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The effects of stand structure on ground-floor bryophyte assemblages in temperate mixed forests

S. Márialigeti · B. Németh · F. Tinya · P. Ódor

Abstract The effect of tree species composition, stand structure characteristics and substrate availability on ground-floor bryophyte assemblages was studied in mixed deciduous forests of Western Hungary. Species composition, species richness and cover of bryophytes occurring on the soil and logs were analysed as dependent variables. The whole assemblage and functional groups defined on the basis of substrate preference were investigated separately. Substrate availability (open soil, logs) was the most prominent factor in determining species composition, cover and diversity positively, while the litter of deciduous trees had a negative effect on the occurrence of forest floor bryophytes. Besides, bryophyte species richness increased with tree species and stand structural diversity, and for specialist epiphytic and epixylic species log volume was essential. Sapling density and light heterogeneity were influential on bryophyte cover, especially for the dominant terricolous species. Many variables of the forest floor bryophyte community can be estimated efficiently by examining stand structure in the studied region. Selective cutting increasing tree species diversity, stand structural heterogeneity and dead wood volume can maintain higher bryophyte diversity in this region than the shelter-wood system producing even-aged, monodominant, structurally homogenous stands.

Keywords Species composition · Species richness · Diversity · Functional groups · Forest structure

S. Márialigeti · B. Németh · P. Ódor (✉)
Department of Plant Taxonomy and Ecology, Loránd Eötvös University,
Pázmány P. stny. 1/C, 1117 Budapest, Hungary
e-mail: ope@ludens.elte.hu

F. Tinya
Department of Plant Pathology, Corvinus University of Budapest,
Ménesi út 44, 1118 Budapest, Hungary

Introduction

The effect of stand structure and tree species composition on bryophyte assemblages in forests has been studied widely (Rose 1992; Vellak and Ingerpuu 2005; Bardat and Aubert 2007). Assemblages on potential substrates (epixylic, epiphytic, epilithic and terricolous) are considerably different and are also determined by stand characteristics (Smith 1982a; Mills and Macdonald 2004, 2005).

Considering epiphytic bryophytes, Barkman (1958) and Smith (1982b) summarized the effects of major abiotic factors (bark type, light, humidity etc.). At regional level, it was shown that not only the presence of relatively old, closed forests, but also the more open or pioneer patches were important for maintaining the abundance and diversity of the epi- phytic bryophyte community (Vanderporten et al. 2004). Intensive forest management impoverished the epiphytic bryophyte communities all over Europe (Rose 1992). Never- theless, even in the most intensively managed Atlantic regions, forest stand structure remains one of the most important factors determining the bryophyte assemblages (Aude and Poulsen 2000).

Another basic substrate in forest bryophyte communities is deadwood (Harmon et al. 1986). Plenty of species appear on decaying wood, many of which are obligate epixylic species (Samuelsson et al. 1994; Jonsson et al. 2005). In the epixylic communities, suc- cession appears: the species composition on wood of different decay stages is different, thus simultaneous presence of different stages can increase diversity considerably (McCullough 1948; Söderström 1988a; Ódor and van Hees 2004). The size of woody debris is also crucial: bigger trunks host more species due to the greater variance of microhabitats and these trunks remain available for a longer period as well (Rambo and Muir 1998; Kruys et al. 1999; Ódor and van Hees 2004; Ódor et al. 2006). Since managed and near-natural forests differ mainly in the amount of deadwood, several comparative studies have shown that epixylic bryophyte communities are the most dissimilar to one another in different forests (Gustafsson and Hallingbäck 1988; Söderström 1988b; An- dersson and Hytteborn 1991; Lesica et al. 1991; Rambo and Muir 1998; Ódor and Standovár 2001). Deadwood can also affect the bryophyte assemblages on other substrates. Ódor and Standovár (2002) have shown that the species composition of epixylic and epilithic communities considerably overlap in a near-natural Hungarian beech forest. The accumulation of dead woody material between outcrops increased the diversity of epilithic assemblages. In addition to the structural features of living and dead wood, in case of epixylic bryophyte communities microclimate is also very important. It has been shown that humid, cool conditions maintain more diverse epixylic bryophyte assemblages, regardless of the characteristics of deadwood (Lindström 2003; Ódor and van Hees 2004; Heilmann-Clausen et al. 2005; Ódor et al. 2006).

Soil inhabiting bryophytes are often inhibited in deciduous forests by litter accumula- tion, thus they grow on disturbed patches where litter is not present (e.g. roadsides, root plates etc., von Oheimb et al. 2007). Deciduous litter limits the growth of bryophytes both by shading and direct allelopathic effects (Rincon 1988; Startsev et al. 2008). In the zone of temperate deciduous forests, high bryophyte cover develops on the forest floor only under special edaphic conditions (swamp forests, acidic forests of steep slopes, rocky ravines and mixed pine-deciduous forests). In boreal forests, the bryophyte diversity of undisturbed forest floor is relatively low, dominated by a few feather moss species. However, fine scale soil disturbances can maintain high bryophyte diversity, thanks to quick colonisation from soil diaspore bank or airborne propagules (Jonsson and Esseen 1990). This phenomenon is observable both in forest types dominated by fine scale disturbances creating pits and

mounds (Schaetzl et al. 1989; Kimmerer 2005), and in forests affected by fire (De Las Herras et al. 1990). Although feather moss species (like *Hylocomium splendens*) regenerate relatively fast after disturbances (Rydgren et al. 2001), the effects of coarse scale disturbances are perceivable in bryophyte species composition even after decades (Brulisauer et al. 1996). In both deciduous beech forests and boreal forests, bryophyte assemblages are more dependent on fine scale disturbances than vascular plants (Jonsson and Esseen 1998; von Oheimb et al. 2007).

The most important factors affecting the diversity and composition of forest-floor bryophyte assemblages are the amount and heterogeneity of potential substrates and microsites (Mills and Macdonald 2004, 2005). The availability of these microsites (dead wood, open patches, pits and mounds), and microclimatic conditions are considerably influenced by forest management such as slash harvesting (Astrom et al. 2005), different felling treatments (Jalonen and Vanha-Majamaa 2001; Fenton and Frego 2005), dead wood management (Ódor and Standovár 2001; Jonsson et al. 2005) and management history (Rose 1992).

This investigation aims at exploring the effects of tree species composition, stand structure, substrate availability and landscape characteristics on ground-floor bryophyte assemblages in mixed deciduous-coniferous forests in Western Hungary. Species composition, species richness and cover of the entire assemblage and of functional groups were studied. These groups were formed on the basis of substrate preference, we distinguished terricolous, mineral soil inhabiting, wood inhabiting and opportunistic (i.e. species without distinct substrate preference) categories. All species living on wood were included in the wood inhabiting category, but we also formed separate subcategories for the specialist epixylic and epiphytic species. The relationships between the species richness and cover of bryophytes and understory vascular vegetation were analysed with respect to cover and species richness.

Materials and methods

Study area

This study was carried out in the Őrség National Park, Western Hungary (N46°51–55′ and W16°07–23′). The elevation is between 250 and 350 m above sea level and the topography consists of hills and wide valleys. Mean annual precipitation is ca. 800 mm and mean yearly temperature is 9.1°C (Marosi and Somogyi 1990). The bedrock is alleviated gravel mixed with loess. The soil is acidic and nutrient poor, the most common soil type on hills is pseudogleyic brown forest soil, while in the valleys mire and meadow soils can be found. This part of Hungary is unique because many different forest types and tree species combinations appear under similar site conditions. It is typical to the region that many tree species (*Quercus robur*—pedunculate oak, *Quercus petraea*—sessile oak, *Fagus sylvatica*—beech, *Carpinus betulus*—hornbeam, *Pinus sylvestris*—Scotch pine, *Picea abies*—Norway spruce) are found with relatively high abundance and various proportions in the stands, and besides, the occurrence of different mixing species (*Betula pendula*—birch, *Populus tremula*—aspen, *Castanea sativa*—chestnut, *Prunus avium*—wild cherry, *Acer spp.*—maple, *Tilia* spp.—lime-tree) is also considerable. The various species composition has phytogeographic, climatic and land use historical reasons. The western borderland of Hungary has always had special agriculture. After the twelfth century, the area was characterized by extensive farming, which led to considerable deforestation (Tímár et al. 2002). Besides the felling of forests, there were other effects contributing to the changes of

vegetation: litter collecting in forests and a special form of tillage, ridging, which also resulted in the acidification of the area and the increased erosion of soil. These effects are advantageous to Scotch pine, an acidofrequent herbaceous layer and high terricolous bryophyte cover (*Pleurozium schreberi*, *Pseudoscleropodium purum*, *Dicranum polysetum*, *Polytrichastrum formosum*). From the nineteenth century, extensive farming was repressed, a large part of the arable lands was gained back by forests, mainly by Scotch pine and pioneer species linked to it (birch, aspen). Later, land use became stable, selective cutting has been performed in forests by farmers, which, along with industrial shelter-wood system, is still typical here. The alteration of agriculture and the development of industrial forestry in our days lead to changes in tree species composition: the dominance of Scotch pine is decreasing, and deciduous species take its place (Tímár et al. 2002). This phenomenon is not unique, and is observed also in Poland (Dzwonko and Gawronski 2002). Thus we find highly mixed stands in the area.

Data collection

We measured characteristics of stand structure and tree species composition, herbaceous and bryophyte vegetation of the forest floor, substrate (soil, litter, deadwood), canopy closure and relative light conditions.

Thirty-five forest stands (2–15 ha each) were selected for this study by stratified random sampling from the stand structural database of the Hungarian National Forest Service. All stands were 70–100 years old and located on plain area not directly influenced by water. The stratification criterion was tree species composition, the selected stands represent different combinations of the main tree species (oak, beech, Scotch pine, Norway spruce and hornbeam) of the area.

Stand structure records were taken in 40×40 m^2 blocks of the stands. Species identity, height, diameter at breast height (DBH) and the position of every tree specimen (including snags) with DBH larger than 5 cm was recorded. Saplings (including shrubs) slimmer than 5 cm DBH but taller than 0.5 m were also counted. The mean diameter and length of logs with more than 5 cm in diameter were recorded. The derived variables of tree species composition and stand structure can be found in Table 1. Tree species diversity was expressed as the Shannon diversity of species abundances using natural logarithm (Shannon and Weaver 1949). The volume of trunks was calculated by species specific equations using DBH and height as parameters (Sopp and Kolozs 2000). In the case of "mean DBH of dominant trees", DBH of the 30 largest trees was considered. Trees were classified into 6 DBH categories (5–10, 11–20, 21–30, 31–40, 41–50, larger than 50 cm). Structural diversity was expressed as the Shannon diversity of tree abundances in different DBH categories (Magurran 2004).

The inventory of understory vegetation (including herbs and tree-shrub seedlings shorter than 0.5 m), bryophytes, substrates and light was taken in 30×30 m^2 plots, positioned in the middle of the blocks. The plots were divided into 36 contiguous quadrates of 5×5 m^2. Absolute cover (dm^2) was estimated for every species, mineral soil, deadwood and litter in the quadrats. In the middle of the quadrats canopy openness was estimated with a spherical densiometer (Lemmon 1957). Relative diffuse light (diffuse non-interceptance) was calculated based on parallel measurements in the quadrats and nearby open fields with LAI-2000 Plant Canopy Analyzer instruments (LI-COR Inc 1990). Proportion of landcover types was estimated in circles of 300 m radius around the plots by remote sensing based on aerial photos and maps. Stands of pure beech, oak, pine, spruce older than 20 years (relative volume of a species is higher than 0.55) and mixed stands were separated. The

Table 1 Potential explanatory variables included in the study

Tree species composition
Tree species richness
Tree species diversity
Relative density of tree species (beech, hornbeam, oaks, pine, spruce, mixing species)
Relative volume of tree species (beech, hornbeam, oaks, pine, spruce, mixing species)
Stand structure
Distribution of DBH [mean, standard deviation, mean DBH of dominant trees, structural diversity, density of DBH categories (stems/ha)]
Sapling density (stems/ha)
Timber volume (m³/ha)
Dead wood volume (m³/ha)
Log volume (m³/ha)
Substrate types
Cover (m²/ha) of mineral soil, litter and dead wood
Light conditions
Canopy openness (mean, standard deviation)
Relative diffuse light (mean, standard deviation)
Landscape variables
Proportion of landcover types (old beech, oak, pine, spruce and mixed forests; young forests; non-forested areas)

category of "young-forests" included all stands younger than 20 years. Non-forest areas were mainly meadows and arable lands.

Stand measurements were performed between summer 2005 and autumn 2006, inventory of understory and bryophyte vegetation was taken in summer 2006. The nomenclature for vascular plants follows Tutin et al. (1964–1993), for mosses Hill et al. (2006) and for liverworts Grolle and Long (2000). We did not discriminate between *Quercus petraea* and *Q. robur* (considering both as *Q. petraea*), and did not identify the microspecies within *Rubus fruticosus agg*. The bryophytes were arranged in functional groups based on literature data (Boros 1968; Smith 1980) and field experience (Appendix 1). According to substrate preference, terricolous, mineral soil inhabiting, epixylic (on decaying wood), epiphytic (on bark), general wood inhabiting (including all species occurring on bark or wood) and opportunistic species were distinguished.

Data analysis

Data structure was explored by ordination: detrended correspondence analysis, principal component analysis and redundancy analysis (Podani 2000). Species data were centred and logarithmically transformed. Only species with higher frequency than five were included in the analyses. Since gradient length along the axes of detrended correspondence analysis was lower than 1.7 standard deviation unit, redundancy analysis was used as direct ordination. In this, explanatory variables were selected by manual forward selection. The effects of factors were tested by *F*-statistics via Monte–Carlo simulation, the number of permutations was 499 (ter Braak and Smilauer 2002). The significance of all canonical axes was tested similarly to the explanatory variables.

The relationship between biological variables and explanatory factors was revealed by linear regression models. Before building models, pilot studies were performed to check correlations between biological variables and single explanatory factors. Finally 5–10 independent explanatory factors were selected as the basis for the regression models. The regression analyses were performed with General Linear Modelling (Faraway 2005). To assure normality of a biological variable, in some cases natural logarithm transformation was used. To get the minimal adequate model, factors were taken out one by one from the full model, and changes in the model were checked with deviance analysis, using *F*-test. While accomplishing the models, not only the value of the coefficient of determination and the results of statistical testing were taken into account, but also the graphical diagnostics of the models (normality of residuals, homogeneity of variance of residuals, relative weight of samples). Linear models are prepared for estimating the species richness and cover of the whole bryophyte assemblage and also of different functional species groups: cover of wood inhabiting species, terricolous and opportunistic species, mineral soil inhabiting species; species richness of specialist epiphytic and epixylic species.

Correlations between both species richness and cover of understory (herbs and seedlings) and bryophyte layer were also calculated (Zar 1999.)

For multivariate analyses, Canoco for Windows 4.5 (ter Braak and Smilauer 2002), for linear regressions *R 2.6.2* (The R Development Core Team 2008), and for normality and correlation analyses and graphical representation Statistica 7.0 (Statsoft 2006) was used.

Results

Multivariate analysis

The first four axes of the principal component analysis explained 69.6% of variance, while the four canonical axes of redundancy analysis explained 59.7% (37.2, 10.9, 6.94.7%, respectively). The effect of litter cover overwhelmed the other variables, although the effect of sapling density and of the size of dominant trees was also considerable (Table 2). The first axis correlated mainly with litter cover and the heterogeneity of canopy openness; the second with the relative volume of spruce, the size of dominant trees, the density of saplings and the total volume of dead wood; the third with the relative density of oak and the proportion of surrounding oak forests; while the fourth with the density of trees between 6 and 10 cm DBH and the size of dominant trees (Fig. 1; Table 2). Nearly all of the species had positive scores on the first axis, indicating the negative effect of litter cover on bryophytes. The dominant terricolous species of the bryophyte assemblage (*Polytrichastrum formosum*, *Pseudoscleropodium purum*, *Hylocomium splendens*, *Pleurozium schreberi*, *Dicranum polysetum*) had especially high scores on the first axis, which shows negative correlation with litter cover and positive with the heterogeneity of light. There are only a few epixylic species in the assemblage (*Lophocolea heterophylla*, *Herzogiella seligeri*, *Tetraphis pellucida*). These had high scores on the first three axes, positively correlating with light heterogeneity, dead wood volume and relative spruce volume. The group of bryophytes occurring on mineral soil did not separate from the functional groups of epiphytic and wood-living species. Some of them had low scores on the third axis, correlating positively with the relative volume of oak and the proportion of oak forests in the landscape (*Atrichum undulatum*, *Dicranella heteromalla*, *Pohlia nutans*, *Ditrichum pallidum*, *Bryum rubens*). Some common wood-inhabiting species (*Hypnum cupressiforme*, *Platigyrium repens*) and epiphytes (*Ptilidium pulcherrimum*, *Ulota crispa*) had similar position.

Table 2 Explained variance (%) of canonical axes in redundancy analysis [Var (%)], and the correlation of the explanatory variables with the axes (only absolute values higher than 0.4 are shown)

	Var (%)	F-test	Axis 1	Axis 2	Axis 3	Axis 4
Litter cover	23	9.63**	−0.757			
Sapling density	10	4.9**	0.482	0.427		
Mean DBH of dominant trees	10	5.41**	−0.458	0.598		0.450
Relative spruce volume	6	3.87**		0.768	0.405	
Relative oak density	5	2.83**			−0.793	
Proportion of surrounding oak forests	3	2.1*			−0.478	
Tree density, 6–10 cm DBH	3	1.67*	0.433			0.512
Total tree density	3	1.95*			0.414	
Dead wood volume	3	1.79*		0.409		
Proportion of surrounding pine forests	2	1.99*				
Heterogeneity of canopy openness	2	1.72*	0.752			

The effects of the explanatory variables were tested by F-test

* $P < 0.05$, ** $P < 0.01$

Linear modelling of biological characteristics (Table 3)

In agreement with the ordination results, we found that the most important factor influencing total bryophyte cover is litter cover: it had a very strong and significant negative effect. The size of the dominant trees and the number of medium trees also showed a negative, but less significant relationship with the studied character. The number of saplings had the only positive, albeit weak effect. The model explained 79% of the total variance.

For the cover of wood-inhabiting bryophytes, we found only two significant explanatory factors, both with a negative sign. Far more important of the two is litter cover, the other is the proportion of beech. In spite of the few explanatory factors, our model explained 62% of the total variance.

Five almost equally significant explanatory factors were found for the cover of terricolous and opportunistic bryophytes. Factors showing positive effect were proportion of surrounding pine forests and the standard deviation of canopy openness, while those with a negative effect were total timber volume, number of medium trees and, with the least importance, litter cover. Explained variance was 71%.

A highly specialised group among bryophytes is that of the mineral soil inhabiting species. According to the model, the three most important factors in determining their cover were number of medium trees, litter cover and the mean of relative diffuse light. They were all similarly important, and the first two had a negative, while the third (connected with the amount of light) had a positive influence. The explained variance of our model was 44% of the total.

Bryophyte species richness also showed negative correlation with litter cover and the number of medium trees, but in this case tree species richness and the standard deviation of DBH had a positive effect. Litter cover had the strongest effect, the other factors were of similar importance. The model explained 56% of the total variance.

The group of specialist epixylic and epiphytic bryophytes is of special conservational interest. In the model concerning their species richness, litter cover again had a negative,

Fig. 1 Ordination plots of the first and second (**a**), and the third and fourth (**b**) axes of redundancy analysis. Species abbreviation consists of the first three letters of the genus and the species names, upper case letters refer to the substrate preference of species. EPH—specialist epiphyte; EX—specialist epixyl; MS—mineral soil; O—opportunistic; T—terricolous; W—wood inhabiting. Abbreviations of explanatory variables: litter—litter cover; sapling—sapling density; DBH dom.—mean DBH of dominant trees; rel. spruce—relative spruce volume; rel. oak—relative oak density; amb. oak—proportion of surrounding oak forests; DBH 6–10—tree density, 6–10 cm DBH; amb. pine—proportion of surrounding pine forests; total tree—total tree density; cwd—dead wood volume; std openness—heterogeneity of canopy openness

Table 3 Significant explanatory variables of the different regression models

Variable	Sign	Variance %	F-value, significance
Bryophyte cover; $R^2 = 0.79$			
Litter cover	−	35.6	57.4***
Sapling density	+	6.8	10.9**
Mean DBH of dominant trees	−	6.4	10.4**
Density of DBH category 30–40 cm	−	2.7	4.4*
Cover of wood-inhabiting bryophytes; $R^2 = 0.62$			
Litter cover	−	43.7	39.5***
Relative density of beech	−	7.1	6.4*
Cover of terricolous and opportunist bryophytes; $R^2 = 0.71$			
Timber volume	−	5.2	6.1*
Density of DBH category 30–40 cm	−	5.1	5.9*
Proportion of surrounding pine forests	+	4.8	5.6*
Standard deviation of canopy openness	+	4.2	4.9*
Litter cover	−	3.3	3.9·
Cover of mineral soil inhabiting species; $R^2 = 0.44$			
Density of DBH category 30–40 cm	−	8.0	4.9*
Litter cover	−	7.1	4.3*
Mean of relative diffuse light	+	5.0	3.0·
Bryophyte species richness; $R^2 = 0.56$			
Litter cover	−	15.5	11.9**
Standard deviation of DBH	+	8.3	6.4*
Abundance of DBH category 30–40 cm	−	7.4	5.8*
Tree species richness	+	4.0	3.1·
Species richness of specialist epiphytic and epixylic bryophytes; $R^2 = 0.42$			
Structural diversity	+	14.2	8.3**
Log volume	+	9.6	5.6*
Litter cover	−	5.3	3.1·

R^2 is the coefficient of determination of the models; *Sense* is the sense of the parameter of the variables in the regression equation; *Variance %* is the percentage of the explained variance by the variable within the model. The significance of explained variance was tested by F statistics: ·$P < 0.1$,* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

but not too strong effect, while structural diversity and log volume had a strong positive effect.

Relationships between bryophytes and vascular assemblages (Fig. 2)

The correlation between cover and species number of bryophytes and understory plants was significantly positive: $r = 0.53$; $P < 0.01$; and $r = 0.66$; $P < 0.001$, respectively.
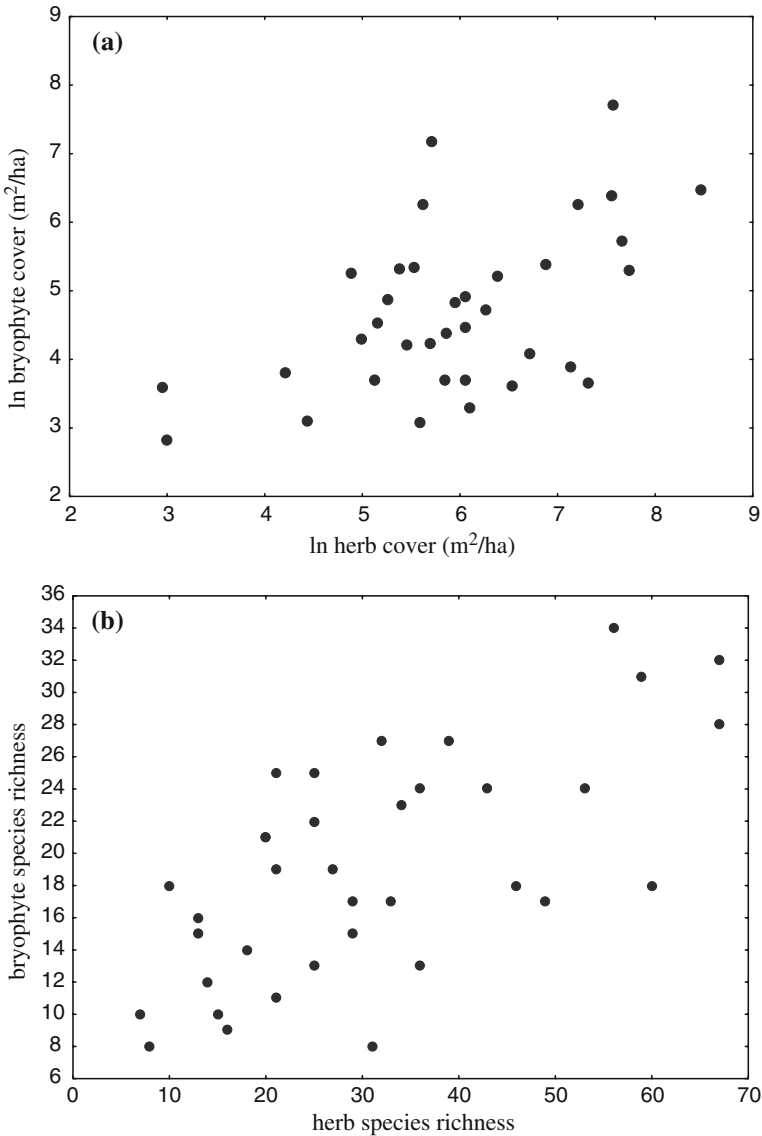
Fig. 2 Correlations between herb and bryophyte layer in terms of (**a**) cover, $r = 0.53$; $P < 0.01$ and (**b**) species richness, $r = 0.66$; $P < 0.001$

Discussion

The effects of explanatory factors

One of the most important explanatory factors proved to be litter cover, both in multi-variate and in linear modelling. The species showed in general strong negative correlations with litter cover. This phenomenon has various reasons. The most obvious is that litter covers the suitable substrates, thus inhibiting the development of a bryophyte layer. Legare

et al. ([2005](#)) and Startsev et al. ([2008](#)) showed that the litter of *Populus tremuloides* had direct allelopathic effects on forest floor bryophytes, especially feather moss species in boreal forests. In modelling total species richness of bryophytes, litter cover was found to have the most important negative influence. Similarly, Dzwonko and Gawronski ([2002](#)) showed in a 16-year field experiment that litter removal from a mixed pine-oak woodland caused increase in both herbaceous and bryophyte species richness.

Another important explanatory factor is sapling density, which often showed positive correlations with bryophytes. In our redundancy analysis this variable correlated strongly with some dominant species of the forest floor: *Hypnum cupressiforme*, *Atrichum undulatum*, *Brachytecium rutabulum* and *Brachyteciastrum velutinum*. Also in the linear model built for assessing total bryophyte cover, the number of saplings had an important positive effect. This phenomenon has partly historical explanation (Tímár et al. [2002](#)). In pine forests in Western Hungary, which used to support a nearly continuous bryophyte layer in the past, nowadays strong regeneration of deciduous trees can be experienced. Deciduous saplings find better germination and growth conditions on the light mineral soil of the pine forests' floor than in closed deciduous forests. Conifer saplings are fewer because of forest soil eutrophication, due to the lack of traditional litter removal from forests (see also Dzwonko and Gawronski [2002](#)). Thus, in conifer forests we find many saplings, but the understory vegetation still holds a coniferous feature, so bryophyte cover is large. Probably the bryophyte layer will also change, but with some years of delay.

In this study the size of dominant trees, which often correlates with the overall age of the stand and timber volume especially in managed forests, has a basically negative effect. Most species show negative correlation with the size of the dominant trees in the plot, and this variable also has a negative effect on bryophyte cover. In many studies large trees act positively on the bryophyte assemblage, but these studies consider mostly epiphytic assemblages (Aude and Poulsen [2000](#); McGee and Kimmerer [2002](#); Bardat and Aubert [2007](#)). For epiphytic species the presence of large trees is favourable, because of the increase in the number of microhabitats (McGee and Kimmerer [2002](#)), the changes in bark structure (Gustafsson and Eriksson [1995](#)) and elongation in colonisation time (Snall et al. [2003](#); Lobel et al. [2006](#)). Also in our study area, analyses with epiphytic species led to similar results (Lengyel-Király [2008](#)). However, large trees had indirect negative effects on forest floor bryophytes in the studied region. The largest trees are usually beech, with high litter production and closed canopy, both of which inhibit bryophyte growth. The dominant trees are not very old (70–100 years), thus they do not provide deadwood, which would enhance the number of potential substrates and microsites. Conditions are unfavourable for bryophytes in managed, closed, even-aged stands of large beech trees.

In the studied forests of this area, spruce does not form monodominant stands, but is present as a mixing species. Many studies have shown that in the boreal region, where spruce is the dominant forest forming species, the presence of deciduous species (e.g. aspen, *Populus tremula*, Berg et al. [1994](#); Gustafsson and Eriksson [1995](#); Esseen et al. [1997](#)) has a positive effect on bryophyte species richness. On the contrary in our case, in the basically deciduous forests, the presence of spruce had a similar positive effect. The presence of spruce creates suitable microhabitats for abundant, acidofrequent feather moss species (e.g. *Eurynchium angustirete*), which are common in the boreal region. Some regionally rare, epixylic bryophytes (e.g. *Nowellia curvifolia*, *Riccardia palmata*) also prefer spruce logs.

The relative density of oak in a forest and the proportion of oak forests in the surrounding woods had an important effect on species composition. Oak forests are usually more open than other forests of the region, explaining the strong correlation of the proportion of oak with one of the most dominant terricolous species in the region, the light-demanding *Polytrichastrum formosum* (Bao 2005). The proportion of oak also shows positive correlation with the most common bryophyte of the region, *Hypnum cupressiforme*. This species is wood-inhabiting, and has the largest cover on deadwood and also on bark (Lengyel-Király 2008). The bark of oak is also favourable for many epiphytic species, as it is mesotrophic and rough, thus giving a variation of convenient microhabitats (Barkman 1958). The proportion of oak forests in the surrounding woods (radius 300 m) is important, as these forests may serve as propagule sources.

The proportion of surrounding pine forests was also a considerable factor, in the overall species composition and in the case of the cover of terricolous species as well. The latter positive correlation again may be the result of spore dispersal between stands. We found the proportion of surrounding pine forests to be correlated with some terricolous species (*Polytrichastrum formusum*, *Leucobryum glaucum*, *Eurynchium angustirete*, *Pseudoscleropodium purum*). These are favoured by better light availability (Bao 2005; Moora et al. 2007), lower litter cover and acidic soil conditions.

In the studied area, specialist bryophytes appearing on logs are either epixylic (dominant species: *Lophocolea heterophylla*, *Herzogiella seligeri*) or epiphytic (abundant species: *Dicranum montanum*, *Radula complanata*). Their species richness is closely correlated with the amount of deadwood. This factor is an indicator of forest naturalness (Canterello and Newton 2008)—the amount of deadwood is one of the most striking differences between natural and managed forests (Gustafsson and Hallingbäck 1988; Söderström 1988b; Lesica et al. 1991; Ódor and Standovár 2001). It is an inevitable substrate for many endangered species, which are getting rarer with the increasing intensity of forest management. Also, as some experiments show, the addition of dead wood to managed forests does improve species richness (Vanha-Majamaa et al. 2007).

Light had an important effect on bryophyte species richness and on the cover of mineral soil inhabiting species. However, literature on the effects of light is contradictory. Some studies suggest that there is no significant relationship between light conditions and the composition of bryophyte assemblages in many forest types (Hardtle et al. 2003). In forest fragments bryophyte diversity was higher in shaded, more humid forest interior than near the edges (Gignac and Dale 2005). Nevertheless, Moora et al. (2007) found that light availability enhances species richness at a fine spatial scale. In the boreal region, considering ground floor bryophytes, light proved to be an important explanatory variable at a fine scale (Mills and Macdonald 2005). Often, more light is available in disturbed patches (von Oheimb et al. 2007).

The diversity of stand structure is a very important explanatory factor, represented by more variables in our linear models. Tree species richness and structural diversity (standard deviation of DBH and the diversity of trees based on size categories) had positive, while the number of medium trees (DBH 30–40 cm) had negative effects. One or more of these factors appeared significant in most of our models. All three positive factors partly act through habitat (Weibull and Rydin 2005) and substrate diversity (e.g. Lohmus et al. 2007; Ódor et al. 2006), as the indicators of forest naturalness (Canterello and Newton 2008). These factors showed significant correlations with total bryophyte species richness and the group of specialist epiphytic and epixylic bryophytes, which contains many rare species. On the other hand, the number of medium trees correlates negatively with the first three variables, thus refers to structural homogeneity. This factor had significant negative effects

on bryophyte cover and species richness, and also on the cover of terricolous and mineral soil inhabiting species groups. Our results indicating the importance of stand structural diversity in the composition of bryophyte assemblages are in accordance with many studies from various forest types (Lesica et al. 1991; Aude and Lawesson 1998; Humphrey et al. 2002; Bardat and Aubert 2007).

Correlations between bryophyte and understory layer

We found that bryophyte assemblages and understory layer are strongly positively correlated in the case of species number as well as cover. This result may have several biological explanations. One possibility is that both layers react positively to the same explanatory effects, so their correlation is only indirect. These factors may be climatic (humidity, temperature etc., Lee and La Roi 1979), edaphic (e.g. chemical characteristics of soil) or the effects of former management. To detect these explanatory factors, further investigations are necessary.

Another possible reason is that the two groups affect each other directly (Aude and Ejrnaes 2005), the likely direction is that the understory layer acts positively on bryophytes. However, previous results are contradictory in this regard. Herbaceous cover negatively influenced the bryophyte cover and diversity in several studies, chiefly because of litter production (e.g. Virtanen et al. 2000; Bergamini et al. 2001). Nevertheless, these investigations were carried out in grasslands or mires, where herbaceous layer is more dominant than in forests. In boreal forests after the addition of fertilisers, herbaceous cover increased and bryophyte cover decreased (Turkington et al. 1998). In our case it is possible that the herbaceous layer changes the microclimate of the forest floor in a way favourable for bryophytes. This positive effect may overwhelm the negative effect of shading in case of shade-tolerant, forest-dwelling bryophyte species.

Conservational considerations

Studies based on observations cannot explore the limiting factors as precisely as experiments, but they can comprehend a much wider range of potential effects. Although in our study many presumably important explanatory variables were missing (measurements of microclimate and soil conditions), the calculated models explained a relatively large proportion of different characteristics of the bryophyte assemblages of the studied region. Practical applicability of our models to biological conservation is increased because they relied upon simply measurable variables, many of which are used by forest managers as well.

Our results showed that the most essential factor influencing the composition of the forest floor bryophyte assemblage was the availability of different substrates, principally mineral soil and dead wood. The most significant inhibiting factor was deciduous litter, which covered the suitable substrate surfaces.

Another basically important explanatory factor was the diversity of stand structure and tree species, responsible for more favourable conditions for bryophytes.

Forest management basically influences forest stand structure and tree species composition. According to this study, selective cutting resulting in heterogeneous structure and species composition, is more favourable for the forest floor bryophyte assemblage than the industrial shelter-wood system. Another important recommendation for conservationists is that the amount of dead wood in these forests should be increased as much as possible.

Appendix 1 List of the recorded bryophyte species, their substrate preference in the region, generalist–specialist type for their substrates and frequency (number of occurrences)

Code	Species	Preferred substrate	Frequency
ambser	*Amblystegium serpens*	W	4
ambsub	*Amblystegium subtile*	W	1
anoatt	*Anomodon attenuatus*	EPH	2
atrund	*Atrichum undulatum*	MS	29
brarut	*Brachytecium rutabulum*	O	22
brasal	*Brachytecium salebrosum*	W	16
bravel	*Brachyteciastrum velutinum*	O	34
brycap	*Bryum capillare*	MS	4
bryrub	*Bryum rubens*	MS	6
bryrud	*Bryum rudelare*	MS	5
buxaph	*Buxbaumia aphylla*	MS	1
calazu	*Calypogeia azurea*	MS	1
calfis	*Calypogeia fissa*	MS	3
calmue	*Calypogeia muellerana*	MS	1
cepbic	*Cephalozia bicuspidata*	MS	1
cerpur	*Ceratodon purpureus*	MS	1
dichet	*Dicranella heteromalla*	MS	35
dicmon	*Dicranum montanum*	EPH	33
dicpol	*Dicranum polysetum*	T	7
dicsco	*Dicranum scoparium*	O	27
dictau	*Dicranum tauricum*	EPH	1
dipfol	*Diphyscium foliosum*	MS	1
ditpal	*Ditrichum pallidum*	MS	10
eurang	*Eurhynchium angustirete*	T	7
fisbry	*Fissidens bryoides*	MS	5
fistax	*Fissidens taxifolius*	MS	11
frudil	*Frullania dilatata*	EPH	5
hersel	*Herzogiella seligeri*	EX	27
homtri	*Homalia trichomanoides*	EPH	3
hylspl	*Hylocomium splendens*	T	10
hypcup	*Hypnum cupressiforme*	W	35
isoalo	*Isothecium alopecuroides*	EPH	7
leprep	*Lepidozia reptans*	W	2
leprip	*Leptodictyum riparium*	O	1
leugla	*Leucobryum glaucum*	T	13
lophet	*Lophocolea heterophylla*	EX	33
metfur	*Metzgeria furcata*	EPH	4
nowcur	*Nowellia curvifolia*	EX	3
ortaff	*Orthotrichum affine*	EPH	5
ortpal	*Orthotrichum pallens*	EPH	1
ortspe	*Ortotrichum speciosum*	EPH	4
ortstr	*Orthotrichum stramineum*	EPH	4
oxyhia	*Oxyrrhynchium hians*	O	3

Appendix 1 continued

Code	Species	Preferred substrate	Frequency
oxysch	*Oxyrrhynchium schleicheri*	T	1
parlon	*Paraleucobryum longifolium*	EPH	2
plaaff	*Plagiomnium affine*	T	17
placav	*Plagiothecium cavifolium*	T	3
placus	*Plagiomnium cuspidatum*	W	9
pladen	*Plagiothecium denticulatum*	W	11
plalae	*Plagiothecium laetum*	W	16
planem	*Plagiothecium nemorale*	W	4
plarep	*Platygyrium repens*	W	33
plasuc	*Plagiothecium succulentum*	W	2
plaund	*Plagiomnium undulatum*	T	1
plesch	*Pleurozium schreberi*	T	16
plesub	*Pleuridium subulatum*	MS	3
pohnut	*Pohlia nutans*	MS	19
polfor	*Polytrichastrum formosum*	T	35
poljun	*Polytrichum juniperinum*	MS	2
psepur	*Pseudoscleropodium purum*	T	15
ptipul	*Ptilidium pulcherrimum*	EPH	5
pylpol	*Pylaisia polyantha*	EPH	1
radcom	*Radula complanata*	EPH	14
rhipun	*Rhizomnium punctatum*	EX	4
rhysqu	*Rhytidiadelphus squarrosus*	T	1
rhytri	*Rhytidiadelphus triquetrus*	T	1
scanem	*Scapania nemorea*	MS	3
scipop	*Sciuro-hypnum populeum*	O	4
tetpel	*Tetraphis pellucida*	EX	7
thudel	*Thuidium delicatulum*	T	3
thutam	*Thuidium tamariscinum*	T	1
ulocri	*Ulota crispa*	EPH	9
weibra	*Weissia brachycarpa*	MS	1
weirut	*Weissia rutilans*	MS	1

EPH specialist epiphyte, *EX* specialist epixyl, *MS* mineral soil, *O* opportunistic, *T* terricolous, *W* wood inhabiting

Maintaining high spatial heterogeneity of substrate and light is prerequisite to an increased bryophyte diversity of forest communities.

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