Substrate specificity and community structure of bryophyte vegetation in a near-natural montane beech forest

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Abstract: Bryophyte vegetation on volcanic rock outcrops and dead wood is studied in a near-natural montane beech stand in northern Hungary. Substrate specificity of the species and the existing interspecific relationships are described. The most important species combinations and their diversity are evaluated using information theoretical functions and Monte-Carlo simulations.

All analyses are based on presence/absence data of 33 species in 1508 100 cm^2 microplots. Most species exhibit strong substrate specificity. Of the species that occurred with frequencies higher than 10, 8 are associated to rock, 5 to dead wood and 5 to both substrate types. Analyses of interspecific associations and agglomerative classification reveal that frequent species of species-poor bare rocks are separated from species-rich assemblages of humus-rich outcrops and coarse woody debris.

Monte Carlo simulations reveal that many species combinations are significantly more frequent than expected under the assumption of random combining of species. Observed number, diversity and evenness of species combinations are significantly lower, whereas interspecific constraint (expressed as associatum) is significantly higher than under the neutral models even when data are stratified according to substrate type.

The presence of coarse woody debris, not only provides habitat for wood inhabiting bryophytes, but also results in diverse rupicolous bryophyte assemblages on humus-rich outcrops.

Abbreviation: CWD - coarse woody debris.

Nomenclature: Corley and Crundwell (1991) and Corley et al. (1981) for mosses; Grolle (1983) for liverworts.

Introduction

Concepts of plant communities range from those that emphasize the recurrence of well-organized species groups (Clements 1916, Braun-Blanquet 1964, Westhoff and van der Maarel 1973), to those that propose that assemblages are stochastic (Gleason 1926, Crawley 1997). The former view is often coupled with the presumption that communities are in dynamic equilibrium with their stable, rarely disturbed environment. Their composition and structure are determined by biotic interactions (Hairston et al. 1960, Tilman 1982). The individualistic approach is often connected with a more dynamic view, which emphasizes that environments are heterogeneous, frequently disturbed, and consequently the recruitment of individuals and species primarily determines community structure. According to this non-equilibrium approach,

community structure and richness are determined by recruitment in a patchy environment, where the normal condition is recovery from last disturbance (Watt 1947, Pickett and White 1985, Reice 1994).

Most of the ideas mentioned above are based on studies of vascular plants. In these, it is well known that species' distribution is grossly determined by climate. However, bryophytes are exceptional in that they have special body structures, life cycles, and physiology that make them dependent mainly on substrate (e.g., rock, soil, dead or living tree) at the stand scale (Smith 1982). Fine scale studies showed that distribution is strongly determined by abiotic factors such as air humidity and microtopography on rock (Yarranton and Beasleigh 1968, 1969, Bates 1975, Pentecost 1980, Alpert 1985), dead wood (Söderström 1988a, McAlister 1997, McCullough 1948, Fehér

and Orbán 1981) and living trees (Slack 1976, Rasmussen and Hertig 1977, Palmer 1986, Bates and Brown 1981, Yarranton 1967).

Phytosociological approaches - based on species composition and character species - were applied to describe bryophyte communities as synusia on specific substrate types (Felföldy 1941, Barkman1958, 1973, Hübschmann 1986). This type of classification is based on the recognition of recurring species groups formed by competition. They are supposed to be in equilibrium with their environment.

Many bryological studies have disproved the significance of resource competition as an important factor in shaping community structure. Watson (1980) did not find evidence of niche separation or resource partitioning among *Polytrichaceae* species. On the contrary, During (1990) reported in a review that positive density-dependence can often occur among bryophytes. High densities may be advantageous for growth and survival of shoots and for water balance (Proctor 1982). Epilithic and epiphytic bryophytes behave opportunistically; they inhabit any suitable site they can colonise. Species turnover is high, the vegetation is dominated by a few species (Slack 1977). Epixylous (Söderström 1988b, 1989, 1990) and epiphytic (Schuster 1957) communities are mostly limited by dispersal. Species composition is largely determined by colonisation success. Suitability of the substrate changes relatively fast, thus the equilibrium approach cannot be used. For bryophytes occurring in more stable communities, interspecific competition and niche segregation are likely to be important. In peat bogs, strong interspecific competition was found among *Sphagnum* species (Vitt and Slack 1975, Vitt et al. 1975, Rydin 1986). Rassmussen and Hertig (1977) detected strong interspecific associations among bark inhabiting bryophytes: the characteristic vertical differentiation was partly explained by interspecific competition. Kunkel (1975) also found niche separation between bryophytes occurring on exposed granite outcrops in the Rocky Mountains in Colorado.

In deciduous beech and oak forests, the soil surface is covered by a thick litter layer, which inhibits the development of a mossy cover. Unlike boreal and alpine spruce forests, where a mossy ground layer is important (Polunin and Walters 1985, Esseen et al. 1997), the main habitats for bryophytes are rocky outcrops, decaying wood and bark. The forest floor is only inhabited after soil disturbance (e.g., uprooting) by colonist species (Jonsson 1993).

The structure and composition of shrubs, herbs and seedlings are strongly influenced by the canopy layer through affecting light conditions (Canham and Marks 1985, Collins et al. 1985, Emborg 1998). However, heterogeneous light conditions under a complex canopy have much less effect on the diversity and patterns of bryophytes than on those of vascular assemblages. Structural and compositional heterogeneity (e.g., multi layered canopy, large proportion of associate trees and large amount of dead wood) provides many habitats suitable for bryophytes, especially for epiphytic and epixylous types (Gustafsson and Hallingbäck 1988, Söderström 1988b, McCune and Antos 1981, Ódor and Standovár 2001).

In Central Europe, bryophyte vegetation has been studied by using biogeographic (Boros 1968) and phytosociological (Felföldy 1941, Fehér and Orbán 1981) approaches. No quantitative studies are available for describing substrate dependence and interspecific relationships of bryophytes in beech forests.

This study examines the structure and organisation of bryophyte vegetation on volcanic rock outcrops and dead wood in a near-natural montane beech stand in northern Hungary. Quantitative methods are applied to evaluate the effects of substrate type on the distribution of species. In addition, interspecific relationships and multispecies assemblages are also studied to test whether there are conservative multispecies combinations, and which are the most important assemblages. The study site is one of the last reference areas in the lower mountains in the Carpathian basin, where the structure and organization of bryophyte communities can be studied in a naturally complex forest stand.

Materials and methods

Study area

Kékes, in the Mátra Mts., is the highest point in Hungary (1014 m). Mean annual temperature is 5.7 °C, the relatively continental climate has low winter temperatures (-4.7 °C in January), high summer temperatures (15.5 °C in July), and ca. 840 mm of rainfall of which 480 mm falls during the growing season. The bedrock is andesite and the topography is extremely steep, scree slopes being characteristic. The shallow brown forest soils are mainly covered by montane beech wood (*Aconito-Fagetum*) and on humid rocky sites maple-ash-lime mixed woodland (*Phyllitidi-Aceretum subcarpaticum*) (Kovács 1968). Kékes Forest Reserve (63 ha) is one of the last remnants of near-natural Central-European montane beech woods in the inner Carpathian mountains. The stand is a mosaic of different forest developmental

phases, with trees older than 200 years occurring together with many other age classes (Czájlik 1996). Accumulations of coarse woody debris (CWD) are characteristic of this near-natural stand, mean volume of dead wood is 98,7 m^3ha^{-1} (Ódor and Standovár, unpub.), but in large gaps its volume can reach 230 m^3/ha (Ódor and Standovár 2001). Understorey layer is scarce, consisting mostly of advanced regeneration of beech. *Daphne mezereum, Sambucus racemosa* and *Ulmus glabra* can be found on scree sites. In the ground layer, *Galium odoratum, Mercurialis perennis, Dentaria bulbifera, Viola sylvestris* and *Oxalis acetosella* are the most frequent vascular species, together with seedlings of *Fagus sylvatica* and *Acer pseudoplatanus*. In the scree site, *Urtica dioica, Impatiens nolitangere, Solanum dulcamara* and *Athyrium filix-femina* are the dominant species. The moss layer has a high cover and is species rich both on rocks and coarse woody debris (Ódor 2000, Ódor and Standovár 2001). The dominant species on rocks are *Hypnum cupressiforme, Paraleucobryum longifolium, Grimmia hartmanii* and *Isothecium alopecuroides*. Logs are dominated by *Lophocolea heterophylla, Hypnum cupressiforme, Brachythecium rutabulum* and *Rhizomnium punctatum*.

As a near-natural reserve that has not been managed for timber production, the vegetation of the Kékes Forest Reserve serves as a valuable reference.

Data collection

A 120 m by 120 m plot with heterogeneous stand structure was studied. As part of a larger project (Standovár 1998), ground vegetation was systematically sampled in 0.5 m by 0.5 m quadrats that were set out on a grid at 5 m intervals. In each of the quadrats, nine 100 cm^2 microplots were set out systematically. In these microplots, presence of bryophyte species and the type of the substrate were recorded. Among possible substrate types, rock, coarse woody debris (CWD), living tree base and soil were distinguished. *Plagiothecium* species (*P. denticulatum, P. nemorale* and *P. ruthei*) were recorded at the genus level. *Amblystegium serpens* and *Brachythecium velutinum* were not separated during field sampling.

Data analyses

Two by two contingency tables were used to test interspecific association and the dependence of species on substrate types (Greig-Smith 1964, Kershaw 1964). An association function (Juhász-Nagy 1976, 1984, Juhász-Nagy and Podani 1983) was calculated between the investigated variables:

$$mI(A,B) = m \log m + a \log a + b \log b + c \log c + d \log d - (a+c) \log (a+c) - (b+d) \log (b+d) - (a+b) \log (a+b) - (c+d) \log (c+d) \qquad (1)$$

where *a, b, c* and *d* denote the elements of the 2x2 contingency table between variables A and B, and *m* = *a* + *b* + *c* + *d* is sample size.

To reveal the most important species groups, the species were classified using Euclidean distance and complete linkage clustering (Podani 2000).

The compositional variation of the bryophyte community was investigated by analysing realised species combinations (florulas). Florula diversity (Eq. 2) and florula evenness (Eq. 3) are Shannon-type diversity measures, which describe the diversity and evenness of realised species combinations based on their relative frequencies:

$$mH = m \log m - \sum_{k=1}^{z} f_k \log f_k \qquad (2)$$

$$H / H_{max} = 1 - (\sum_{k=1}^{z} f_k \log f_k / m \log m) \qquad (3)$$

where f_k= frequency of the *k*th species combination; *m* = sample size; and *z* = number of realised species combinations.

The importance of interspecific associations within the whole community was characterised by the "associatum function" (Eq. 4). This is a generalisation of the interspecific association function (Eq. 1) to many species (Juhász-Nagy 1980). If the community consists of *s* species, associatum is the mutual information of an *s*-dimensional contingency table.

$$mI(s) = (s-1) \, m \log m + \sum_{k=1}^{z} f_k \log f_k$$

$$- \sum_{i=1}^{s} n_i \log n_i + (m - n_i) \log(m - n_i) \qquad (4)$$

where n_i is the frequency of species *i*.

The above functions were described in detail by Juhász-Nagy (1976, 1984), Juhász-Nagy and Podani (1983) and Podani et al. (1993). Applications to different vegetation types were given by Bartha (1990, 1992), Szollát and Bartha (1991) and Bartha et al. (1995a), to mention only a few.

Simple neutral models were used to test if the observed departures from random expectation were significant. Monte-Carlo simulations were performed by keeping the observed frequencies of variables (species and substrate types). For testing dependence between two

Table 1. Observed frequencies and associations of bryophytes to substrate types. The order of species follows first their substrate preference (coarse woody debris, rock, mixed), and secondly their overall frequencies. The substrate preference of species was ascertained by the significance of association function (ASS. (p<.05)) and by qualitative decision (QUALIT. DECISION). R: rock, CWD: coarse woody debris, LT: living tree, S: soil.

SPECIES	ABBREVIATIONS	SUBSTRATE						
		FREQUENCY					ASS.	QUALIT.
		ALL	R	CWD	LT	S	(P<0.05)	DECISION
Lophocolea heterophylla	LOPHET	116	61	51	4	0	CWD	CWD
Bryum flaccidum	BRYFLA	76	45	28	1	2	CWD	CWD
Amblystegium serpens and Brachythecium velutinum	AMBSER	66	33	33	0	0	CWD	CWD
Brachythecium rutabulum	BRARUT	42	11	31	0	0	CWD	CWD
Pseudoleskeella nervosa	PSENER	13	0	13	0	0	CWD	CWD
Blepharostoma trichophyllum	BLETRI	6	1	4	0	1		CWD
Sanionia uncinata	SANUNC	4	1	3	0	0		CWD
Nowellia curvifolia	NOWCUR	2	0	2	0	0		CWD
Calypogeia suecica	CALSUE	1	0	1	0	0		CWD
Grimmia hartmanii	GRIHAR	747	733	11	0	1	R	R
Paraleucobryum longifolium	PARLON	470	446	4	8	11	R	R
Isothecium alopecuroides	ISOALO	290	282	4	0	3	R	R
Plagiochila porelloides	PLAPOR	155	142	8	0	5	R	R
Metzgeria furcata	METFUR	100	97	2	1	0	R	R,
Homalothecium philippeanum	HOMPHI	37	28	7	0	2	R	R
Brachythecium populeum	BRAPOP	48	46	2	0	0	R	R
Homalia trichomanoides	HOMTRI	19	18	1	0	0	R	R
Anomodon viticulosus	ANOVIT	1	1	0	0	0		R
Cynodontium strumiferum	CYNSTR	2	2	0	0	0		R
Plagiomnium cuspidatum	PLACUS	1	1	0	0	0		R
Hedwigia ciliata	HEDCIL	1	1	0	0	0		R
Hypnum cupressiforme	HYPCUP	672	551	110	3	7		R,CWD,S
Dicranum scoparium	DICSCO	158	142	10	0	6		R,CWD
Pterigynandrum filiforme	PTEFIL	126	109	1	16	0	LT	R,LT
Plagiothecium spp.	PLATCH	107	85	15	2	5		R,CWD,LT
Plagiomnium ellipticum	PLAELL	20	14	5	0	1		R,CWD
Rhizomnuim punctatum	RHIPUN	27	17	8	0	2		R,CWD
Eurhynchium striatum	EUSTRI	7	5	2	0	0		R,CWD
Brachythecium salebrosum	BRASAL	6	2	4	0	0		R,CWD
Pohlia nutans	POHNUT	8	4	3	3	0		R,S,CWD
Dicranella heteromalla	DICHET	5	1	1	1	2		R,S,CWD
Polytrichum formosum	POLFOR	6	4	0	0	2		R,S

variables (Eq. 1), 1000 random simulations were performed for each pair of variables. The mean and 95% confidence intervals were calculated from simulated data. For community level characteristics, 100 random simulations were used, and field data were compared with the whole range of simulated values. Observed and expected frequencies of the most common species combinations were also compared with these neutral simulations.

Data from all non-empty microplots were used to study dependence between variable pairs (substrate-species or species-species). Community level characteristics were calculated based on three data sets: a) data from all non-empty microplots, b) data from non-empty microplots on rock, c) data from non-empty microplots on dead wood. Information theoretical analyses were performed by the SYN-TAX program package (Podani 1993).

Results

Of the 5184 microplots, 1508 contained bryophytes. 33 species were recorded (Table 1).

Relationships between species and substrate types

The most frequent substrate was rock (n=1268). CWD was abundant (n=181), whilst soil and living trees were uncommon as substrate types (n=32 and 25, respectively).

From the species occurring more than 10 times in the data set, 5 were associated to coarse woody debris, 8 to rock and 5 to both major substrates. Only *Pterigynandrum filiforme* was associated to living trees (Table 1). The frequency of rare species was too low for statistical analysis, so their substrate preference was determined qualitatively based on field experience and literature (Boros 1968, Orbán and Vajda 1983). Dead wood inhabiting species frequently occurred also on rocks.

Species groups and interspecific associations

Based on the classification of species (Fig. 1) the four most common species: *Grimmia hartmanii* (on rock), *Hypnum cupressiforme* (on all substrates), *Paraleucobryum longifolium* (on rock) and *Isothecium alopecuroides* (on rock) are separated from other bryo-
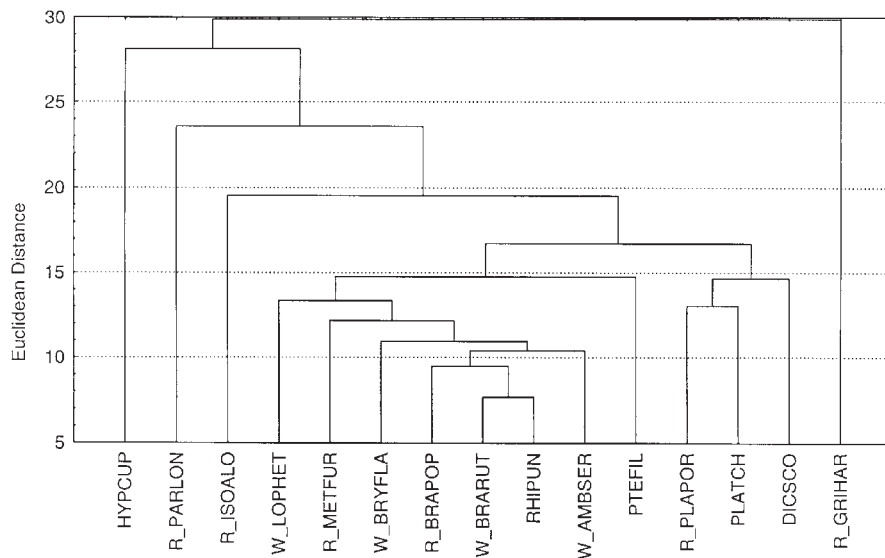
phytes. The rupicolous species *Plagiochila porelloides* is in the same group with *Plagiothecium spp.* and *Dicranum scoparium* (they occur on both major substrates). In the largest species group, dead wood inhabiting species (*Lophocolea heterophylla, Bryum flaccidum, Brachythecium rutabulum, Amblystegium serpens*) are mixed with rupicolous species (*Metzgeria furcata, Brachythecium populeum*) and with *Rhizomnium punctatum*, which occurs on both major substrates. *Pterigynandrum filiforme* (on living trees and rock) is in intermediate position between the two groups.

Figure 2. Significant interspecific associations among dominant and subdominant species on the basis of association function and 1000 Monte Carlo simulations (p<.05). Thick lines: positive associations, thin lines: negative associations. See Table 1, for species names.

Interspecific associations between species are shown in Fig. 2. The most frequent species (*Grimmia hartmanii, Paraleucobryum longifolium, Hypnum cupressiforme*) had only negative associations, mainly with epixylous species (*Lophocolea heterophylla, Bryum flaccidum, Brachythecium rutabulum, Amblystegium serpens*) and with species occurring on both CWD and rocks (*Plagiothecium spp., Rhizomnium punctatum*). The latter two species had positive associations with *Plagiochila porelloides* (rupicole) and *Dicranum scoparium* (occurs on both major substrates).
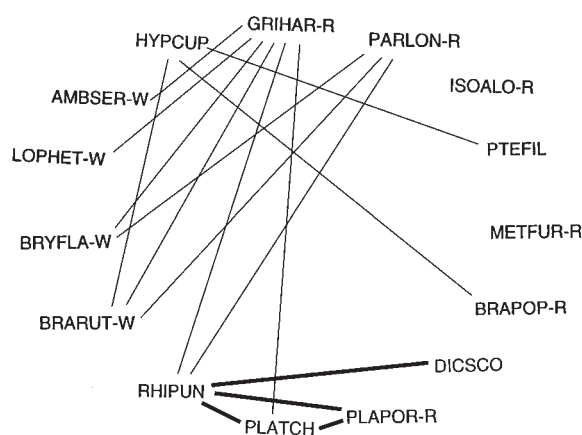
The results of these two methodologically different analyses are very similar. The bryophyte vegetation on rocks is heterogeneous. At this scale of investigation, the four most common species occur separately on rocks, still other rupicolous species occur often together with species occurring on logs or on both substrates. The four most frequent species occur mainly on exposed, dry rock surfaces, whereas others are restricted to more humid fissures rich in humus, where the rupicolous and epixylous species co-occur. In this species-rich group, the rupicolous and epixylous assemblages are not separated.

Analysis of species combinations

Observed species combinations differed significantly from simulated random references both in number and frequency (Table 2). The number, diversity and evenness of species combinations were lower, while associatum (importance of interspecific constraints) was higher than expected. Similar results were obtained for all three data sets, i.e., using all data, and data collected from rock and CWD substrates, respectively (c.f. Table 2). This means that the obtained differences between observed and ex-

Table 2. Comparison of community characteristics of field observations (number of species combinations, florula diversity, florula evenness and associatum) with the mean and range of random references based on 100 random simulations. The functions were calculated on the basis of all plots, plots on coarse woody debris (CWD), and plots on rock (R) separately.

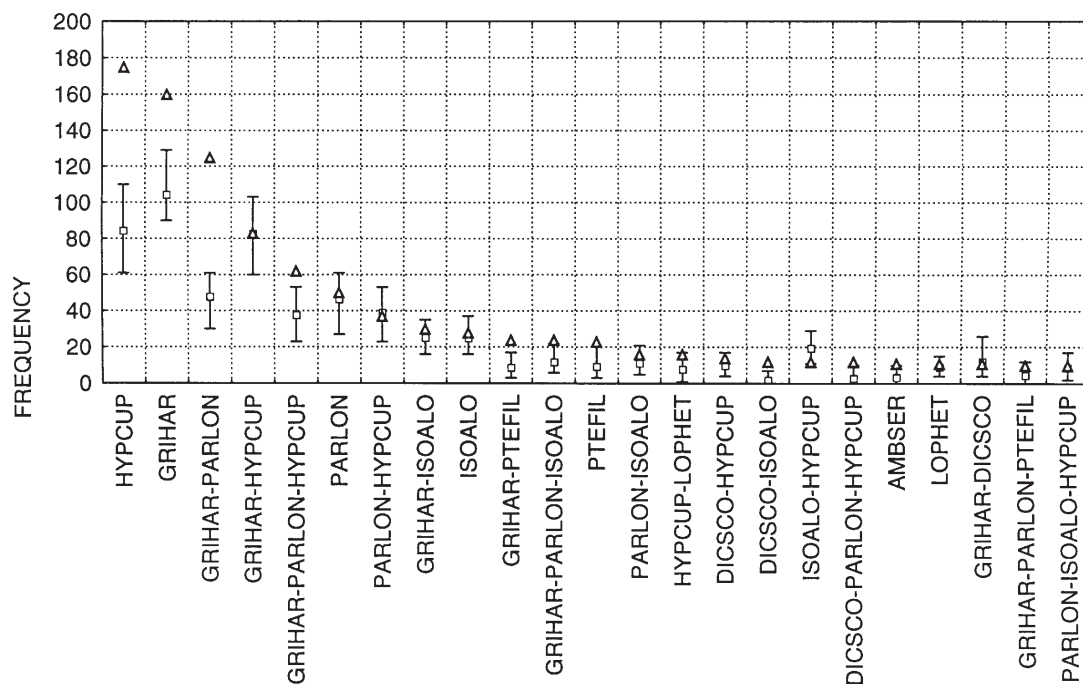|	all plots		plots on CWD		plots on R	
	random	field	random	field	random	field
number of combinations	433.5 [412;448]	364	80.7 [72;92]	71	333.6 [314;349]	299
florula diversity	10688 [10583;10790]	9530	977 [926;1033]	924	8586 [8495;8649]	7621
florula evenness	0.671 [0.665;0.678]	0.598	0.720 [0.682;0.761]	0.681	0.657 [0.650;0.662]	0.583
associatum	1245 [1142;1349]	2403	378 [321;429]	492	882 [820;924]	1847

Figure 3. Observed frequencies of dominant species combinations (△) compared with random references (□-mean ± range) in the case of microplots. See Table 1, for species names.

pected values result not only from substrate specificity of species.

Fig. 3 shows the observed frequencies of some realised species combinations together with the frequency range of simulations. The most frequent species combinations (*Hypnum cupressiforme*; *Grimmia hartmanii*; *Grimmia hartmanii - Paraleucobryum longifolium*) were significantly more frequent than suggested by random simulations. Other combinations (*Grimmia hartmanii - Hypnum cupressiforme*; *Paraleucobryum longifolium*; *Paraleucobryum longifolium - Hypnum cupressiforme*) did not differ from random expectation. Some less fre-

quent combinations (*Pterigynandrum filiforme*; *Grimmia hartmanii - Pterigynandrum filiforme*; *Dicranum scoparium - Isothecium alopecuroides*) were slightly more frequent than expected from random simulations, and only one combination was slightly less frequent than random expectation (*Isothecium alopecuroides - Hypnum cupressiforme*).

For the 12 most frequent bryophyte species, Fig. 4 shows the distribution of microplots among species richness categories. At this scale (100 cm^2), species differed considerably in the average number of species co-occurring with them. *Grimmia hartmanii, Hypnum cupressi-*
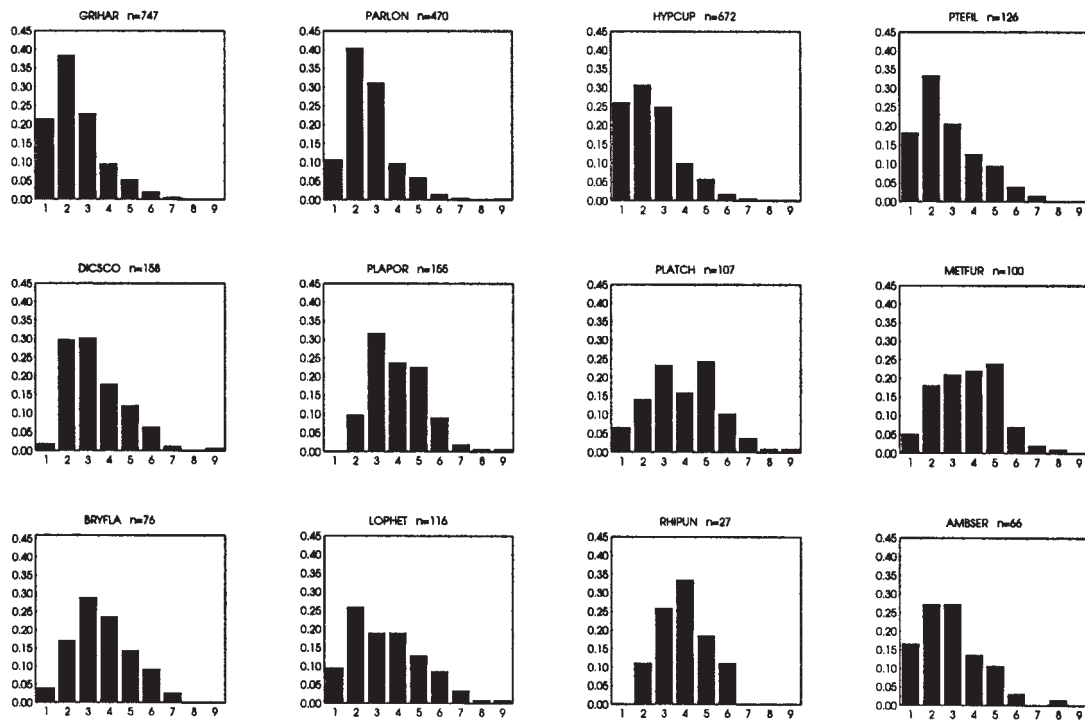
Figure 4. Distribution of microplots among species richness categories for each of the 12 most frequent bryophyte species. X axis: species richness of microplots, Y axis: relative frequency, n: number of microplots containing the species. See Table 1, for species names.

forme, *Paraleucobryum longifolium* and *Pterigynandrum filiforme* occurred mostly in microplots containing only two species. Species on humus-rich outcrops (*Dicranum scoparium, Plagiochila porelloides, Metzgeria furcata*) and dead wood (*Amblystegium serpens*, *Lophocolea heterophylla*, *Bryum flaccidum*) occurred in more diverse microplots, i.e., the proportion of microplots containing 3, 4, 5 species was considerable. *Plagiothecium* spp. and *Rhizomnium punctatum* associated with both rock and CWD - also occurred in more diverse microplots.

Discussion

Classical statistical approaches (e.g., chi-square statistic, Kershaw 1964, Greig-Smith 1964) were frequently used in ecological studies to detect pairwise associations. However, some of the detected associations may be a methodological artefact, because the obtained results depend on the frequency distribution of variables involved (Palmer and van der Maarel 1995). Most real samples are small in size, which in turn limits the number of possible species combinations. Associations of rare variables may be underestimated, whereas those of abundant types can be over represented. The problem of frequency constraints can be overcome by applying neutral models, like finite Monte-Carlo simulations (Bartha and Kertész 1998). In the absence of test statistics for the applied information theoretical functions, Monte Carlo simulations are appropriate for making statistical inference.

This problem was relevant to the present study: more significant pairwise associations were found by the chi-square statistic than by the association function (Eq. 1).

Substrate specificity

Most studied species are associated with a specific substrate type (R, CWD, living tree). *Grimmia hartmanii* was the dominant species on rocky outcrops. It is an initial coloniser of bare rock surfaces; often occurring on relatively dry, vertical surfaces, where other species cannot establish themselves. It has a typical colonist strategy (During 1979, 1992): it does not develop sporophytes, rather it often carries large long-living gemmae. Most often it forms monospecific mats or occurs together with *Paraleucobryum longifolium* or *Pterigynandrum filiforme* (Fig. 3). Depending on bedrock type, different *Grimmia* species dominate the driest epilithic communities (Smith 1982). *Paraleucobryum longifolium* often occurs together with *Grimmia hartmanii* on bare rocks, or sometimes it grows on thin humus layer. *Pterigynandrum filiforme* appears on bare rock surfaces or on the bark of living trees; no humus develops under its mat. It occurs alone, or on outcrops, together with *Grimmia hartmanii* (Fig. 3). These three species rarely grow together with

species characteristic of humus-rich outcrops or CWD. Since only a few species are able to tolerate the xeric circumstances provided by the bare outcrops, they occur in monospecific or species-poor mats (Fig. 4). *Hypnum cupressiforme* was also a very frequent species in this vegetation and it has an interesting behaviour. It appeared both on outcrops and on CWD. Often (25% of its occurrences c.f. Fig. 4) it formed monospecific mats at this spatial scale (100 cm^2). Despite its high frequency, it rarely occurs together with coloniser species, or with species of CWD. In a study of epiphytic vegetation in a *Fagus - Fraxinus* forest in Denmark (Rasmussen and Hertig 1977), *Hypnum cupressiforme* was also found to be negatively associated with many other species.

Shaded wet crevices and fissures with considerable humus supported species-rich bryophyte assemblages (*Plagiochila porelloides, Dicranum scoparium, Plagiothecium* spp., *Metzgeria furcata, Homalia trichomanoides*). These sites also served as habitat for some rare species (*Cynodontium strumiferum, Tritomaria quinquedentata, Barbilophozia barbata*). Organic matter among rocky outcrops originates from CWD. For this reason, there is an overlap between the species pool of humus rich outcrops and that of dead wood. Some CWD inhabiting species (*Lophocolea heterophylla, Bryum flaccidum, Amblystegium serpens*) also occurred in wet rock crevices (see Table 1), whereas *Plagiothecium* spp. and *Rhizomnium punctatum* were not only frequent species, but they also inhabited both humus rich rocks and CWD. These species often occurred in diverse microplots (Fig. 4). *Isothecium alopecuroides* exhibited transitional characteristics between colonists (*Grimmia hartmanii, Paraleucobryum longifolium, Pterigynandrum filiforme*) and species of humus-rich rocks.

These interspecific relations are valid only at very fine (100 cm^2) spatial scale in the investigated bryophyte vegetation. Similarly to the detection of spatial pattern and the clumping scale of populations, the values of interspecific associations and all the vegetation functions used are dependent on the spatial scale of observation, i.e., on sampling unit size (Podani et al. 1993, Bartha et al. 1995b). The characteristic patch sizes of the most frequent species (*Grimmia hartmanii, Paraleucobryum longifolium, Hypnum cupressiforme*) are higher than 100 cm^2, whereas species of humus rich outcrops and CWD are mixed at finer spatial scale. Sadler and Bradfield (2000) found much more positive interspecific associations in the terrestrial bryophyte vegetation of subalpine forest at a bit larger spatial scale (1000 cm^2).

Accumulation of coarse woody debris is a general characteristic of unmanaged semi-natural forests (Kirby

et al. 1998). CWD offers different habitats for many species of bryophytes and other organisms (e.g., Harmon et al. 1986). Since CWD is generally in short supply in most managed stands in Hungary, there were some rare species in our sample (*Calypogeia suecica, Nowelia curvifolia, Blepharostoma trichophyllum, Saionia uncinata,* Table 1) that were confined to large, well decayed logs characteristic only of near-natural forests. As it has been found in many different forest types (McCullough 1948, Söderström 1988c, McAlister 1997), CWD inhabiting species exhibit a range of ecological demands and dispersal abilities. This study suggests that the presence of CWD not only provided habitat for wood inhabiting bryophytes, but also resulted in diverse rupicolous bryophyte assemblages on outcrops rich in humus.

Community organization

In terms of phytosociology (Hübschmann 1986), the species composition of the studied epilithic vegetation corresponds to the *Paraleucobryetum longifolii* synusium (Sjögren 1964) in alliance *Grimmion hartmanii* (Philippi 1956). The described epixylous vegetation is similar to the alliance *Blepharostomion trichophylli* (Barkman 1958). However, there are some problems in interpreting the investigated bryophyte vegetation as stands of these synusia:

- In reality, bryophytes living on decaying woods and outcrops are not separated as distinctly as descriptions suggest. The species composition of humus-rich outcrops is much more different from that of bare rock surfaces than from that of decaying woods.

- The described synusia occur in the colline and montane region of Central Europe on silicate rocks and decaying wood, respectively. However, this approach cannot account for the fact that the composition of bryophyte vegetation (both on outcrops and on CWD) is very much dependent on the forest type (e.g., beech or spruce), stand age, climate (affected by aspect, slope, etc.) and the structural complexity of the forest. The diversity of bryophyte vegetation is strongly affected by the quantity and quality of CWD in the stand.

- Bryophyte vegetation occurring on rocky outcrops cannot be considered as a single association. These outcrops provide heterogeneous habitats, and the occurrence of species combinations is affected by microtopography and associated microclimatic conditions.

In this study, several species showed strong substrate preference (niche segregation). Interspecific association

(expressed as associatum) was very important in the vegetation on both substrates (CWD, R). There were many realised species combinations with significantly higher (or lower) frequencies than expected under the assumption of random mixing, even on seemingly homogeneous surfaces, where it is hard to assume niche segregation. Many studies showed that bryophytes behave opportunistically, the effects of niche segregation are negligible, existing mats have positive feedback to establishment, and mortality is not density dependent (Slack 1977, Lee and La Roi 1979, Watson 1980, Sadler and Bradfield 2000). These could be true for assemblages of humus-rich outcrops and CWD, but not for species of exposed rock surfaces, where fast growing (*Hypnum cupressiforme*) and colonist (*Grimmia hartmanii*) species can dominate. Microtopography and microenvironmental conditions determine the occurrence of epilithic species (Kunkel 1975, Yarranton and Beasleigh 1968, Alpert 1985). In this study area, there were only a few species that were successful on dry exposed rock surfaces; but even there, the number of realised species combinations was limited. More species appeared in humid crevices with accumulations of organic matter. Species composition of humus-rich crevices showed slighter deviation from random expectation. More sophisticated studies of the effect of microtopography to epilithic vegetation might reveal that microenvironmental factors play more important role in determining species composition of outcrops than interspecific relationships. Dispersal and establishment are important in determining the composition of epixylous vegetation, especially in the case of those rare species that are confined to well decayed large logs of mostly fragmented semi-natural forests (Söderström 1988a, 1989, 1990).

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