

DIVERSITY AND COMPOSITION OF DEAD WOOD INHABITING BRYOPHYTE COMMUNITIES IN EUROPEAN BEECH FORESTS

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Abstract: Species composition and diversity of bryophyte communities occurring on dead beech trees were analyzed in five European countries (Slovenia, Hungary, The Netherlands, Belgium and Denmark). Altogether 1.009 trees were inventoried in 19 beech dominated forest reserves. The differences in the composition of bryophyte communities were high among countries and it overwhelms the effect of decay stages, which affect the species composition at local scale. Well decayed trees were dominated by epixylic species in Slovenia, while in other countries the proportion of opportunistic bryophytes was much higher and in Atlantic countries uproot species are also common. In Slovenia hepatics, in Hungary and Denmark pleurocarps, and in The Netherlands and Belgium acrocarps were the most frequent. Diversity of communities differed considerably among regions. Slovenian sites were the hotspot of bryophyte diversity characterized by high species richness (both tree and country level) and a high fraction of rare and threatened species. This richness is most likely caused by the combination of high air humidity combined with a very high degree of naturalness of the Slovenian sites. The diversity of Hungarian stands was intermediate reflecting the relatively high naturalness of the study sites, as well as a rather continental climate sub-optimal for epixylic liverworts. Atlantic forests have deteriorated bryophyte communities on dead trees, dominated by a few opportunistic species. This is partly a result of habitat fragmentation and past and recent management of forest. Most of the stands the amount and quality of dead wood is not suitable for species rich epixylic bryophyte communities.

INTRODUCTION

An important feature of natural forests is that they possess high amounts of coarse woody debris (CWD) in all stages of decay and also high proportion of old, living trees with dead parts (Maser & Trappe, 1984; Harmon *et al.*, 1986; Ferris-Kaan *et al.*, 1993; Peterken, 1996; Csóka, 2000). Apart from bryophytes these different CWD types provide important habitats for

a diversity of organisms, including fungi, lichens, invertebrates, amphibians, cavity nesting birds and small mammals (Maser & Trappe, 1984; Harmon *et al.*, 1986; Eckloff & Ziegler, 1991; Ferris-Kaan *et al.*, 1993; Samuelsson *et al.*, 1994; Esseen *et al.*, 1997; Csóka, 2000; Siitonen, 2001; Heilmann-Clausen & Christensen, 2003).

In temperate European beech (*Fagus sylvatica*) forests fine scale gap dynamics, based on the death of individual or small groups of trees, is the main form of natural disturbance, providing a continuous presence of dead wood of different size and decay categories over time (Korpel, 1995; Peterken, 1996; Emborg *et al.*, 2000; Standovár & Kenderes, 2003).

Man has heavily influenced the European beech forest landscape for centuries (Rose, 1992; Peterken, 1996), causing artificial stand structure and disturbance regime in most present-day beech forests. Many structural elements important for forest dwelling organisms, e.g. water bodies, veteran trees, dead wood, intermixing tree species, have decreased considerably both in quantity and quality (Christensen and Emborg, 1996; Kirby *et al.*, 1997). For CWD it has been estimated that the decline in availability has been in the range of 90-98% in the Fennoscandian region (Siitonen, 2001). In the European beech forest zone the degree of decline in available CWD is not known with certainty, but it is estimated to be comparable to the degree in Fennoscandia (Christensen *et al.*, 2005). Forest fragmentation has imposed additional difficulties for dispersal of dead wood dependent forest organisms between remaining old-growth stands (Saunders *et al.*, 1991; Söderström & Jonsson, 1992). Especially, sites retaining natural characteristics are now widely separated at the regional and continental scales. The combination of forest management and forest fragmentation has led to a substantial decline in the populations of most forests dwelling organisms, and especially of species depending on dead wood, of which many have decreased or gone extinct locally and regionally (Rose, 1992; ECCB, 1995; Siitonen, 2001; Söderström & Jonsson, 1992). Many bryological studies proved from different forest types that the bryophyte vegetation of managed stands is impoverished comparing to old-growth forests, especially true epixylic liverworts are sensitive for forest management and fragmentation (Gustafsson and Hallingbäck, 1988; Söderström, 1988a; Andersson & Hytteborn, 1991; Lesica *et al.*, 1991 Rambo & Muir, 1998; Ódor & Standovár, 2001). Generally, remnants of semi-natural beech stands are more widespread and less influenced by human activities in the mountains of Central Europe and the Dinaric region, than in the Atlantic lowlands of northwest Europe (Peterken, 1996; Standovár and Kenderes, 2003).

Among bryophytes many species occur on dead wood obligatorily (true epixyls) or facultatively (epiphytic, terricol and epilithic species). Successional studies focusing on one habitat type typically show a clear compositional change of bryophyte vegetation during the decay of trees (McCullough, 1948; Söderström, 1988a, 1993; Heilmann-Clausen *et al.*, 2005; Ódor & van Hees, 2004). At the continental scale a lot of bryophyte species has a relatively restricted distribution, hence phytogeographic and climatic factors are the major determinants of species composition (Barkmann, 1958; Phillippi, 1965; Hübschmann, 1986; Marstaller, 1986; Qian *et al.*, 1999). At the regional scale other factors such as forest types, management

type, distance from water body, microclimate, tree species composition, soil/bedrock type are highly important (McCullough, 1948; Raschendorfer, 1949; Barkman, 1958; Muhle & LeBlanc, 1975; McAlister, 1997; Aude & Poulsen, 2000).

This present study aims to compare the community composition, diversity and functional groups of bryophytes inhabiting decaying beech trees in five countries of Europe in semi-natural beech reserves.

MATERIAL AND METHODS

Study sites

Altogether 19 forest reserves were selected for this study in Slovenia, Hungary, The Netherlands, Belgium and Denmark. The selected sites represent, as closely as possible, the best natural reference of beech dominated forests for investigated countries. In each country approximately 200 fallen dead trees were selected for the study. In Belgium only one site was selected, but it was divided into two parts based on different age and forest history. In Hungary and Slovenia two sites were studied, each represented by c. 100 trees. In Denmark five sites were included representing four regions. Finally, The Netherlands is represented by eight sites with a variable numbers of studied trees. The high number of study sites in The Netherlands reflects the low amount of CWD available at each site.

Some general features of the investigated sites relating to naturalness, age, stand structure, soil type and climate are shown in Table 1.

Bedrock and soil characteristics (acidity, nutrient content, etc.) differ considerably among sites, both between and within countries, but in Atlantic countries the selected sites were much more heterogenous compared to Slovenian and Hungarian forests.

All stands were dominated by beech, but in some sites other tree species are also important. Forest history differs considerably among sites and countries. Some stands were cut completely in the past and have a rather uniform age structure, with dominant tree ages between 100 and 250 years. Some of these stands have unbroken forest continuity (e.g. Óserdő in Hungary, part of Strødam in Denmark, the Dutch reserves on sandy soils) while others were used as arable or pasture land for a long time breaking forest continuity (e.g. Dutch reserves on clay soil). Other sites have a more complex history of human use, including periods of forest grazing, selective cutting and even small-scale agriculture, but have never been cut totally in the past. These forests are characterized by uneven age structure, and the ones with the least human influence (e.g. Suserup in Denmark, Kékes in Hungary, Krokár in Slovenia) by structures and gap dynamics similar to those reported from virgin forests (Korpel, 1995; Hartman, 1999; Emborg *et al.*, 2000; Standovár & Kenderes, 2003). However, there is only one site, Rajhenav in

Slovenia that seems to support a true virgin forest, which has suffered minimal, if any direct human intervention (Bončina, 1999).

The observed features of CWD differ considerably among the investigated stands. The volume of CWD is generally 40-70 m³/ha in the Dutch sites, 100-180 m³/ha in other sites and very high, 300 m³/ha in Rajhenav, Slovenia (Kraigher *et al.*, 2003; Christensen *et al.*, 2005). All investigated reserves hold large dead beech trees (diameter at breast height (DBH) larger than 80 cm), but in the reserves in Belgium and The Netherlands strongly decayed trees (decay phase 4, 5, 6) are missing or scarce.

Dead tree selection and description

Trees were selected using two criteria: decay and size (DBH). Decay stages were classified using a six-class system based on outer physical features of trees (presence of bark, branches, softness and surface of wood, shape of trunk, Ódor & van Hees, 2004). Most dead trees represent a mixture of different decay stages, therefore the dominant decay class was used during the analysis.

Inventory of bryophytes

Bryophytes occurring on the selected trees were recorded in each country in summer and autumn 2001. The inventory included the log, the uprooting part of the log, the snag (if present), and the major branches of the crown (if present). The nomenclature used follows Corley *et al.* (1981) and Corley and Crundwell (1991) for mosses, and Grolle (1983) for hepatics. *Plagiochila porelloides* and *P. asplenioides* were not separated and *Plagiothecium* species follow Frisvoll *et al.* (1995).

Data analysis

The general structure of the data sets was explored by detrended correspondence analysis (DCA, Hill & Gauch, 1980; Jongman *et al.*, 1987; Økland, 1990) using CANOCO 4.5 (ter Braak & Šmilauer, 2002). Species with less than five records and trees with less than five species recorded were excluded from the analysis. Between sample scores of different DCA axes and countries heterogeneity analysis was carried out using chi² statistics, sample scores on DCA axes were classified according to the quartiles (Zar, 1999). In the case of decay stages Spearman rank correlation was calculated with the ordination axes (Zar, 1999).

Diversity of bryophytes were compared among countries based on the whole dataset investigating the following descriptors: species richness, number of occurrences and tree level species richness, which was compared among countries by ANOVA and Tukey-type multiple comparison after logarithmic transformation of the original data (Zar, 1999).

Country	Reserve	Size (ha)	Age (yr) ¹	Other trees ²	Living volume (m ³ /ha)	CWD volume (m ³ /ha)	No. of sampled trees	DBH of CWD (cm) ³	Decay stages of CWD ⁴	Elevation (m)	Bedrock	Tave (°C) ⁵	Tmin (°C) ⁶	Tmax (°C) ⁷	Precipitation (mm) ⁸
Slovenia (S)	Rajhenav (R)	51	old	Abies alba	813	299	110	50 (17, 97)	1-6	865	limestone	7.7	-1.9	16.9	1579
	Krokar (K)	73	old	Abies alba	633	153	101	37 (10, 98)	1-6	1120	limestone	8.4	-1.6	17.8	1526
Hungary (H)	Kékes (KEK)	63	old	Tilia platyphyllos, Acer pseudoplatanus, A. platanoides	454	99	97	55 (23, 125)	1-6	850	andesite	5.7	-4.7	15.5	840
	Oserdo (OSE)	25	200	-	765	164	110	66 (18, 135)	1-6	850	limestone	6.1	-4.1	15.5	896
The Netherlands (N)	Speuldebos (SB)	27	200	Q. robur, Q. petraea	457	44	42	46 (25, 83)	1-4	42	sand	9.4	2.2	17.2	876
	Drie (DR)	5	200	Q. robur, Q. petraea	457	44	21	51 (21, 90)	1-3	35	sand	9.4	2.2	17.2	876
	Gortelsebos (GB)	15	200	Q. robur, Q. petraea	507	66	11	62 (14, 95)	2-3	45	sand	9.4	2.2	17.2	873
	Weversbergen (WB)	12	100	-	469	49	32	55 (18, 120)	1-3	80	loam-sand	9.4	2.2	17.2	856
	Wuiperhorst (WH)	3	200	Q. robur, F. excelsior, Carpinus betulus	701	72	44	68 (36, 120)	2-4	3	clay	9.4	2.8	17.2	827
	Oostbroek (OB)	3	150	Q. robur, F. excelsior	-	-	10	71 (57, 88)	2	2	clay	9.4	2.8	17.2	827
	Dassenberg (DB)	12	200	Q. robur, Q. petraea	402	63	37	67 (18, 105)	1-3	96	sand	9.4	2.2	17.2	906
	Amelisseweerd (AW)	3	150	Q. robur, F. excelsior	-	-	5	73 (60, 90)	1-3	2	clay	9.4	2.8	17.2	827
Belgium (B)	Zoniënwood (ZON)	80	150	Q. robur, Q. petraea	602	24	67	45 (15, 118)	1-5	105	loess	9.4	3.4	18.2	829
	Zoniënwood - Kern (ZOK)	18	220	-	794	139	125	69 (15, 117)	1-5	105	loess	9.4	3.4	18.2	829
Denmark (D)	Knagerne (KNA)	6	230	-	449	152	25	72 (27, 108)	1-4	80	sand	7.5	0	15.5	719
	Velling (VEL)	24	275	-	489	114	25	53 (20, 93)	1-6	70	sand	7.5	0	15.5	839
	Suserup (SUS) Mons	19	old	F. excelsior, Ulmus glabra, Q. robur	674	176	50	76 (24, 131)	2-6	20	loam-sand	8.1	0.8	16.7	644
	Klinteskov (MON)	25	350	-	201	100	50	48 (21, 86)	1-6	100	chalk	7.9	0.2	16.2	586
	Strodam (STR)	25	250	Q. robur	490	181	50	77 (21, 127)	1-6	23	loam-sand	7.7	-0.5	16.2	697

Table 1. Stand structural and climatic features of the selected forest stands. 1: Age since last cutting or plantation; old: the stand was never cut in the past. 2: Tress with min. 5% stand volume besides beech. 3: Mean diameter at breast height (DBH) based on the investigated dead trees, minimum and maximum are in brackets. 4: Minimum number of trees from the same decay stage is 3 from one site. 5: Mean annual temperature. 6: Mean temperature of the coldest month. 7: Mean temperature of the warmest month. 8: Annual precipitation.

Species were classified based on their taxonomical status (hepatics, acrocarpic and pleurocarpic mosses, although pleurocarpic and acrocarpic are not real taxonomic categories) and their substrate preference using the following ecological groups: epixylic (occurring mainly on well decayed wood), epiphytic (occurring mainly on bark), opportunistic (no special substrate preference), terricolous (occurring on forest floor and litter), uproot (occurring on the mineral soil of the vertical uprooting part of the logs), epilithic (occurring on rocks). The ecological classification was based on different handbooks (Frey & Frahm, 1995; Smith, 1978, 1990; Dierssen, 2001), quantitative studies (Söderström, 1988a; Ódor & van Hees, 2004) and field experiences of the authors. Appendix 1 contains the list of bryophytes, their number of occurrences per country, and their classification into taxonomic and ecological types. Relative frequencies of these ecological and taxonomic groups were compared among countries using heterogeneity analysis of contingency tables (Zar, 1999).

Apart from the general analyses of species richness, special emphasis was given to species that are considered to be threatened all over or regionally in Europe. The *Red Data Book of European Bryophytes* (ECCB, 1995) was the major reference for Europe, but regional red lists for different countries (Martinčič, 1992; Papp *et al.*, 2001) were also used.

RESULTS

Species composition of bryophytes

The whole dataset contained 8986 occurrences of 161 species present on 1009 trees. The dataset used for ordination contained 102 species and 732 trees after deleting species with less than five occurrences and logs with less than five species. The eigenvalues of the first two axes were 0.57 and 0.27, with gradient lengths of 3.99 and 3.90 SD units, respectively. The samples were separated according to the countries along the first ordination axis in the order Slovenia, Hungary, Denmark, Belgium and The Netherlands (Fig 1a). The χ^2 value between the first axis quartiles and countries were 1227 (df=12, $p<0.001$), while the same statistics between second axis and countries were 293 (df=12, $p<0.001$). The second axis was highly correlated with decay stages ($r_s=-0.413$, $p<0.001$), the earlier decay stages had higher, while the later ones had lower scores on it (Fig. 1b). The correlation between decay stages and the first axis was weaker ($r_s=-0.094$, $p<0.05$). The effect of decay along the second axis was very pronounced in Slovenia, distinct in Hungary and Denmark, and not important in The Netherlands and Belgium (Fig 1a). The Slovenian samples represented very high variation along the axis, which is definitely related to the high variation in decay stage. The two Hungarian sites had similar axis scores and exhibit small variation along both axis. The species composition of the Danish samples was very heterogeneous covering a large variation along both axis. The species

composition of the Belgian sites was homogeneous, while Dutch samples were separated mainly along the second axis.

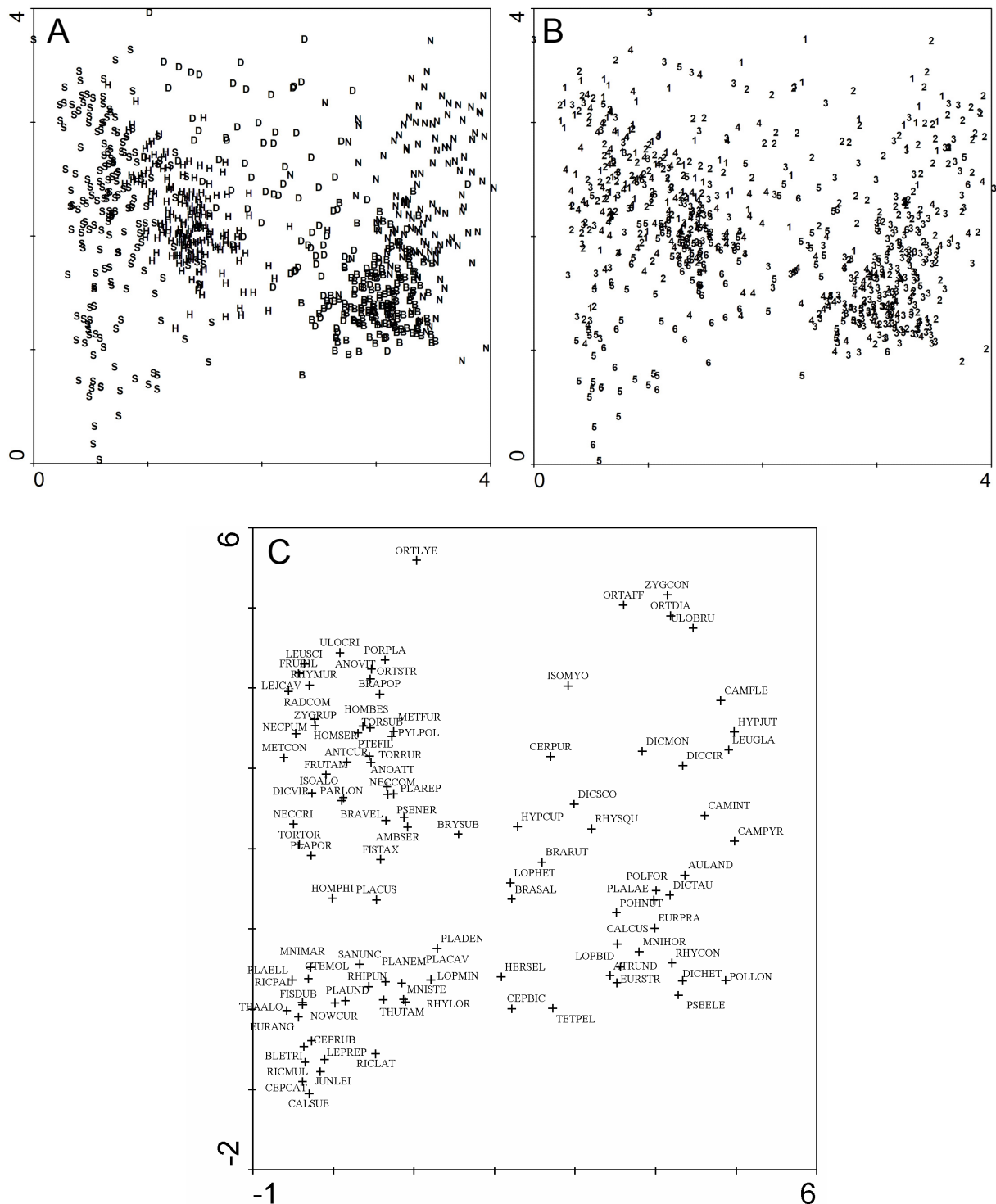


Figure 1. Position of samples (A-B) and species (C) along the first two axes of DCA analysis. Samples are labelled by country codes (A) and decay stages (B). Species codes are based on the first three letters of the genus and the species name found in Appendix 1.

The positions of species in the ordination diagram mainly reflected regional differences (Fig. 1c). The central species group in the middle of the diagram included frequent and widespread species: *Herzogiella seligeri*, *Lophocolea heterophylla*, (obligate epixyls), *Hypnum cupressiforme*, *Brachythecium rutabulum*, *Brachythecium salebrosum*, *Dicranum scoparium*, *Bryum subelegans*, (opportunistic species). *Tetraphis pellucida* (obligate epixyl) had a low score along the second axis, because it is frequent in Slovenia and The Netherlands, but rare in the Hungarian, Belgian and Danish sites. Species with low first axis scores preferred the Dinaric and Central-European sites and several of them occurred mainly in the Slovenian sites. True epixylic liverworts had low scores on both axis and missing or very rare in other countries, e.g. *Calypogeia suecica*, *Jungermannia leiantha*, *Cephalozia catenulata*, *Riccardia multifida*, *Blepharostoma trichophyllum*, *Cephaloziella rubella*, *Nowellia curvifolia*. Some epiphytes with high scores along the second axis were also restricted to the Slovenian forests (*Lejeunea cavifolia*, *Zygodon rupestris*, *Neckera crispa*, *Ulota crispa*, *Dicranum viride*), while other species occurred both in Slovenian and Hungarian sites (*Orthotrichum stramineum*, *Pylaisia polyantha*, *Pterygynandrum filiforme*). Species that have most of their occurrences in Hungary are mainly epiphytes (*Anomodon viticulosus*, *Platygyrium repens*, *Pseudoleskeella nervosa*, *Homalia besseri*). Species occurring on strongly decayed trees in Hungary belong to the opportunistic and epixylic species of the central species group (*Plagiothecium denticulatum*, *Herzogiella seligeri*, *Lophocolea heterophylla*). Danish trees were dominated mainly by opportunistic species that are frequent everywhere. Species with high first axis scores were specific for the Atlantic region. Species with low second axis scores were mainly terricol species occurring on mineral soil attached to the uprooted parts of fallen trees and on the bases of broken dead trees (*Pohlia nutans*, *Atrichum undulatum*, *Mnium hornum*, *Pseudotaxiphyllum elegans*), while high scores were obtained by a number of epiphytes (*Zygodon conoideus*, *Ulota bruchii*, *Dicranoweisia cirrata*, *Dicranum tauricum*). A number of opportunistic and epixylic species obtained intermediate second axis scores (*Campylopus species*, *Leucobryum glaucum*, *Aulacomnium androgynum*, *Eurhynchium praelongum*).

Species richness and functional groups

The highest species richness of bryophytes was recorded in Slovenia, 103, whereas it was between 50 and 70 in the other countries (Table 2). More than one third of all the records (3397 of 8986) were made in Slovenia. Tree level species richness showed similar differences among countries (ANOVA; df = 4, 1003; F value 71.71). It was the lowest in Denmark and The Netherlands, intermediate in Belgium and Hungary and the highest in Slovenia.

The relative frequency of hepatics, acrocarpic and pleurocarpic mosses considerably differed among countries (Table 2, $\chi^2=807$, df=8, $p<0.001$). Comparing the countries in Slovenia the relative frequency of hepatics was very high, in Hungary and Denmark the pleurocarps, in The Netherlands and Belgium the acrocarps were the most important.

The relative frequency of ecological groups (Table 2) was significantly different among countries ($\chi^2 = 1590$, $df = 20$, $p < 0.001$). The proportion of epixylic species c. 22% in Slovenia, c. 20% in Hungary, c. 14-16% in The Netherlands and Belgium, and lowest (c. 9%) in Denmark. In Slovenia the species richness of this group was much higher (27) than in other countries (7-10). The relative frequency of epiphytes was also higher in Slovenia than in other countries. The proportion of opportunistic species was similar in all countries (0.44-0.52) except Slovenia (0.30). Species occurring on mineral soil (mainly on uprooted part of logs and at the leg of snags) were important in the Atlantic countries.

Variable	Slovenia	Hungary	The Netherlands	Belgium	Denmark	Whole data set
Diversity						
Number of trees	213	207	197	192	200	1009
Number of species	103	65	56	48	69	161
Number of occurrences	3397	1928	1170	1525	966	8986
Tree level species richness ¹	15.95±9.81 ^a	9.31±5.31 ^b	5.94±4.76 ^c	7.94±4.11 ^b	4.83±3.66 ^c	8.91±7.21
Taxonomical groups						
Hepatics	0.28	0.12	0.07	0.10	0.13	0.17
Pleurocarps	0.43	0.65	0.40	0.51	0.60	0.51
Acrocarps	0.29	0.22	0.53	0.39	0.26	0.32
Ecological groups						
Epixylic	0.22	0.20	0.15	0.16	0.09	0.18
Epiphyte	0.38	0.28	0.27	0.11	0.26	0.29
Opportunistic	0.30	0.50	0.44	0.45	0.52	0.41
Terricol	0.04	0.00	0.01	0.04	0.02	0.03
Uproot	0.02	0.01	0.13	0.23	0.09	0.07
Epilythic	0.04	0.01	0.00	0.00	0.01	0.02

Table 2. The values of diversity variables and relative frequencies of taxonomical and ecological groups in different countries. 1: mean±standard error. Tree level species richness significantly differed among countries (ANOVA, $F(4,1004)=71.71$, $p < 0.001$), the letters show the results of multiple comparison test.

Conservation issue of bryophytes

The whole data set contained 7 threatened species listed in the European (ECCB, 1995) or country level red lists (Martinčič, 1992, Table 3). Most of these occurrences were recorded in the virgin forest Rajhenav, Slovenia. These species occurred with very low frequencies, except for *Dicranum viride*, which was recorded very frequently in Rajhenav, where it occurred on almost all of the fallen trees in early stage of decay. This forest seems to hosts one of the largest and most important local population of this threatened species in Europe

Species	Red list	Threat category	Country	Site	N. of occurrences	Substrate type
<i>Anacamptodon splachnoides</i>	European	endangered	Slovenia	Rajhenav	1	epixyl
<i>Buxbaumia viridis</i>	European	vulnerable	Slovenia	Rajhenav	2	epixyl
<i>Antitrichia curtipendula</i>	Slovenian	vulnerable	Slovenia	Rajhenav	5	epiphyte
<i>Antitrichia curtipendula</i>	Slovenian	vulnerable	Slovenia	Krokar	1	epiphyte
<i>Dicranum viride</i>	European	vulnerable	Slovenia	Rajhenav	60	epiphyte
<i>Dicranum viride</i>	European	vulnerable	Slovenia	Krokar	1	epiphyte
<i>Dicranum viride</i>	European	vulnerable	Hungary	Oserdo	out of sample, rare	epiphyte
<i>Lophozia ascendens</i>	European	rare	Hungary	Kekes	2	epixyl
<i>Riccardia latifrons</i>	Dutch	extinct	The Netherlands	Weversberg	2	epixyl
<i>Zygodon forsteri</i>	European	vulnerable	Slovenia	Rajhenav	out of sample, rare	epiphyte

Table 3. Occurrences of threatened (locally or all over Europe) bryophytes in the investigated forest stands.

DISCUSSION

The found geographical community gradients to be complex: the investigated beech forests are different both in their climate and both in the past and recent human influence for their stand structure and dead wood characteristics. Dutch and Belgian stands at one extreme, where the original forest landscape had become highly fragmented and present day forests have transformed structure, and in many cases broken continuity. In Denmark there is a slightly more natural remnant of the original forest landscape. In Hungary and Slovenia there are large tracks of beech-dominated forests with unbroken continuity and close to original tree species composition. However it is only in Slovenia, where managed forests have rather natural structure and some remnants of truly natural forests have survived.

Regional differences in the composition of bryophyte communities are distinct and overwhelm the effect of decay stages, which affect the species composition at local scale. Thus, the succession of bryophytes during log decay differed principally among the countries. In earlier decay stages epiphytes were the most important species group in all countries, but their proportion is higher in Slovenia than in other countries. However well decayed trees were dominated by epixylic species in Slovenia, while in other countries the proportion of

opportunistic bryophytes was much higher and in Atlantic countries uproot species were more common.

Slovenian virgin forests were biodiversity hotspots of dead wood living bryophytes. Both the tree level species richness and the whole species pool was very high, and there were some species occurring in these site, which were extremely rare elsewhere in Europe. The proportions of relatively frequent, sub-ordinate species were very high, and there were many obligate epixylic liverworts among them (e.g. *Nowellia curvifolia*, *Riccardia multifida*, *R. palmata*, *R. latifrons*, *Cephalozia catenulata*, *Calypogeia suecica*, *Lepidozia reptans*, *Jungermannia leiantha*, *Blepharostoma trichophyllum*, cf. Hočevár *et al.*, 1995; Ódor & van Dort, 2003). Although most of these epixylic liverworts are broadly distributed in boreal and montane regions, they are generally rare and have been suggested to be good indicators of old-growth forests (Gustafsson and Hallingbäck, 1988; Söderström, 1988b; Samuelsson *et al.*, 1994; Ódor & Standovár, 2001). This species require a continuous presence of logs in intermediate decay and high and stable air humidity. The high diversity of Slovenian stands are due to their long history of preservation as unmanaged forest reserves supporting a continuous presence of dead wood and the uneven aged forest stand with high structural heterogeneity in combination with high precipitation.

In Hungary the distribution of obligate epixylic liverworts is limited by climate rather than substrate availability. It is well known that dry climate can act as an effective limiting factor for a lot of epixylic bryophytes, especially liverworts (Clausen, 1964; Proctor, 1982). In most of the continental beech stands air humidity is too low for these species, independently of the presence of dead wood. In this region rich epixylic communities can exist only in more humid ravines and exposed north-facing slopes (Ódor & Hees, 2004). It is supposed that the local frequency of epixylic species would be relatively low in this region even if more natural conditions prevailed, but definitely it would be higher than nowadays if more natural forest structures were recreated. These characteristics reflect the relatively high naturalness of the study sites as well as the continental climate.

The studied Atlantic beech forests have a modified, reduced bryoflora, almost lacking several important functional groups including obligate epixylic species. This is partly a result of habitat fragmentation in time and space that led to the extinction of dispersal limited species (Söderström & Jonsson, 1992; Rose, 1992). In addition, the amount and quality of dead wood is not suitable for species rich epixylic bryophyte vegetation in most of the remaining stands. In some parts of Western Europe (e.g. Denmark, The Netherlands) the majority of forests have experienced a dramatic desiccation during the last 150 yr, although it is not valid for historically dry sites. The possible reasons for this development are drainage, planting of exotic coniferous tree species and increased water extraction that altogether deteriorate a moist forest microclimate. Based on investigation of Danish forests the most important factors influencing epiphytic bryophyte composition of beech forests were identified to be the management regime and stand structure (Aude & Poulsen, 2000). Most of the epixylic

liverworts are widely distributed in Europe and we suppose that they used to be richly represented in the natural Atlantic forested landscape, but that they have vanished after centuries of deforestation and other human activities (Rose, 1992). Several of the Danish sites are rather small and situated in a matrix of cultural forests and/or arable land causing rather windy conditions, which may be detrimental to many epixylic bryophytes. Among acrocarpic and pleurocarpic bryophytes there was more species that was able to survive because of their better dispersal abilities and drought resistance. In Belgium and mainly in the Netherlands the amount of dead wood is relatively low and large trees and later decay stages are underrepresented. The climate of this region is favorable for bryophyte growth, which resulted very high frequency and cover of a few opportunistic species. Current forest management in Atlantic countries takes efforts to reconstruct more natural forest conditions (e.g. higher amount of dead wood, multi-layered canopy) and it is probable, that some epixylic species will be able to recolonize the region. New records of formerly extinct *Riccardia latifrons* in The Netherlands (van Dort, 2002), and *Nowellia curvifolia* in Belgium (van Dort & van Hees, 2002) support this possibility. With increasing age of the forest stands and the availability of new substrates a higher diversity may be expected in the future, especially if the area of protected forests increases in the region. The distinctly altered community composition may however slow down this process, because of the competitive advantage gained by unspecialized opportunists, which have benefited from centuries of human disturbance.

Both because of the absence of well-decayed trees and the reduced species pool, the effect of decay stage on species composition was less pronounced in Atlantic stands than in the more natural Slovenian and Hungarian sites. While the variation of samples within countries at the second ordination axes could be explained by decay stage effect in Slovenia and Hungary, in Atlantic countries the large differences among sites of clay and sand bedrock was also important. In conclusion, the large differences among countries in the species composition and diversity seem to be explained more by management-influenced factors than the climatic conditions.

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APPENDIX 1

Number of occurrences of bryophytes in different countries and in the whole data set (Total). Tax.: Taxonomical groups (A-acrocarp, P-pleurocarp, H-hepatics), Ecol.: Ecological groups (X-epixylic, E-epiphytic, O-opportunistic, T-terricol, U-uproot species (mineral soil), L-epilythic). Countries are: Slovenia (S), Hungary (H), The Netherlands (N), Belgium (B), Denmark (D).

SPECIES	CODE	TAX.	ECOL.	S	H	N	B	D	TOTAL
<i>Amblystegium riparium</i> (Hedw.) Br. Eur.	AMBRIP	P	O	1	1	0	0	0	2
<i>Amblystegium serpens</i> (Hedw.) Br. Eur.	AMBSER	P	O	37	120	1	1	14	173
<i>Amblystegium subtile</i> (Hedw.) B., S. & G.	AMBSUB	P	O	0	1	0	0	0	1
<i>Amblystegium varium</i> (Hedw.) Lindb.	AMBVAR	P	O	0	1	0	0	2	3
<i>Anacamptodon splachnoides</i> (Brid.) Brid.	ANASPL	P	X	1	0	0	0	0	1
<i>Anomodon attenuatus</i> (Hedw.) Hüb.	ANOATT	P	E	0	11	0	0	0	11
<i>Anomodon longifolius</i> (Brid.) Hartm.	ANOLON	P	E	0	1	0	0	0	1
<i>Anomodon viticulosus</i> (Hedw.) Hook. & Tayl.	ANOVIT	P	E	1	8	0	0	3	12
<i>Antitrichia curtipendula</i> (Hedw.) Brid.	ANTCUR	P	E	6	0	0	0	1	7
<i>Apometzgeria pubescens</i> (Schrank) Kuwah.	APOPUB	H	L	1	0	0	0	0	1
<i>Atrichum undulatum</i> (Hedw.) Br. Eur.	ATRUND	A	U	20	4	15	104	14	157
<i>Aulacomnium androgynum</i> (Hedw.)	AULAND	A	X	0	0	29	21	2	52

Schwaegr.										
<i>Barbula unguiculata</i> Hedw.	BARUNG	A	U	0	1	1	0	0	2	
<i>Blepharostoma trichophyllum</i> (L.) Dum.	BLETRI	H	X	33	0	0	0	0	33	
<i>Brachythecium populeum</i> (Hedw.) B., S. & G.	BRAPOP	P	O	8	0	1	0	0	9	
<i>Brachythecium rutabulum</i> (Hedw.) B., S. & G.	BRARUT	P	O	119	104	132	178	134	667	
<i>Brachythecium salebrosum</i> (Web. & Mohr.) B., S. & G.	BRASAL	P	O	78	102	14	121	45	360	
<i>Brachythecium velutinum</i> (Hedw.) B., S & G.	BRAVEL	P	O	126	161	1	1	10	299	
<i>Bryum argenteum</i> Hedw.	BRYARG	A	U	0	0	1	0	0	1	
<i>Bryum erythrocarpum</i> aggr.	BRYERI	A	O	0	0	0	0	2	2	
<i>Bryum subelegans</i> Kindb.	BRYSUB	A	O	94	146	8	57	22	327	
<i>Buxbaumia viridis</i> Brid. ex Moug. & Nestl.	BUXVIR	A	X	2	0	0	0	0	2	
<i>Calliergonella cuspidata</i> (Hedw.) Loeske	CALCUS	H	O	0	0	1	6	2	9	
<i>Calypogeia azurea</i> Stotler et Crotz	CALAZU	H	T	4	0	0	0	0	4	
<i>Calypogeia muellerana</i> (Schiffn.) K. Müll.	CALMUE	H	O	1	0	0	0	0	1	
<i>Calypogeia suecica</i> H. Am et J. Press.) K. Müll.	CALSUE	H	X	17	0	0	0	0	17	
<i>Campylopus flexuosus</i> (Hedw.) Brid.	CAMFLE	A	O	0	0	17	0	1	18	
<i>Campylopus introflexus</i> (Hedw.) Brid.	CAMINT	A	O	0	0	28	7	3	38	
<i>Campylopus pyriformis</i> (K. F. Schultz) Brid.	CAMPYR	A	O	0	0	9	0	0	9	
<i>Cephalozia bicuspidata</i> (L.) Dum.	CEPBIC	H	O	4	0	0	0	11	15	
<i>Cephalozia catenulata</i> (Hüb.) Lindb.	CEPCAT	H	X	18	0	0	0	0	18	
<i>Cephaloziella divaricata</i> (Sm.) Schiffn.	CEPDIV	H	O	0	0	0	1	0	1	
<i>Cephaloziella hampeana</i> (Nees) Schiffn.	CEPHAM	H	X	1	0	0	0	0	1	
<i>Cephaloziella rubella</i> (Nees) Warnst.	CEPRUB	A	X	15	0	0	0	0	15	
<i>Ceratodon purpureus</i> (Hedw.) Brid.	CERPUR	A	O	5	19	13	10	9	56	
<i>Chiloscyphus polyanthos</i> (L.) Corda	CHYPOL	H	X	3	0	0	0	0	3	
<i>Climacium dendroides</i> Web. et Mohr.	CLIDEN	P	T	0	1	0	0	0	1	
<i>Ctenidium molluscum</i> (Hedw.) Mitt.	CTEMOL	P	L	69	0	0	0	1	70	
<i>Cynodontium polycarpon</i> (Hedw.) Schimp.	CYNPOL	A	L	0	1	0	0	0	1	
<i>Dicranella heteromalla</i> (Hedw.) Schimp.	DICHET	A	E	0	2	26	46	4	78	
<i>Dicranodontium denudatum</i> (Brid.) Britt.	DICDEN	A	X	2	0	0	0	0	2	
<i>Dicranoweisia cirriata</i> (Hedw.) Lindb. Ex Milde	DICCIR	A	U	0	0	74	50	12	136	
<i>Dicranum montanum</i> Hedw.	DICMON	A	E	12	17	106	8	0	143	
<i>Dicranum scoparium</i> Hedw.	DICSCO	A	O	40	22	74	35	71	242	
<i>Dicranum tauricum</i> Sap.	DICTAU	A	E	0	1	16	53	0	70	
<i>Dicranum viride</i> (Sull. and Lesq.) Lindb.	DICVIR	A	E	61	3	0	0	0	64	
<i>Didymodon vinealis</i> (Brid.) Zander	DIDVIN	A	U	0	0	1	0	0	1	
<i>Ditrichum pallidum</i> (Hedw.) Hampe	DITPAL	A	U	0	1	0	0	0	1	
<i>Drepanocladus aduncus</i> (Hedw.) Warnst.	DREADU	P	T	0	0	0	0	1	1	
<i>Drepanocladus</i> sp.	DRESPE	P	T	0	0	0	0	2	2	
<i>Encalypta streptocarpa</i> Hedw.	ENCSTR	A	L	2	1	0	0	0	3	
<i>Eucladium verticillatum</i> (Brid.) B., S. & G.	EUCVER	A	L	0	0	0	0	1	1	
<i>Eurhynchium angustirete</i> (Broth.) T. Kop.	EURANG	P	T	27	2	0	0	0	29	
<i>Eurhynchium hians</i> (Hedw.) Sande Lac.	EURHIA	P	U	2	0	1	0	0	3	
<i>Eurhynchium praelongum</i> (Hedw.) B., S. & G.	EURPRA	P	L	2	0	58	117	11	188	
<i>Eurhynchium striatulum</i> Spruce (B., S. & G.	EURLUM	P	O	0	0	0	0	1	1	
<i>Eurhynchium striatum</i> (Hedw.) Schimp.	EURSTR	P	T	6	0	13	23	0	42	
<i>Fissidens adianthoides</i> Hedw.	FISADI	A	O	0	0	0	0	1	1	
<i>Fissidens bryoides</i> Hedw.	FISBRY	A	U	0	0	1	1	0	2	
<i>Fissidens dubius</i> P. Beauv	FISDUB	A	L	54	0	0	0	0	54	
<i>Fissidens taxifolius</i> Hedw.	FISTAX	A	U	12	0	0	2	0	14	
<i>Frullania dilatata</i> (L.) Dum.	FRUDIL	H	E	65	3	0	0	0	68	
<i>Frullania tamarisci</i> (L.) Dum.	FRUTAM	H	E	5	0	0	0	0	5	
<i>Funaria hygrometrica</i> Hedw.	FUNHYG	A	T	0	0	0	2	0	2	
<i>Grimmia hartmanii</i> Schimp.	GRIHAR	A	L	1	2	0	0	0	3	
<i>Grimmia</i> sp.	GRISPE	A	L	1	0	0	0	0	1	
<i>Hedwigia ciliata</i> (Hedw.) P. Beauv.	HEDCIL	A	L	1	1	0	0	0	2	
<i>Herzogiella seligeri</i> (Brid.) Iwats.	HERSEL	P	X	87	118	20	84	34	343	

<i>Homalia bessereri</i> Lob.	HOMBES	P	E	0	7	0	0	0	7
<i>Homalia trichomanoides</i> (Hedw.) Brid.	HOMTRI	P	L	2	0	0	0	0	2
<i>Homalothecium philippeanum</i> (Spruce.) B., S. & G.	HOMPHI	P	L	7	4	0	0	0	11
<i>Homalothecium sericeum</i> (Hedw.) B., S. & G.	HOMSER	P	E	62	13	0	0	18	93
<i>Homomallium incurvatum</i> (Brid.) Loeske	HOMINC	P	E	0	0	0	0	1	1
<i>Hygrohypnum luridum</i> (Hedw.) Jenn.	HYGLUR	P	L	1	0	0	0	0	1
<i>Hylocomium splendens</i> (Hedw.) Br. Eu.	HYLSPL	P	T	0	0	0	0	2	2
<i>Hypnum cupressiforme</i> Hedw.	HYPCUP	P	O	199	184	144	154	162	843
<i>Hypnum jutlandicum</i> Holmen & Warncke	HYPJUT	P	U	0	0	18	1	0	19
<i>Isothecium alopecuroides</i> (Dubois) Isov.	ISOALO	P	E	157	38	0	0	7	202
<i>Isothecium myosuroides</i> Brid.	ISOMYO	P	E	1	0	22	3	66	92
<i>Jungermannia leiantha</i> Grolle	JUNLEI	H	X	22	0	0	0	0	22
<i>Lejeunea cavifolia</i> (Ehrh.) Lindb.	LEJCAV	H	E	30	0	0	0	0	30
<i>Lepidozia reptans</i> (L.) Dum.	LEPREP	H	X	30	0	0	1	0	31
<i>Leucobryum glaucum</i> (Hedw.) Angstr.	LEUGLA	A	X	0	0	42	0	1	43
<i>Leucodon sciuroides</i> (Hedw.) Schwaegr.	LEUSCI	P	E	32	7	0	0	0	39
<i>Lophocolea bidentata</i> (L.) Dum.	LOPBID	H	X	0	0	0	14	8	22
<i>Lophocolea heterophylla</i> (Schrad.) Dum.	LOPHET	H	T	143	146	61	125	40	515
<i>Lophocolea minor</i> Nees	LOPMIN	H	X	1	10	0	0	0	11
<i>Lophozia ascendens</i> (Warnst.) Schust.	LOPASC	H	X	0	2	0	0	0	2
<i>Marchantia polymorpha</i> L.	MARPOL	H	T	0	0	0	1	0	1
<i>Metzgeria conjugata</i> Lindb.	METCON	H	E	42	0	0	0	0	42
<i>Metzgeria furcata</i> (L.) Dum.	METFUR	H	E	134	54	12	0	53	253
<i>Mnium hornum</i> Hedw.	MNIHOR	A	U	0	0	23	98	34	155
<i>Mnium marginatum</i> (Dicks) P. Beauv.	MNIMAR	A	X	13	0	0	0	0	13
<i>Mnium stellare</i> Hedw.	MNISTE	A	X	3	1	0	0	1	5
<i>Mnium thomsonii</i> Schimp.	MNITOM	A	X	1	0	0	0	0	1
<i>Neckera complanata</i> (Hedw.) Hüb.	NECCOM	P	E	41	2	0	0	29	72
<i>Neckera crispa</i> Hedw.	NECCRI	P	E	52	0	0	0	1	53
<i>Neckera pumila</i> Hedw.	NECPUM	P	E	11	0	0	0	0	11
<i>Nowellia curvifolia</i> (Dicks.) Mitt. in Godman	NOWCUR	H	X	55	3	0	2	1	61
<i>Odontoschisma denudatum</i> (Mart.) Dum.	ODODEN	H	X	1	0	0	0	0	1
<i>Orthodontium lineare</i> Schwaegr.	ORTLIN	A	E	0	0	0	0	1	1
<i>Orthotrichum affine</i> Brid.	ORTAFF	A	E	2	0	8	5	5	20
<i>Orthotrichum diaphanum</i> Brid.	ORTDIA	A	E	0	1	7	1	0	9
<i>Orthotrichum lyellii</i> Hook. & Tayl.	ORTLYE	A	E	10	1	3	0	0	14
<i>Orthotrichum speciosum</i> Nees	ORTSPE	A	E	0	0	0	0	3	3
<i>Orthotrichum stramineum</i> Hornsch. ex Brid.	ORTSTR	A	E	67	35	3	0	11	116
<i>Paraleucobryum longifolium</i> (Hedw.) Loeske	PARLON	A	E	115	36	0	0	0	151
<i>Pellia epiphylla</i> (L.) Corda	PELEPI	H	T	0	0	0	1	0	1
<i>Plagiochila porelloides</i> (Torrey ex Nees) Lindenb.	PLAPOR	A	T	113	6	0	0	0	119
<i>Plagiomnium affine</i> (Bland.) T. Kop.	PLAAFF	P	U	4	0	0	0	0	4
<i>Plagiomnium cuspidatum</i> (Hedw.) Kop.	PLACUS	A	O	46	70	0	0	3	119
<i>Plagiomnium ellipticum</i> (Brid.) Kop.	PLAELL	P	X	44	0	0	0	0	44
<i>Plagiomnium rostratum</i> (Schrad.) T. Kop.	PLAROS	A	O	1	1	0	0	0	2
<i>Plagiomnium undulatum</i> (Hedw.) Kop.	PLAUND	P	E	40	0	0	3	2	45
<i>Plagiothecium cavifolium</i> (Brid.) Iwats.	PLACAV	P	E	14	5	0	0	12	31
<i>Plagiothecium denticulatum</i> (Hedw.) Br. Eur.	PLADEN	P	X	4	45	2	0	4	55
<i>Plagiothecium laetum</i> Br. Eur.	PLALAE	H	O	1	1	10	0	3	15
<i>Plagiothecium latebricola</i> Br. Eur.	PLALAT	P	E	0	0	0	0	1	1
<i>Plagiothecium nemorale</i> (Mitt.) Jaeg.	PLANEM	A	O	84	9	0	12	5	110
<i>Plagiothecium undulatum</i> (Hedw.) Br. Eur.	PLTUND	A	T	0	0	1	0	0	1
<i>Platygyrium repens</i> (Brid.) B., S. & G.	PLAREP	P	T	16	51	1	0	3	71
<i>Pleurozium schreberi</i> (Brid.) Mitt.	PLESCH	P	T	1	2	0	0	1	4
<i>Pogonatum aloides</i> (Hedw.) P. Beauv.	POGALO	A	U	0	0	1	0	0	1
<i>Pohlia melanodon</i> (Brid.) Shaw	POHMEL	A	U	0	1	0	0	0	1
<i>Pohlia nutans</i> (Hedw.) Lindb.	POHNUT	A	U	0	1	2	0	3	6
<i>Polytrichum formosum</i> Hedw.	POLFOR	A	U	9	0	57	80	20	166

<i>Polytrichum longisetum</i> Brid.	POLLON	A	O	0	0	15	0	0	15
<i>Polytrichum piliferum</i> Hedw.	POLPIL	A	U	0	0	1	0	1	2
<i>Porella platyphylla</i> (L.) Pfeiff.	PORPLA	H	E	13	0	0	0	12	25
<i>Pottia</i> sp.	POTSPE	A	U	0	0	0	0	1	1
<i>Pseudoleskeella nervosa</i> (Brid.) Nyh.	PSENER	P	U	3	100	0	0	0	103
<i>Pseudoscleropodium purum</i> (Hedw.) Fleisch.	PSEPUR	P	E	0	0	1	2	0	3
<i>Pseudotaxiphyllum elegans</i> (Brid.) Iwats.	PSEELE	P	T	0	0	2	22	0	24
<i>Pterigynandrum filiforme</i> Hedw.	PTEFIL	P	E	148	129	0	0	0	277
<i>Ptilidium pulcherrimum</i> (G. Web.) Vainio	PTIPUL	H	O	0	0	2	1	0	3
<i>Pylaisia polyantha</i> (Hedw.) Schimp.	PYLPOL	P	E	4	5	0	0	2	11
<i>Radula complanata</i> (L.) Dum.	RADCOM	H	E	119	14	0	0	0	133
<i>Rhizomnium punctatum</i> (Hedw.) Kop.	RHIPUN	A	X	105	51	0	5	2	163
<i>Rhynchostegium confertum</i> (Dicks.) B., S. & G.	RHYCON	P	E	0	0	25	48	0	73
<i>Rhynchostegium murale</i> (Hedw.) B., S. & G.	RHYMUR	P	T	17	0	0	0	0	17
<i>Rhytiadelphus loreus</i> (Hedw.) Warnst.	RHYLOR	P	L	8	0	1	1	4	14
<i>Rhytiadelphus squarrosus</i> (Hedw.) Warnst.	RHYSQU	P	T	0	0	0	2	4	6
<i>Rhytiadelphus triquetrus</i> (Hedw.) Warnst.	RHYTRI	P	T	4	0	0	0	0	4
<i>Riccardia latifrons</i> (Lindb.) Lindb.	RICLAT	H	X	11	0	2	0	0	13
<i>Riccardia multifida</i> (L.) S. Gray	RICMUL	H	X	14	0	0	0	0	14
<i>Riccardia palmata</i> (Hedw.) Carruth.	RICPAL	H	X	62	0	0	0	0	62
<i>Sanionia uncinata</i> (Hedw.) Loeske	SANUNC	P	O	51	27	0	1	0	79
<i>Scapania umbrosa</i> (Schrad.) Dum.	SCAUMB	H	X	1	0	0	0	0	1
<i>Tetraphis pellucida</i> Hedw.	TETPEL	A	X	11	1	17	0	1	30
<i>Thamnobryum alopecurum</i> (Hedw.) Gang.	THAALO	P	E	6	0	0	0	0	6
<i>Thuidium tamariscinum</i> (Hedw.) B., S. & G.	THUTAM	P	T	41	0	1	8	0	50
<i>Tortella tortuosa</i> (Hedw.) Limpr.	TORTOR	A	L	35	0	0	0	1	36
<i>Tortula ruralis</i> (Hedw.) Gaertn.	TORRUR	A	U	1	5	0	0	0	6
<i>Tortula subulata</i> Hedw.	TORSUB	A	O	0	5	0	0	0	5
<i>Ulota bruchii</i> Hornsch. Ex Brid.	ULOBRU	A	E	0	0	13	4	1	18
<i>Ulota crispa</i> (Hedw.) Brid.	ULOCRI	A	E	49	0	0	0	9	58
<i>Weissia condensa</i> (Voit.) Lindb.	WEICON	A	U	2	0	0	0	0	2
<i>Zygodon conoideus</i> (Dicks.) Hook. & Tayl.	ZYGCON	A	E	0	0	12	0	6	18
<i>Zygodon rupestris</i> Schimp. Ex Lor.	ZYGRUP	A	E	37	0	0	0	6	43
<i>Zygodon viridissimus</i> (Dicks.) Brid.	ZYGVIR	A	E	0	0	0	2	0	2