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BRYOPHYTE DIVERSITY AND VASCULAR PLANTS

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PRESS

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CONTENTS

LIST OF PAPERS

The present thesis is based on the following papers which are referred to in the text by the Roman numerals.

I Ingerpuu, N., Vellak, K., Kukk, T. and Pärtel, M. 2001. Bryophyte and vascular plant species richness in boreo-nemoral moist forests and mires. *Biodiversity and Conservation* 10: 2153–2166.

II Ingerpuu, N., Vellak, K., Liira, J. and Pärtel, M. Bryophyte and phanerogam responses to environmental conditions in primeval deciduous forests at the North-Estonian limestone escarpment. (Submitted)

III Ingerpuu, N., Kull, K. and Vellak, K. 1998. Bryophyte vegetation in a wooded meadow: relationships with phanerogam diversity and responses to fertilisation. *Plant Ecology* 134: 163–171.

IV Ingerpuu, N. and Pärtel, M. Influences of vascular plants on bryophytes: species-specific effects in a grassland experiment. (Submitted)

V Ingerpuu, N. and Pärtel, M. Bryophyte and vascular plant rarity types in Estonian grasslands. (Manuscript)

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INTRODUCTION

The role of bryophytes in different ecosystems has often been overlooked. Their small body size does not always mean inferiority in plant interactions. The boreal bog is one conspicuous example where dwarfs may become giants. But, even without their striking biomass accumulation, the influence of bryophytes in several ecosystems can be remarkable. Well-known is the ability of bryophytes and lichens to inhabit inorganic surfaces as pioneers and promote soil formation, or cover soils almost immediately after fires, and, by stabilising soil temperature and moisture regime, make it inhabitable for vascular plants (Longton 1992). They play an important role in nutrients and water retention in tundra, forest, and mire ecosystems (Sveinbjörnsson and Oechel 1992, Vitt and Kuhry 1992, O'Neill 2000), but also in grasslands in winter (van Tooren *et al.* 1987, 1988). The seed germination and juvenile growth of vascular plants can be enhanced or suppressed by bryophytes (Hein 1966, Keizer *et al.* 1985, Zamfir 2000).

Bryophytes form the only habitat for many insects (Gerson 1982). They provide food for several invertebrates (Longton 1992) and nest material for many birds (Breil and Moyle 1979). Besides being eaten or out-competed, bryophytes can be promoted by other organisms. They can be distributed by animals (Marino 1997, Heinken *et al.* 2001, Ignatov and Ignatova 2001), and can be supported with nutrients or shade, and protected through the suppression of other competitors, by vascular plants (During and Verschuren 1988, Weibull 2001, Levine 1999). The balance of suppression and facilitation between different groups of organisms depends on numerous environmental factors and species-specific interactions. Even the terms "suppression" and "facilitation" have a relative meaning for a species. It is often useful for the existence of a species if its growth is somehow limited — the development of parasites, diseases, soil exhaustion etc. is limited then as well.

The maintenance of organism diversity is of ultimate importance for the maintenance of separate species, as well as for the wellbeing of humans. In the world of environmental pollution, and destruction and damaging of communities and species on vast areas, the networks of natural interactions between the organisms in ecosystems are often broken or distorted, which can enable, for example, the invasion of alien organisms (Lyons and Schwartz 2001) and can further damage the ecosystems. *Homo sapiens* itself can be treated as an alien organism, which can invade almost every ecosystem. Using the tool that has enabled humans to suppress all other organisms — the intellect, which is guided by an inner sympathy, may allow us to stabilise the damaged ecosystems and may bring us to a world where the coexistence of humans with numerous other organisms will be enabled for a longer time. For this, an understanding of the needs and interactions of different organism groups in their natural habitats is essential. High species diversity that has been maintained by traditional moderate human activity in seminatural communities, such as grasslands, can be destroyed by more intensive management if the functioning rules of these habitats are ignored.

In Estonia, there are still many natural and seminatural communities that are inhabited by quite a rich flora and fauna in spite of the fact that the area of primeval forests, mires, and seminatural grasslands has diminished drastically during last century. This gives a good opportunity to study the structure and functioning, also the protection and restoration, of the communities still present here.

I hope that our studies promote just a little the understanding about the coexistence of different plant groups and have a small impact on the survival of the diversity of communities and species.

The present work concentrates on the relations of bryophytes and vascular plants in different communities and in different conditions.

The aims of the work were:

1. To test if correlation between vascular plant and bryophyte species richness is same in different scales and in different communities.
2. To find out if environmental factors influence the diversity of these plant groups similarly.
3. To study the influence of vascular plants on the growth of bryophytes.
4. To compare the distribution into different forms of rarity for bryophytes and vascular plants.
5. To give some argumented guidance for community conservation.

MATERIAL AND METHODS

Study areas and field data

The data for the five papers was collected from different parts of Estonia.

Estonia covers an area of 47 450 km^2 and belongs to the boreo-nemoral vegetation zone (Sjörs 1965). The mean temperature in January is between –2°C and –7°C and in July between +16°C and +17.5°C, the mean annual precipitation is between 650 and 750 mm, the mean snow cover duration between 80 and 130 days (Jaagus 1999). Due to the proximity to the sea the western part of Estonia has higher temperatures in winter and lower temperatures in summer and also shorter snow cover duration. The bedrock consists of Ordovician and Silurian limestones in the northern and western part of Estonia and of Devonian sandstones in the southern part of Estonia. There are more than 1000 islands and islets near the coast of the mainland. Estonia has two major geobotanical divisions — the western part belongs to the Central-European province and the eastern part belongs to the East-European province (Lippmaa 1935). About 47% of Estonia is covered by woodland (Varblane 1998) and 23% by mires (Orru *et al.* 1992). In the first half of the 20th century the area of seminatural grasslands was 24,5% of the whole territory of Estonia (Laasimer 1965). This area has decreased enormously during the last century. The number of bryophyte species found in Estonia is 535 (Ingerpuu *et al.* 1998, Vellak *et al.* 2001). The number of native vascular plant species and subspecies is 1538 (Kukk 1999).

The data for the first paper (I) was collected in 1996–1999 from two wetland nature reserves in the central part of Estonia (Alam-Pedja Nature Reserve and Soomaa National Park). The study areas together cover about 520 km^2. Nine forest types and two mire types were included in the study. Vegetation was described in homogeneous 1 ha stands belonging to one community type. All bryophyte and vascular plant species were registered in every stand.

The study for the second paper (II) included only one forest type — primeval broad-leaved forest at the North-Estonian limestone escarpment. Twenty-three sites along the escarpment's 200 km length from east to west were studied in 1999. Bryophyte and vascular plant species lists (here defined as species richness) were compiled, and covers for herb and bryophyte layers estimated on 217, 1×1 m plots. The species composition of trees, herbs and bryophytes was described from an area of 0.1 ha around the 1×1 m plots (defined as community species pool). Two soil samples from every site were taken for the estimation of nitrogen, pH, and soil specific area. Additionally, 125 plots of 20×20 cm with bryophyte cover only were analysed on five different substrata types (soil, tree trunks, logs, sandstone rocks, and limestone rocks).

In the third paper (III), the influence of fertilizing was studied in 1995 on a wooded meadow in Laelatu, situated in the western part of Estonia. The species composition and cover of vascular plants and bryophytes was analysed on twelve 1x1 m plots at two fertilized and two control sites.

The fourth paper (IV) summarises the results of an experiment, where three grassland vascular plant species (*Trifolium pratense, Festuca pratensis* and *Prunella vulgaris*) were grown in pots (21×32 cm) together with two bryophyte species (*Brachythecium rutabulum* and *Rhytidiadelphus squarrosus*) during the years 2000 and 2001. The bryophytes were collected from a nearby meadow, dried and cut into lengths of 1–2 cm and then equal masses were sown into pots. The vascular plants were grown from seeds and planted to pots as juveniles in four densities (3, 6, 12 and 24 plants to a pot). Control pots were left without vascular plants. The pots were kept outside, in half-shade. At the end of the growing seasons the covers of bryophytes and vascular plants were estimated and the vascular plants were cut to simulate grassland management.

The fifth paper (V) includes material from three grassland types — alvar, meso-eutrophic meadow and spring fen. Ten sites of each type were studied. At each study-site species lists were compiled and covers estimated for both bryophytes and vascular plants on five 1×1 m plots. The alvar study sites were situated on two large western islands — Saaremaa and Muhu. The meso-eutrophic meadow and spring fen sites were situated in the southern part of Estonia.

Analyses

Regional species pools of nine forest and two mire types were compiled for bryophytes and vascular plants from the species pool of the whole Estonian flora. All species potentially capable of growing in a certain community type were included in the regional species pools of the studied communities. The species were selected according to literature data about the Estonian flora (Eesti NSV floora 1953–1984, Kuusk 1975, Laasimer *et al.* 1993, Ingerpuu *et al.* 1994, Kuusk *et al.* 1996, Leht 1999), and personal experience (paper I)).

The minimum number of stands needed for maintenance of the regional species pool for the particular community type was calculated by using the species richness accumulation curves. To obtain mean richness from one to the total number of stands for a particular community type a bootstrap method was used. Mean richness per a number of stands was always significantly linearly related to the natural logarithm of the number of stands. Using the linear regression formula, we calculated the exponent for the base of the natural logarithm, and the number of stands needed to reach the regional species pool of typical species. Rare species (less than ten localities known in Estonia, Kukk 1999, Ingerpuu *et al.* 1994) were excluded from the regional pools, since, for the distribution of rare species, factors other than the number of suitable sites may be more important (paper I).

To study bryophyte species' substrate affiliations, the effect of environmental conditions on bryophyte and herb species richness (paper II), and the influence of vascular plant cover on bryophyte cover (paper IV), the General Linear Mixed Model (GLMM, proc mixed, SAS ver 6.12, SAS Institute Inc. 1992) was used. In paper II species richness estimates for bryophytes and herbs were treated as repeated measurements within the plot (defined as variable 'Layer'). Significance of the variable 'Layer' indicates differences between bryophyte and herb richness. If interaction between an independent parameter and 'Layer' was significant, it meant that bryophyte and herb richness were differently related to the independent parameter, and regression slopes with their significance were presented separately for bryophytes and herbs. In paper IV the responses of bryophyte cover to the factors: 'year', 'absence of vascular plants', 'bryophyte species', 'vascular plant species', and their interactions, were tested, where 'year' was a repeated variable. GLMM was used to calculate regression slopes between bryophyte and vascular plant covers for each bryophyte species — vascular plant species — and observation year combination.

The relationship between species pool composition and environmental conditions was studied separately for bryophytes and herbs using CCA in the CANOCO 4.0 program (ter Braak and Šmilauer 1998). Monte Carlo permutation tests were used to estimate the significance of the environmental conditions (paper II).

The degree of spatial autocorrelation for mean species richness and species pool composition was measured using a Mantel type of test (Legendre 1993, Pärtel *et al.* 2001). All combinations of forest fragment pairs from a total of 23 fragments were established. Geographical distance between fragments in a pair was defined by the rank order of the fragments along the North Estonian escarpment. Difference in mean species richness between fragments in a pair was calculated as the larger value minus the smaller one. Floristic similarity between fragments in a pair was calculated by Jaccard's similarity index (number of common species from two fragments divided by the number of all species in those fragments). Correlation coefficients were calculated between geographical distance and difference in species richness, or between geographical distance and floristic similarity, using all pairs. Significance was calculated by a randomisation process, where the geographical distance of the 253 pairs was randomly ordered and then correlation calculated (paper II).

To analyse the species structure of three grassland types all species were divided into eight rarity forms following Rabinowitz (1981). The division into large and small geographical range was made according to the frequency estimations in the regional species pool (Kukk 1999, Ingerpuu *et al.* 1994) where the species are divided into seven groups. The five rarer groups were considered to have "small regional distribution" and the two more frequently occurring groups to have "large regional distribution". Species were considered to have "narrow habitat specificity" when they occurred only in one grassland type of the three, and to have "wide habitat specificity" when they occurred in two or three grassland types. The species were defined as "small-populational" if they were occurring on one or two plots at a site, and "large-populational" if they were occurring on 3 to 5 plots at a site. The differences between the distribution of the bryophyte and grass layers into these groups were estimated with the chi-square and Kolmogorv-Smirnov tests. The same tests were used to compare the distribution into rarity groups between vascular plants in Estonia and in other regions. The differences of the Ellenberg (1991) index values between the small- and large-populational species in the most rare group, were analysed with ANOVA.

RESULTS

Correlation between bryophyte and vascular plant species richness and cover in different plant communities (I, II, V)

Species richness, large scale (>100 m²)
The regional species pools of bryophytes and vascular plants (I), compiled for nine forest and two mire types from the whole flora of Estonia were significantly correlated ($r = 0.755$, $P = 0.007$). The richness per ten stands (stand size 1 ha) was also significantly correlated ($r = 0.707$, $P = 0.015$). The correlations between the species richness of vascular plants and bryophytes of the stands were significantly positive in eight community types, but the correlation between mean richness per stand was marginally non-significant ($r = 0.585$, $P = 0.058$). When Bonferroni correction was used, the relationship in stands remained significant only in poor paludified forest and in drained peatland forest. However, all 11 community types showed a positive relationship between bryophyte and vascular plant species richness per stand, which means an overall positive relationship (Sign test, $Z = 3.0$, $P = 0.003$).

No significant correlation was found between bryophyte and herb species pool sizes (on 0.1 ha) in the primeval deciduous forests below the limestone escarpments (II).

There were also no significant correlations between the species richness of vascular plants and bryophytes in alvar and meso-eutrophic meadow sites (site size 100–400 m²) (V). In fens the species richnesses of sites were significantly positively correlated ($r = 0.67$, $P = 0.033$).

The species richness in different plant communities varies differently among bryophytes and vascular plants (Fig. 1.). The mean species richness per stand over all studied communities (I, V) is lowest in mire communities, both for bryophytes and vascular plants. The values of mean bryophyte species richness are similar in forests and grasslands, while mean species richness of vascular plants is much higher in grasslands.

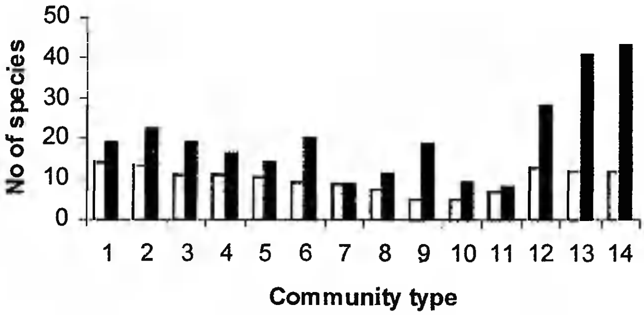

Figure 1. Mean species richness per site in different community types: 1 — nemoral forest; 2 — eutrophic swamp forest; 3 — rich paludified forest; 4 — drained peatland forest; 5 — boreal forest; 6 — floodplain forest; 7 — poor paludified forest; 8 — mixotrophic bog forest; 9 — eu-mesotrophic swamp forest; 10 — mixotrophic mire; 11 — ombrotrophic bog; 12 — spring fen; 13 — dry alvar; 14 — meso-eutrophic meadow. White columns — bryophytes; black columns — vascular plants.

Species richness, small scale (1 m²)

In primeval deciduous forests below the limestone escarpments (II), residuals of bryophyte and herb species richness, in the GLMM model, were significantly negatively correlated ($r = -0.287$, $P < 0.001$). For comparison, the Pearson correlation coefficient between bryophyte and herb species richness was positive ($r = 0.128$, $P = 0.06$) when the significant effect of environmental variation was not taken into account (Fig. 2.).

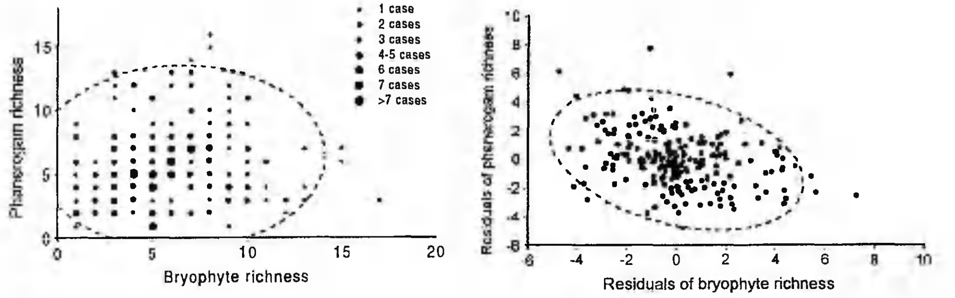

Figure 2. The correlation between bryophyte and herb species richness and between their residuals after the elimination of the influence of environmental factors.

There was no significant correlation between the small-scale species richness of bryophytes and vascular plants in grasslands (V).

Cover (1 m²)

The correlation between bryophyte and herb cover in primeval deciduous forests below the limestone escarpment (II) was significantly negative ($r = -0.444$, $P < 0.001$). The cover of these plant groups was also significantly negatively correlated on alvars ($r = -0.45$, $P = 0.001$) and meadows ($r = -0.48$, $P < 0.001$), while the correlation in fens was non-significant (V).

Environmental factors influencing the moss and field layer (II, III)

In primeval deciduous forests below the limestone escarpment (II), species richness of both bryophytes and herbs had a unimodal dependence on their cover, with highest richness values at intermediate cover values for the layer (the regression parameters of the second order polynomial had significant negative values, Table 1.). Species richness of both layers was significantly negatively affected by human disturbance. Only bryophyte species richness was significantly negatively influenced by the soil nitrogen content and positively affected by soil specific surface area, while herb species richness showed no significant relationship with soil parameters. We did not find the soil pH, forest fragment size, and site distance from the sea to be significant predictors of bryophyte or herb species richness in the forests studied.

Table 1. The effect of environmental conditions on the bryophyte and herb species richness (defined as Layer), in GLMM analysis. Only significant effects are shown. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

Source	$F_{1,372}$	Regression coefficient (SE)	
		Bryophytes	Herbs
Herb cover	6.3 *		
Herb cover × Layer	4.0 *	0.0036 (0.0253)	0.0827 (0.0271)**
Herb cover²	12.5 ***		
Herb cover² × Layer	3.3 **	–0.0002 (0.0002)	–0.0009 (0.0003)***
Bryophyte cover	10.7 **		
Bryophyte cover × Layer	29.2 ***	0.1517 (0.0237)***	–0.0421 (0.0253)
Bryophyte cover²	9.6 **		
Bryophyte cover² × Layer	18.8 ***	–0.0015 (0.0003)***	0.0003 (0.0003)
Human impact	13.6 ***		
Human impact × Layer	4.4 *	–1.8882 (0.7843)*	–3.3553 (0.8033)***
Soil N × Layer	9.3 **	–4.0467 (1.6206)*	0.6759 (1.6653)
Soil specific surface × Layer	9.1 **	0.0164 (0.0065)*	–0.0017 (0.0067)

Human disturbance altered significantly the species compositions of both plant groups (II), (Table 2). Both bryophyte and herb species compositions were related to their cover, but only the bryophyte composition was additionally related to the distance from the sea and to forest fragment size. The cumulative variance of the first four axes of species data for bryophytes was 51%, and for herbs, 34%, and, of species-environmental relation for bryophytes, 77%, and for herbs, 62%.

Table 2. The effect of environmental conditions on the species composition of bryophytes and herbs. Only significant effects are shown. * $P < 0.05$; ** $P < 0.01$

Variable	Bryophytes		Herbs	
	Eigenvalue	*F*	Eigenvalue	*F*
Herb cover	0.09	1.25	0.26	1.57*
Bryophyte cover	0.50	5.74**	0.24	1.36
Human impact	0.14	1.88*	0.34	1.90**
Forest size	0.17	2.1**	0.14	0.89
Distance to sea	0.20	2.42**	0.17	1.07

The tree species pool size was significantly positively correlated with both bryophyte and herb species pool sizes (II).

Bryophyte species richness per 0.04 m² plots differed significantly between substrates ($F_{4, 106} = 2.8$, $P = 0.031$). The most species-rich substrate for this community was limestone cliffs (mean 4.1), the most species-poor was soil (mean 2.6; Fig. 3) (II).

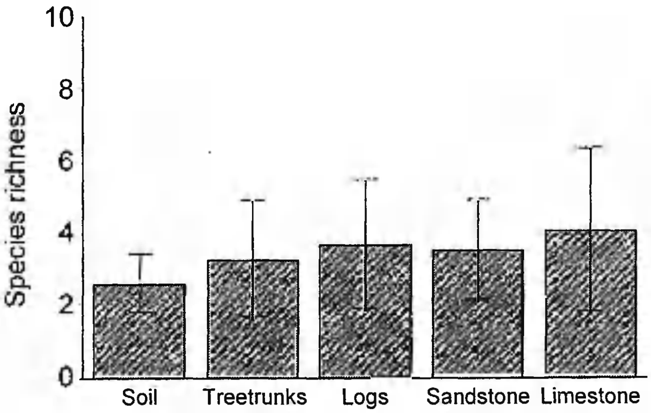

Figure 3. Bryophyte species richness per 20x20 cm plots (mean ±SD) on different substrates in the studied forests.

Fertilisation influenced significantly the species richness and cover of bryophytes and vascular plants in a wooded meadow (III). The species richness of bryophytes increased and the species richness of vascular plants decreased in fertilised plots, while the cover of bryophytes decreased and the cover of vascular plants increased in the same plots (Table 3).

Table 3. Vascular plant and bryophyte community parameters in F (fertilised) and C (control) plots. *t* — significance of difference between the paired means of F and C plots (* $P < 0.05$; **$P < 0.01$)

	Parameter	F_1	F_2	C_1	C_2	*t*
Bryophytes	Mean no of species per sample plot	8	8	5	4	**
	No of species pooled	14	15	6	7	**
	Cover (%)	45	55	55	65	*
Vascular plants	No of species pooled	46	64	72	68	*
	Cover (%)	90	85	65	70	**
	Aboveground biomass (g/m²)	260	180	170	154	**

Effect of vascular plant cover on the growth of bryophytes in a pot experiment (IV)

The absence of vascular plants had significantly positive effect on the cover of bryophytes, showing competitive effect from vascular plants (Table 4). The interaction of bryophyte species and vascular plant absence was not significant, showing that both bryophyte species responded similarly. Also, vascular plant absence and 'year' had no significant interaction, showing that the effect of vascular plants on bryophytes was consistent in time.

Vascular plant cover, however, was significantly positively correlated with bryophyte cover (Fig. 4.). There were significant positive correlations between the cover values of *Brachythecium* and *Trifolium* (both years, Fig. 4a), *Brachythecium* and *Festuca* (second year only, Fig. 4b), and *Rhytidiadelphus* and *Festuca* (second year only, Fig. 4e).

Significant interaction occurred between vascular plant cover and 'year', showing that the second year positive influences were stronger than the first year relationships (Table 4.). Significant interaction occurred between vascular plant species and vascular plant cover. The occurrence of significant interaction between 'vascular plant cover', 'vascular plant species' and 'bryophyte species' indicates a high species specificity in the biotic effects between vascular plant and bryophyte species. *Trifolium* and *Festuca* had positive effects, but *Prunella* showed no such effect.

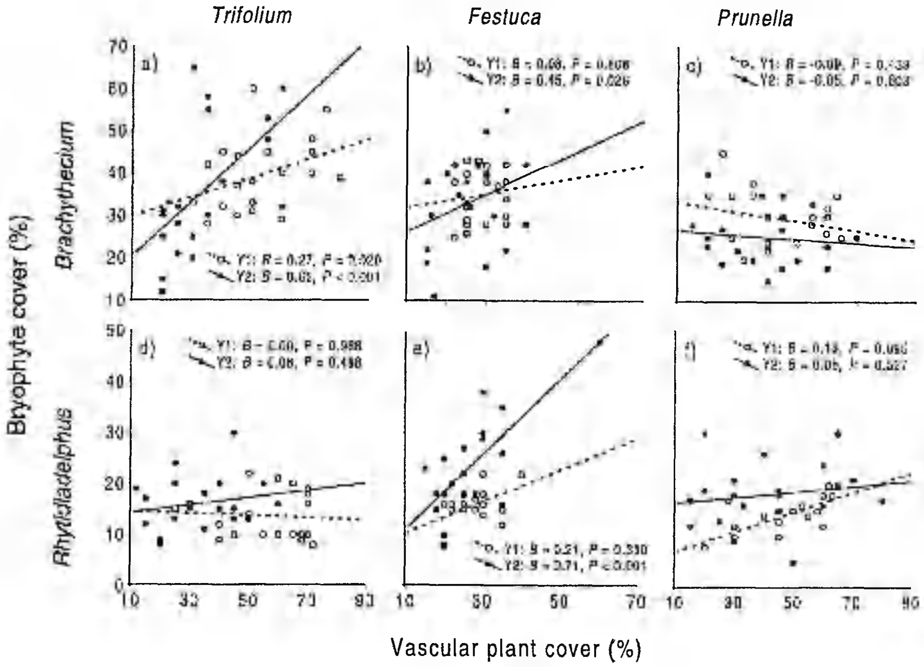

Figure 4. Cover of two bryophyte species in relation to cover of three vascular plant species during two years (Y).

Table 4. The dependence of bryophyte cover on vascular plant cover, year, bryophyte species, and vascular plant species (GLMM). Significant effects only shown. Abbreviations: YR — year; BS — bryophyte species; A — absence of vascular plants; VS — vascular plant species; VC — vascular plant cover

Source	Df	F	P
BS	1.12	44.1	<0.001
YR*BS	1.11	8.3	0.005
A	1.12	45.3	<0.001
VC	1.11	16.2	<0.001
VC*YR	1.11	4.7	0.032
VC*VS	1.11	4.6	0.012
VC*YR*VS	1.11	3.0	0.055
VC*BS*VS	1.11	6.8	0.002

The distribution of grassland bryophytes and vascular plants into different rarity forms (V)

The species of three different grassland types (dry alvar, meso-eutrophic meadow and spring fen) were divided into rarity forms according to Rabinowitz (1981). The distributions of bryophytes and vascular plants into these forms (Table 5) are similar in all grasslands and in different grassland types except meadows, where it was significantly different ($\chi^2 = 15.08$; df = 7; $P = 0.035$).

Table 5. The percentage of grassland species in different rarity forms

Regional distribution	Large				Small			
Habitat specificity	Wide		Narrow		Wide		Narrow	
Population size	Large	Small	Large	Small	Large	Small	Large	Small
Alvar								
Bryophytes	13	24	16	18	3	5	8	13
Vascular plants	27	28	8	11	4	5	9	7
Meadow								
Bryophytes	10	36	5	26	2	7	0	14
Vascular plants	26	24	11	26	4	2	1	6
Fen								
Bryophytes	12	21	18	18	6	3	15	6
Vascular plants	18	13	21	24	0	1	7	14
All								
Bryophytes	10	14	17	29	4	1	10	16
Vascular plants	19	11	18	29	3	1	7	13

This is due to the smaller number of regionally large-distributional species with large populations and the larger number of regionally small-distributional species with small populations among bryophytes in this grassland type. The proportion of regionally small-distributional species is 23–31% for bryophytes and 13–24% for vascular plants. The number of species with small populations is similar for vascular plants in all community types (52–59%), but the proportion of bryophytes with small populations is much higher in alvars (61%) and meadows (83%) than in fens (48%). The proportion of regionally small-distributional species with large populations is similar for bryophytes and vascular plants (varying between 0–14%) except in fens, where it is much larger for bryophytes (22%) than for vascular plants (9%). The number of habitat specific species with small populations is much smaller for bryophytes in alvars and meadows, and for vascular plants in fens.

The comparison of the ecological demands of the large-populational habitat-specific species and the small-populational habitat-specific or non-habitat-specific species showed significant differences in a majority of cases.

Comparing data from different regions, grouped according to the three major divisions of Rabinowitz (1981), we can see that the summarised groups of regional distribution do not differ significantly between the selected groups of British (Rabinowitz *et al* 1986) and Estonian plants, but, of course, French and Spanish endemic plants (Médail and Verlaque 1997; Blanca *et al* 1998) have significantly less (χ^2 = 69.96; P<0.001 and χ^2 = 7.33; P = 0.007) species with regionally large distribution. The distribution into habitat specificity groups does not differ significantly between different regions.

Results connected with nature conservation (I, II, V)

The greatest number of Red-Listed bryophyte species — 20, was counted in the primeval deciduous forests at the limestone escarpments (II), showing the great importance of the conservation of this community type for rare and vulnerable bryophyte species. Most of the Red-Listed bryophytes were found growing on cliffs (both limestone and sandstone). The number of Red-Listed bryophytes in other studied community types, and of vascular plants in all studied community types, was less than 5.

The minimum number of stands (of size at least 1 ha) required for the maintenance of the regional species pools of the studied nine forests and two mire types was roughly between 300 and 5,300 for bryophytes and roughly between 400 and 35,900 for vascular plants (II). Only in eutrophic-mesotrophic swamp forests did the number of sites needed for the bryophyte regional species pool exceed that for the vascular plant species pool. In general, more stands are needed to maintain vascular plant regional species pools.

Species richness and species composition of both bryophyte and vascular plant layers were significantly negatively affected by human disturbance in broad-leaved forests (II).

The most vulnerable rarity form includes species with small regional distribution, narrow habitat specificity and small populations. The grassland study (V) showed that the number of such species is much higher for bryophytes in alvars and meadows, and for vascular plants in fens. Consequently, rare bryophytes are more endangered in alvars and meadows, and rare vascular plants, in fens.

DISCUSSION

There are very few community types that consist only of vascular plants or only of bryophytes. Usually representatives from both plant groups coexist, their numbers and covers being balanced by numerous interactions with each other and the environment. The small body-size of bryophytes may leave them almost unnoticed in some grassland communities with dense grass layer cover, while in forests with sparse grass layer they usually form a conspicuous layer. However, our studies showed that the bryophyte mean species richness does not differ significantly between grasslands and forests while the species richness of field layer is much higher in grasslands (I, II, V, Fig. 1.). The species richness of the field layer is more than that of the moss layer suppressed by the tree cover. The majority of bryophytes is shade-tolerant plants in comparison with the majority of vascular plants (Valanne 1984, Proctor 2000). They reach an optimal photosynthesis level very often at lower light intensity compared with vascular plants (Green and Lange 1995). In fact, very many bryophytes even need shade, since their metabolism relies on the amount of external water that is held between their stems and leaves, and also in the upper layer of the growing substrate. Without shade from vascular plants the higher temperature and stronger wind could dry them up too quickly. In open habitats they form very dense growth-forms, which enable them to retain water in the small capillary rooms around their body for a longer time, and also reduce the influence of winds, since the evaporation from the surface of a dense moss cushion has been measured to be almost the same as from the surface of a smooth hemisphere (Proctor 1984). Bryophyte and vascular plant relations are often contradictory. On one hand bryophytes are often suppressed by a lack of light and space, which is illustrated by the mainly significantly negatively correlated covers of the bryophytes and vascular plants (II, IV), but, on the other hand, they can be facilitated by nutrients arriving with the throughfall from the vascular plant canopy (Weibull 2001, Norden 1991, 1994) and by evaporation and temperature reducing shade of moderate vascular plant cover. Our experiment with grassland plants (IV, Fig. 4) was proof of such a facilitative effect of vascular plant cover, which is usually left unnoticed in the field, where the grass densities are often too high and the suppressing effect is prevalent. The switch from facilitative effect to suppressing effect may be apparent only in communities with varying vascular plant cover, as shown by the unimodal correlation of vascular plant leaf area index and bryophyte biomass in the mountain fens of Switzerland (Bergamini *et al* 2001) and in Estonian alvars (unpublished data of T. Pesur).

The species richness of vascular plants and bryophytes across different community types may have little in common (Dirkse and Martakis 1998), while within the community types they can be positively correlated (Ejrnæs and Poulsen 2001). Our studies (I, II, V) showed that the correlations on 1 m^2 are mainly insignificant, but in larger scales they often become significant, especially in forest communities (I). This may be mainly due to the higher number of different microhabitats in larger scales. The competitive effect is more important in smaller scales, where the resources are more evenly distributed. Still, due to different morphology and physiology, bryophytes and vascular plants can use the same resources in different rates and ways, so that soil properties can be of different importance to them. Bryophytes are known to receive nutrients mainly from precipitation. Anyhow, soil can also be an important source of nutrients for bryophytes as shown by van Tooren *et al* (1990). The study of broad-leaved forests (II) showed that bryophyte species richness and composition was significantly dependent, and in some cases in different ways than vascular plants, on the studied environmental factors (soil moisture, soil nitrogen content, distance from the sea and forest size). The grass layer was not significantly influenced by the measured factors. The correlation between field data of species richness of bryophytes and vascular plants was positive. After the elimination of the effects of environmental factors in the model, the correlation between the residuals of bryophyte and vascular plant species richness was found to be significantly negative, referring to possible competition (Fig. 2).

Our studies showed that the soil factors can have a different effect on species richness of bryophytes in different community types. In the broad-leaved forests higher soil nitrogen content was negatively correlated with the bryophyte species richness (II), while in the wooded meadow study (III) it was positively correlated. Fertilisation with small amount of nitrogen has been shown to promote the growth of some bryophytes (Rincon and Grime 1989, Jauhiainen et al. 1998) while higher nitrogen content in fertilizers usually inhibits bryophyte growth (Bergamini and Pauli 2001). The species richness in the wooded meadow study increased mainly due to the addition of several new species, presumably tolerant to higher nutrient concentrations. The cover of species more sensitive to fertilisers diminished and left space for the new species. Some of these are also more light demanding, which may limit their growth in forest communities.

The species richness of bryophytes is additionally influenced by the number and character of available substrata. Bryophyte richness was highest on limestones and lowest on soil in the broad-leaved forests (II). The differences can partly be explained by differences in the stability of substrata and the average size of species on them. Limestone cliffs should be the most stable substrate of the studied five, and species inhabiting this substrate usually have small size. Soil is presumably the most unstable substrate, since the changing phanerogam growth pattern and falling leaves provide a dynamic environment. Soil inhabiting bryophyte species are often also larger-sized.

The only studied factors that had similar effects on bryophytes and vascular plants were ‘number of tree species’ and ‘human impact’. The number of tree species was significantly positively correlated with the species richness of both plant groups in a larger scale, presumably due to allelopathic effects (Nordén 1991, 1994).

The human disturbance had strong negative influence on the species richness and it altered the species composition of both bryophytes and vascular plants (II). Human disturbance is one of the main reasons for the extinction and rarity of many species. Forest management causes the impoverishment of bryoflora, since the microhabitats for several species, like logs, large tree-trunks, wet soil, etc., are eliminated. This has been shown in numerous studies (Söderström 1987, Gustafsson and Hallingbäck 1988, Andersson and Hytteborn 1991, Vellak and Paal 1999, Trass *et al* 1999). On the other hand, grasslands as habitat types cannot be preserved without the maintenance of traditional management in the majority of cases. Management of grasslands and wooded meadows is needed for the continued existence of many species (During and Willems 1986). If it is accepted that high species diversity is important, efforts must be made to stop further elimination and fragmentation of the habitat diversity. This is only possible if maximum diversity of different communities is preserved in every geographical region. In order to retain its species diversity, every community type must cover a reasonable area. We calculated this area for several Estonian plant community types. The analysis did not include important factors such as distance between different sites, balance between extinction and colonisation, dispersal ability, etc. If these factors were included, the minimum area for the maintenance of the species pool typical for a community would be much larger. From this we can conclude that the whole area of several rare community types, like floodplain forests and forests on the North-Estonian escarpment talus, should be taken under nature conservation. The analysis, which included forests and mires (I), showed that less area is usually required for bryophytes than for vascular plants in order to retain the species composition typical for a community. If different forms of rarity (Rabinowitz 1981) are taken into account, the area may be more limiting for rare bryophytes than vascular plants in some grassland types such as alvars and meso-eutrophic meadows (V). The distribution into rarity forms is similar for grassland vascular plants and bryophytes, showing, however, some differences in the most vulnerable rarity form (species with small regional distribution, narrow habitat-specificity and small populations). The proportion of this form is larger for bryophytes in alvars and meso-eutrophic meadows.

In conclusion, our studies showed that the relationship between the species diversity of bryophytes and vascular plants can not be explained uniformly. It changes in different directions and in different rates depending on ecological conditions and species composition. The only studied factor that was found to have a uniformly negative effect on both bryophytes and vascular plants was human disturbance.

CONCLUSIONS

1. The relationships between species richness of the bryophyte and herb layers and their responses to different environmental factors may be different in different plant community types.
2. The large-scale species richness of bryophytes and herbaceous plants is usually positively correlated in forest communities.
3. The small-scale species richness of bryophytes and herbaceous plants in forests is negatively correlated if the effect of environmental heterogeneity is eliminated.
4. Species richness of moss and herb layer respond to different environmental factors differently, with a few exceptions: the number of tree species a has positive effect, and human disturbance a negative effect, on both plant groups.
5. The division of grassland bryophytes and vascular plants into groups according to their regional distribution, habitat specificity and population size is similar — the majority of grassland plants have a large regional distribution, but a narrow habitat specificity. Among species with narrow habitat specificity small populations prevail.
6. In general, more area is needed by vascular plants to maintain their community species pools.
7. In order to retain the overall species diversity, the whole area of the rarest plant communities should be taken under nature protection and the decline of other natural and seminatural plant communities should be halted.

SUMMARY IN ESTONIAN

Sammaltaimede mitmekesisus ja seosed soontaimedega
Kokkuvõte

Samblad on väga oluliseks osaks paljudes taimekooslustes. Väikese kasvu tõttu on neid tihti peetud kooslustes vähetähtsateks ning võrreldes soontaimedega konkurentsinõrkadeks. Olenevalt keskkonnatingimustest võivad aga samblad teatud regioonides ja kooslustes nagu arktilised tundrad, boreaalsed sood ning metsad, saavutada ülekaalu kas biomassis või liigirikkuses. Sellistes kooslustes reguleerivad nad kaasnevate soontaimede kasvu võime tõttu toitainetevaestes tingimustes efektiivsemalt ära kasutada sademetega saabuvaid toitaineid. Samblad võivad mõjutada nii oma kasvuvormi kui eritatavate ainete mõjul ka soontaimede idanemist ja juveniiltaimede kasvu.

Käesolev töö uurib sammaltaimede liigirikkust mõjutavaid põhjuseid ning seoseid sammal- ja soontaimede mitmekesisuse vahel mitmetes Eesti taimekooslustes väliuuringute põhjal ning ka potikatsete abil.

Töö eesmärkideks olid:

1. Leida seoseid sammalde ja soontaimede liigirikkuste vahel erinevates skaalades ja erinevates taimekooslustes.
2. Uurida keskkonnafaktorite mõju sambla- ja rohurinde mitmekesisusele. Kas samad faktorid mõjutavad erinevaid taimede rühmi sarnaselt?
3. Selgitada katseliselt soontaimede katvuse mõju sammalde kasvule.
4. Võrrelda, kas sammalde ja soontaimede jaotumine erinevatesse harulduseusvormidesse on sarnane.
5. Anda teoreetiliselt põhjendatud suuniseid taimekoosluste liigilise mitmekesisuse kaitseks.

Andmed doktoritöö jaoks koguti mitmetest erinevatest taimekooslustest üle Eesti: metsakoosluste andmestik Kesk-Eestist Alam-Pedja ja Soomaa kaitsealadelt ning Põhja-Eesti pangaalusest piirkonnast, niidukoosluste andmestik Lõuna-Eestist ning Muhu- ja Saaremaalt. Väetuse mõju uuriti Lääne-Eestis Laelatu puisniidul ning potikatse viidi läbi Tartus, TÜ botaanikaaia territooriumil.

Töö käigus kogutud andmed erinevate taimekoosluste suureskaalalise liigirikkuse kohta näitavad, et kui soontaimede liigirikkus oli niitudel suurem kui metsades, siis sammalde liigirikkuses olulist erinevust ei esinenud. Erinevates metsakasvukohtüüpides ühe-hektarilistel proovialadel oli sammalde ja soontaimede liigirikkuste vaheline korrelatsioon enamasti oluliselt positiivne. Väikseses skaalas (1m^2) selgus, et seos oli küll positiivne, kuid statistiliselt ebaoluline nii metsades (pangametsade uurimuse alusel) kui ka erinevates niidukooslustes. Pangametsade andmestiku statistilisel analüüsil ilmnes aga, et peale keskkonnafaktorite mõju eemaldamist osutusid soontaimede ja sammalde liigirikkuste jäägid oluliselt negatiivselt korreleerituks. See viitab nimetatud taimerühmade vahel eksisteerivatele konkurentsisuhetele, mida maskeerib keskkonnatingimuste heterogeensus.

Keskkonnatingimuste mõju analüüsil (pangametsade näitel) selgus, et samade faktorite mõju liigirikkusele ja liigilisele koosseisule oli sammaldele ja soontaimedele mõnel juhul vastassuunaline, kuid statistiliselt oluline ainult sammaldele. Erandiks oli siin kasvukoha reostatus, mis avaldas olulist negatiivset mõju liigirikkusele ning muutis oluliselt liigilist koosseisu nii sammaldel kui soontaimedel. Mullaparameetritest oli oluline positiivne mõju sammalde liigirikkusele mulla niiskusesisaldusel ning oluline negatiivne mõju mulla lämmastikusisaldusel. Mulla pindmise kihi veesisaldusel on oluline tähtsus sammalde kasvule, kuna juurte puudumise tõttu võtavad samblad vett ja toitained vastu kogu kehapinnaga ning kehaga otseses kontaktis oleva keskkonna suurem niiskusaste soodustab fotosünteesi kestmist. Mulla lämmastikusisaldusel oli metsasammalde liigirikkusele oluline negatiivne mõju, kuid puisniidu väetuskatsete analüüs näitas, et väetatud aladel sammalde liigirikkus suurenes. Puisniidu väetamise tagajärjel vähenes väetamisele tundlike liikide katvus, mis võimaldas lisanduda uutel liikidel. Lisandusid ka mõned valguslembesed ning toitaineterikkamale mullastikule iseloomulikud liigid, kes taluvad ilmselt suuremat väetuskoormust, kuid vähem varjutatust. Sammalde liigirikkust mõjutab lisaks veel substraatide rohkus ning iseloom. Erinevate substraatide hulk oli eriti suur pangametsades. Suurim oli liigirikkus lubjakivikaljudel ning väikseim maapinnal. Väikeseskaalalist liigirikkust soontaimevabadel proovialadel mõjutab ka substraadi kestvus ning liikide suurus. Lubjakivikaljud on uuritud koosluses kaheldamatult kõige pikaealisem substraat, siin esinevad aga sagedamini väikesekasvulised liigid. Mullapind on soontaimede võimaliku pealekasvu, vihmauhte ning metsavarise tõttu küllaltki muutlik ning väikeseskaalaline sammalde hävimine toimub siin tihedamini. Samas on maapinnal kasvavad samblad ka enamasti suuremakasvulised.

Sammalde ja soontaimede katvuste vahelised korrelatsioonid üheruutmeetristel proovialadel olid väliandmetel nii metsas kui niitudel oluliselt negatiivsed. Potikatse tulemusel osutus aga soontaimede ja sammalde katvus positiivselt seotuks. Kontrollseeria näitas siiski oluliselt suuremat sammalde kasvu soontaimede täieliku puudumise korral, mis viitab valguskonkurentsile. Eksperimendiseerias kasutati suhteliselt väikseid soontaimede tihedusi, mis ei tekitanud veel sammalde kasvu täielikult pärssivat katvust. Soontaimede katvuse tõttu vähenenud valgustingimustes osutub eriti oluliseks fotosünteesiks vajaliku niiskusperioodi pikkus ning optimaalne temperatuur. Mõõdukas soontaimede katvus vähendab oluliselt tuule kuivatavat mõju samblavaibale ja pindmisele mullakihile ning alandab temperatuuri päikeselistel päevadel. Erinevate soontaimeliikide puhul oli täheldatav ka erinev mõju sammalde katvusele.

Analüüsides rohumaade sammalde ning soontaimede jaotumist erinevatesse haruldusvormidesse nende geograafilise leviku, kooslusspetsiifilisuse ja populatsoonide suuruse alusel Rabinowitz'i (1981) järgi, selgus, et see ei erine oluliselt. Nii sammalde kui soontaimede puhul kuulus enamus liike laia geograafilise levikuga ning kitsa kasvukoha eelistusega liikide hulka. Looduskaitseliselt kõige ohustatuma grupi, väikese geograafilise levikuga, kitsa kasvukohaeelistusega ning ainult väikeseid populatsioone moodustavate liikide osakaalu järgi on haruldased samblad rohkem ohustatud loodudel ja aruniitudel, soontaimed aga allikasoodes.

Harulduse mõistet võib käsitleda mitmeti ning väga haruldaste liikide kaitse on üsna komplitseeritud sõltudes paljudest nii liigi bioloogiat kui keskkonnatingimusi puudutavatest asjaoludest. Siiski on selge, et eelkõige oleks vajalik kõigi regioonile iseloomulike kooslusetüüpide ning neile vastavate tüüpiliste liigifondide säilimine. Metsa- ja sookoosluste analüüs näitas, et enamikel juhtudel on sammalde liigifondi säilimiseks vajalik pindala väiksem (300–5300 ha) kui soontaimedel (400–35900 ha). Kuna analüüsis polnud arvesse võetud paljusid olulisi asjaolusid, nagu aladevaheline distants, liikide levimisvõime ja väljasuremise vaheline tasakaal jmt., siis peaksid arvutatud pindalad liigifondi tegelikuks säilimiseks olema veelgi suuremad. Sellest järeldub omakorda, et praegu niigi väikese pindalaga esindatud kooslusetüübid nagu näiteks lammimetsad ja pangametsad, tuleks täies ulatuses võtta Eestis kaitse alla.

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PAPERS

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Bryophyte and vascular plant species richness in boreo-nemoral moist forests and mires

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Abstract. We compare species richness of bryophytes and vascular plants in Estonian moist forests and mires. The material was collected from two wetland nature reserves. Bryophyte and vascular plant species were recorded in 338 homogeneous stands of approximately 1 ha in nine forest and two mire types. Regional species pools for bryophytes and vascular plants were significantly correlated. The correlations between the species richnesses of bryophytes and vascular plants per stand were positive in all community types. The relative richnesses (local richness divided by the regional species pool size) were similar for bryophyte species and for vascular plant species. This shows that on larger scales, conservation of the communities rich in species of one taxonomic plant group, maintains also the species richness of the other. The minimum number of stands needed for the maintenance of the regional species pool of typical species for the every community type was calculated using the species richness accumulation curves. Less stands are needed to maintain the bryophyte species pools (300–5300 for bryophytes and 400–35 000 for vascular plants).

Key words: bryophytes, conservation of species diversity, species accumulation curve, species pool, vascular plants

Introduction

The importance of maintaining species richness has become more pressing in recent years, especially due to the loss and fragmentation of natural habitats (Fischer and Stöcklin 1997; Rozensweig 1999). In Estonia, the main attention in plant species richness studies has been on grasslands (Pärtel and Zobel 1995, 1999; Zobel et al. 1996; Pärtel et al. 1998). Plant species richness in forests and wetlands has been studied much less (Zobel 1993). Forests and mires form the typical climax vegetation for the boreo-nemoral zone (Sjörs 1963) although natural forests and wetlands have almost disappeared from Western Europe due to agriculture and forest cultivation (Navid 1994; Noss and Csuti 1994). In Estonia the situation is much better, 47% of the territory of Estonia is covered by woodland (Varblane 1998) and 23% by mires (Orru et al. 1992). Land ownership reform has intensified forest utilization in Estonia in recent years. Background information about the variation of species richness in forests and mires is urgently needed for nature protection policy planning.

Bryophyte and vascular plant species diversity has only rarely been considered together in one study (Wilson and Sykes 1988; Glaser et al. 1990; Rey Benayas 1995; Såstad and Moen 1995; Aude and Lawesson 1998; Ingerpuu et al. 1998; Gould and Walker 1999). Bryophyte species richness and coverage can be especially high in forests and mires, sometimes exceeding the vascular plant richness. It is not yet clear what determines the differences in species richness in these two plant groups in different communities. A close relationship between the number of bryophytes and vascular plant species richness has been described from a North American peatland (Glaser et al. 1990). In a North American arctic riverside community, bryophyte and vascular plant species richnesses had different relationships to environmental gradients (Gould and Walker 1999). Different responses of vascular plants and bryophytes to fertilization were observed in an Estonian wooded meadow (Ingerpuu et al. 1998). Hence, it is still unclear whether the variation in species richness of these two plant taxonomic groups follows similar trends and whether the same strategies can be used for maintaining species richness of bryophytes and vascular plants.

Species richness patterns and processes in different stands are dependent on the potential set of species present in the region and able to grow in a particular community type. This set of species is called the species pool (Taylor et al. 1990; Eriksson 1993; Zobel 1997). Species pools may be defined by species ecological requirements (Pärtel et al. 1996) or by phytosociological belonging to particular community types (Gough et al. 1994; Zobel et al. 1998; Pärtel et al. 1999; Dupré 2000). The species pool defines the maximum potential richness for each community type, but also the typical species composition. In nature, different habitat types may form a mosaic, which may obscure the general pattern of richness of typical species for a particular community type. Therefore, one should separately consider only the species that are defined as typical for this community type, and belonging to the species pool.

To compare species richness in different community types and different taxonomic groups, differences in potential richness can be considered. One possibility is to divide the richness by the species pool size, obtaining the relative richness (Zobel and Liira 1997), also called community completeness (Rabotnov 1987).

Species richness is scale dependent. Knowing the mean richness per one stand, we cannot estimate richness for a higher number of replicates without knowing the species accumulation curves. These functions describe the relationship between regional and local richness, allowing the estimation of richness for a particular number of areas (Miller and Wiegert 1989). Here we propose an opposite method: to calculate the number of stands (in our study of 1 ha size) needed for preserving the regional species pool. This issue is related to the well-known species-area relationships (Dony 1977; McGuiness 1984). Several separated stands, however, generally have more species than a single stand of the same area (Sætersdal 1994) and the number of stands and their total area cannot be mixed.

The objective of the present work was to compare the variation in species richness of bryophytes and vascular plants in Estonian moist forests and mires. We addressed the following questions: (i) How is the species richness of bryophytes and vascular plants correlated in different community types? (ii) What is the relative richness of the studied community types for bryophytes and vascular plant species, and is it different? (iii) How many stands will be needed to maintain the regional species pool of bryophytes and vascular plants for each community type?

Materials and methods

Study area

The material was collected from two wetland nature reserves in Estonia – Alam-Pedja Nature Reserve and Soomaa National Park. Alam-Pedja Nature Reserve (260 km^2) is situated in the eastern-central part of Estonia in a landscape area called the Võrtsjärv Basin. Soomaa National Park (367 km^2) lies in the southwestern part of Estonia. The distance between the two study areas is ca. 100 km and the territories covered by them lie between 58°35′ and 58°19′ N, 24°53′ and 26°31′ E. The majority of the territory is covered with mires and moist forests. Forest management in these areas has been stopped at least 10 years ago, in some areas much earlier. The reserves are bordered and crossed by several rivers. In spring, large areas of meadows and forests are flooded. The mean annual temperature is 4.5–5.0 °C and the mean annual precipitation is 500–700 mm. The plant communities and the natural conditions in both study areas are similar (Ader and Tammur 1997; Allilender 1999).

Field works were carried out in 1996–1999. We included only mature forest in our study, of an age of at least 40 but often up to 100 years. Forests were classified according to Lõhmus (1984) and mires according to Masing (1975). The forest or mire types and type groups of these classifications are referred to in this work as community types. Vegetation was described in homogeneous 1 ha stands belonging to one community type in nine forest, and two mire types (Table 1). The approximate areas of the forest types in Estonia are given by Karoles (1995), and of the mire types by Ilomets (1998) (Table 2).

Data

Species richness parameters were determined for each community type, separately for bryophytes and vascular plants.

Regional species pools – the set of species, from the Estonian flora, which are potentially capable of growing in a certain community type – were determined for each community type in the study area. The phytosociological method was applied

Table 1. General characteristics of the studied forest and mire types. Nomenclature: bryophytes according to Ingerpuu et al. (1994), vascular plants according to Leht (1999).

Type – abbreviation and name	Main tree species	Dominant under-story species	Soil
BF – Mesic boreal forests	*Picea abies* *Betula pendula* *Pinus sylvestris*	*Pleurozium schreberi* *Hylocomium splendens* *Vaccinium myrtillus* *Oxalis acetosella*	Mineral, mesic
NF – Mesic nemoral forests	*Betula pendula* *Populus tremula* Various broad-leaved species	*Cirriphyllum piliferum* *Eurhynchium angustirete* *Aegopodium podagraria* *Mercurialis perennis*	Mineral, mesic
FF – Floodplain forests	*Betula pubescens* *Alnus glutinosa* Various broad-leaved species	*Climacium dendroides* *Calliergonella cuspidata* *Carex cespitosa* *Filipendula ulmaria*	Mineral, periodically flooded by rivers
RPF – Rich paludified forests	*Betula pubescens* *Alnus glutinosa*	*Climacium dendroides* *Aulacomnium palustre* *Athyrium filix-femina* *Filipendula ulmaria*	Mineral or with peat up to 30 cm, high fluctuating ground water level
PPF – Poor paludified forests	*Pinus sylvestris*	*Pleurozium schreberi* *Sphagnum* spp. *Vaccinium uliginosum* *Ledum palustre*	Peat up to 30 cm, high fluctuating ground water level

EMSF – Eu-mesotrophic swamp forests	*Betula pubescens*	*Aulacomnium palustre* *Calliergonella cuspidata* *Calamagrostis canescens* *Carex* spp.	Peat more than 30 cm, high ground water level, long flooding periods
ESF – Eutrophic swamp forests	*Alnus glutinosa* *Betula pubescens*	*Climacium dendroides* *Calliergon cordifolium* *Filipendula ulmaria* *Calla palustris* *Caltha palustris*	Decomposed peat more than 30 cm, fluctuating ground water level, periodically flooded
TBF – Mixotrophic bog forests	*Pinus sylvestris*	*Sphagnum* spp. *Pleurozium schreberi* *Carex lasiocarpa* *Calamagrostis canescens*	Peat more than 30 cm, permanently saturated with water
DPF – Drained peatland forests	*Pinus sylvestris*	*Pleurozium schreberi* *Hylocomium splendens* *Vaccinium myrtillus* *Oxalis acetosella*	Drained decomposing peat, mesic or moist
TM – Mixotrophic mires	–	*Sphagnum* spp. *Warnstorfia* spp. *Trichophorum alpinum* *Carex lasiocarpa*	Peat, high ground water level, sometimes flooded
OB – Ombrotrophic bogs	–	*Sphagnum fuscum* *Sphagnum magellanicum* *Ledum palustre* *Calluna vulgaris*	Peat, permanent saturation by precipitation water

Table 2. Mean species richness values for eleven moist forest and mire types. Abbreviations for the community type are given in Table 1. Stand size is 1 ha. Mean richness per stand is given with 95% confidence limits.

Community type	BF	NF	FF	BPF	PPF	EMSF	ESF	TBF	DPF	TM	OB
Area in Estonia (ha, ×1000)	222	182	*	444	81	101	20	141	182	10	165
Number of stands described	15	18	30	48	17	33	54	35	45	20	23
Bryophytes											
Regional species pool	88	156	90	143	112	59	95	70	68	49	48
No. of rare species in regional pool	13	32	3	28	21	3	7	9	8	5	13
Species richness per stand	10.7	14.3	9.2	10.9	8.9	5.0	13.3	7.5	10.8	5.1	6.7
	±2.5	±2.3	±2.0	±1.5	±2.1	±0.9	±1.0	±0.9	±1.1	±1.0	±0.9
Species richness per ten stands	31.3	46.1	36.0	40.2	30.3	19.3	41.3	27.5	33.5	19.6	18.4
Relative richness (%)	35.6	29.6	40.0	28.1	27.1	32.7	43.5	39.3	49.3	40.0	38.3
a	10.8	14.7	8.6	8.2	8.3	5.1	13.9	5.9	10.8	3.8	6.8
b	8.9	13.6	11.6	13.9	9.6	5.9	12.0	9.4	9.8	6.7	4.8
No. of stands needed for regional pool without rare species (×1000)	1.4	3.1	0.8	2.1	5.3	5.2	0.5	0.3	1.5	0.4	0.3
Vascular plants											
Regional species pool	210	270	231	263	157	190	248	101	177	110	27
No of rare species in regional pool	67	34	25	33	32	18	27	9	15	10	1
Species richness per stand	14.1	19.3	20.0	19.4	8.6	18.9	22.5	11.3	16.6	9.3	8.2
	±4.7	±3.0	±3.0	±2.0	±2.0	±2.5	±1.6	±1.3	±2.0	±2.6	±0.8
Species richness per ten stands	44.4	71.5	79.9	73.3	33.0	66.7	76.8	39.7	60.5	36.7	16.4
Relative richness (%)	21.1	26.5	34.6	27.9	21.0	35.1	31.0	39.3	34.2	33.4	60.7
a	13.8	17.9	16.9	17.1	7.0	19.7	22.5	12.2	18.2	7.5	9.7
b	13.2	22.7	27.7	24.4	11.3	19.7	23.4	12.0	17.1	12.4	2.8
No of stands needed for regional pool without rare species (×1000)	17.5	14.9	0.9	6.1	35.9	2.3	4.8	0.8	3.8	1.8	0.4

* The area of FF is considered jointly under ESF.

The variables *a* and *b* are from species accumulation curves: richness = $a - b * \ln(\text{stands})$.

The number of stands needed to maintain the regional species pool is calculated as: stands = $\exp((\text{regional species pool} - \text{number of rare species} - a)/b)$.

using literature data about the Estonian flora (Eesti NSV floora 1953–1984; Kuusk 1975; Laasimer et al. 1993; Ingerpuu et al. 1994; Kuusk et al. 1996; Leht 1999), and personal experience.

All bryophyte and vascular plant species were registered in all stands. Some atypical species, not belonging to the species pool of a particular community type, were always found, due to exceptional microhabitats or accidental invasion from neighboring communities. The percentage of atypical species per stand was generally less than 25% for bryophytes and less than 15% for vascular plant species. In the following analyses we considered only those species which were included in the regional species pool. Tree species were omitted from further analysis. All data is available on request from the authors.

Mean species richness per stand was calculated for each community type. Mean cumulative species richness per ten stands was calculated to obtain a larger scale species richness. A bootstrap method was used, where ten stands were selected randomly from the total number of stands of a particular community type. The mean over 100 iteration was calculated.

Relative richness was calculated as the mean richness per 10 stands divided by the regional species pool, multiplied by 100 to obtain percentage.

The minimum number of stands needed for maintenance of the regional species pool for the particular community type was calculated by using the species richness accumulation curves. A similar algorithm as for mean richness per ten stands was used to obtain mean richness from one to the total number of stands for a particular community type. Mean richness per a number of stands was always significantly linearly related to the natural logarithm of the number of stands. Using the linear regression formula, we calculated the exponent for the base of the natural logarithm, and the number of stands needed to reach the regional species pool of typical species. Rare species (less than ten localities known in Estonia, Kukk 1999; Ingerpuu et al. 1994) were excluded from the regional pools, since, for the distribution of rare species, other factors than the number of suitable sites might be more important.

Pearson correlation was used to obtain the relationships between bryophyte and vascular plant regional species pools, mean richnesses per ten stands and mean richnesses per one stand. Pearson correlation was also used to find relationships between bryophyte and vascular plant species richnesses within each community type. Bonferroni correction was considered for these multiple comparisons, where traditional significance level $P = 0.05$ was divided by the total number of comparisons: 11, resulting in the actual level of $P = 0.005$. The sign test was used to check whether there are more positive or negative relationships across the community types, whether the relative richnesses of bryophyte communities and vascular plant communities differ, or whether more stands are needed to preserve the regional species pools for bryophytes or for vascular plant communities.

Results

In total, 196 bryophyte and 301 vascular plant species were recorded from 338 stands. This is approximately one third of the Estonian bryophyte flora and about one fifth of the vascular plant flora. In spite of extensive recording, observed number of rare species was very small (0–4 per vegetation type). Thus, our study cannot give any general suggestions for rare species conservation. The size of the species pool, mean values of species richness per stand and per ten stands, and relative richness are given in Table 2. The largest species pools for both bryophytes and vascular plants were found in the mesic nemoral forest, but the mean vascular plant richness per stand was highest in the eutrophic swamp forests.

The regional species pools of bryophytes and vascular plants were significantly correlated ($r = 0.755$, $P = 0.007$). The richnesses per ten stands were also significantly correlated ($r = 0.707$, $P = 0.015$), but the correlation between mean richnesses per stand was marginally non-significant ($r = 0.585$, $P = 0.058$).

The correlations between the species richnesses of vascular plants and bryophytes were significantly positive in eight community types (Figure 1). However, when Bonferroni correction was used, the relationship remained significant only in poor paludified forest and in drained peatland forest. However, all 11 community types showed a positive relationship between bryophyte and vascular plant species richness per stand, which means overall positive relationship (Sign test, $Z = 3.0$, $P = 0.003$).

The relative richness in both taxonomic groups was lowest in poor paludified forest, and highest in drained peatland forest for bryophytes, and in ombrotrophic bog for vascular plants. The Sign test did not reveal a difference in bryophyte and vascular plant species relative richness ($Z = 1.2$, $P = 0.228$).

The minimum number of stands (of size at least 1 ha) needed to maintain the regional species pools of the studied community types was approximately between 300 and 5300 for bryophytes and between 400 and 35 900 for vascular plants (Table 2). Only in eutrophic-mesotrophic swamp forests was a larger number of sites needed for the bryophyte regional species pool than for the vascular plant species pool. In general, more stands are needed to maintain vascular plant regional species pools (Sign test, $Z = 2.8$, $P = 0.004$).

Discussion

Bryophyte and vascular plant species richnesses were positively related in all studied community types, as also described in a peatland study from North America (Glaser et al. 1990). This means that similar methods can be used to protect the large-scale richness of those two taxonomic groups in moist forests and mires in the boreo-nemoral zone. In our previous study on a grassland, bryophyte richness increased and

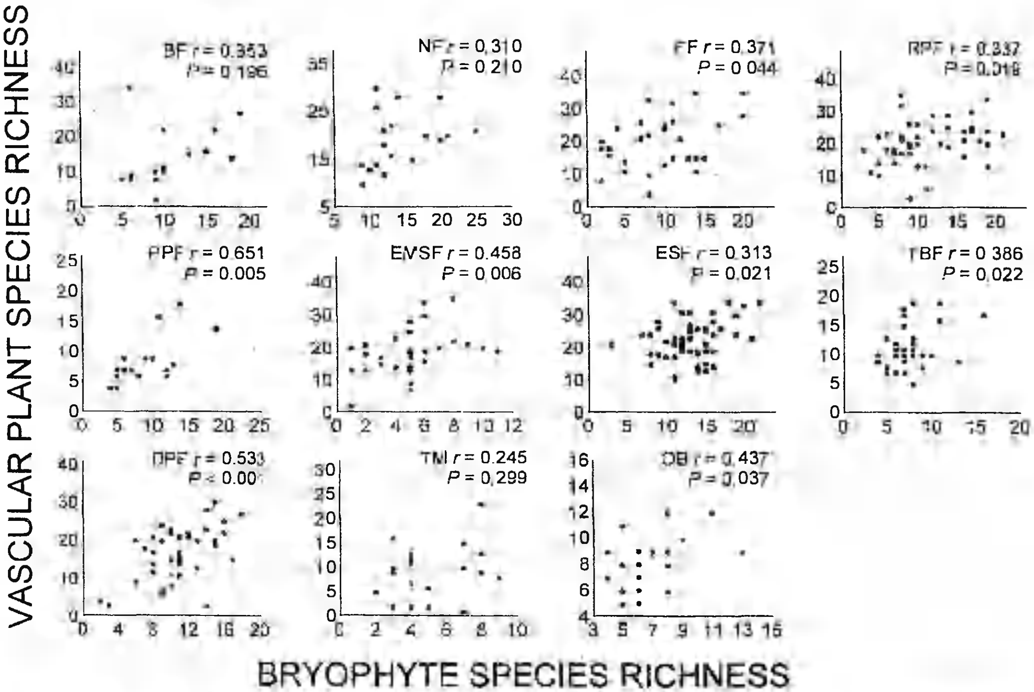

Figure 1. Correlations between bryophyte and vascular plant species richness in 11 forest and mire types. Sample size is 1 ha. Abbreviations of the community types are given in Table 1.

vascular plant richness decreased in a long-term fertilization experiment, suggesting differential behavior between those two taxonomic groups (Ingerpuu et al. 1998). Our present results suggest that the behavior of species diversity of different taxonomic groups is similar in larger scale. The scale both in time and space is an important aspect to consider species diversity relationships (Huston 1999). The importance of scale is corroborated by the fact that the correlation between bryophyte and vascular plant species diversities was strong at the regional species pool level and decreased gradually if richnesses per ten stands, or per one stand was used. Larger scale allows the incorporation of habitats suitable only for bryophytes (tree trunks, stones, shady micro-niches etc.), as well as habitats supporting a great variety of vascular plant species (humus-rich soil areas, forest gaps etc.). Our results expect that bryophyte and vascular plant species preferences in the studied communities are similar along the main environmental gradients, in contradiction to a study from the Canadian arctic (Gould and Walker 1999).

The bryophyte and vascular plant species relative richnesses were not significantly different in most cases, the local richness is rather a constant proportion of the regional species pool for both taxonomic groups. This supports the species pool hypothesis that large-scale richness pattern is primarily determining small-scale richness (Lawton 1996; Pärtel et al. 1996). Similar results were received from an Estonian wooded meadow, where richness per sample plot was 22% of the total bryophyte flora and 25% of the total vascular plant flora of the locality (Ingerpuu et al. 1998). Although the dispersal strategy of bryophytes differs considerably from that of most vascular plant species, the richness patterns seem to be quite similar. High relative richness indicates similarity across stands in one community type (actually, our relative richness is $1/\beta$ diversity, according to Whittaker 1972). Indeed, the ombrotrophic bog with relatively small variation in environmental factors and small regional species pool showed exceptionally high relative richness for vascular plants. In bryophyte communities this relationship is not so clear, which may be explained by a different scale of ecological variability for bryophytes. In the ombrotrophic bog the conditions for vascular plants are evenly nutrition-poor, well illuminated and mostly quite moist; for bryophytes there is a gradient of extremely moist (pools) to dry (higher hummocks, cortex of sparse trees), a gradient of high to low illumination (small cavities in the peat and under the roots) and a gradient of extremely nutrition-poor to nutrient-rich (decomposing higher plants and animal dung). Number of microhabitats has been found to explain a large part of the variation in bryophyte species richness in peatlands (Vitt et al. 1995).

The calculations of minimal standnumber for preserving the regional species pool for different community types showed that less stands are needed to maintain the bryophyte species pools than the vascular plant species pools. This is even the case if the regional species pools of vascular plants are of the same size as those of bryophytes. This indicates that the difference in species composition between stands is much greater in the vascular plant group. In the field we examined stands with an area of approximately 1 ha. However, each described stand represented a much larger forest or mire area, and had probably higher richness than it would be in a stand with the size exactly 1 ha. The effect of total stand size on bryophyte richness on a smaller sample size has been shown on New Zealand forested islands (Tangney et al. 1990). Our estimated number of stands is based on the assumption that no local species extinctions occur. However, this is not likely to be true and to maintain the regional species pool, a larger set of stands is needed to allow persistent metapopulations (Hanski and Gilpin 1997). This means that the number of protected areas we suggest should be scattered and the area needed for conservation is much larger than the area obtained by multiplying the number of stands by 1 ha.

At present, we do not know the exact area of the studied community types that are protected. Anyhow, especial attention should be paid to the rare community types. The rarest of the studied community types in Estonia is floodplain forest. Together with the eutrophic swamp forests they form about 5000 km^2 in Estonia (Lõhmus 1984) and the majority of the territory of these site types should be maintained as nature reserves (Paal 1998).

Rare species have been the first object of conservation biology (Meffe and Carroll 1994), but in recent years the number of species typical for a specific community type has been considered valuable (Sansen and Koedam 1996). Protection of the typical species composition and richness provide a basis for rare species conservation too, which, however, needs additional specific conservation efforts. We did not include rare species in our calculations because very few were actually found during the survey. The occurrence of rare species is influenced by too many different biological and environmental factors that could not be accounted for in the calculations (Ingerpuu and Vellak 1995). Protection of rare species cannot be realized only by protecting a certain number of sites suitable for those species, since it depends on the specificity of distribution, ecology and biology of a species (Giplin and Soulé 1986; Hallingbäck 1995). Bryophyte richness is further influenced by availability of different substrata, which is directly influenced by forest management practice (Vellak and Paal 1999). High habitat specialism is the main reason for herbaceous species rareness in central England (Thompson et al. 1999).

In conclusion, the species richness between bryophytes and vascular plants is positively correlated on larger scales, and conservation of communities rich in species of one plant group maintains also the species richness of the other. Since the relative richness was not different between those taxonomic groups, and local richness tends to be a quite constant proportion of the regional species pool, it is an indication that large-scale richness determines the average richness per one stand. Our calculations for preserving typical species compositions for different forest and mire vegetation types can only serve as additional recommendations for already existing nature conservancy, giving information about the approximate number of sites required for it.

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Bryophyte and phanerogam responses to environmental conditions in primeval deciduous forests at the North-Estonian limestone escarpment

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Abstract. Forests at the base of the North-Estonian limestone escarpment are exceptional in terms of the specific environmental conditions and rich flora there. The total species list in the 23 studied forest fragments consisted of 145 bryophytes and 154 phanerogams. Twenty bryophyte species and three phanerogams were Red-Listed. Bryophytes and phanerogams differed in their diversity and species composition patterns in relation to environmental conditions. Human activity was found to reduce species richness and alter species composition significantly for both bryophytes and phanerogams. Other environmental conditions had significant effects only on bryophytes: higher soil nitrogen content reduced and higher soil water retention increased bryophyte species richness; forest size and distance to the sea influenced bryophyte species composition. Small-scale species richness of bryophytes was further influenced by the type of substrate, being highest on limestone cliffs and lowest on soil. After eliminating the effects of environment, species richness, as well as covers, of soil bryophytes and phanerogams, were found to be negatively correlated. Both bryophyte and phanerogam species compositions, but only phanerogam species richness showed significant spatial autocorrelation. Due to the uniqueness and small area of these forests we recommend protection and restoration of disturbed sites.

Keywords: species richness, human impact, soil, substrata, spatial autocorrelation
Nomenclature: Ingerpuu et al. (1994) for bryophytes, Leht (1999) for phanerogams.
Abbreviations: CCA = Canonical Correspondence Analysis; GLMM = General Linear Mixed Model.

Introduction

Biodiversity studies are among the most serious tasks of contemporary ecological science (Margules & Pressey 2000, Tilman 2000). The diversity of plant species is one of the main factors supporting the diversity of other organisms (Myers *et al.* 2000). Plant diversity is often described in terms of phanerogams alone. Bryophytes also belong to the plant kingdom, and although they inhabit most plant communities, they are often neglected.

Bryophytes differ from phanerogams in regard to a large variety of physiological and life-history parameters; they are evolutionarily older and more widely distributed. As a rule, phanerogams grow on soil, but bryophytes inhabit several substrata. Bryophytes and phanerogams have a different function in ecosystems and they support different heterotrophic species (Schofield 1992). Therefore, the diversity patterns of these plant groups may differ significantly. Some studies have found correlation between bryophyte and phanerogam diversities (e.g. Slack 1977, Glaser *et al* 1990, Fensham & Streimann 1997, Ingerpuu *et al.* 2001) while others have failed (e.g. McCune & Antons 1981, Ewald 2000). In order to know if and when phanerogam diversity can be used as a surrogate for bryophyte diversity (Pharo *et al.* 2000), more detailed studies on those diversities are needed. If there are fundamental differences in the bryophyte and phanerogam diversities, both should be taken into account in the community protection.

Plant diversity patterns may be determined by differences in the ecological requirements of species in the regional species pools (i.e., the potential set of species for a habitat). This, in turn, is defined by evolutionary and historical processes for each region (Pärtel *et al.* 1996, Zobel 1997). Bryophyte and phanerogam diversity has been found to be differently related to environmental gradients in several studies (Gould & Walker 1999, Pausas 1994, Ingerpuu *et al.* 1998). In contrast, Ferris *et al.* (2000) found that diversities of both plant groups were similarly negatively related to soil nitrogen in British planted forests.

In addition to large-scale processes, biotic interactions can influence richness patterns (Huston 1999, Pärtel *et al.* 2000). Although it is expected that phanerogams have an asymmetrically stronger effect on small bryophytes, creating a shaded environment for them (Fitter 1987), bryophyte cover can still both inhibit or facilitate the regeneration of different vascular plants (Hein 1966, Zamfir 2000). The direct effect of biotic interactions should be studied at a scale relevant to plants (Huston 1999, Pärtel et al. 2000). Biotic interactions among bryophyte species and among phanerogam species can be estimated by analyzing relationships between their biomass (or cover) and richness. Dominance and competition should decrease richness at high levels of cover (Grime 1979, Grace 1999).

Furthermore, the diversity patterns can be influenced by human activity. Ewald (2000) pointed out, that correlations between the species richness of different forest layers has been found more often in natural vegetation than in habitats with long-lasting human impact. For example, in secondary Dutch forests, bryophyte and phanerogam diversity patterns had little in common (Dirkse & Martakis 1998), but in Estonian unmanaged moist forests and wetlands we found positive correlation between the richness of bryophytes and phanerogams (Ingerpuu *et al.* 2002). Human disturbance can influence bryophytes and phanerogams differently. Ewald (2000) found that the silvicultural practice of replacing natural *Fagus sylvatica* forest with more profitable *Picea abies* stands had no influence on phanerogams, but increased bryophyte diversity.

Besides changing ecosystem parameters *in situ*, human influence also results in community fragmentation (Dzwonko & Loster 1989, Grashof-Boktam 1997, Bruun 2000). Studies from naturally fragmented communities help to predict the effect of human induced fragmentation (Haig *et al.* 2000). Fragmentation leads both to reduced habitat size and increased isolation. Bryophytes are often dispersed by small spores, while most phanerogams have much larger diaspores, ferns and orchids being exceptions. Pharo *et al.* (1999) found that bryophyte richness in an Australian forest was correlated with fern richness and not with seed plant richness, suggesting that dispersal may influence richness pattern. Although bryophytes are expected to be easily dispersed, Tangney *et al.* (1990) described positive effect of island size and negative effect of isolation for bryophyte diversity on lake islands in New Zealand. Thus, the effect of dispersal distance should not be neglected when studying bryophytes. The effect of isolation is reflected by the degree of spatial autocorrelation — sites closer to each other are more similar in species composition and richness than distant sites (Legendre 1993, Koenig 1999). If there were differences in the degree of spatial autocorrelation for bryophytes and vascular plants, it would indicate that dispersal differences may be important for the diversity pattern, too.

The proportions of bryophytes and phanerogams in plant communities vary. Often bryophytes form the minor part; exceptions are peatlands and boreal forest communities with very few phanerogams (Pharo & Vitt 2000, Ingerpuu *et al.* 2002). In the temperate region, old broad-leaved forests are characterized by both high bryophyte and phanerogam diversity (Kalda 1960, 1981, Sjögren 1964, 1971, 1995, Diekmann 1999).

In this paper we analyse bryophyte and phanerogam species diversitiy and composition patterns in the primary broad-leaved nemoral forests at the base of the North-Estonian Klint. Our aims were 1) to check whether environmental conditions influence bryophyte and phanerogam species richness and composition similarly, 2) to test whether the bryophyte and phanerogam species richness and cover are correlated, 3) to test whether the degree of spatial autocorrelation of species richness and composition is similar for bryophytes and phanerogams.

Material and methods

North-European broad-leaved forest

Broad-leaved forests are rare in Northern Europe, and their area has decreased considerably during the last centuries (Laasimer 1965, Diekmann 1994, 1999). This forest type is considered to be very valuable from the nature-conservation point of view and is listed as a priority habitat type in the Habitat Directive of the European Union. In Estonia, broad-leaved forests are on the northern limit of their distribution area and they constitute just 0.6% (8000 ha) of the whole forest area in Estonia (Kalda 1962, 1995). The majority of the broad-leaved forests were cut during the last two centuries (Laasimer 1965). The present stands have developed through the selective cutting of coniferous trees and the overgrowing of grasslands. A specific type of Estonian broad-leaved nemoral forest grows in narrow strips at the base of limestone cliffs along the northern coastline of Estonia, where the North-Estonian plain suddenly ends with a steep escarpment — the North-Estonian Klint.

The North-Estonian Klint is fragmented and stretches for more than 200 km (Fig. 1). The height of the escarpment varies between 24 and 67 m over sea level, being lower in the west and higher in the east. The upper part of the escarpment is almost vertical and exposes the layers of calcareous rocks from the Ordovicium. The lower layers consist of clays, silts, sandstones and argillites from the Cambrium and Ordovicium (Miidel 1997). The base of the escarpment is a slope formed of rocky debris which is more or less covered by soil. The distance from the sea is different for different parts of the escarpment. In some places it falls straight into the sea, in other places it may be up to 6 km away. In contrast to other locations, forests at the base of the escarpment are mostly primary; in the majority of cases their management has been too difficult since they lie on a slope between a steep cliff and the sea (Kalda 1962). In addition, closeness to sea and shelter from the escarpment creates a unique microclimate, which supports a diverse flora, exceptional for the Nordic biota (Paal 1998). Similar habitats have been described from Ontario, Canada along the Niagara Escarpment (Larson *et al.* 1989).

Study sites and data collection

Estonia belongs to the boreo-nemoral vegetation zone (Sjörs 1965). The mean temperature on the North-Estonian coast is –5°C in January and +16.5°C in July, the mean annual precipitation is 650 mm (Jaagus 1999).

The escarpment base forest was analyzed along all of its 200 km length in 217 randomly placed, 1x1 m plots from 23 forest fragments, 9–10 plots per fragment (Fig. 1) in the summer of 1999. Bryophyte and phanerogam species were recorded from each plot and species richness was calculated separately for bryophytes and phanerogams. In the following, we shall use the term ‘herb’ for the phanerogams in the field layer. If not specified differently, by ‘species richness’ we mean the number of species per 1 m^2 plot. Total bryophyte and herb coverage was determined for each plot. To study bryophyte small-scale richness on different substrates, randomly placed 125 plots of 20×20 cm were analyzed on soil, treetrunks, logs, sandstone rocks and limestone rocks. The smaller plot size was due to the small size of some substrates. All these plots lacked herbs. From each forest fragment the size and composition of the community species pool was determined for bryophytes, herbs and trees from an area of approximately 0.1 ha, surrounding the 1×1 m plots. ‘Species pool’ is used for community species pool in the following text (Pärtel & Zobel 1999).

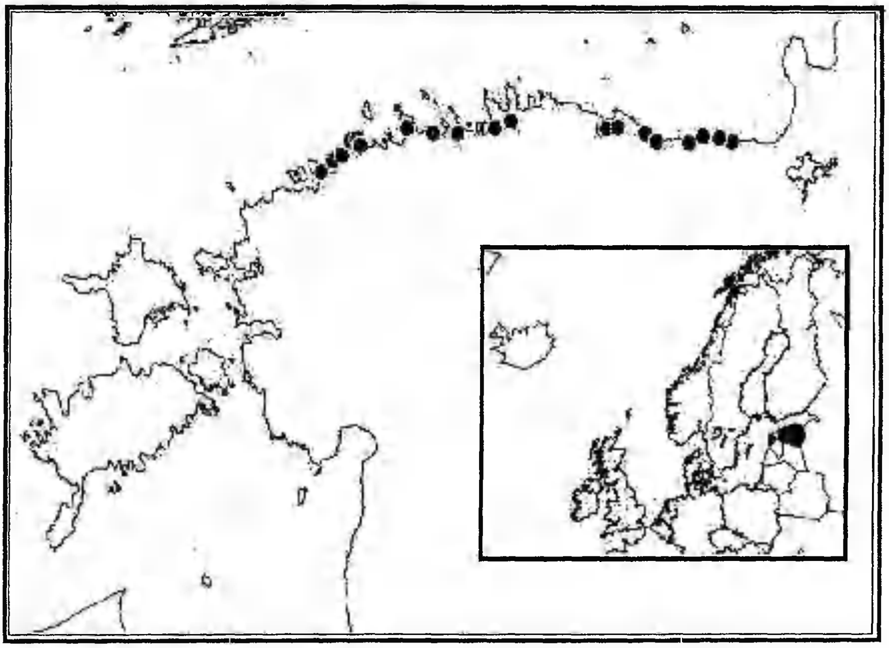

Figure 1. Locations of the studied forests along the North-Estonian Klint.

From each forest fragment, two soil samples were taken so that half of the vegetation plots were closer to the first soil sample and the other half to the second soil sample. Soil pH was determined in water solution potentiometrically (pH-meter Jenway 3071), nitrogen content was analyzed according to the Kjeldahl volumetric method (Ranst *et al.*, 1999), and determination of soil specific surface (m^2/g), followed Puri and Murari (Kitse & Rooma, 1984). All analyses were made on the basis of the fine fraction of the soil (particles < 2 mm). Soil pH often influences the species composition and richness in Europe for both phanerogams (Grubb 1987) and bryophytes (Pausas 1994), nitrogen is one of the main plant nutrition elements in the soil and soil specific surface area is related to the soil water retention capacity (Kitse 1978).

The length of the forest fragment (>10 km / 5–10 km / <5 km) and its distance from the sea (<1 km / greater) was determined on a map (1:150,000). The presence of human impact was determined for each forest fragment. Human influence meant mainly that much waste (including sometimes also chemicals) had been thrown down the cliff, in such places there were also often several pathways or traces of tree felling.

Data analysis

Total species lists of bryophytes and herbs for all examined forest fragments were compiled and Red Data Book species (Lilleleht 1998) were outlined. Bryophyte species substrate affiliations were determined using the General Linear Mixed Model (GLMM, proc mixed, SAS ver 6.12, SAS Institute Inc. 1992), where forest fragments were considered as random factors.

GLMM with repeated design was built to compare the effect of biotic and environmental conditions (bryophyte and herb cover, soil parameters, forest fragment length, distance to sea, and human influence) on bryophyte and herb species richness. Species richness estimates for bryophytes and herbs were treated as repeated measurements within the plot (defined as variable 'Layer'). Significance of the variable 'Layer' in the performed GLMM's indicates differences between bryophyte and herb richness. Forest fragments and soil sampling locations within fragments were considered as random factors. Polynomial relationships between species richness and cover for both bryophytes and herbs were added based on a preliminary graphical data survey where the "hump-back" relationship between cover and species richness was evident (Fig. 2). If interaction between an independent parameter and 'Layer' was significant, it meant that bryophyte and herb richness was differently related to the independent parameter, and regression slopes with their significance were presented separately for bryophytes and herbs.

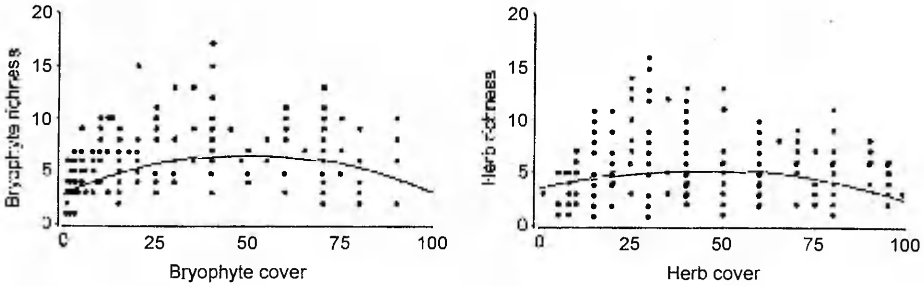

Figure 2. The relationship between species richness and cover.

The relation between the species pool composition (on 0.1 ha plots) and environmental conditions was studied separately for bryophytes and herbs using CCA in the CANOCO 4.0 program (ter Braak and Šmilauer 1998). Monte Carlo permutation tests (n=2000) were used to estimate the significances of the environmental conditions.

The covariance structure of the GLMM was used to estimate correlation between bryophyte and herb species richness or cover. The significance of the correlation was tested with the Likelihood Ratio Test comparing difference in –2log-likelihood of GLMM models with and without covariance structure. The correlation between bryophyte, herb, and tree species pool sizes was estimated from the covariance structure between layers within GLMM models, using 23 fragments as replicates. Environmental conditions were considered as factors in each of these models, in order to consider environmental variation between sites.

In order to compare bryophyte and herb cover on plots, similar repeated design GLMM analysis was used with cover as an independent variable. The significance of the factor 'Layer' indicates a difference in bryophyte and herb cover. Bryophyte and herb species pool sizes were compared by the t-test for dependent samples.

The degree of spatial autocorrelation for mean species richness and species pool composition was measured using a Mantel type of test (Legendre 1993, Pärtel *et al.* 2001). All combinations of forest fragment pairs from a total of 23 fragments were established (253 combinations). Geographical distance between fragments in a pair was defined by rank order of fragments along the North Estonian escarpment. Difference in mean species richness between fragments in a pair was calculated as the larger value minus the smaller. Floristic similarity between fragments in a pair was calculated by Jaccard's similarity index (number of common species from two fragments divided by the number of all species in those fragments). Correlation coefficients were calculated between geographical distance and difference in species richness, or between geographical distance and floristic similarity, using all pairs. Significance was calculated by a randomization process where the geographical distance of the 253 pairs was randomly ordered and then correlation calculated. This process was iterated 5000 times. The P value was the proportion of iterations where the calculated correlation was more negative than the correlation from empirical data.

Results

Altogether, 145 bryophyte species and 154 herb species were recorded in the broad-leaved forests of the North-Estonian Klint. Dominant trees were *Ulmus glabra, Fraxinus excelsior, Acer platanoides, Tilia cordata,* in fewer cases *Alnus incana, Betula pendula* or *Picea abies*. Dominant herb species were *Aegopodium podagraria, Matteuccia struthiopteris, Lunaria rediviva, Mercurialis perennis, Galeobdolon luteum* and *Urtica dioica* and dominant bryophytes were *Brachythecium rutabulum, Eurhynchium hians, Anomodon longifolius, Eurhynchium angustirete* and *Rhytidiadelphus triquetrus.* Twenty Red-Listed bryophyte species, but only three Red-Listed herbs (Lilleleht 1998) were found in study areas (Table 2). Most of the Red-Listed bryophytes were found growing on cliffs (both lime- and sandstone).

Table 1. Community species pool sizes, mean species richness per 1 m², cover and soil parameters in 23 forest fragments

	Mean	(Range)
Bryophyte species pool size	18.9	(4–33)
Herb species pool size	18.4	(6–28)
Tree species pool size	5.7	(2–9)
Bryophyte species richness	5.7	(1.3–11.6)
Herb species richness	5.6	(2.4–12)
Bryophyte cover (%)	22.7	(0.1–61.0)
Herb cover (%)	43	(20–79)
Soil pH	7.0	(5.1–7.7)
Soil N %	0.7	(0.17–1.7)
Soil specific surface (m^2/g)	209	(65–480)

Table 2. Red-Listed bryophytes and phanerogams, their growing substrata and percentage of forest fragments where species occurred (out of 23)

Species	Substrates	Occurrence (%)
Bryophytes:		
Fissidens gracilifolius	Limestone	69.6
Fissidens pusillus	Soil	4.4
Gymnostomum aeruginosum	Limestone	4.4
Gyroweisia tenuis	Limestone	8.7
Jungermannia confertissima	Sandstone	4.4
Jungermannia hyalina	Sandstone, clay	8.7
Jungermannia sphaerocarpa	Sandstone	4.4
Neckera pennata	Treetrunks	21.7
Plagiothecium latebricola	Sandstone	4.4
Platydictya jungermannioides	Limestone	4.4
Porella cordaeana	Limestone, treetrunks	4.4
Rhynchostegium murale	Limestone	26.1
Scapania lingulata	Sandstone	4.4
Scapania mucronata	Sandstone	4.4
Seligeria calcarea	Limestone	4.4
Seligeria donniana	Limestone	4.4
Seligeria pusilla	Limestone	34.8
Thamnobryum alopecurum	Soil	4.4
Timmia bavarica	Sandstone, limestone	17.4
Timmia megapolitana	Sandstone	4.4
Phanerogams:		
Allium ursinum	Soil	4.4
Asplenium trichomanes	Limestone cliff crevices	4.4
Lunaria rediviva	Soil	34.8

The bryophyte species were differently distributed according to their substrate affiliation: 42.1% (61 species) of bryophytes were found on soil, 17.2% (25) on tree trunks, 22.1% (32) on rocks, 4.8% (7) on decaying wood, 4.8% (7) on tree trunks and rocks, 4.1% (6) on soil and rocks, 3.5% (5) on soil and on tree trunks, 1.4% (2) on tree trunks and decaying wood. Bryophyte species richness per 0.04 m^2 plots differed significantly between substrates ($F_{4, 106} = 2.8$, $P = 0.031$). The most species-rich substrate for this community was limestone cliffs (mean 4.1), the most species-poor was soil (mean 2.6; Fig. 3).

GLMM analysis showed that species richness of both bryophytes and herbs had an unimodal dependence on their cover, with highest richness values at intermediate cover values for the layer (the regression parameters of the second order polynomial had significant negative values, Fig. 2, Table 3). Species richness of both layers was significantly negatively affected by human disturbance. Only bryophyte species richness was significantly negatively influenced by the soil nitrogen content and positively affected by soil specific surface area, while herb species richness showed no significant relationship with soil parameters. We did not find the soil pH, forest fragment size, and site distance from the sea to be significant predictors of bryophyte or herb species richness in the forests studied.

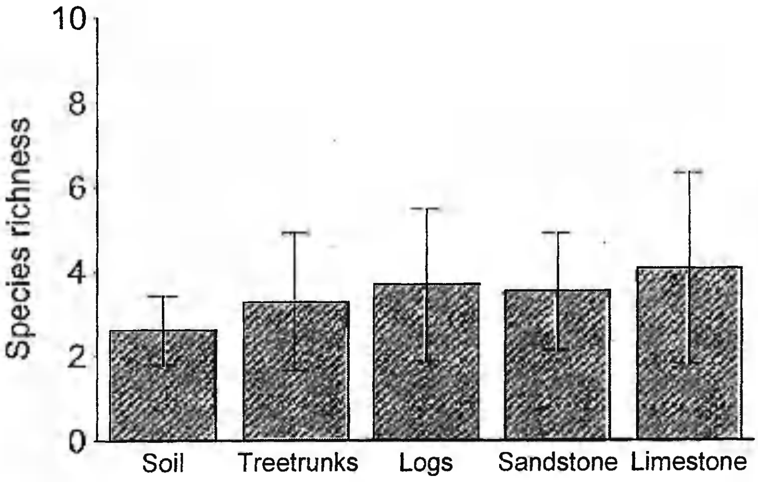

Figure 3. Bryophyte species richness per 20x20 cm plots (mean ±SD) on different substrata in the studied forests.

Table 3. The effect of environmental conditions on the bryophyte and herb species richness (defined as Layer), in GLMM analysis. * $P<0.05$; ** $P<0.01$; *** $P<0.001$

Source	$F_{1,372}$	Regression coefficient (SE)	
		Bryophytes	Herbs
Layer	0.1		
Herb cover	6.3*		
Herb cover × Layer	4.0*	0.0036 (0.0253)	0.0827 (0.0271)**
Herb cover^2	12.5***		
Herb cover^2 × Layer	3.3**	–0.0002 (0.0002)	–0.0009 (0.0003)***
Bryophyte cover	10.7**		
Bryophyte cover × Layer	29.2***	0.1517 (0.0237)***	–0.0421 (0.0253)
Bryophyte cover^2	9.6**		
Bryophyte cover^2 × Layer	18.8***	–0.0015 (0.0003)***	0.0003 (0.0003)
Human impact	13.6***		
Human impact × Layer	4.4*	–1.8882 (0.7843)*	–3.3553 (0.8033)***
Forest size	0.1		
Forest size × Layer	0.2		
Soil pH	2.8		
Soil pH × Layer	0.1		
Soil N	1.4		
Soil N × Layer	9.3**	–4.0467 (1.6206)*	0.6759 (1.6653)
Soil specific surface	1.6		
Soil specific surface × Layer	9.1**	0.0164 (0.0065)*	–0.0017 (0.0067)
Distance to sea	2.0		
Distance to sea × Layer	0.7		

Table 4. Correlations between bryophyte, herb and tree species pool sizes, bryophyte and herb species richness, and cover after removal of the effects of environmental conditions. *** $P<0.001$ of the Likelihood Ratio test (*df*=1)

Comparison	*N*	G^2	*R*
Bryophyte species richness & herb species richness	217	16.5	–0.287***
Bryophyte species pool & herb species pool	23	0.89	0.230
Tree species pool & bryophyte species pool	23	27.4	0.575***
Tree species pool & herb species pool	23	20.3	0.153***
Bryophyte cover & herb cover	217	39.4	–0.444***

Human disturbance altered significantly the species compositions of both plant groups (Table 5). Both bryophyte and herb species compositions were related to their cover, but only the bryophyte composition was additionally related to the distance from the sea and to forest fragment size. The eigenvalues of the first two axes for bryophytes were 0.60 and 0.24, and for herbs 0.54 and 0.41. The cumulative variance of the first four axes of species data for bryophytes was 51%, for herbs 34% and of species-environmental relation for bryophytes 77%, and for herbs 62%.

According to the Likelihood Ratio Test, residuals of bryophyte and herb species richness were significantly negatively correlated (Table 4). For comparison, the simple Pearson correlation coefficient between bryophyte and herb species richness was merely positive (r = 0.128, P = 0.06; Fig. 4) when the significant effect of environmental variation (Table 3) was not taken into account. In contrast, no significant correlation was found between bryophyte and herb species pool sizes. The correlation between bryophyte and herb cover was significantly negative. The tree species pool size was significantly positively correlated with both bryophyte and herb species pool sizes.

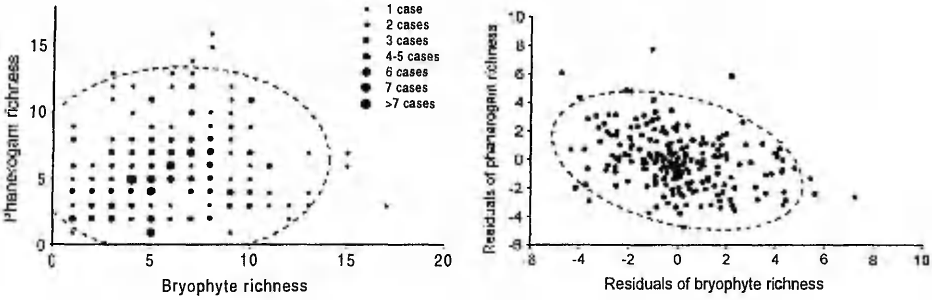

Figure 4. The correlation between bryophyte and herb species richness and between their residuals after the elimination of the influence of environmental factors. Dashed line indicates 95% prediction interval ellipse.

There were no differences between the species richness of bryophytes and herbs ($F_{1,372}$ =0.12, P=0.732), or in their species pool sizes (t=0.2, df=22, P=0.810), but the herb coverage was higher than that of bryophytes ($F_{1,392}$ =12.8, P<0.001, Table 1).

Both bryophyte and herb species pool composition, but only herb species richness showed significant spatial autocorrelation. Species pool sizes for bryophytes or herbs showed no significant spatial autocorrelation (Table 6).

Table 5. The effect of environmental conditions on the species composition of bryophytes and herbs — results of CCA analysis; significance was calculated by Monte Carlo tests.
* P<0.05; ** P<0.01

Variable	Bryophytes		Herbs	
	Eigenvalue	*F*	Eigenvalue	*F*
Herb cover	0.09	1.25	0.26	1.57 *
Bryophyte cover	0.50	5.74**	0.24	1.36
Human impact	0.14	1.88*	0.34	1.90 **
Forest size	0.17	2.1**	0.14	0.89
Soil pH	0.13	1.84	0.21	1.22
Soil N%	0.09	1.47	0.21	1.27
Soil specific area	0.06	0.92	0.21	1.34
Distance to sea	0.20	2.42**	0.17	1.07
Tree species pool	0.06	0.94	0.18	1.09

Table 6. The spatial autocorrelation of bryophyte and herb species richness, species pool sizes and species pool compositions. Pearson correlation between geographical distance of forest fragment and floristic similarity between forest stands (Jaccard), significance is calculated by a Mantel type test. * $P<0.05$; *** $P<0.001$

Parameter	Bryophytes	Herbs
Species richness	–0.06	–0.12*
Species pool size	–0.03	–0.04
Species pool composition	–0.11*	–0.38***

Discussion

Calcareous cliff substrata, shade from the cliff, and proximity of the sea in the primeval deciduous forest at the base of the North-Estonian Klint form an exceptional habitat for the temperate zone, showing similarly high diversity for bryophytes and phanerogams. The number of rare bryophyte species found in this forest type was also high: 14% of the total number of bryophyte species found, while in other forest types it was only up to 5% (Ingerpuu *et al.* 2002). Bryophytes and phanerogams demonstrated remarkable differences in their diversity and species composition responses to environmental conditions. Only human influence (waste depositing, pathways, tree damage) significantly decreased both bryophyte and herb species richness, and altered their species composition. Several other environmental conditions had an effect on bryophytes but not on herbs: soil nitrogen decreased and soil water holding retention increased bryophyte richness; forest size and distance to the sea determined bryophyte species composition. If the effect of environmental conditions was eliminated, significant negative correlation between bryophytes and herbs in richness and cover appeared, suggesting the possible effect of biotic interactions.

Phanerogam richness showed no relationships with any soil factors, but soil nitrogen was negatively, and soil specific surface area was positively related to bryophyte richness (Table 3). A negative relationship between soil nitrogen content and bryophyte richness was also described in British conifer plantations (Ferris *et al.* 2000). In contrast, bryophyte richness increased in a wooded meadow after fertilisation (Ingerpuu et al. 1998), suggesting that this relationship depends on habitat type. Both the effects of large scale processes (different species pools for low and high fertility, Taylor *et al.* 1990) and biotic interactions (e.g., competitive effect from larger phanerogams at high fertility) evidently determine the shape of ‘soil nitrogen — species richness’ relationships. Fewer bryophyte species can survive in dry conditions, which explains why bryophyte richness was positively correlated with soil water holding retention, measured as soil specific surface area. Surprisingly, soil factors had no effect on either bryophyte or phanerogam species composition (Table 5). Bryophyte species composition can, however, still be influenced by air moisture, since forest distance from the sea was significantly related to bryophyte composition. Soil pH in the temperate zone is generally positively correlated with phanerogam richness (Grubb 1987, Pärtel 2000), as well as with bryophyte richness (Glime & Vitt 1987, Pausas 1994, Virtanen et al. 2000). We did not find any effect of soil pH on richness. This is probably due to the limited range of soil pH in the forests investigated. Most of the forests had a high soil pH, while positive correlation between soil pH and richness is more probable at low actual pH values (Pärtel 2000).

The number of tree species was positively related with the size of bryophyte and phanerogam species pools (Table 4). Differences between the throughfall and litter chemistry of tree species are very large (Bergvist & Folkeson 1995, Nordén 1991, 1994). This creates a patchy forest floor, important for rootless bryophytes growing directly on litter and depending on the nutrients in throughfall. A positive relationship between bryophyte and tree species richness has been described by several authors (During & Verschuren 1988, Pharo *et al.* 1999, Weibull 2000), although McCune & Antons (1981) did not find any correlation. Bryophyte richness was additionally influenced by substrate, which can be explained by differences in the durability of substrate and the average size of shoots of the characteristic species on them (Fig. 2). Bryophyte richness was highest on durable limestone cliffs with species characterized by small size; and lowest on soil, where the changing phanerogam growth pattern and falling leaves provide a dynamic environment suitable for larger-sized bryophytes (La Roi & Stringer 1975).

Both bryophyte and herb richness had unimodal relations with their cover (Fig. 3.), richness being highest at intermediate cover values. Cover is related to biomass, and the well-known 'hump-back' biomass-richness curve (Grime 1979, Grace 1999) was found in the case of both plant groups. This is interesting, since clonal bryophyte mats are considered to be ecologically functional units, compared to spatially separated phanerogam ramets (Bates 1998). Lower richness at higher biomass values may be due to several reasons, like more intense competition (Grime 1979), smaller species pool size (Taylor *et al.* 1990), or larger size and consequently smaller number of plant individuals per area (Oksanen 1996) in fertile conditions. Competition among bryophytes has been described on sandstone rocks (Zittová-Kurková 1984). Økland (1994), however, found that interactions between coniferous forest bryophytes were rather facilitative than competitive. If we consider the significant relationships between cover and composition in the case of both bryophytes and herbs in our study (Table 5), we may suggest the effect of species pool differences (there are more species for intermediate fertility), or the species size differences (large species form high cover).

The cover and richness of bryophytes were significantly negatively correlated with that of phanerogams if the influence of environmental conditions was eliminated (Table 4), indicating competition between those plant groups. Biotic interactions are important on scales comparable for plant sizes (Huston 1999). We found insignificant positive relationships between bryophyte and herb community species pool size (Table 4), showing no significant effect of biotic interactions at large scale. Thus, both the species pool effect and the biotic interactions were influencing bryophyte and phanerogam diversity (Pärtel *et al.* 2000). Similar competitive effect from large-sized to small-sized life-form (trees to herbs) has been described from a wooded meadow (Zobel *et al.* 1996). This is one explanation for the variability of results concerning bryophyte and phanerogam diversity relations: in some ecosystems and at larger scales the effect of species pools prevails, in other ecosystems and at smaller scales biotic interactions may be more important.

No effect of forest area on bryophyte or herb richness could be detected (Table 3). There was also no relationship between cliff area and bryophyte richness at Niagara Escarpment in Canada, while cliff area was positively related to phanerogam richness (Haig *et al.* 2000). In contrast, in New Zealand lake-islands bryophyte richness was positively related to island area (Tangney *et al.* 1990), while phanerogam richness had no relationship (Kelly *et al.* 1989). Unlike the findings in Niagara Escarpment cliff communities (Larson *et al.* 1989, Haig *et al.* 2000), our study shows bryophyte species composition to be related to stand size (Table 5). Both bryophyte and phanerogam species pool composition were significantly spatially autocorrelated, but only phanerogam richness showed the same effect (Table 6). Thus, in broad-leaved forests, bryophyte composition may be as vulnerable to habitat isolation as phanerogam composition, being even more related to fragment size.

Presently, only approximately one third of the North-Estonian Klint forests are protected. Human impact in these primeval forests is destructive. The numbers of both bryophytes and phanerogams decreased in influenced sites (Table 3), and their species composition was affected (Table 5). Due to the unique habitat, species composition, primeval state, and small area all these forests must be protected as nature reserves (Laasimer 1981, Paal 1998). Human influence should be excluded totally, and the disturbed sites restored as much as possible.

In summary, the unique set of primeval broad-leaved forests along the North-Estonian Klint revealed significant differences between bryophyte and phanerogam species richness and composition patterns in respect to soil conditions, distance from the sea, and the rate of spatial autocorrelation. The species pool determined local bryophyte and phanerogam community species richness levels and compositions. Biotic interactions were important between bryophytes and phanerogams, which resulted in a negative correlation between the species richness of these plant groups. The strongest effect that decreased richness and changed composition for both bryophytes and phanerogams was still human disturbance.

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Bryophyte vegetation in a wooded meadow: relationships with phanerogam diversity and responses to fertilisation

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Abstract

In the Laelatu wooded meadow in Estonia, famous for its phanerogam diversity, the bryophyte community has been investigated in order to compare its flora and diversity relationships with those of the vascular plant community. Ninety-six bryophyte species were found, 13 of them are hepatics; the majority of the bryophytes are epigeic species common to meadows and forests, including many calciphilous species. Vascular plants and bryophytes display opposite responses to fertilisation. For vascular plants, fertilisation increases the coverage and diminishes the number of species, while for bryophytes it diminishes coverage and increases the number of species. The relationship between the number of species in small plots and the total number of species in the area is similar for vascular plants and bryophytes. No significant changes in the bryophyte community in Laelatu wooded meadow has been detected during the last 30 years.

Nomenclature:
For bryophytes Ingerpuu et al. (1994), for vascular plants Laasimer et al. (1993–97).

Introduction

Areas of exceptional high species richness are interesting from both the theoretical and conservational point of view. Considering the scale-dependence of species richness records (Stoms 1994), it is important to distinguish between species-rich sites of different scale. On a small scale (10 m^2 and less) some particular types of grassland represent the most species-rich vascular plant communities in the world (Sanders 1995). In a very small number of sites, the number of vascular plant species exceeds 60 species per 1 × 1 m plot – among these, published data exist for Strelets meadow steppe in Russia (Afanaseva & Golubev 1962), and for West-Estonian wooded meadows (Kull & Zobel 1991).

We define a wooded meadow as a natural sparse woodland with a regularly mown herb layer. Wooded meadows were typical and traditional in many areas around the Baltic Sea, but have almost all disappeared due to changes in management regimes during the last half century (Hæggström 1983). The remaining few on calcareous soils have been found to have some of the highest known vascular plant species-richness values on the small scale (Kull & Zobel 1991). It is, however, unclear whether the other components of the ecosystem are also rich in species and whether they contain rare species (e.g., Talvi 1995).

Bryophytes constitute a permanent part of the flora of calcareous grasslands. Variations in the species composition of the bryophyte layer are mainly determined by the same factors that influence the vascular plant community – management regime, topography, bedrock (During 1990), but their relationship to the variation in the vascular plant community has still not been explained completely. Herben (1987) has compared fluctuations in bryophyte and phanerogam communities. There are several studies on the influence of the bryophyte layer on the emergence of seedlings (e.g., Tooren 1990; Hein 1966), and on the effect of the density of the vascular plant community or community gaps on bryophytes (Jonsson & Esseen 1990). The influence of differences in the management of vegetation on bryophytes has also been described (Brown 1992; Tooren et al. 1988; During & Tooren 1988). During & Tooren (1990) emphasized the possible importance of the mutualistic relationships between bryophytes and other plants. The relationships between species richnesses are less well studied.

Since the 1950s, vascular plant coverage, productivity, phenology, and seed-bank composition have been studied at Laelatu wooded meadow (Hein 1966; Krall & Pork 1970; Kull & Zobel 1991). However, until now data about bryophytes were rather scarce. In 1962–63 the moss vegetation in some plots on Laelatu meadow was described in connection with an experiment on meadow fertilisation, and changes in the bryophyte community were recorded (Kalda & Kannukene 1966). The aims of the present study are (1) to characterise the bryophyte vegetation in the wooded meadow community richest in vascular plant species at Laelatu, (2) to compare diversity trends in bryophyte and vascular plant communities on fertilised and unfertilised ground, and (3) to see if the bryophyte vegetation of some sample plots has changed since 1963.

Study area

Laelatu wooded meadow is situated in the western part of Estonia, close to the Baltic Sea, between the Mõisa, Kase, and Hein bays, and covers an area of about 100 ha. The meadow had regularly mown for over 300 years, but the mown area has now decreased to only ca 15 ha.

The mean temperature for July is 17.0 °C, and for January –5.0 °C. The mean annual precipitation is 500 mm. The soil is a rendzic leptosol with a pH of 6.7–7.2 (Niinemets & Kull 1997), formed on calcareous silurian bedrock. It is characterized by a thin humus layer (15–20 cm) and is relatively poor in available nutrients (Sepp & Rooma, 1970). Soil moisture content varies, both dry and wet meadow sites are represented.

The tree layer (crown projections) covers 30–50% of the ground in typical sites (more open sites or those which have a more closed canopy also exist) and consists of *Quercus robur, Betula pendula, Betula pubescens, Fraxinus excelsior* a.o. The undergrowth includes *Fraxinus excelsior* and *Populus tremula*, with many species of shrubs (*Corylus avellana, Sorbus aucuparia, Rhamnus cathartica, Viburnum opulus,* a.o.). The field layer is very rich in species, being one of the richest known (at least in temperate Eurasia) at a small scale – the number of vascular plant species on 1 × 1 m plot exceeds 60 (Kull & Zobel 1991), with a recorded maximum of 68 species. There are almost no dominant species. Characteristic species are *Sesleria coerulea, Filipendula hexapetala, Festuca rubra, F. ovina, Carex flacca, Succisa pratensis, Prunella vulgaris, Plantago lanceolata, Convallaria majalis, Centaurea jacea, Cirsium acaule* (Krall & Pork 1970). The vascular plant flora in Laelatu wooded meadow (without adjacent habitats) contains 371 species.

Methods

In 1961, a meadow fertilisation experiment was set up by K. Pork at a typical, quite uniform and relatively dry site in Laelatu wooded meadow. The main experiment used twelve 10 × 30 m permanent plots that are still used for long-term succession research. Nine plots were fertilised during the period 1961–1981. Since 1982, no plots were fertilised. The plots were mown every year in July, and the hay was removed. In the present study, we analysed four of these plots – two fertilised plots F_1 and F_2 (numbers 4 and 11 of the original experiment, which have received 3.5 g m^{-2} nitrogen, 2.6 g m^{-2} phosphorus and 5 g m^{-2} potassium annually), and two controls – C_1 and C_2 (6 and 10, respectively). The plots represent very old wooded meadow vegetation, which has been regularly mown without any great changes during at least the last three centuries. The only difference between the F plots and controls has been the 20 year period of fertilisation. F_1 and C_1 are close together and are 200 m from the other close pair F_2 and C_2. At the end of June 1995, three sample plots (a to c) of 1 × 1 m in each of the larger plots were used for the description of the bryophyte vegetation. The above-ground biomass and the number of vascular plant species were measured from 20 randomly placed 20 × 7.5 cm sample plots within the 10 × 30 m plot. The Student's *t*-test was used for statistical analysis.

Table 1. Bryophytes of Laelatu wooded meadow. The frequency is marked as following: C – common; O – occasional; R – rare; not-marked – recorded only in literature or herbarium data. The pH classes represent the ecological indices by Düll (1991) (1 – pH<4; 3 – pH 4–5; 5 – pH 5–6; 7 – pH 6–6.9; 9 – pH>6.9; 2, 4, 6, and 8 represent intermediate values), and substrata reaction groups by Apinis & Diogucs (1933) and Apinis & Lācis (1936) (I hyperacidophilous, II mesoacidophilous, III acidophilous, IV neutroacidophilous, V neutromesoacidophilous, VI euryionic, VII hypoacidophilous, VIII neutrohypoacidophilous, IX neutrophilous, X meioeuryionic, XI basihypoacidophilous, XII basineutrophilous, XIII basiphilous).

Table 1. Continued

	pH		Frequency
	Alpinis	Düll	
EPIGEIC			
Atrichum undulatum	III	4	
Aulacomnium palustre	VI	3	O
Barbula convoluta	XI	6	R
Barbula unguiculata	XII	7	R
Brachythecium oedipodium	III	3	C
Brachythecium rivulare	XI	5	R
Brachythecium salebrosum	V	5	O
Bryum argenteum	XI	6	R
Bryum caespiticium	V	6	O
Bryum inclinatum	VII	7	R
Bryum pallescens	–	7	R
Bryum pseudotriquetrum	X	7	R
Calliergonella cuspidata	X	7	
Campylium stellatum	XI	7	C
Ceratodon purpureus	VI	–	C
Chiloscyphus pallescens	II	7	O
Cirriphyllum piliferum	X	6	C
Climacium dendroides	X	5	C
Conocephalum conicum	VI, X	7	R
Ctenidium molluscum	XII	8	C
Dicranum polysetum	III	5	C
Dicranum scoparium	III	4	C
Didymodon rigidulus	XII	7	R
Ditrichum flexicaule	XI	9	O
Drepanocladus aduncus	VI	7	O
Drepanocladus cossonii	X	8	C
Drepanocladus lycopodioides	XII	9	
Encalypta vulgaris	XI	8	R
Eurhynchium angustirete	–	7	O
Eurhynchium hians	VIII?	7	O
Eurhynchium praelongum	XI	5	
Fissidens adianthoides	VI, X	5	C
Fissidens taxifolius	XI	7	O
Funaria hygrometrica	X	6	O
Homalothecium lutescens	XI	8	C
Hylocomium splendens	IV	5	C
Lophocolea minor	V	8	
Marchantia polymorpha	VI	5	R
Mnium stellare	X	7	R
Plagiochila asplenioides	IV	6	O
Plagiochila porelloides	–	7	O
Plagiomnium affine	X	5	C
Plagiomnium elatum	–	6	R
Plagiomnium ellipticum	–	3	O
Plagiomnium undulatum	V	6	C
Pleurozium schreberi	IV	2	C
Polytrichum piliferum	III	2	
Ptilidium ciliare	II	2	
Racomitrium canescens	III	6	R
Rhizomnium punctatum	V	4	O
Rhodobryum roseum	II	7	O
Rhytidiadelphus squarrosus	III	5	O
Rhytidiadelphus triquetrus	IV	5	C
Scleropodium purum	III	5	C
Scorpidium scorpioides	XI	9	
Thuidium abietinum	XI	7	O
Thuidium delicatulum	II?	7	C
Thuidium philibertii	X	7	C
Thuidium recognitum	X	6	O
Thuidium tamariscinum	IV	4	
Tomentypnum nitens	X	8	R
Tortula ruralis	X	6	C
Warnstorfia fluitans	III?	1	R
EPILITHIC			
Barbilophozia barbata	III	5	O
Brachythecium populeum	XI	7	O
Dicranum fuscescens	III	2	
Grimmia pulvinata	VIII	7	R

Table 1. Continued

	pH		Frequency
	Alpinis	Düll	
Hedwigia ciliata	II	2	C
Metzgeria furcata	–	6	O
Orthotrichum anomalum	XII	8	R
Orthotrichum rupestre	XI	6	R
Orthotrichum speciosum	II	5	O
Paraleucobryum longifolium	II	1	O
Schistidium apocarpum	X	7	C
EPIPHYTIC			
Amblystegium serpens	XI	6	C
Amblystegium subtile	IX	6	R
Anomodon longifolius	XI	8	R
Antitrichia curtipendula	II,(IV)	6	O
Brachythecium velutinum	V	6	R
Campylium polygamum	XII	4	O
Dicranum montanum	I	2	C
Frullania dilatata	II	5	R
Homalia trichomanoides	VII	7	O
Homalothecium sericeum	XII	7	R
Hypnum pallescens	II?	2	O
Leucodon sciuroides	X	6	C
Plagiothecium laetum	III	2	O
Pseudoleskella nervosa	XII	6	O
Pylaisia polyantha	VIII	7	O
Radula complanata	II	7	R
Sanionia uncinata	V	3	C
EPIXYLIC			
Aulacomnium androgynum	III, IV	2	R
Hypnum cupressiforme	IV	4	C
Lophocolea heterophylla	III	3	O
Pohlia nutans	III	2	R
Ptilidium pulcherrimum	–	2	C

The present list of bryophytes in Laelatu wooded meadow has been compiled from literature (Kalda & Kannukene 1966; Nurk 1983) and the herbarium of the Institute of Zoology and Botany, in addition to the collections of the authors from 1987 and 1995 from the whole area and from the 12 experimental plots described above. Three frequency classes have been used based on the estimations of collectors. The unpublished material of L. Kannukene from 1975 and M. Leis from 1989 has also been used.

Results

The total number of bryophyte species found at Laelatu is 96 (thirteen of which are hepatics); they belong to 30 families and 61 genera (Table 1). The majority of the species (63) are epigeic. According to the existing ecological classifications (Apinis & Diogucs 1933; Apinis & Lācis 1936; Düll 1991), nine calciphilous (seven of them epigeic) and 26 acidophilous (14 of them epigeic) species were found, the other species having a wide amplitude, being either neutral, or lacking precise data. About one third of the species prefer moist habitats (meso-hygro-, hygro- and hydrophytes), and one third prefer dry habitats (xero- and xero-mesophytes), the others are mesophytes or have a wide amplitude (Ingerpuu et al. 1994). Among the epigeic species, the ratio between moisture-preferring species and dry-habitat species is approximately 2:1.

The number of bryophyte species found within the experimental plots (which represent an area of 0.12 ha) in this study was 21, whereas the number of vascular plant species found from the same area was 94.

The number of bryophyte species in previously fertilized (F) plots was considerably higher than in control (C) plots, which is especially noticeable when using the pooled data (Table 2, Table 4).

The difference in bryophyte species richness in the F and C plots is due to the presence of additional species in the F plots. C plots contained only one species which was not present in the F plots whereas 12 species found in the F plots were absent from the C plots (Table 3).

The F plots had more species than the C plots, whereas the opposite was the case for vascular plants (Table 4). The F plots have lower bryophyte cover than the C plots (only in one case did the cover value exceed 55 in the F plots, and only once was it lower than 60 in the C plots), whereas the aboveground biomass and cover of vascular plants is higher in the F than in the C plots.

Discussion

The bryoflora of Laelatu wooded meadow includes many ecologically quite different species. The occurrence of so many species with different ecological requirements can be explained by the existence of

Table 2. Species list and the cover values (%) of sample plots. F – fertilised, C – control plots.

	F_{1a}	F_{1b}	F_{1c}	F_{2a}	F_{2b}	F_{2c}	C_{1a}	C_{1b}	C_{1c}	C_{2a}	C_{2b}	C_{2c}
Amblystegium serpens	1											
Barbula convoluta	+	+										
Barbula unguiculata	+											
Brachythecium salebrosum		1		+								
Bryum sp.	+											
Campylium stellatum						+						
Chiloscyphus pallescens						+						
Cirriphyllum piliferum			+									
Eurhynchium hians		+			+						+	
Fissidens taxifolius	+					+					+	
Hylocomium splendens			10		10		15	25	45	5	10	
Plagiochila asplenioides					+	+		+	+	+	+	
Plagiomnium affine	5		1	1	1							
Plagiomnium undulatum	15	5	5		+	5						
Pleurozium schreberi									5			
Rhodobryum roseum					+							
Rhytidiadelphus squarrosus	5	40	35	+	20		15	5	5			
Rhytidiadelphus triquetrus		5	5	40	10	45	30	15	5	60	55	55
Sanionia uncinata						+						
Scleropodium purum	+	+	5	10	10	10	5	5	+	1	5	5
Thuidium delicatulum				5	+	1						1
Total bryophyte cover	25	50	55	55	50	60	60	50	60	65	70	60
Number of species	9	7	7	6	10	9	4	5	6	4	6	3

Table 3. Comparison of species presence and absence in F (fertilised) and C (control) plots.

	Absent in C		Absent in F	
	Present in F_1 and F_2	Present in F_1 or F_2	Present in C_1 or C_2	Present in C_1 and C_2
Brachythecium salebrosum	+			
Plagiomnium affine	+			
Plagiomnium undulatum	+			
Amblystegium serpens		+		
Barbula convoluta		+		
Barbula unguiculata		+		
Bryum sp.		+		
Campylium stellatum		+		
Chiloscyphus pallescens		+		
Cirriphyllum piliferum		+		
Rhodobryum roseum		+		
Sanionia uncinata		+		
Pleurozium schreberi			+	

various microniches with different moisture and pH conditions at the site. The majority of the species are common epigeic meadow and forest species (Table 1). A large number of species characteristic to moist and paludifying meadows can be found here (*Drepanocladus* spp., *Calliergonella cuspidata*, *Aulacomnium palustre*, *Fissidens adianthoides*, *Tomentypnum nitens*, *Plagiomnium affine*). The occurence of calciphilous

Table 4. Vascular plant and bryophyte community parameters in F (fertilised) and C (control) plots. t – significance of the difference between the paired means of F and C plots ($^{*}P < 0.05$, $^{**}P < 0.01$).

	Parameter	F_1	F_2	C_1	C_2	t
Bryophytes	mean no. of species per sample plot	8	8	5	4	**
	no. of species pooled	14	15	6	7	**
	cover (%)	45	55	55	65	*
Vascular plants	no. of species pooled	46	64	72	68	*
	cover (%)	90	85	65	70	**
	aboveground biomass (g/m^2)	260	180	170	154	**

species is characteristic. There are also many species inhabiting tree trunks. Epixylic species are scarcer due to the lack of suitable substrata (decaying wood, stumps) in the seminatural area. Bryophytes inhabiting stones are represented by a smaller group. According to the List of Estonian Bryophytes (Ingerpuu et al. 1994) the following species found on Laelatu meadow are "relatively rare" in Estonia (up to 20 localities): *Frullania dilatata*, *Mnium stellare*, *Thuidium tamariscinum*, *Campylium polygamum*, *Scleropodium purum*, *Encalypta vulgaris* and *Antitrichia curtipendula*. *Antitrichia curtipendula* and *Aulacomnium androgynum* are distributed only in the western part of Estonia. No "rare" bryophyte species (less than 8 localities in Estonia) were found in Laelatu wooded meadow, although there are a remarkable number of rare vascular plants (Krall & Pork 1970). This could be explained by the absence of some habitats that are suitable for many Estonian rare bryophyte species (shady virgin forests, alvars, spring mires), or in other words, a wooded meadow (despite now being rare itself) does not provide rare microhabitats.

The species composition and density at Laelatu show a similarity to those in similar meadows in Western Europe (e.g., Rijnberk & During 1990). 4–10 bryophyte species were counted in 1 m^2 plots on Laelatu meadow. The number of species counted on several bog plots (4–10 m^2 in size) was 2–19 (Kask 1965). Hence the species richness seems to be higher on meadow plots. It is also higher than in Estonian forests: 2–7 species per 1 m^2 in Vilsandi pine forest (Ratas et al. 1993a). The number of epigeic bryophytes in the decidous forests of Öland on 1 m^2 plots was 4–12 (Sjögren 1964). The Vilsandi alvar meadow has 10–14 species per 1 m^2 plot (Ratas et al. 1993b). The number on species-rich Dutch chalk grasslands, 6–12 species as a mean in 1 × 1 m plots (Tooren et al. 1990; During & Willems 1986), is comparable to the number found in Laelatu meadow. We also noticed the similarity in species composition of Laelatu's bryophyte vegetation to that of Strelets meadow steppe (Utehin 1965).

Models which are developed in order to explain the mechanisms of species co-existence often view a plant community as a closed system in relation to species composition within a time period of about a decade (e.g., Tilman 1988). According to the view of the community as an open system, the absolute number of species in a plot is the result of a balance between immigration from the species pool and extinction. In our study, the number of bryophyte species in the 1 × 1 m plots (for the mean 50% of the plots) has been found to be in the range 23–34% of their number in the whole set of plots (from the 0.12 ha area), the latter representing 22% of the whole list of Laelatu bryophytes. The respective figures for vascular plant species in plots of the same size are 30–50%, and 25%. Consequently, although a tendency towards a higher concentration of phanerogam species in smaller plots could be noticed, we cannot detect any remarkable difference in the relationships of bryophyte and vascular plant communities to their species pools. The species pool as an important factor which determines the small-scale species richness requires much more attention in bryophyte communities. Until now, the relationship between species number in small plots and their species pools has mainly been investigated for vascular plant communities (Pärtel et al. 1996).

A decrease in the moss cover together with an increase in the cover of the herb layer, caused by fertilisation, as shown by our data, is a well known pattern (Mickiewicz 1976; Brown 1982). Our study shows that the number of bryophyte species increases as the abundance decreases. We recorded no bryophyte species specific to calcicolous semi-natural meadow communities with a rich herb layer (cf., Table 3). After the changes in these communities, including diminished bryophyte cover as a result of fertilisation and increased herb biomass (still evident 14 years after the last fertiliser application), a series of new bryophyte species immigrated to the plots.

A possible explanation of these results has been derived from the observation that in both layers (bryophyte and herb communities), more species are found in conditions of lower cover or layer biomass. According to the general unimodal species-biomass curve of Grime (1977), species richness increases with decreasing community biomass, up to the rather low value of community biomass corresponding to the maximum diversity. The opposite behaviour of herb and bryophyte layer biomass should consequently lead to contrariwise trends in species richness, as observed in our experiment. The assumption used in this explanation (the independent behaviour of different layers) is supported by the results of Kull et al. (1995) which showed that different layers are well separated by their nitrogen-use-efficiency (which is considerably higher in bryophytes than in herbs).

A different explanation, partly supporting the previous one, comes from the findings of an experiment which showed that the species richness of bryophyte communities increases as a result of fertiliser application together with complete or partial removal of competing phanerogams (Brown 1982). It means that more species can grow on a more fertile soil if this effect is not suppressed by competition.

A comparison of our recent data with the results of the study made more than 30 years earlier (in 1962–63) of the same plots shows a great similarity and only minor changes in the bryophyte community throughout this period. The overall number of bryophyte species found in 1995 (21) is close to that found in 1962–63 (19) (Kalda & Kannukene 1966) on the same plots. The dominant species, *Rhytidiadelphus triquetrus* and *Scleropodium purum*, are the same as in 1962–63. Some species formerly found were not recorded in the plots in 1995: e.g., *Thuidium philibertii*, *Ctenidium molluscum*, but this may be due to the low frequency of these species. The cover values in 1962–63 for vascular plants (F plots – 80, C plots – 65) and bryophytes (F plots – 35, C plots – 50) are close to those described in 1995 (Table 4). Thus, we could not detect any significant changes in the bryophyte community of this site during the last three decades, in contrast to Dutch chalk grasslands which have been strongly impoverished (Tooren et al. 1990). This is probably due to continued traditional management in Laelatu wooded meadow.

The phanerogam community in Laelatu wooded meadow showed a relatively quick response to fertilisation during the first 5–7 years of the experiment in both biomass and species composition, and a very long reversion time (especially concerning species composition and to a lesser extent biomass) after the cessation of fertilizer application, which has also been demonstrated by similar experiments elsewhere (Olff & Bakker 1991). However, the recovery has been considerably slower in our experiment than that reported in some other studies (Mountford et al. 1996; Willems & Nieuwstadt 1996). Bryophytes also exhibited a quick response to fertilisation (Kalda & Kannukene 1966), and a slow recovery of the bryophyte community composition is implied by the present study.

Tooren et al. (1990) showed in experiments on Dutch chalk grasslands that fertilisation had only a minor effect on bryophytes at moderate fertilization levels. Dirkse & Martakis (1992) described a significant rise in the abundance of several bryophyte species as a result of forest fertilisation. Brown & Bates (1990) reached the conclusion that fertilizer additions often reduce bryophyte biomass by the overgrowth of other plants, but when this problem is avoided, fertilizers frequently fail to change the bryophyte cover.

Several papers show the species specificity of responses to fertilizers (e.g., Mickiewicz 1976; Lambert et al. 1986). The most sensitive appears to be forest species (Kellner & Marshagen 1991; Gerhardt & Kellner 1986). In a forest fertilization experiment, *Hylocomium splendens* and *Pleurozium schreberi* declined strongly at nitrogen doses of over 3 g m^{-2} per year (Dirkse & Martakis 1992). This data fits well with the results of Kalda and Kannukene (1966) who also found that the first species to disappear in response to fertilizing were *Hylocomium splendens* and *Pleurozium schreberi* and the most tolerant species was *Rhytidiadelphus squarrosus*. This tendency corresponds with the results of the present study (Table 2). The preference for more fertile sites may also explain the distribution pattern of *Rhytidiadelphus squarrosus*, which was sparse in the meadow in 1995, growing almost only on the experimental plots, and mainly on the plots previously fertilised.

A problem which should not be overlooked when comparing the dynamics of diversity in vascular plants and bryophytes, is the possible direct interaction between these two plant groups in communities. One aspect of these interactions is the role of bryophytes in phanerogams' recruitment from seed. According to the study by Krall & Pork (1970) from the same Laelatu area, the C plots with more extensive bryophyte cover have a lower seedling frequency than the F plots, but a higher frequency of species having mycotrophic juveniles. This may be a result of shading provided by bryophytes and the chemical compounds derived from them. It has been shown (Tooren 1990; Hein 1966) that mosses may decrease herb germination. Herbs with large and nutrient-rich seeds, as well as bacteriotrophic, mycotrophic or hemiparasitic herbs, are more tolerant to bryophyte cover. In this way, bryophytes could have a certain role in the functioning of the species-rich meadow community. By diminishing the generative reproduction of dominant phanerogam species and increasing a chance for mutualistic relationships (During & Tooren 1990), they could give some less-frequent species a greater opportunity to coexist. However, these effects are probably not very strong, since vegetative reproduction plays a major role in these communities.

Conclusions

The epigeic bryophyte flora on Laelatu wooded meadow is relatively rich in species. It is characterised by the occurrence of several calciphilous species. Vascular plants and bryophytes respond in opposite ways to fertilisation – it increases the coverage and diminishes the number of species in vascular plants, but diminishes coverage and increases the number of species in bryophytes. The relationship between the number of species in a small plot and the number of species in the species pool of the same area is similar for both vascular plants and bryophytes. No significant changes in the bryophyte community could be detected in Laelatu wooded meadow during the last three decades.

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Ingerpuu, N. and Pärtel, M.
Influences of vascular plants on bryophytes:
species-specific effects in a grassland experiment. (Submitted)

Vascular plants species-specific effects on bryophytes in a grassland experiment

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Abstract

In grassland communities vascular plants and bryophytes form two distinct layers. In order to understand the factors responsible for plant community structure, more information about interactions between these plant groups is needed. Here we tested experimentally whether different grassland vascular plant species (*Trifolium pratense, Festuca pratensis, Prunella vulgaris*) had different influences on the cover of two bryophyte species (*Rhytidiadelphus squarrosus, Brachythecium rutabulum*). In a two-year garden pot experiment, bryophytes were planted at a constant density. Some pots were left without vascular plants, in the others vascular plants were planted in four densities, one bryophyte species and one vascular plant species per pot. The absence of vascular plants favoured the growth of bryophyte species, showing the competitive effect of vascular plants. At the same time the cover of both bryophyte species increased with increasing vascular plant cover, showing the facilitative effect of vascular plants. Bryophyte responses to vascular pant species were species-specific. *Festuca* had significantly positive effects on both bryophyte species in the second year, and *Trifolium* on *Brachythecium* in both years, whereas *Prunella* had no significant effect on bryophytes. The competitive effect was constant in time but the facilitation increased in the second year. In summary, both competition and facilitation occur between different grassland layers. The biotic effects between bryophytes and vascular plants are species-specific and they can have a strong influence on the plant community structure.

Key words: bryophytes, competition, facilitation, grassland, vascular plants.

Introduction

Plant communities are driven by both large-scale processes — the species pool effects (Ricklefs 1987, Zobel 1992, Pärtel *et al.* 1996), and small-scale processes — biotic interactions (Tilman and Pacala 1993, Brown *et al.* 2001). The relative importance of these aspects depends on the abiotic conditions, e.g. the species pool effect is more important in unproductive habitats and competition is more important in productive habitats (Huston 1999, Pärtel *et al.* 2000, Foster 2001).

Biotic interactions include both negative and positive effects, which often act simultaneously (Callaway and Walker 1997, Brooker and Callaghan 1998, Pugnaire and Luque 2001). The role of competition has been emphasised in several species coexistence theories, but facilitation has been found to be important more recently (Callaway 1995, Stachowicz 2001, Callaway *et al.* 2002). Biotic interactions are important for determining plant community structure, e.g., presence of distinct layers. For example, tree establishment in prairies is facilitated by the shrub layer (Li and Wilson 1998), and woody species are excluded from prairies through intense root competition from grasses (Pärtel and Wilson 2002).

Compared to interactions between tree, shrub and field layers, bryophyte interactions with vascular plants have been studied less. Most of these studies consider bryophytes on the forest floor. For example, bryophyte species composition differed between coniferous and hardwood forests in Northern America (Rambo and Muir 1998), and epilithic bryophyte composition in Scandinavia differed under a variety of tree species (Weibull 2001). In contrast, under predominately coniferous forests, no correlation between tree and bryophyte species compositions has been found (McCune and Antos 1981, Pharo and Vitt 2000). Due to large differences in size and longevity, trees affect bryophytes mostly through the "engineering" of abiotic conditions: light, temperature, moisture, nutrient status and other chemical properties of substrates (Jones *et al.* 1997).

Bryophytes also form a distinct layer in grassland communities under herbaceous vascular plants. There are very few investigations where the effects of established herbaceous vascular plants on bryophytes have been studied experimentally (Levine 1999). Bryophyte species composition is correlated to the vascular plant species composition in some temperate grasslands (During and Lloret 1996, Zamfir *et al.* 1999, Ejrnæs and Poulsen 2001), but no correlations have been found in other locations (Herben 1987). Biomass of bryophytes and vascular plants, however, has been found to be negatively correlated in most studies (Ingerpuu *et al.* 1998, Zamfir *et al.* 1999, Virtanen *et al.* 2000, Bergamini *et al.* 2001).

Bryophytes' influence on herbaceous vascular plant germination and juvenile survival is mostly negative (Hein 1966, Hörnberg *et al.* 1997, Zamfir 2000). In grassland communities, most of the vascular plants are perennials (Eriksson and Jakobsson 1998) and regeneration from seeds is common only after disturbances (Foster 2001). However, bryophytes have almost no biotic effects on established vascular plants (During and van Tooren 1990), which means that the bryophyte layer in grassland communities may be regulated by vascular plants through their biotic effect. Biotic interactions in ecological communities occur both above and below ground, often giving contrasting effects (Callaway 1997). In the herbaceous vascular plant — bryophyte system, below ground interactions are almost missing, making it more easy to study only the above ground biotic interactions.

Established herbaceous vascular plants can influence bryophytes both negatively and positively. A negative effect is the reduction of light availability. Grassland bryophytes are known to need relatively high light levels (Rincon and Grime 1989). In an Estonian wooded meadow, bryophytes were only common under a sparse upper layer (Kull *et al.* 1995). Another negative effect is competition for space. Perennial vascular plants can easily fill most of the space and bryophytes can only use the remaining space. Positive effects include protection from drought and the provision of nutrients captured through the symbiosis with N-fixing bacteria, or captured from the air (Callaway 1995).

Biotic interactions may be general when the influencing species are determining abiotic conditions making it more suitable for one group of species and less suitable for another group of species (Jones *et al.* 1997). In contrast, biotic interactions may be highly species specific (Callaway 1998). To detect species specificity, experimental work with selected species pairs are needed.

Here we studied how three grassland vascular plant species affect two bryophyte species in a two-year garden experiment. Our null hypothesis was that vascular plant cover has no general or species-specific effect on bryophyte cover, and that this relationship does not vary in time.

Material and methods

We used two bryophyte species common in European grasslands (*Brachythecium rutabulum* (Hedw.) B., S. & G. and *Rhytidiadelphus squarrosus* (Hedw.) Warnst.), and three vascular plant species (a legume — *Trifolium pratense* L., a grass — *Festuca pratensis* Huds. and a forb — *Prunella vulgaris* L.) in a garden pot experiment where a bryophyte species was grown alone or under varying degrees of cover of a vascular plant species for two years (2000–2001). Hereafter species are referred to by genus.

The bryophytes were collected from a natural grassland 30 km south of the experiment garden, air dried, and cut into pieces of 1–2 cm. A constant mass of bryophytes (0.2 g) was planted evenly into pots (21 x 32 cm, 8 cm deep, filled with a low fertility soil — mixture of sieved natural grassland soil and sand), one species per pot. Planting of vegetative parts allows a good establishment of the bryophyte cover (Mulder *et al.* 2001). Five *Brachythecium* and five *Rhytidiadelphus* pots were left without vascular plants (the control group), other pots were planted with the vascular plants, one vascular plant species per pot (the experimental group). The vascular plants were grown from seeds in a greenhouse and planted evenly as two-weeks old juveniles in four densities: 3, 6, 12 and 24 plants in a pot, in order to obtain different degrees of cover. The pots with both bryophyte and vascular plant species had five replicates for each combination (two bryophyte species, and three vascular plant species at four densities). At the beginning of the experiment in May 2000, the cover of bryophytes was 3% and that of vascular plants 0.5–12%.

The pots were kept outside, on the ground and in half-shade in a garden, located at the University of Tartu (58°22' N, 26°44' E). The pots were displaced randomly several times during the summers, watered during longer dry periods and weeded regularly. At the end of the growing seasons the covers of bryophytes and vascular plants were determined in percentages and the vegetation was cut at a height of 1–2 cm to simulate grassland management. The difference of temperature and radiation on moss layer between pots with and without vascular plant cover was measured in the end of the second growing season. The intensity of photosynthetic radiation was measured using Line Quantum Sensor LI-COR. The temperature and radiation under vascular plant cover in experimental pots were lower than in control pots without vascular plants — mean difference, respectively, 3.5°C and 35%. The temperature in moss cover without vascular plants was more than 30°C in sunny days. Vascular plant cover was found to be suitable for further analysis, since it was significantly related to light reduction ($r = 0.188$, $P = 0.044$) and temperature reduction ($r = 0.221$, $P = 0.018$).

In order to analyse the effect of vascular plants on two bryophyte species coverage, a General Linear Mixed Model (GLMM, proc mixed, SAS Institute 1992) was defined. The general effect of the presence of vascular plants was estimated as difference between control group (only bryophytes) and pooled experimental groups (samples with vascular plants present). The factor 'vascular plant presence' was tested in interaction with bryophyte species and repeated factor 'year'. The vascular plant species specific effects on bryophytes' cover was tested within experimental groups (nested into factor 'vascular plants presence'). In the experimental group, regression slopes were calculated between bryophyte and vascular plant covers for each bryophyte species — vascular plant species — and observation year combination.

Results

Bryophyte cover was found to be constant in time (Table 1, Fig. 1). Bryophyte species differed significantly in their cover, *Brachythecium* having twice the cover as *Rhytidiadelphus.* There was a significant interaction between year and bryophyte species, since cover of *Brachythecium* decreased slightly in the second year, but the cover of *Rhytidiadelphus* increased. Vascular plants significantly decreased the cover of both bryophyte species to a similar extent. Vascular plant presence and year had no significant interaction, showing that the effect of vascular plants on bryophytes was consistent in time.

Table 1. The dependence of bryophyte cover on vascular plant cover, year, bryophyte species, vascular plant presence, and vascular plant species (GLMM). Abbrevations: YR — year; BS — bryophyte species; VP — vascular plant presence; VS — vascular plant species; VC — vascular plant cover

Source	Df	F	P
YR	1, 110	1.1	0.292
BS	1, 122	44.1	<0.001
YR*BS	1, 110	8.3	0.005
VP	1, 122	45.3	<0.001
YR*VP	1, 110	0.8	0.381
BS*VP	1, 122	1.0	0.321
YR*BS*VP	1, 110	0.2	0.660
VS (VP)	2, 122	0.5	0.632
YR*VS (VP)	2, 110	1.2	0.305
BS*VS (VP)	2, 122	1.7	0.189
YR*BS*VS (VP)	2, 110	0.3	0.721
VC	1, 110	16.2	<0.001
VC*YR	1, 110	4.7	0.032
VC*BS	1, 110	0.0	0.972
VC*YR*BS	1, 110	0.3	0.561
VC*VS (VP)	2, 110	4.6	0.012
VC*YR*VS (VP)	2, 110	3.0	0.055
VC*BS*VS (VP)	2, 110	6.8	0.002
VC*YR*BS*VS (VP)	2, 110	0.3	0.724

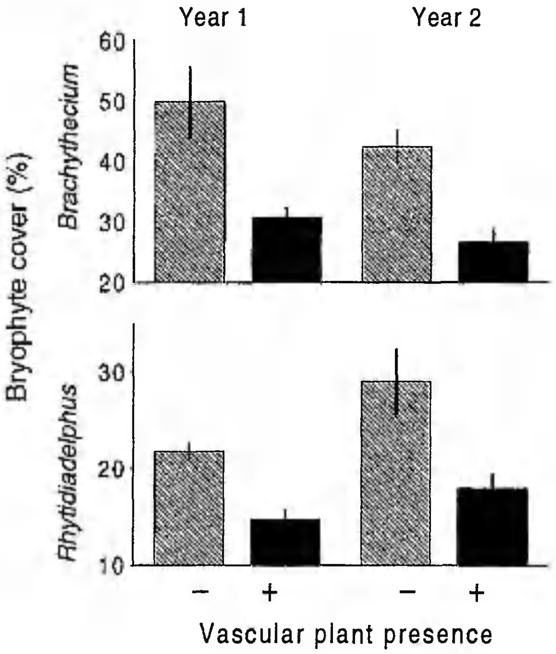

Figure 1. Cover of two bryophyte species at the end of growing season in the control group (without vascular plants) and in the experimental group (with vascular plants) during two years (mean ± SE).

Vascular plant cover in the experimental group, however, was significantly positively correlated with bryophyte cover (Fig. 2). There were significant positive correlations between the cover values of *Brachythecium* and *Trifolium* (both years, Fig. 2a), *Brachythecium* and *Festuca* (second year only, Fig. 2b), and *Rhytidiadelphus* and *Festuca* (second year only, Fig. 2e).

Significant interaction occurred between vascular plant cover and year, showing that in the second year positive influences were stronger than in the first year (Table 1). A significant interaction occurred between vascular plant species and vascular plant cover. *Trifolium* and *Festuca* had positive effects, but *Prunella* showed no such effect. The occurrence of significant interaction between vascular plant cover, vascular plant species and bryophyte species indicates a high species specificity in the biotic effects between vascular and bryophyte species.

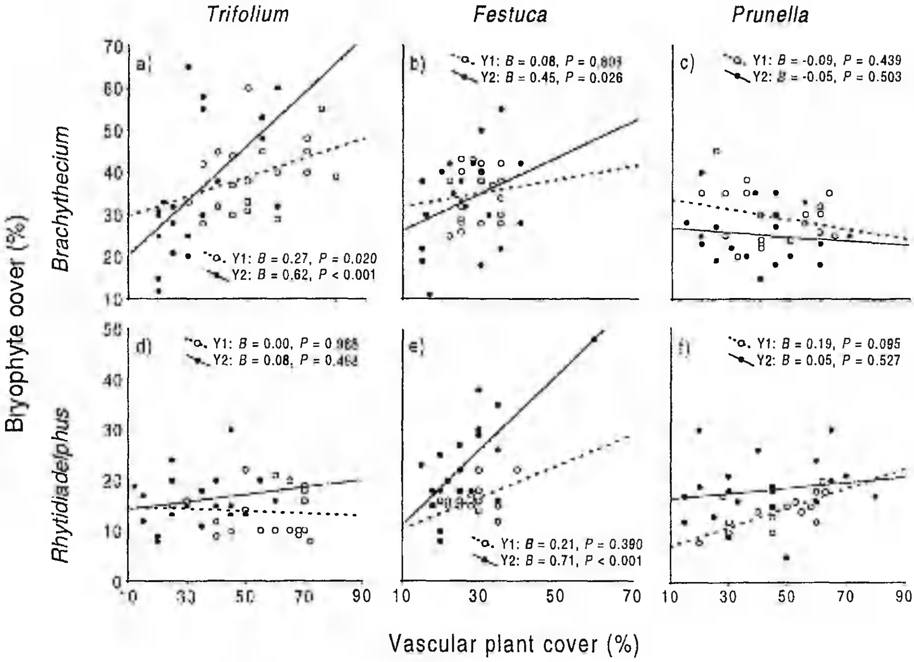

Figure 2. Cover of two bryophyte species in relation to cover of three vascular plant species in the experimental group during two years (Y).

Discussion

Grassland vascular plants had simultaneously occurring competitive and facilitative effects on bryophytes. Bryophyte cover in pots without vascular plants was higher than in pots with vascular plants. Bryophyte cover in pots with varying vascular plant cover, however, was generally positively related to the density of vascular plant cover. Thus, a less dense cover of vascular plants suppresses bryophytes more than a higher cover density, where facilitative effects dominate. The facilitative effects and responses were significantly species-specific.

The study system used is a simplified model of a grassland with different pairs of bryophyte and vascular plant species, giving us an excellent possibility to study species-specific effects. Since the communities were planted, we expect only extremely asymmetric effects from vascular plants to bryophytes (During and van Tooren 1990).

Competition dominated over facilitation, if pots with and without vascular plants were compared (Fig. 1). One reason for this is competition for space. Perennial vascular plants can easily increase their density and bryophytes are able to fill only the space left. *Prunella* was the only species that had no positive effects on bryophytes. Due to its basal leaf rosettes, it fills space more efficiently than the higher *Trifolium* or *Festuca*, which allow bryophytes to grow under the field layer. Another reason is the competition for light. Most of grassland bryophytes require good light conditions (Rincon and Grime

1989, Kull *et al.* 1995). In our study systems, there was 35% less light under vascular plants compared to the control pots with only bryophytes.

Facilitation of bryophytes by vascular plants dominated over competition, when pots with varying vascular plant cover were compared (Fig. 2). Positive effects among different bryophyte species are often described (Økland 1994, Zamfir and Goldberg 2000, Mulder *et al.* 2001). The possible facilitative mechanisms are improvement of moisture and nutrient conditions. Bryophytes absorb water and nutrients using their full shoot surface. That is why the availability of rainwater or dew is often much more important for them than the presence of soil water. Bryophytes are poikilohydric plants and the length of the optimal photosynthesizing period depends on the length of time that the bryophyte mat can retain water (Proctor 1984, Green and Lange 1995). This is favoured by dense bryophyte shoots, but also by a vascular plant canopy over the bryophyte mat, which reduces temperature and thus evaporation, that in turn extends the photosynthesizing time. The lower temperature has a special facilitative effect, while the optimal photosynthesis temperature for many bryophytes has found to be lower than 25°C (Proctor 1982). In our study pots vascular plant cover was significantly related to temperature reduction. Nutrient conditions can be improved by vascular plants by fixing airborne nitrogen in symbiosis with bacteria (Callaway 1995). N-fixing *Trifolium*, however, had no stronger positive effect on bryophytes than *Festuca*, making this explanation less probable. For comparison, in an alpine tundra a *Trifolium* species facilitated forbs and competed against graminoids, resulting in no difference in the total biomass of neighboring plants (Thomas and Bowman 1998). Another way in which vascular plants can improve the nutrient status is the ability to alter the chemical composition of rainwater (Nordén 1991, 1994) that will be washed down to bryophytes, however, further experiments are needed to estimate its importance.

Facilitation has been described mostly from harsh abiotic conditions — arctic-alpine communities (Gold and Bliss 1995, Thomas and Bowman 1998, Kikvidze and Nakhutsrishvili 1998), salt marshes (Bertness and Hacker 1994, Hacker and Gaines 1997), and arid regions (Pugnaire and Luque 2001, Tielborger and Kadmon 2000, Caldwell *et al.* 1998). Vascular plant facilitative effects on bryophytes have been described only very rarely (Sohlberg and Bliss 1984, Levine 2000) and they can be quite complicated, for example, through suppressing a competing plant (Levine 1999). Vascular plant facilitative effects on bryophytes in our experiment indicate that this relationship is probably more widespread than has been described before, but is often obscured by simultaneous competition.

Both bryophyte species responded similarly to the nonspecific competitive effect of vascular plants (Fig. 1), facilitative influences, however, were significantly different among species (Table 1), supporting the idea of species-specific positive interactions (Callaway 1998). The two bryophyte species differ in their growth form: *Brachythecium* is creeping and *Rhytidiadelphus* has upright growth. *Brachythecium* was facilitated more strongly than *Rhytidiadelphus* (Fig. 2). In addition, *Brachythecium* produced plentiful sporophytes during the second year, while *Rhytidiadelphus* remained vegetative (data not shown).

The competitive effect remained constant between years, but the facilitation was significally stronger in the second year (Table 1). Evidently the competitive effect was reduced during late autumn and early spring, when the field layer was not present, but bryophytes were able to grow (Grime *et al.* 1990).

We measured the net effects of both competition and facilitation. Controversial results show that the balance between competition and facilitation varies and that the net effect has a nonlinear nature. We expect that the bryophyte cover in natural meadows will be unimodally related to the overall cover of the vascular plant layer. This kind of relationship has been shown between bryophyte biomass and vascular plant leaf area index in calcareous fens (Bergamini *et al.* 2001). Usually the vascular plant cover is quite high in natural meadows and many studies report the second part of the unimodal relationship, i.e. the negative relationships between vascular plants and bryophytes (Ingerpuu *et al.* 1998, Zamfir *et al.* 1999, Virtanen *et al.* 2000). In our experiment, mean vascular plant covers were relatively low (ca 40%, Fig. 2) and revealed the first facilitative part of the unimodal relationship.

In summary, simultaneously occurring competition and species specific facilitation determine grassland community structures. In the future, experiments are needed to separate the different mechanisms of competition and facilitation.

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Ingerpuu, N. and Pärtel, M.
Bryophyte and vascular plant rarity types in Estonian grasslands.
(Manuscript)

Bryophyte and vascular plant rarity types in Estonian grasslands

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Abstract

The distribution into rarity groups according to Rabinowitz (1981) was not different between bryophyte and vascular plant species of Estonian grasslands. The majority of grassland plants have large regional distribution, but narrow habitat specificity. The differences appeared in the most vulnerable rarity form — small regional distribution, narrow habitat specificity and small populations. The proportion of species included in this form was larger for bryophytes in alvars and meadows and larger for vascular plants in fens. The ecological demands of species with narrow habitat specificity were significantly different between the large-populational and small-populational group. Similarities in the distributions into rarity forms between Estonian grassland plants and British plants were found.

Introduction

The concept of "rarity" does not have a uniform definition. Its meaning depends on the criteria used by a researcher (Kunin and Gaston 1993). Rarity is closely associated with diversity. Usually there is a positive relationship between these two concepts. Different types of rarity arise from high α-, β- and γ-diversity (Cody 1986). According to Cody (1986) high α- diversity may result in a disproportionately high number of rare species, since the resources are divided between a greater number of species. High β-diversity, being itself mainly a result of high habitat heterogeneity, is closely related to a growing number of rare species with narrow habitat specificity. High γ-diversity relies on high number of ecologically equivalent, but geographically isolated species (endemic and vicarious species). All kinds of dispersal barriers may lead to high numbers of rare species. A system that takes all these rarity aspects into account has been worked out by Rabinowitz (1981). This system distinguishes eight forms representing possible causes of rarity of particular species. Species are divided according to their range of geographical distribution (large or small), habitat specificity (wide or narrow), and population size (large or small). Only species with large geographical range, wide habitat specificity and large populations are counted as not-rare species. Very few studies have, however, used this system to analyse what the general pattern of species rarity in a certain area may be (Sætersdal 1994, Blanca *et al.* 1998, Médail & Verlaque 1997, Pitman *et al.* 1999).

We chose species-rich Estonian seminatural grasslands to apply this system for both bryophytes and vascular plants, and see if the results are comparable with other studies. Grasslands are habitats for many rare or protected plant species. The number of rare (less than 25 localities) vascular species that can be found in grassland communities constitutes more than one third of all rare species in Estonia (Kull *et al.* 2002). In particular, grasslands are habitats for about 25% of the vascular plants and about 15% of the bryophytes included in the Red Data Book of Estonia (Lilleleht 1998). By the term "seminatural grasslands" we mean almost treeless sites with spontaneous vegetation, where human management is limited only to mowing or grazing (Krall & Pork 1980). These grasslands are usually less productive, but more species-rich than hay fields that are frequently ploughed, fertilised and sown.

The area of seminatural grasslands has diminished drastically during the last century due to the abandonment of traditional management in Estonia, as well as in the whole of Europe. Seminatural grasslands were very extensive in Estonia untill the 1950. From 1950 to 1975 the majority of Estonian seminatural grasslands were turned into fields or woodland (Pork 1979). From the end of the 20th century a lot of grasslands were abandoned and they began to overgrow with trees and bushes in the course of natural succession. Several grassland communities have become very rare (Paal 1998). More recently, from the end of 1990, the restoration of seminatural grasslands has begun, first as voluntary rescue, and later also as a state program.

Three grassland types (alvars, meso-eutrophic meadows and spring fens) were chosen for the study due to their high species-richness and due to the ever growing threat that these communities will become very rare or even extinct in Estonia. All these grassland types are characterized by high soil pH; grasslands on acid soils have in most cases been influenced by fertilisation (Pärtel *et al.* 1996) and are not appropriate for high biodiversity studies.

The aims for the study were:

1. To establish the distribution of grassland vascular plant and bryophyte species among the rarity forms defined by Rabinowitz (1981).
2. To test whether the pattern of rarity forms differs between vascular plants and bryophytes, between different grassland types and between Estonian grasslands and analogous areas in other regions.
3. To test how the rarity forms are related to each other.
4. To search for possible reasons for the species rarity in different community types.

Material and methods

We chose three species-rich calcareous seminatural grassland types, which represent different positions along the moisture gradient: alvar grasslands on dry mineral soil, meso-eutrophic meadows on fresh mineral soil, and spring fens on wet peaty soil. The mean pH was 6.8 in alvars, 6.5 in meso-eutrophic meadows and 7.4 in spring fens (measurements of soil water solution at every study site).

The alvar grasslands are found only in the northern and western part of Estonia and on the western islands. Our study sites were located on the two largest islands — Saaremaa and Muhu. Meso-eutrophic meadows and spring fens are distributed sparsely all over Estonia. The study sites were situated in the southern part of Estonia.

Ten sites from each grassland type were analysed. At each site, five sample plots of an area of 1 m^2 were described. The species lists were compiled and covers estimated, separately for bryophyte and vascular plant layers.

Pearson correlations were used to study the relationship between the species-richnesses and covers. In order to classify species into certain rarity forms according to Rabinowitz (1981), the decision on classification into large or small geographical range was made on the basis of the distribution types in the regional species pool (Kukk 1999, Ingerpuu *et al.* 1994), where the species are divided into seven groups. The five rarer groups were estimated to have "small regional distribution" and the two common groups to have "large regional distribution". Species were defined as with "narrow habitat specificity" when they occurred in only one grassland type of the three, and with "wide habitat specificity" when they occurred in two or three grassland types. Species were classified as small-populational when they occurred only on one or two plots at a site, and as large-populational when they occurred on 3 to 5 plots at a site.

The differences between the distribution of the bryophyte and grass layer species into these rarity forms were estimated with the chi-square and Kolmogorv-Smirnov tests. The differences between the ecological demands of large- and small-populational species with narrow habitat specificity, defined as Ellenberg index values (Ellenberg 1991), were analysed with ANOVA. We compared also the distribution of Estonian grassland vascular plant species among rarity forms of Rabinowitz (1981) with analogous works done in United Kingdom (Rabinowitz *et al.* 1986), France (Médail & Verlaque 1997) and Spain (Blanca *et al.* 1998). The work of Sætersdal (1994) was neglected, because plants only from one forest type were included in this study.

Results

The total number of bryophytes in these grasslands was 83 and the number of vascular plants, 239. The species pool was largest in meso-eutrophic meadows and smallest in the spring fens, both for bryophytes and vascular plants (Table 1).

Table 1. Species pools and covers of vascular plants (Vas) and bryophytes (Bry) in three grassland types

	Alvar		Meso-eutrophic meadow		Spring fen	
	Bry	Vas	Bry	Vas	Bry	Vas
Species pool size	38	99	43	142	33	91
Mean cover per 1 m² (%)	51.8	52.1	46.1	72	82.1	51.1

There was no significant correlation between the species richness of vascular plants and bryophytes across all grassland types nor in separate types, except in fens, where the species richness of sites was significantly positively correlated ($r = 0.67$; $P = 0.033$). The covers of these plant groups were significantly negatively correlated on alvars ($r = -0.45$; $P = 0.001$) and in meadows ($r = -0.48$; $P < 0.001$), while the correlation in fens was non-significant. The correlation between cover and species richness on plots in different grassland types was significantly positive only for vascular plants in fens ($r = 0.375$; $P = 0.007$).

The occurrence of species at different sites showed a similar pattern in all grassland types and among both plant groups — the majority of species occur only at one or a few sites (Fig. 1).

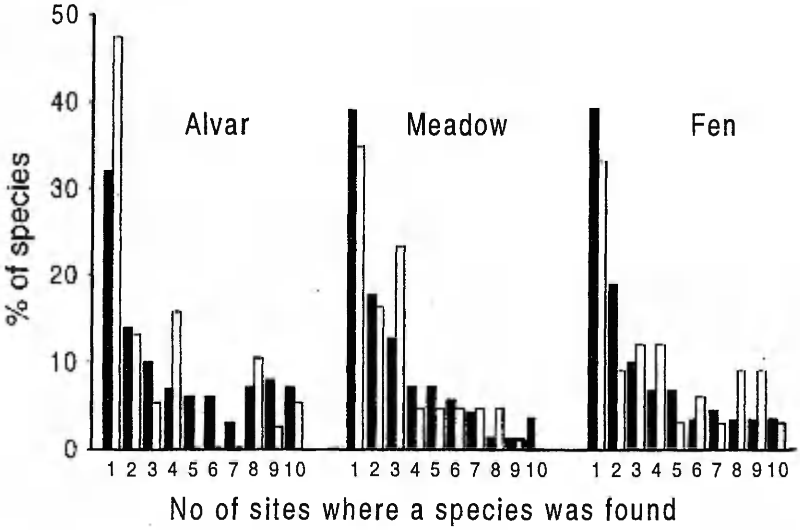

Figure 1. Species occurrence in alvar, meadow and fen grassland sites. White columns bryophytes, black columns — vascular plants

There were less species with a regionally small distribution among all grassland plants (Fig. 2). The proportion of species with a regionally small distribution, in different grassland types, was 23–31% for bryophytes and 13–24% for vascular plants. The majority of grassland plants showed narrow habitat specificity, but the division into small- and large populational groups did not show much difference (Fig. 2). The data for the rarity forms according to Rabinowitz (1981) is presented in Table 2. The distributions of bryophytes and vascular plants among these forms was similar, except in the case of meadows, where it was significantly different ($\chi^2 = 15.08$; df = 7; $P = 0.035$). This was due to the smaller number of species with a regionally large distribution and with large populations and a larger number of species with a regionally small distribution and with small populations among bryophytes. Some significant differences were found in the species distribution among different grassland types. The percentage of vascular plants with narrow habitat specificity was significantly higher in fens (68%) than in meadows (44%) or alvars (36%). The proportion of bryophytes with small populations was much higher in meadows (83%) than in fens (48%). The proportion of species with a regionally small distribution and large populations was similar for bryophytes and vascular plants (varying between 0–14%), except in fens, where it was significantly larger among bryophytes (22%) than among vascular plants (9%). The number of species that are rare according to all three rarity criteria (small regional distribution, narrow habitat specificity and small populations) was much larger for bryophytes than for vascular plants in alvars and meadows, while in fens the opposite was true (Table 2).

The species with a regionally small distribution and narrow habitat specificity are listed in Table 3.

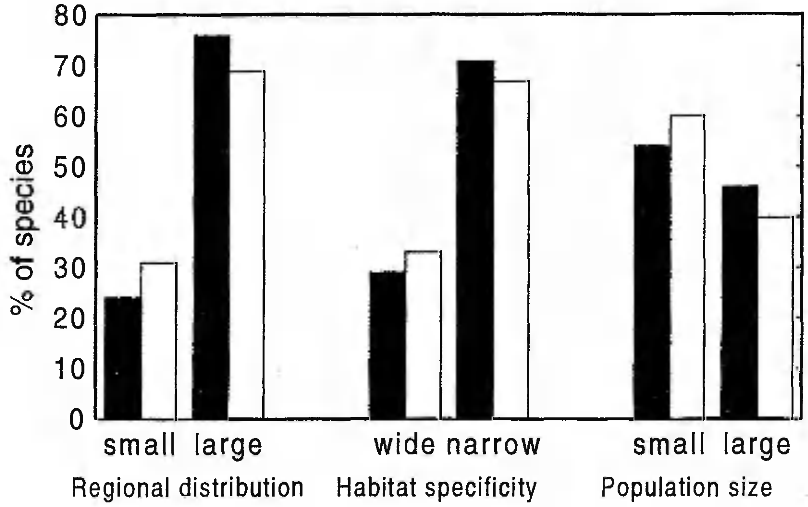

Figure 2. The distribution of all grassland species according to regional distribution, habitat specificity and population size. White columns — bryophytes, black columns — vascular plants

Table 2. The percentage of grassland plant species in different rarity forms

Regional distribution	Large				Small			
Habitat specificity	Wide		Narrow		Wide		Narrow	
Population size	Large	Small	Large	Small	Large	Small	Large	Small
Alvar								
Bryophytes	13	24	16	18	3	5	8	13
Vascular plants	27	28	8	11	4	5	9	7
Meadow								
Bryophytes	10	36	5	26	2	7	0	14
Vascular plants	26	24	11	26	4	2	1	6
Fen								
Bryophytes	12	21	18	18	6	3	15	6
Vascular plants	18	13	21	24	0	1	7	14
All								
Bryophytes	10	14	17	29	4	1	10	16
Vascular plants	19	11	18	29	3	1	7	13

Table 3. Species with a regionally small distribution and narrow habitat specificity in three grassland types. Species that form large populations are given in bold. Nomenclature of bryophytes according to Ingerpuu *et al.* (1994), of vascular plants according to Kukk (1999)

	Bryophyte species	Vascular plant species
Alvar	*Campylium elodes,* ***Encalypta rhaptocarpa,*** *Eurynchium praelongum,* ***Fissidens dubius*** *,* ***Fissidens taxifolius,*** *Lophocolea minor, Pottia bryoides,* ***Scorpidium turgescens,*** *Weissia brachycarpa*	*Arabis hirsuta,* ***Anthyllis vulneraria,*** *Artemisia rupestris,* ***Asperula tinctoria,*** *Carex montana,* ***Carex tomentosa, Carlina vulgaris, Cirsium acaule, Helianthemum nummularia, Herminium monorchis, Plantago maritima, Melampyrum cristatum,*** *Ononis arvensis, Potentilla neumanniana, Rubus caesius, Viola hirta*
Meso-eutrophic meadow	*Cephaloziella hampeana, Chiloscyphus polyanthos, Ditrichum pusillum, Fissidens bryoides, Hypnum lindbergii, Pottia intermedia*	*Botrychium lunaria,* ***Clinopodium vulgare,*** *Jasione montana, Luzula campestris, Melampyrum nemorosum, Polygala vulgaris, Potentilla reptans, Saxifraga granulata, Trifolium aureum, Trifolium hybridum, Vicia angustifolia, Vicia hirsuta,*
Spring fen	***Calliergon stramineum,*** *Cephalozia lunulifolia,* ***Cinclidium stygium, Hamatocaulis vernicosus, Helodium blandowii,*** *Lophozia bantriensis,,* ***Paludella squarrosa***	***Betula humilis, Calla palustris,*** *Cardamine pratense, Carex appropinquata,* ***Carex limosa,*** *Dactylorhiza maculata,* ***Epipactis palustris,*** *Eriophorum latifolium, Impatiens noli-tangere, Liparis loeselii, Lysimachia thyrsiflora, Pedicularis sceptrum-carolinum, Polygonum bistortum, Rumex aquatica, Saxifraga hirculus,* ***Swertia perennis,*** *Trichophorum alpinum,* ***Trichophorum caespitium,*** *Utricularia minor*

The comparison of the ecological demands of large-populational habitat-specific species (species which are well adapted to this grassland type) and small-populational habitat-specific, or habitat-non-specific, species showed significant differences in the majority of cases (Table 4). The differences with the non-specific group were, in the majority of cases larger.

The distribution between eight rarity forms was significantly different between Estonian grassland vascular plants and the selected vascular plants of the United Kingdom, France, and Spain ($\chi^2 > 45.7$; df = 7; $P < 0.0001$). Similarities appeared, if the species were grouped according to the three major rarity criteria. The summarized groups of regional distribution did not differ significantly between the selected groups of British and Estonian plants. Among French and Spanish endemic plants there were significantly less species with a regionally large distribution (Table 5, respectively $\chi^2 = 69.96$; $P < 0.001$ and $\chi^2 = 7.33$; $P = 0.007$). The distribution into habitat specificity groups does not differ significantly between different regions. Differences appear also in the summarized groups of large- and small-populational species. The high proportion of large-populational species in British plants ($\chi^2 = 52.11$; $P< 0.001$) is partly due to the species selection that contained more common plants than the whole flora. The proportion of large-populational species in French endemic vascular plants is the same as in the Estonian grassland plants, while there are much less large-populational plants among Spanish endemic vasular plants ($\chi^2 = 12.83$; $P < 0.001$).

Table 4. The differences in ecological demands between narrow habitat-specificity large-populational (narrow-large), narrow habitat specificity small-populational (narrow-small) and wide habitat specificity small-populational (wide-small) groups. Significance: * $P < 0.05$; ** $P < 0.01$; ***$P < 0.001$. > higher in first group; < lower in first group

	Bryophytes	Vascular plants
Alvars Narrow-large vs. narrow-small	Reaction * >	Nitrogen * <
Narrow-large vs. wide-small	Reaction ** >	Nitrogen * <
Meadows Narrow-large vs. narrow-small	–	–
Narrow-large vs. wide-small	–	Moisture * <
Fens Narrow-large vs. narrow-small	Light * > Temperature ** <	Moisture * >
Narrow-large vs. wide-small	Light *** > Temperature** < Moisture *** >	Moisture *** >

Table 5. Percentage distribution according to regional distribution, habitat specificity, and population size in Estonian grassland, British selected (Rabinowitz *et al.* 1986), southeast French endemic (Médail and Verlaque 1997), and southern Spanish endemic (Blanca *et al.* 1998) vascular plants

Plant groups	Regional distribution		Habitat specificity		Population Size	
	Large	Small	Wide	Narrow	Large	Small
Estonian vascular plants	76	24	41	59	46	54
British vascular plants	85	15	41	59	93	7
French endemic vascular plants	17	83	34.5	65.5	46	54
Spanish endemic vascular plants	58	42	30	70	21.5	78.5

Discussion

According to our study, only about one tenth up to one fourth of the Estonian grassland species (both vascular plants and bryophytes) are not rare in a certain sense according to Rabinowitz (1981), i.e. they belong to the group of species with regionally large distribution, wide habitat specificity, and large-populations. A high proportion of sparsely distributed species in communities have also been found in several other studies (Pärtel *et al.* 2001, Vitt and Belland 1997, Gaston 1994, Jackel and Poschold 1996). Yet the majority of grassland species studied by us are quite common on a larger scale, having a large regional distribution (Fig. 2). Here we come to the paradox that majority of species can be rare sometimes. The decision whether a species is rare depends on the scale of observation. Diminishing of the scale increases the possibility of a species being classified as rare. If we expand the scale, very few species can be classified as rare. This has been shown also in the study of Murray *et al.* (1999), where a careful search in a larger area led to a great decrease in the number of "everywhere-sparse" species. In a world of devastating human impact on nature, it is reasonable to study and protect rarity on smaller scales in order to avoid major fragmentation of habitats and species distribution areas, which could lead to a growing rate of rarity among all species, and on a larger scale. Using rarity forms according to Rabinowitz (1981) makes it possible to look at the problem of rarity in a more general context and to pay attention to all species that can be rare in different ways. Usually species that are more numerous in some habitats, and have large populations somewhere, are neglected in studies concerning species protection. But these might be just the species that are crucial for the resistance of invasive species and for the maintenance of a certain community (Lyons and Schwartz 2001).

It was surprising to find great similarity in the distribution between rarity forms for vascular plants and bryophytes (Table 2). This refers to possible common forces behind the distributional pattern of these two groups of plants. The majority of grassland plants have a large regional distribution, but narrow habitat specificity. Species with narrow habitat specificity tend to form more small populations than species with wide habitat specificity. The greatest differences between bryophyte and grass layer species were found in the group with small regional distribution, narrow habitat specificity and small populations over all grassland types (Table 2). This group consists of the most vulnerable species from the conservational point of view. The proportion of species belonging to this group is higher in the bryophytes of alvars and meadows and in the vascular plants of spring fens. Thus, bryophytes can be more endangered in alvars and meadows and vascular plants in fens. At the same time the greatest number of species with small regional distribution was found among fen bryophytes, but the majority of them form large populations there.

There is a common trend if we compare distribution into rarity forms of British (Rabinowitz *et al.* 1986) and Estonian plants (Table 5). The majority of species are either regionally large-distributional and/or with narrow habitat specificity. Very few plants have small regional distribution, but wide habitat specificity. This number is higher in endemic plants of France (Médail & Verlaque 1997) and Spain (Blanca *et al.* 1998). The number of large-populational species is not lower in the endemic plants of France. The low number of small-populational species among British plants is partly caused by the fact that the proportion of common plants, among those selected for the study, is larger than that in the whole British flora. The method of the evaluation of population size was also different — relying mainly on personal experience. The similarities revealed by our study seem to be valid only among herbaceous vascular plants and bryophytes, or only in temperate regions, since a study of tropical tree species (Pitmann *et al.* 1999) showed a totally different distribution.

Human disturbance is one of the main reasons for rarity among various organisms. But quite a number of species tend to be rare even without any human influence. This may be due to their traits, such as floral longevity (Kunin and Shmida 1997) or low seed production (Jackel and Poschold 1996) in vascular plants and certain type of life history (During 2000) or low sporophyte production (Longton 1992, Laaka-Lindberg *et al.* 2000) in bryophytes. This happens also due to regional distribution history, since species can be relicts from former climatic periods. The comparison of the ecological demands of the species which are well adapted to the community type, forming large populations (core species sensu Hanski (1982) and Pärtel *et al.* (2001)), with the ecological demands of small-populational species, showed several significant differences (Table 4). The ecological conditions that showed a potential limiting effect on small-populational species were different for bryophytes and vascular plants. For example, on alvar grasslands, the small-populational bryophyte species preferred significantly lower pH values, while small-populational vascular plants preferred higher soil nitrogen content. Such differences have been found also in a study of forest vascular plants, where threatened species preferred higher soil pH and nitrogen content than non-threatened species. (Gustafsson 1994). The differences in ecological demands between large-populational and small-populational species refer to the fact that some of the species with narrow habitat specificity, and even more with wide habitat specificity, may be really limited due to their different ecological demands. This was, however, not the case in meadow bryophytes, where presumably other reasons, such as distributional limitations or biotic interactions, play a major role.

In conclusion, the comparison of rarity groups according to Rabinowitz (1981) revealed a common pattern among grass and bryophyte layer species. The reasons for rarity very often lay in the different ecological demands of the species. More studies in different parts of the world and at different scales are needed to find out if the similarity trends found in this study are valid in other conditions, referring that rarity may have similar causes.

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Education

1961–1972	II Secondary School of Tartu
1972–1977	Univerity of Tartu, Faculty of Biology and Geography, botany
1997	M.Sc. in botany, University of Tartu
1997–2002	PhD student at the Institute of Botany and Ecology, University of Tartu

Professional employment

1977–1978	Tallinn Botanical Garden
1979–2002	Institute of Zoology and Botany

Main fields of research

Composition of Estonian bryoflora, species richness of bryophytes in relation to ecological conditions and vascular plants, impact of forest management on bryophyte diversity, rarity of bryophytes.

Membership in scientific organizations

Estonian Naturalists' Society
Editorial Board of "Folia Cryptogamica Estonica"
Expert group of the Estonian Red Data Book
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Teaching

Participated in teaching of the following courses at Tartu University: bryology, field course in floristics, field course in biodiversity.

Publications

Ingerpuu, N. & Vellak, K. 1995. The distribution and some ecological characteristics of Estonian rare bryophytes. —*Arctoa* 5: 143–148.

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Publikatsioonid

Ingerpuu, N. & Vellak, K. 1995. The distribution and some ecological characteristics of Estonian rare bryophytes. — *Arctoa* 5: 143–148.

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