Diversity of dead wood inhabiting fungi and bryophytes in semi-natural beech forests in Europe

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ABSTRACT

Saproxylic organisms are among the most threatened species in Europe and constitute a major conservation problem because they depend on the most important forestry product – dead wood. Diversity of fungal and bryophyte communities occurring on dead beech trees was analyzed in five European countries (Slovenia, Hungary, The Netherlands, Belgium and Denmark) considering tree level species richness (TLSR), country level species richness (CLSR), frequency distributions of species, occurrence of threatened species and relations between TLSR and decay stage, tree size and countries. Altogether 1009 trees were inventoried in 19 beech dominated forest reserves.

The number of fungi in the full dataset was approximately three times larger (456 versus 161 species) and the proportion of low frequent species was higher than among bryophytes. The species richness of bryophytes and fungi was significantly different among countries considering both TLSR and CLSR. In addition the diversity patterns deviated considerably between the two groups of organisms. Slovenian sites appeared to be biodiversity hotspots for bryophytes characterized by high TLSR and CLSR and a high fraction of threatened species. Hungarian sites had somewhat lower bryophyte diversity, while the Atlantic region had deteriorated assemblages. Fungal species richness was very high in Denmark, but the Hungarian and Slovenian sites were richer in threatened and low frequency species. Tree size was better able to explain variation in TLSR in both organism groups than decay stage. TLSR was found to vary significantly between countries but the difference was most considerable in the case of bryophytes.

The diversity patterns of both organism groups along the investigated geographical gradient appear to be influenced by both climatic and management related factors (forest history, dead wood availability and continuity, habitat fragmentation). There is no doubt that an increase in the abundance of dead wood in European beech forests will benefit diversity

of saproxylic fungi and bryophytes, especially if a continuous presence of large diameter logs are secured within individual stands.

1. 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 proportions of old, living trees with dead parts (Harmon et al., 1986; Peterken, 1996). These different CWD types provide important habitats for a diversity of organisms, including fungi, bryophytes, lichens, invertebrates, amphibians, cavity nesting birds and small mammals (Maser and Trappe, 1984; Harmon et al., 1986; Samuelsson et al., 1994; Esseen et al., 1997; Csóka, 2000; Siitonen, 2001; Ódor and Standovár, 2002; Bobiec et al., 2005).

In temperate European beech (*Fagus sylvatica*) forests the death of individuals 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 (Korpel, 1995; Peterken, 1996; Standovár and Kenderes, 2003).

Humans have heavily influenced the European beech forest landscape for centuries (Rose, 1992; Peterken, 1996), creating artificial stand structures and disturbance regimes in most present-day beech forests. For CWD it has been estimated that the decline in availability at landscape scale has been in the range of 90–98% in the Fennoscandian conifer forest 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 found 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; Edman et al., 2004). The combination of forest management and forest fragmentation has lead 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; Söderström and Jonsson, 1992; Siitonen, 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).

Fungi are the principal agents of wood decay in terrestrial habitats and hence they open up the wood resource for most other organisms living in dead wood (Boddy, 2001). Decay stage appears consistently to be the most important variable for understanding fungal community composition on decaying wood, but also tree species, tree size, microclimatic conditions, cause of death and the original position of the dead wood in the tree are key variables influencing species composition (Keizer and Arnolds, 1990; Renvall, 1995; Boddy, 2001; Heilmann-Clausen, 2001; Heilmann-Clausen and Christensen, 2003, 2004; Ódor et al., 2003; Nordén et al., 2004; Heilmann-Clausen et al., 2005).

Among bryophytes many species occur on dead wood obligatorily or facultatively. Successional studies focusing on one habitat type typically show a clear compositional change of bryophyte vegetation during the decay of trees (McCullough, 1948; Muhle and LeBlanc, 1975; Söderström, 1988a, 1993; McAlister, 1997; Ódor and van Hees, 2004; Heilmann-Clausen et al., 2005).

Most studies dealing with dead wood dwelling fungi or bryophytes concentrate on a relatively small region describing the effect of decay and other factors for species composition (e.g. McCullough, 1948; Söderström, 1988a; Renvall, 1995; Heilmann-Clausen, 2001; Lindhe et al., 2004; Ódor and van Hees, 2004) or compare the diversity of sites characterized by different management regimes (e.g. Söderström, 1988b; Bader et al., 1995; Rambo and Muir, 1998; Sippola and Renvall, 1999; Ódor and Standovár, 2001; Penttilä et al., 2004). No studies so far have dealt with the diversity of wood dwelling fungi or bryophytes in European broad-leaved forest zone at the continental scale.

This study is an attempt to analyze the diversity of two species groups on a broad geographical scale, fungi that are the major biological factors of wood decomposition (Boddy, 2001), and bryophytes that follow decomposition processes in a more passive way (Ódor and van Hees, 2004). It aims to compare the diversity of fungi and bryophytes inhabiting decaying beech trees in forest reserves occurring in different regions of Europe (Slovenia, Hungary, The Netherlands, Belgium and Denmark). In the case of both organism groups: (1) tree level species richness (TLSR); (2) country level species richness (CLSR); (3) frequency distribution of species; and (4) occurrence of threatened species were compared among countries. The importance of decay stage and tree size for TLSR were also analyzed in different countries. Finally, the importance of management influenced (dead wood characteristics, forest and dead wood continuity, fragmentation) versus climatic and geographical factors are discussed in relation to the recorded diversity patterns of fungi and bryophytes.

2. Materials and methods

2.1. Study sites

Altogether 19 forest reserves were selected for this study in Slovenia, Hungary, The Netherlands, Belgium and Denmark. The sites were selected according to the following criteria: (a) beech should be dominant, and (b) the sites should represent, as far as possible, the best natural reference of beech forests for the country. In Belgium only one site was selected, but it was divided into two parts based on dominant tree age and forest history. In Hungary and Slovenia two sites were studied, each represented by ca. 100 trees. In Denmark five sites in four regions were included, each represented by 50 trees. Finally, The Netherlands is represented by eight study

sites, each including variable numbers of studied trees. The high number of study sites in The Netherlands reflects the low amount of available fallen trees at each site.

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

Climatic conditions vary considerably among the selected forest stands. The climate of sites in Denmark, Belgium and The Netherlands is more or less Atlantic, in Hungary it is mid-European continental, while in Slovenia it has a mountainous character.

The bedrock is generally formed by young deposits in Atlantic sites (sand, clay, loess, and chalk) while dolomite, limestone and andesite characterize the Slovenian and Hungarian sites. Generally, soil acidity is higher, and nutrient content is lower in sites characterized by sand or andesite compared to soils developed on clay, loess or limestone. Therefore, the soil characteristics (acidity, nutrient content, etc.), differ considerably among sites, both between and within countries.

All stands are dominated by beech, but in some sites other tree species are also important (especially *Abies alba* in Slovenian sites, *Quercus robur* and *Fraxinus excelsior* in some Atlantic forests, Table 1). 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 still have unbroken forest continuity (e.g., Öserdö in Hungary, part of Strødam in Denmark, Dutch reserves on sandy soil) 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 they show the least effects of human influence (e.g., Suserup in Denmark, Kékes in Hungary, Krokar in Slovenia), i.e., they possess structures and gap dynamics similar to those reported from virgin forests (Korpel, 1995; Standovár and 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 (Table 1). The volume of CWD is generally 40–70 m^3/ha in the Dutch sites, 100–180 m^3/ha in other sites and very high, 300 m^3/ha in Rajhenav, Slovenia (Christensen et al., 2005; Kraigher et al., 2003). 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 and 6) are missing or underrepresented.

2.2. Dead tree selection and description

In each country approximately 200 dead beech trees were selected. It is proved from different forest types that the size and decay stage of dead trees are very important factors influencing species richness and composition of fungi and bryophytes (Söderström, 1988a; Renvall, 1995; Heilmann-Clausen, 2001; Heilmann-Clausen and Christensen, 2004; Ódor and van Hees, 2004). Before selection all dead beech trees occurring in the investigated sites were measured and classified into DBH and decay stage categories. Based on a stratified random selection procedure different decay stages and size (diameter at breast height) categories were as evenly distributed among the selected trees per country as possible. Because of the absence of well-decayed trees in The Netherlands and Belgium the later decay stages (4–6) are considerably underrepresented in these countries. The selected trees could have uprooted plate or a standing dead part (snag), but minimum 70% of the stem should have soil contact. Selected dead trees were described by their decay stage and size expressed as diameter at breast height. Decay stages were classified into six classes following the definitions of Ódor and van Hees (2004) based on outer physical features of trees (presence of bark, branches, softness and surface of wood, outline and shape of trunk). Most dead trees represent a mixture of different decay stages (decay is not homogenous at different parts of the tree), therefore the dominant decay class was used during the analysis. Diameter at breast height was accurately measured on trees of earlier decay stages (either on the standing or the lying part) but in later stages, when the original shape of the trunk is altered, the diameter of the original (living) tree was estimated.

2.3. Inventory of bryophytes and fungi

The presence/absence of species was recorded on each individual dead tree. One record (or occurrence) of a species means its presence on a tree independently from its abundance or cover. The recordings from different tree parts were merged including: (a) the log, (b) the uprooting part of the log (if present), (c) the snag up to 2 m (if present), and (d) the major branches of the crown (diameter >10 cm, if present).

Bryophytes occurring on the selected trees were recorded once in summer and autumn 2001. Nomenclature follows Corley et al. (1981) and Corley and Crundwell (1991) for mosses, and Grolle (1983) for liverworts. *Plagiochila porelloides* and *P. asplenioides* were not separated and nomenclature of *Plagiothecium* species follows Frisvoll et al. (1995).

Fungi were recorded on three occasions on each tree during two growing periods: 2000 late autumn, 2001 spring and 2001 late summer – early autumn. The records of the three inventories were merged in the analyses. On each occasion, each dead tree was inventoried for fungal sporocarps occurring strictly on dead wood. Sporocarps were either identified in the field or collected for microscopic identification. Within the *Basidiomycetes* all morphological groups, excluding fully resupinate corticoid fungi, were included, while non-stromatic *Pyrenomycetes* and inoperculate *Discomycetes* with sporocarps regularly smaller than 10 mm were excluded from the *Ascomycetes*. The excluded groups are, according to our experiences, not very important for wood decay in CWD in European beech forests, though they constitute an important component of species diversity. The required sampling and microscopy time, as well as serious taxonomic knowledge gaps did not allow us to include these groups in this study. Nomenclature for fungi in general follows Hansen and Knud-

Country	Reserve	Size (ha)	Age (yr)[a]	Other trees[b]	Living tree volume (m³/ha)[c]	Dead wood volume (m³/ha)[c]	No. of sampled trees	DBH of dead wood (cm)[d]	Decay stages of dead wood[e]	Elevation (m)	Bedrock	T_{ave} (°C)[f]	T_{min} (°C)[g]	T_{max} (°C)[h]	Precipitation (mm)[i]
Slovenia (S)	Rajhenav	51	Old	*Abies alba*	813	299	110	50 (17, 97)	1–6	865	Limestone	7.7	−1.9	16.9	1579
	Krokar	73	Old	*Abies alba*	633	153	101	37 (10, 98)	1–6	1120	Limestone	8.4	−1.6	17.8	1526
Hungary (H)	Kékes	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
	Öserdö	25	200	–	765	164	110	66 (18, 135)	1–6	850	Limestone	6.1	−4.1	15.5	896
The Netherlands (N)	Speuldebos	27	200	*Quercus robur*	457	44	42	46 (25, 83)	1–4	42	Sand	9.4	2.2	17.2	876
	Drie	5	200	*Quercus robur*	457	44	21	51 (21, 90)	1–3	35	Sand	9.4	2.2	17.2	876
	Gortelsebos	15	200	*Quercus robur*	507	66	11	62 (14, 95)	2,3	45	Sand	9.4	2.2	17.2	873
	Weversbergen	12	100	–	469	49	32	55 (18, 120)	1–3	80	Loam-sand	9.4	2.2	17.2	856
	Wulperhorst	3	200	*Quercus robur, Fraxinus excelsior, Carpinus betulus*	701	72	44	68 (36, 120)	2–4	3	Clay	9.4	2.8	17.2	827
	Oostbroek	3	150	*Quercus robur, Fraxinus excelsior*	–	–	10	71 (57, 88)	2	2	Clay	9.4	2.8	17.2	827
	Dassenberg	12	200	*Quercus robur*	402	63	37	67 (18, 105)	1–3	96	Sand	9.4	2.2	17.2	906
	Amelisweerd	3	150	*Quercus robur, Fraxinus excelsior*	–	–	5	73 (60, 90)	1,3	2	Clay	9.4	2.8	17.2	827
Belgium (B)	Zoniënwoud	80	150	*Quercus robur, Quercus petraea*	602	24	67	45 (15, 118)	1–5	105	Loess	9.4	3.4	18.2	829
	Zoniënwoud – Kern	18	220	–	794	139	125	69 (15, 117)	1–5	105	Loess	9.4	3.4	18.2	829
Denmark (D)	Knagerne	6	230	–	449	152	25	72 (27, 108)	1–4	80	Sand	7.5	0	15.5	719
	Velling	24	275	–	489	114	25	53 (20, 93)	1–6	70	Sand	7.5	0	15.5	839
	Suserup	19	Old	*Fraxinus excelsior, Ulmus glabra, Q. robur*	674	176	50	76 (24, 131)	2–6	20	Loam-sand	8.1	0.8	16.7	644
	Møns Klinteskov	25	350	–	201	100	50	48 (21, 86)	1–6	100	Chalk	7.9	0.2	16.2	586
	Strødam	25	250	*Q. robur*	490	181	50	77 (21, 127)	1–6	23	Loam-sand	7.7	−0.5	16.2	697

a Age since last cutting or plantation; old: the stand was never cut in the past.
b Trees with min. 5% stand volume besides beech.
c Mean volume of living trees and dead wood are based on Christensen et al. (2005).
d Mean diameter at breast height (DBH) based on the investigated dead trees, minimum and maximum are in brackets.
e Minimum number of trees from the same decay stage is three from one site. The six level of decay stages are defined in Ódor and van Hees (2004).
f Mean annual temperature.
g Mean temperature of the coldest month.
h Mean temperature of the warmest month.
i Annual precipitation.

sen (1992, 1997, 2000), but special taxonomical works were consulted for certain groups (e.g., *Pyrenomycetes*).

The field inventory protocol was designed to secure standardized, comparable data from different countries. For this reason, different persons working in different regions used the same standards, taxonomical restrictions, sampling intensity during the fieldwork. It is supposed that most bryophyte species living on the selected dead tree were recorded during the inventory, because the longevity of most epixylic and epiphytic species is several years. The efficiency of the fungal inventory is without doubt lower, even though each tree was inventoried on three occasions during two successive years. Many fungi present in wood as mycelia do not develop fruit bodies, while other species produce infrequent and/or short-lived fruit bodies, which are easily missed even if a rather extensive sampling protocol is used (Boddy, 2001; Berglund et al., 2005). The weather of different years has considerable effect on the fruit body production of fungi. Generally the precipitations in the two studied years (2000 and 2001) were close to the averages for most sites. In both years Belgium, The Netherlands and Western Denmark received slightly more precipitation than normal during the main fungal growing season, while the opposite was the case in Hungary. In Eastern Denmark and Slovenia precipitation was very close to normal when both sampling years are summarized (source: www.weatheronline.co.uk). This might have affected the production of sporocarps, but effects appear to be limited with respect to the recorded species diversity. Thus, there is no obvious relationship between average species richness per tree, total species richness per country and precipitation deficits or surpluses (cf. Table 3). We therefore feel convinced that both datasets are sufficiently complete among countries to allow statistical comparisons of species richness, but do not claim the fungal dataset to be fully complete neither on tree nor on country level.

2.4. Data analysis

Diversity of dead wood dwelling fungi and bryophytes was compared among countries based on the whole dataset investigating the following descriptors: (1) tree level species richness (TLSR): mean species richness of individual dead trees; (2) country level species richness (CLSR): species pool of the selected dead trees from each country; (3) the number of occurrences: sum of species presences in the sample of each country; and (4) species rank – relative frequency curves (Begon et al., 1996). TLSR was compared among countries by ANOVA and Newman–Keuls multiple comparison (Zar, 1999). In the case of bryophytes the original species richness data were logarithmic transformed before the statistical comparison, because of the inhomogeneity of variances. The effects of decay stage, tree size (DBH) and geographical region (country) on species richness (TLSR) were analysed by multiple regression models (McCullagh and Nelder, 1983; Crawley, 1993). During the analysis a general linear model was used with the following criteria: (1) dependent variable: TLSR; (2) explanatory variables: decay stage (factor), DBH (interval), country (factor); (3) error structure: normal; (4) link function: square root. Although for species richness data it is more convenient to use Poisson error structure and logarithmic link function

during this analysis (Crawley, 1993) the goodness-of-fit of the models were worse using these conditions (the coefficient of determination was 0.259 versus 0.402 for bryophytes and 0.502 versus 0.549 for fungi). The model building was based on backward elimination from the full model (including all interactions). During the selection the effects of eliminations were tested by deviance analysis (McCullagh and Nelder, 1983; Crawley, 1993). The effects of decay stage and DBH were analyzed in different countries by comparing the predicted values of the selected model.

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. For bryophytes the "Red Data Book of European Bryophytes" (ECCB, 1995) was used with regional red lists for different countries (Martinčič, 1992; Papp et al., 2001). In the lack of a common European red list for fungi a number of species were classified as "Species of Special Interest" (SSI) based on data from several national red lists (Benkert et al., 1992; Wojewoda and Ławrynowicz, 1992; Arnolds and van Ommering, 1996; Stoltze and Pihl, 1998; Rimóczi et al., 1999; Gärdenfors, 2000). This classification was only carried out for truly lignicolous species. Three classes of SSI were defined. Class A includes widespread species regarded as very rare and severely threatened (IUCN threat categories "Endangered" to "Critically Endangered") everywhere in Europe. Class B includes widespread species regarded as rare all over Europe, and threatened in several countries (IUCN threat categories "Near Threatened" to "Vulnerable"). Finally, class C encompasses species that are considered to be threatened (IUCN threat categories "Vulnerable" to "Critically Endangered") in one or several of the covered European countries/regions, but being frequent in others. A few poorly known but apparently rare species are also included in this category.

The list of bryophyte and fungi species included in this study, their frequencies in different countries, and for fungi their threat (SSI) status can be found as supplementary data (suppl1.doc for fungi and suppl2.doc for bryophytes).

3. Results

3.1. Species richness of fungi

The complete dataset contained 12,896 occurrences representing 457 species occurring on 1008 trees. CLSR was the highest in Denmark, followed by Hungary, Slovenia, Belgium and The Netherlands in decreasing order (Table 2). Considering the number of records per country a different pattern emerged with the highest number of records in Belgium and the lowest in Slovenia. TLSR was significantly different among countries (ANOVA; df = 4, 1003; F value 28.08, p < 0.001). It was lowest in Slovenia, intermediate in Hungary and The Netherlands and highest in Denmark and Belgium. Comparing the species rank – relative frequency curves among countries the curves are relatively steep in the case of the Dutch and the Belgian samples, while they are less steep for the Slovenian, the Hungarian and the Danish samples (Fig. 1). In The Netherlands and Belgium the proportion of frequent species (relative frequency above 0.01) is relatively high, while in the three other countries the proportion of sub-

Table 2 – Species richness of fungal communities in different countries						
Variable	Slovenia	Hungary	The Netherlands	Belgium	Denmark	Whole data set
Number of trees	211	207	198	192	200	1008
CLSR	207	227	155	190	257	457
Number of occurrences	1819	2635	2300	3204	2938	12,896
TLSR (mean ± SD)	8.62 ± 8.06^a	12.73 ± 7.88^b	11.62 ± 7.40^b	16.69 ± 8.52^d	14.69 ± 9.13^c	12.79 ± 8.65

TLSR significantly differed among countries (ANOVA, F-value $(4, 1003) = 28.08$, $p < 0.001$), the letters show the results of multiple comparison test. CLSR: country level species richness. TLSR: tree level species richness.
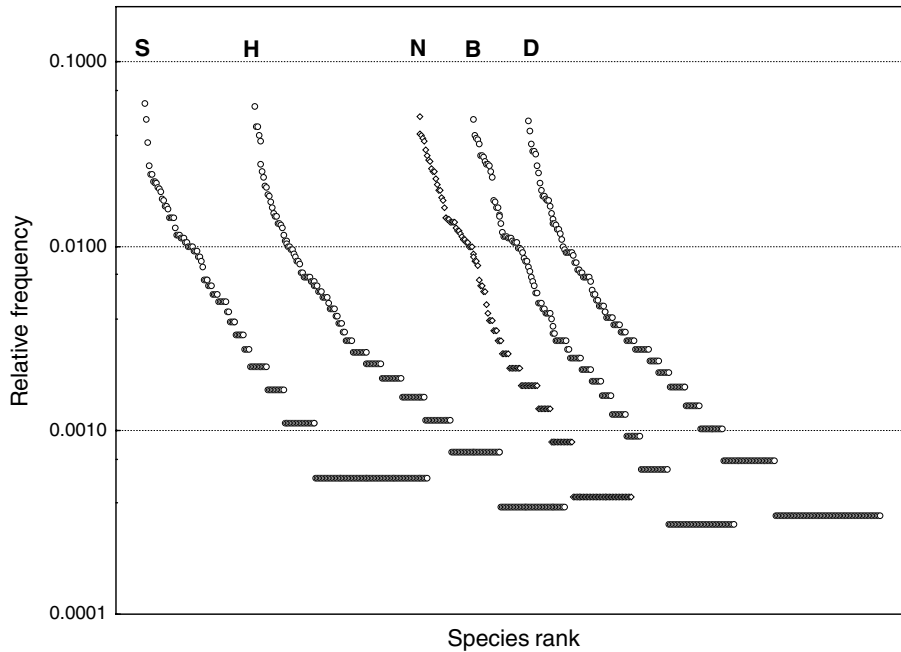
Fig. 1 – Species rank – relative frequency curves of fungi in Slovenia (S), Hungary (H), The Netherlands (N), Belgium (B) and Denmark (D).

ordinate (relative frequency between 0.001 and 0.01) and rare (relative frequency below 0.001) species is high.

Based on the multiple regression model, tree size was the most important factor explaining species richness per tree (expressed as DBH, F-value 357.0), although the effects of decay stage (DS, F-value 33.5) and geographic region (COUNTRY, F-value 22.7) were also considerable (Table 3). Although the effects of second level interaction factors were less important than the main factors (F values between 3 and 11), they were significant and included to the model. The effect of the third level interaction was not significant. It is obvious that some of the differences found in TLSR among countries were related to the differences in size and decay class distributions of study trees within countries. Based on the predicted values TLSR increased with tree size in all countries (Fig. 2), but the increment was steeper in Slovenia (the range of predicted average TLSR was between 5 and 30 from DBH = 20 to 110 cm), compared to the other countries (range 5–20). In The Netherlands the increase is only weak (range 8–15). In all countries TLSR was recorded to be highest on trees in decay stages 2 and 3. For Belgium and The Netherlands the figures for the late decay stages are highly uncertain due to the low number of trees represented.

3.2. Species richness of bryophytes

The whole dataset contained 8954 occurrences of 161 species on 1008 trees. The highest CLSR of bryophytes was recorded in Slovenia, 103, whereas it was between 48 and 69 in the other countries (Table 4). It is notable that more than one third of all species records (3381 of 8954) were made in Slovenia. TLSR showed similar differences among countries (ANOVA; df = 4, 1003; F-value 72.96, $p < 0.001$). It was low in Denmark and The Netherlands, intermediate in Belgium and Hungary and the highest in Slovenia. The differences among species rank – relative frequency curves from different countries are more distinct than for fungi, mostly because of the peculiar species frequency distribution in Slovenia (Fig. 3). In Slovenia the frequency distribution of species is much more even than in other countries, the proportion of frequent and subordinate species is very high, and the number of rare species is also considerable. For Hungary and Belgium the curves were steeper than in The Netherlands and Denmark. In the two latest countries the proportion of frequent species is relatively high, country level species richness is low, and there are only a few subordinate and rare species in the samples.

Table 3 – Steps of multiple regression model building of species richness of fungi during backward selection

Steps	SS_e	DF_e	MS_e	dSS_e	dDf_e	dMS_e	F	p
Without regression	1499.4	1007	1.489	–	–	–	–	–
+ Full model				−838.7	−56	−14.946	10.058	***
	660.7	969	0.695					
−DBH × DS × COUNTRY				14.7	18	0.816	1.173	n.s.
	675.4	969	0.697					
−DBH × DS				17.3	5	3.462	4.967	***
−DBH × COUNTRY				29.4	4	7.342	10.534	***
−DS × COUNTRY				44.9	19	2.362	3.388	***
−All interaction	770.0	997	0.772					
−DS				129.5	5	25.900	33.549	***
−DBH				357.0	1	357.000	462.430	***
−COUNTRY				70.2	4	17.542	22.723	***

The error estimation was normal, the link function was square root. SS_e, DF_e, MS_e: sum of squares, degrees of freedom and mean square of the error part of regression. dSS_e, dDF_e, dMS_e: deviation in sum of squares, degrees of freedom and mean square of error after the regression step. Explanatory variables are country (COUNTRY, factorial variable of five level), decay stage (DS, factorial variable of 6 level) and diameter at breast height (DBH, continuous variable). "p" is the significance level of deviance analyses using F statistics, n.s.: not significant, $^*p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$. Based on the backward selection the minimum adequate model was COUNTRY + DBH + DS + DBHxDS + DBHxCOUNTRY + DSx-COUNTRY. R^2 value of the regression was 0.5495.
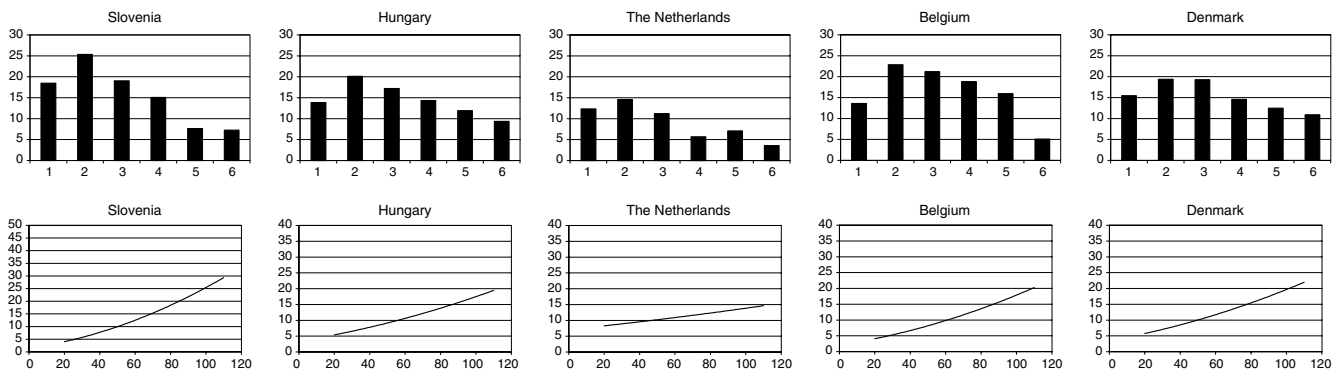
Fig. 2 – Tree level species richness of fungi. First row: predicted values of species richness (Y axes) at different decay stages (X axes) in different countries. Tree DBH is fixed at 80 cm. Second row: predicted values of species richness (Y axes) depending on DBH values (X axes) in different countries. Decay stage of trees is fixed at 3 (in case of other decay stages the curves are similar).
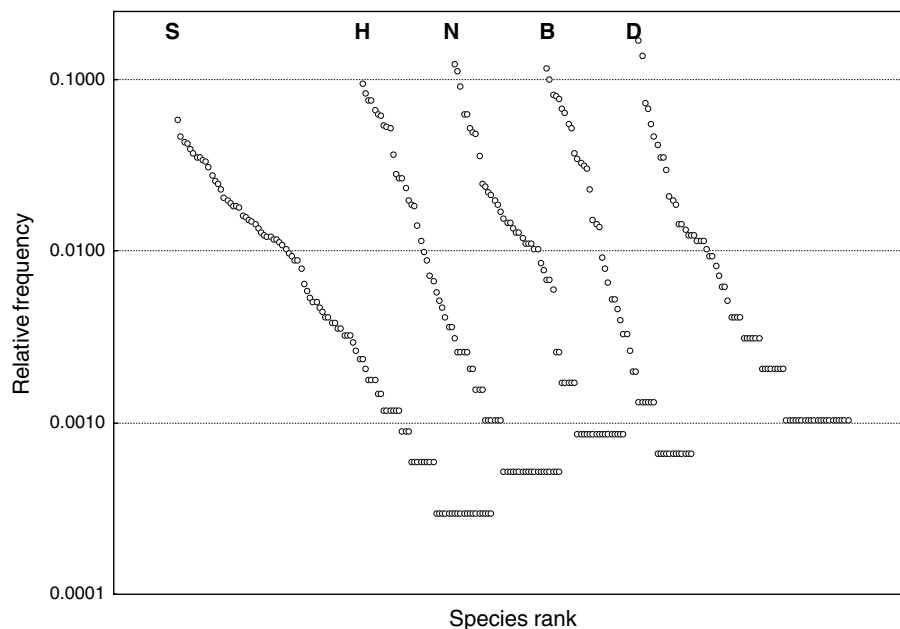
Table 4 – Species richness of bryophyte communities in different countries

Variable	Slovenia	Hungary	The Netherlands	Belgium	Denmark	Whole data set
Number of trees	211	207	198	192	200	1008
CLSR	103	65	56	48	69	161
Number of occurrences	3381	1928	1155	1525	965	8954
TLSR (mean ± SD)	16.02 ± 9.82[a]	9.31 ± 5.31[b]	5.83 ± 4.65[c]	7.94 ± 4.11[b]	4.82 ± 3.66[c]	8.88 ± 7.21

TLSR significantly differ among countries (ANOVA, F-value $(4, 1003) = 72.96$, $p < 0.001$), the letters show the results of multiple comparison test. CLSR: country level species richness. TLSR: tree level species richness.

Unlike the case for fungi, multiple regression modeling showed that the effect of geographic region (COUNTRY, F-value 123.0) was more important than that of tree size (DBH, F-value 97.6) in explaining bryophyte TLSR (Table 5). The effect of decay stage was even less important though still highly significant (DS, F-value 3.6). Among the two-way interactions DBH × COUNTRY had far the strongest effect in the model, indicating that the importance of tree size was different for each country. TLSR increased considerably with tree size in Slovenia, moderately in Hungary and Belgium, while tree size had hardly any effect in The Netherlands and Denmark (Fig. 4). Reflecting the relatively weak effect of decay stage

Fig. 3 – Species rank – relative frequency curves of bryophytes in Slovenia (S), Hungary (H), The Netherlands (N), Belgium (B) and Denmark (D).

Table 5 – Steps of multiple regression model building of species richness of bryophytes during backward selection

Steps	SS_e	DF_e	MS_e	dSS_e	dDf_e	dMS_e	F	p
Without regression	1377.3	1007	1.368	–	–	–	–	–
+ Full model				−571.7	−56	−10.209	7.463	***
	805.6	951	0.847					
−DBH × DS × COUNTRY				11.51	18	0.639	0.755	n.s.
	817.1	969	0.843					
−DBH × DS				6.0	5	1.210	1.435	n.s.
−DBH × COUNTRY				38.2	4	9.552	11.331	***
−DS × COUNTRY				40.4	19	2.125	2.520	***
−All interaction	903.8	997	0.906					
−DS				16.3	5	3.260	3.598	***
−DBH				88.4	1	88.400	97.572	***
−COUNTRY				445.6	4	111.400	122.958	***

The error estimation was normal, the link function was square root. SS_e, DF_e, MS_e: Sum of squares, degrees of freedom and mean square of the error part of regression. dSS_e, dDF_e, dMS_e: Deviation in sum of squares, degrees of freedom and mean square of error after the regression step. "p" is the significance level of deviance using F statistics, n.s.: not significant, $^*p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$. The minimum adequate model was based on the backward selection of COUNTRY + DBH + DS + DBH × COUNTRY + DS × COUNTRY. R^2 value of the regression was 0.402.

in the model, the predicted TLSR values differ only slightly among decay stages in all countries.

3.3. Threatened species of fungi

In total 99 species defined as species of special interest (SSI) were recorded. Of these, 11 species were regarded as highly threatened all over Europe (SSI-A), 41 species as rare and potentially threatened (SSI-B), and 47 as threatened only in some of the included countries (SSI-C). The total number of SSI's recorded was the highest in Hungary (51), slightly lower in Slovenia (43) and Denmark (41) and very low in The Neth-

erlands (27) and Belgium (24). Of the most threatened species (SSI-A) six were reported from Hungary and only one to three species from each of the other countries included. In total 1084 records of SSI's were made during the study. The highest numbers of records were obtained in Hungary (301), with slightly lower values from Denmark (258), Slovenia (235), and low values from Belgium (175) and The Netherlands (115). 66 % of the 29 SSI-A records were made in Hungary.

If the numbers of records of SSI's are related to the total numbers of records for each country, it is evident that the proportion of SSI's was considerably larger in Slovenia and Hungary (>10% of records), intermediate in Denmark (9%) and low
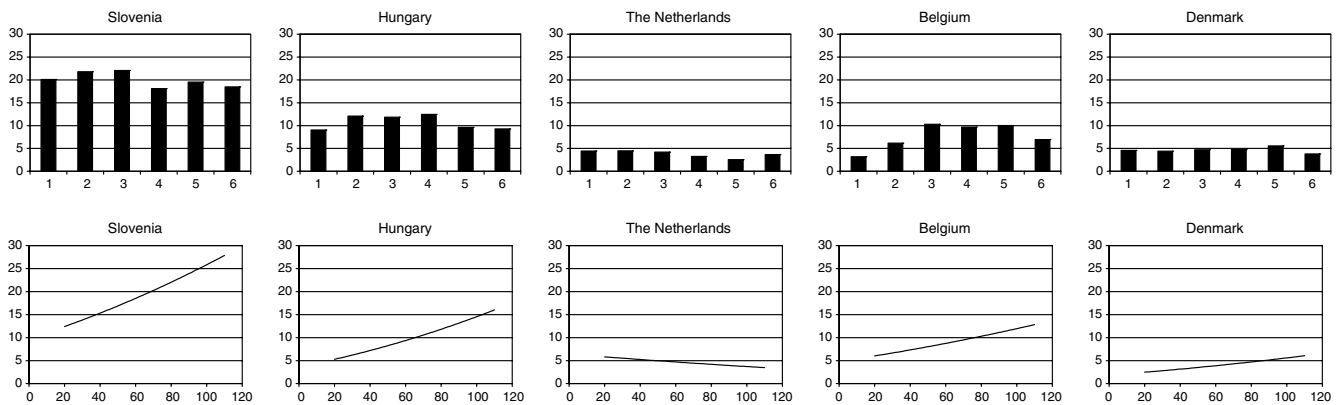
Fig. 4 – Tree level species richness of bryophytes. First row: predicted values of species richness (Y axes) at different decay stages (X axes) in different countries. Tree DBH is fixed at 80 cm. Second row: predicted values of species richness (Y axes) depending on DBH values (X axes) in different countries. Decay stage of trees is fixed at 3 (in case of other decay stages the curves are similar).

in The Netherlands and Belgium (ca. 5%) (Fig. 5). A χ^2 test confirmed the distinctiveness of theses differences ($\chi^2 = 154$, df = 4; $p < 0.001$), and showed that the observed number of SSI's recorded in Hungary and Slovenia was much higher than the expected value, while the opposite is true for The Netherlands and Belgium.
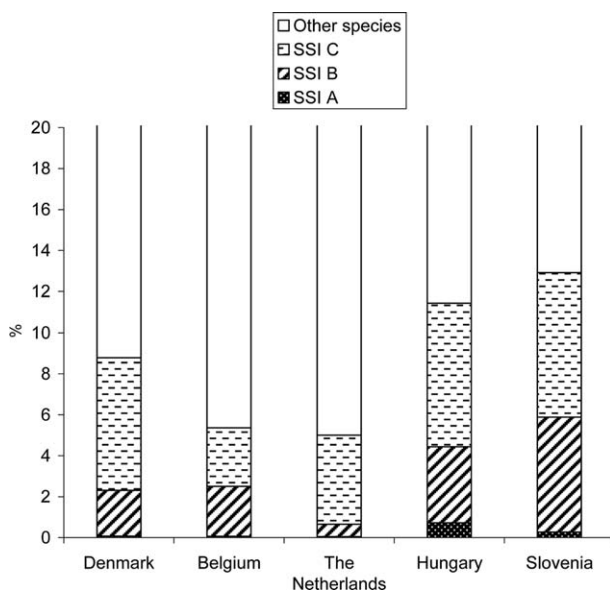
Fig. 5 – Relative frequency (%) of threatened fungi in different countries. SSI, Species of special interest. SSI A, widespread species regarded as very rare and severely threatened (IUCN threat categories "Endangered" to "Critically Endangered") everywhere in Europe. SSI B: widespread species regarded as rare all over Europe, and threatened in several countries (IUCN threat categories "Near Threatened" to "Vulnerable"). SSI C: species that are considered to be threatened (IUCN threat categories "Vulnerable" to "Critically Endangered") in one or several of the covered European countries, but being frequent in others.

3.4. Threatened species of bryophytes

The whole data set contained seven threatened species listed in the European (ECCB, 1995) or Slovenian red lists (Martinčič, 1992) (Table 6). 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 fallen trees in early stage of decay. This forest seems to host a large and very important local population of this threatened species in Europe.

4. Discussion

4.1. Effect of tree size and decay on TLSR in different countries

The present study identified tree size to be more important than decay stage in explaining differences in species diversity in communities of bryophytes and fungi living on dead beech wood in European beech forests. However, an analysis of compositional differences in the same datasets (Ódor et al., 2003), identified decay stage to be much more important than tree size in explaining differences in species composition among both organism groups. This means that there is a considerable directional compositional change (succession) during decay, while the species richness of the different successional stages depends mainly on the size of the trees.

Other studies have also emphasized the importance of tree size for species diversity of fungi (e.g., Bader et al., 1995; Renvall, 1995; Høiland and Bendiksen, 1996; Sippola and Renvall, 1999; Heilmann-Clausen and Christensen, 2004, 2005) and bryophytes (Humprey et al., 2002; Kruys and Jonsson, 1999; Kruys et al., 1999; Söderström, 1988a; Ódor and Standovár, 2001; Ódor and van Hees, 2004). The importance of large trees for species richness seems to involve several different factors. The simplest explanation is the surface area effect: large trees provide more space for species than small ones. Other factors may have a more qualitative effect: (1) large logs decay slower, which allows more time for colonization; (2) the number of

Table 6 – Occurrences of threatened (locally or all over Europe) bryophytes in the investigated forest stands

Species	Red list	Threat category	Country	Site	Number of occurrences	Substrate type
Anacamptodon splachnoides	European	Endangered	Slovenia	Rajhenav	1	Epixyl
Buxbaumia viridis	European	Vulnerable	Slovenia	Rajhenav	2	Epixyl
Antitrichia curtipendula	Slovenian	Vulnerable	Slovenia	Rajhenav	5	Epiphyte
Antitrichia curtipendula	Slovenian	Vulnerable	Slovenia	Krokar	1	Epiphyte
Dicranum viride	European	Vulnerable	Slovenia	Rajhenav	60	Epiphyte
Dicranum viride	European	Vulnerable	Slovenia	Krokar	1	Epiphyte
Dicranum viride	European	Vulnerable	Hungary	Oserdo	*	Epiphyte
Lophozia ascendens	European	Rare	Hungary	Kekes	2	Epixyl
Riccardia latifrons	Dutch	Extinct	The Netherlands	Weversberg	2	Epixyl
Zygodon forsteri	European	Vulnerable	Slovenia	Rajhenav	*	Epiphyte

* The species occurs on some dead beech trees in the site but not on the selected ones of this study.

microhabitats is higher in large trees; (3) small trees may be buried fast into soil and litter, or colonized by fast growing forest floor bryophytes, which may hinder establishment of epixylic bryophytes and late stage, spore dispersed fungi (Bader et al., 1995; Ódor and van Hees, 2004); (4) large trees have more heart-wood and are more likely to be old, with a long infection history as living trees, which may be crucial for the establishment of certain specialized heart rot fungi (Heilmann-Clausen and Christensen, 2005).

We consider the presence of large trees in different stages of decay to be very important for diversity of both organism groups, although even fine woody debris may support species rich bryophyte and fungal communities (Kruys and Jonsson, 1999; Ódor and Standovár, 2001; Nordén et al., 2004). Several specialist heart rot fungi and epixylic bryophytes are, however, unable to thrive on such substrates (Söderström, 1988b; Ódor and Standovár, 2001; Ódor and van Hees, 2004; Heilmann-Clausen and Christensen, 2005) and habitats in which large logs are scarce or missing are accordingly unable to conserve the full range of saproxylic biodiversity. Interestingly, the positive relation between tree size and bryophyte diversity was less pronounced in the Atlantic countries, compared to Slovenia and Hungary. This may reflect that the species pool is limited, with rare and specialized species, preferring large diameter logs being extinct at the landscape scale.

4.2. Bryophytes and fungi – different ecology, different diversity patterns

The realized species pool for fungi was ca. three times larger than for bryophytes (457 versus 161 species), while the difference in TLSR is less pronounced (it was 12.8 for fungi versus 8.9 for bryophytes based on the full dataset). This shows that the proportion of low frequency species was much higher among fungi than bryophytes. This seems to be a general finding in temperate and boreal forests, pointing out fungi, utilizing dead wood directly as a primary nutrient resource, to be much more diverse in dead wood compared to bryophytes, which mainly utilize dead wood as a place to grow (Heilmann-Clausen et al., 2005).

The study confirms that the diversity of fungi and bryophytes living on dead wood is not only dependent of dead wood characteristics, as distinct regional differences in diversity patterns (considering TLSR, CLSR and the occurrence of

threatened species) were identified. The differences in diversity patterns among regions are especially striking for bryophytes, but are also distinct among fungi, especially in relation to the frequency of rare and threatened species. The differences in diversity patterns are also only partly concurrent among the two species groups and some distinct group specific trends are striking. These different trends seem to relate to differences in life styles and habitat requirements among the two groups. Jonsson and Jonsell (1999) and Berglund and Jonsson (2001) found that species richness of bryophytes (including also non saproxylic species) and wood inhabiting fungi was generally weakly correlated in old growth spruce forests. They pointed out habitat characteristics (like the amount and quality of dead wood) to be often better indicators of species richness in one organism group than the species richness in another group. Fungal diversity was in both cases more distinctly correlated with dead wood characteristics than bryophyte diversity. Sætersdal et al. (2004) found that the most important factor influencing the composition of vascular plant and bryophyte communities in a range of Norwegian forests was soil nutrient content while the composition of fungal communities related mainly to dead wood characteristics. Therefore conservation initiatives focusing on wood inhabiting organisms need to focus carefully on wood-inhabiting organisms themselves, and even to distinguish among different groups of wood inhabiting organisms with different habitat requirements. This is important both at the local and the much wider regional or European scales.

In an overall context we conclude that the fragmentation of forests is most detrimental to bryophytes living on dead wood, because many bryophytes are dependent on a moist and protected forest climate. However, the effect of fragmentation may even be crucial for threatened, dispersal limited fungi (Gu et al., 2002). In contrast to the situation among bryophytes, several threatened fungi seem to prefer trees subject to stressful microclimatic conditions. Conservation initiatives aimed on creating dead wood only in damp forest interiors may not benefit these species. In a historical context this preference may even explain the partial lack of congruence in current diversity patterns in fungi and bryophytes along the geographical gradient studied, e.g., the rather high fungal diversity (even regarding SSI) but low bryophyte diversity in Denmark. Forest grazing has been very extensive in parts of

Northwest Europe during the last 5000 years (e.g., Fritzbøger, 1994). This, most likely, has facilitated the development of semi-open landscapes rich in old-grown oaks and beeches, which are superior producers of mast, a valuable source for pig feeding. We believe that this landscape type has been critical for the survival of specialized forest bryophytes, especially epixylic species, while wood-inhabiting fungi have been better able to survive in the dead interior of living trees or on attached dead wood. Further aspects on the relation between diversity patterns and regional factors are discussed below for each organism group.

4.3. Diversity of bryophytes and fungi in different regions

This study shows that the study sites in Slovenia represent diversity hotspots for wood inhabiting bryophytes, considering TLSR and CLSR, as well as the high proportion of threatened species and a high proportion of specialist: obligate epixylic liverworts and epiphytes (see Ódor et al., 2003; Ódor and van Dort, 2003). The study sites in Hungary have a intermediate value for bryophyte diversity, while the Atlantic region seems to have deteriorate assemblages, although CLSR was relatively high in Denmark. The differences in bryophyte diversity among study regions most likely relate to differences in climate, management influenced factors of the stands (availability and continuity of dead wood, stand structure, and stand history), and landscape history (fragmentation of the forested landscape in time and space). The relatively humid, montane climate of the Slovenian sites is favorable for a lot of epixylic bryophytes, especially for obligate epixylic liverworts, all occurring with rather high frequency (*Nowellia curvifolia*, *Riccardia multifida*, *R. palmata*, *R. latifrons*, *Cephalozia catenulata*, *Calypogeia suecica*, *Lepidozia reptans*, *Jungermannia leiantha* and *Blepharostoma trichophyllum*; Ódor and van Dort (2003), suppl2.doc). 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 and Standovár, 2001). They require a continuous presence of large logs in late and intermediate decay stage, and high and stable air humidity. In Hungary, the occurrence of these obligate epixylic liverworts is limited by climate rather than substrate availability. It is well known that a dry microclimate can act as an effective limiting factor for a lot of epixylic liverworts (Clausen, 1964). In most of the continental beech stands air humidity is too low for these species, independently of the presence of dead wood and rich epixylic communities exist only in humid ravines and sheltered north facing slopes (Ódor and van Hees, 2004). It is therefore supposed that the local frequency of epixylic species would be relatively low in this region even if more natural conditions prevailed, but it would be definitely higher than nowadays if more natural forest structures were recreated. In both Slovenia and the studied part of Hungary the landscape has unbroken forest continuity, most of the investigated sites was never clearcut in the past, and creation of dead wood has occurred continuously at least locally. Although forests in these landscapes have been managed for long, populations of dead wood inhabiting organisms have had good chances to survive

and colonize new suitable habitats. In Slovenia the used fine scaled selection felling system saved more structural elements of natural beech forests (e.g., more dead wood) than the larger scaled shelterwood uniform system used in Hungary (Matthews, 1991). This may help explain the high diversity and integrity of bryophytes communities in this country. Further, it is worth to mention that the Dinaric Mountains was one of the refugia for beech in Europe, during the ice age. Slovenia therefore has a much longer beech forest history, compared especially to the Atlantic region (Taberlet et al., 1998; Hewitt, 2000). Whether this has any importance for present day diversity of generally well dispersed organisms like bryophytes (and fungi) remain uncertain.

The modified and impoverished status of the bryophyte communities in the studied Atlantic beech forests is reflected in low TLSR and CLSR and more importantly in a dominance of opportunistic species, and a corresponding scarcity of obligate epixylic elements and rare species. The Atlantic region are all situated in predominantly non forested agricultural landscapes and the diminished bryophyte flora is most likely a result of habitat fragmentation and breaks in forest continuity causing local and regional extinction of dispersal limited species (Söderström and Jonsson, 1992; Rose, 1992). In addition, the amount and quality of dead wood is not suitable for species rich bryophyte vegetation in several sites. Most of the studied sites (especially in The Netherlands and in Belgium) are relatively young stands with broken forest continuity, absence of dead wood for long time in the past and well decayed wood being still underrepresented. In some parts of Western Europe (e.g., Denmark) the majority of forests have experienced a dramatic desiccation during the last 150 year due to drainage, planting of exotic coniferous tree species and increased water extraction. Together with habitat fragmentation this has caused a drier and darker microclimate in the remaining forests. Investigations in Danish beech forests have shown that the dominating management regime focusing on uniform stand structures and rather short rotations are influencing bryophyte diversity and composition negatively (Aude and Lawesson, 1998; Aude and Poulsen, 2000). Current forest management in Atlantic countries takes efforts to reconstruct more natural forest conditions (e.g., higher amount of dead wood, uneven age and species structure, and multi-layered canopy). Hopefully this will help to increase the frequency of rare wood inhabiting bryophyte species depending on special conditions for establishment and propagation (i.e., very old and naturally dying trees) in the region. With increasing age of the forest stands and the availability of more diverse substrates a higher diversity may be expected in the future, especially if the area of protected forests increases in the region. New records of formerly extinct epixylic bryophytes as *Riccardia latifrons* in The Netherlands, and *Nowellia curvifolia* in Belgium support this possibility (van Dort, 2002). In Denmark the relatively high CLSR however indicate that there is a good potential for the recovery of rich bryophyte communities on dead trees, if more or bigger forest reserves are declared and if near-natural forestry is utilized to a wider extent.

For fungi the observed diversity patterns are more complex than for bryophytes: CLSR was highest in Denmark, and also TLSR was high in the Atlantic region (Denmark

and Belgium), while Hungary and Slovenia were richer in rare and threatened species (SSI's).

Several of the defined SSI's are specifically associated with rot in the interior of large living or dead trees, where they cause extensive decay. This is the case for e.g., *Dentipellis fragilis*, *Ischnoderma resinosum*, *Ossicaulis lignatilis*, *Pholiota squarrosoides*, *Spongipellis delectans* and *S. pachyodon*. Some of these are probably heart rot agents with weak pathogenic abilities making them able to extend rot in living trees while others are secondary successors depending on previous heart rot (cf. Niemelä et al., 1995). For simplicity all are denoted heart rot species in the following section, although precise knowledge on their ecological strategies may be lacking. The heart rot species were all recorded most frequently in Hungary and partly in Slovenia, though none of them has a strictly continental or mountainous distribution in Europe. We interpret the higher abundance of these species in Hungary and Slovenia to reflect two different intermingling trends; the general degree of naturalness of the forest landscape and the degree of continentality.

Heart rot species can generally be regarded as stress tolerators, since they are dependent on establishment and growth under inhospitable gaseous and chemical regimes characterizing the interior of living trees (Boddy, 2001). At the local scale forestry activities tend to increase the fraction of uncolonized dead wood (open resources) and small diameter wood relative to the fraction of dead wood already colonized by decay fungi (closed resources) (Boddy, 2001). This is clearly to the benefit of species with ruderal or ruderal-competitive traits (i.e., fast growth, rapid propagation), while heart rot species suffer from the lack of damaged old trees and large diameter wood decaying in the forest floor (cf. Sippola and Renvall, 1999; Penttilä et al., 2004). Thereby forestry activities may change the composition of wood inhabiting fungal communities. The very low frequencies of rare heart rot species and other SSI's in the strongly altered sites in Belgium and The Netherlands seem to reflect this.

In a wider geographical context the Hungarian sites are situated at the southernmost part of the very important beech forest area of the northern Carpathians, which includes several virgin beech forests reserves acting as true hotspots for diversity of wood-inhabiting fungi at the European scale (Christensen et al., 2005). The vicinity of these hotspots may have helped the survival of several rare species in Hungary during past bottlenecks in dead wood abundance. Regional factors most likely play a similar role in Slovenia where the two study sites represent just two out of several virgin forest reserves in the Dinaric region, which is covered with huge expanses of beech dominated forests rich in dead wood.

With respect to the supposed importance of climatic factors we suggest that the adaptations of heart rot species to stressful conditions give these species a competitive advantage in continental climates, with dry and hot summers and large fluctuations in annual and daily temperatures. This could explain the high frequency of rare heart rot species in the distinctly continental Hungarian sites. The slightly lower frequencies of SSI's in Slovenia, compared to Hungary, probably relate to the less stressful, more mountainous climate.

In Atlantic climates several rare heart rot species are most common on trees growing in exposed conditions, e.g., in forest edges, on street trees or in park-like forests (Kresiel, 2000; Heilmann-Clausen and Christensen, 2003), where the microclimatic regime has more continental traits than in forest interiors. Accordingly, conservation initiatives focusing on the conservation of wood inhabiting fungi in Atlantic climates should not only focus on closed forest stands. The high fungal diversity in Denmark is somewhat surprising but may at least partly reflect that the five study sites in Denmark cover higher variation in soil conditions, landscape history and climatic conditions than the much fewer sites in the other countries, except for The Netherlands. Further is should be noticed that simple TLSR of fungi may be quite misleading in a conservation context. From a number of Danish beech forests, Heilmann-Clausen and Christensen (2005) reported TLSR to be negatively correlated with site naturalness indicators (as maximum tree age and dead wood continuity), while diversity of threatened species showed the opposite tendency. The decrease in species diversity per tree in sites with long dead wood continuity can be explained by the competitive exclusion of more opportunistic species (Nordén and Paltto, 2001; Heilmann-Clausen and Christensen, 2005). In this light the rather low fungal TLSR and CLSR in the highly natural beech forests in Slovenia may be less surprising.

Acknowledgements

Appendix A.   Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2006.02.004.

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