gradi-

- ents in the subarctic forest-tundra of North-Western Canada. *The Bryologist* 92(4): 495–512.
- Saetre, P. 1999. Spatial patterns of ground vegetation, soil microbial biomass and activity in a mixed spruce-birch stand. *Ecography* 22: 183–192.
- Scott, G.A.M. 1971. Some problems in the quantitative ecology of bryophytes. *New Zealand Journal of Botany* 9: 744–749.
- Slack, N.G. 1977. Species diversity and community structure in Bryophytes: New York State studies. *New York State Museum* 428: 1–70.
- 1990. Bryophytes and ecological niche theory. *Botanical Journal of the Linnean Society* 104: 187–213.
- StatSoft, Inc. 2001. Statistica (data analysis software system), version 6. www.statsoft.com.
- Stowe, L.G. & Wade, M.J. 1979. The detection of small-scale patterns in vegetation. *Journal of Ecology* 67: 1047–1064.
- Suominen, J. 1969. The plant cover of Finnish railway embankments and the ecology of their species. *Annales Botanici Fennici* 60: 183–236.
- Tamm, C.O. 1953. Growth, yield and nutrition in carpets of a forest moss (*Hylocomium splendens*). *Reports of the Forest Research Institute of Sweden* 43: 1–40.
- ter Braak, C.J.F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67: 1167–1179.
- 1990. Update notes: Canoco version. 3.12. Agricultural Mathematics Group, Wageningen.
- 1995. Ordination. In: Jongman R.H., Ter Braak C.J.F. & van Tongeren O.F.R. (eds.), *Data analysis in community and landscape ecology*. Cambridge University Press, Cambridge. pp. 91–173.
- Uranov, A.A. 1965. [Phylogenetic field]. In: [Problems of modern botany]. Vol. 1. Nauka, Moscow–Leningrad, p. 251–254. (in Russian)
- 1968. [On the association of species in phytocoenoses]. In: [Problems of morphogenesis and population structure of vascular plants]. Nauka, Moscow, p. 183–208. (in Russian)
- Zinke, P.J. 1962. The pattern of influence of individual forest trees on soil properties. *Ecology* 43: 130–133.
- Virtanen, R., Johnston, A.E., Crawley, M.J. & Edwards, G.R. 2000. Bryophyte biomass and species richness on the Park Grass Experiment, Rothamsted, UK. *Plant Ecology* 151: 129–141.
- Weibull, H. 2000. Bryophytes on boulders: diversity, habitat preferences and conservation aspects. *Acta Universitatis Agriculturae Sueciae, Silvestria* 159: 7–24.
- Whittaker, R.H. & Levin, S.A. 1977. The role of mosaic phenomena in natural communities. *Theoretical Population Biology* 12: 117–139.

Total of 69 references