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ORIGINAL PAPER

Wood-inhabiting bryophyte communities are influenced by different management intensities in the past

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Abstract Many studies have underlined the fact that once forest continuity is broken, communities of wood-inhabiting organisms may never be restored to their original status. However, only a few studies have actually presented results from sites that have current old-growth structure, and where the history of human interventions is known. In this study we compared the species richness, nestedness, beta diversity, and composition of bryophytes from living trunks and dead logs of beech (*Fagus sylvatica*) in seven forest stands in the Czech Republic with old-growth structure and various histories of past human impact. Our analysis showed that these communities are nested and that their beta diversity is lower than random. There was a significant proportion of shared species, and rare species were present only in the most heterogeneous and the least man affected habitats. We found that bryophyte communities of forests with more intensive past management were significantly impoverished in terms of both species richness and composition. Beta diversity was not related to management history and reflected current habitat heterogeneity. The effect of decay stage on species richness and beta diversity was stronger than the site effect. Our results demonstrate that the protection of current natural beech-dominated

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forests and improvements to their connectivity in fragmented landscapes are crucial for the survival and restoration of the diversity of wood-inhabiting bryophytes.

Keywords Beech · Beta diversity · Bryophytes · Central Europe · Dead wood · Management history

Introduction

Beech-dominated forests are one of the major types of natural vegetation in the temperate zone of Europe (Bohn et al. 2003; Box and Fujiwara 2005). Due to its broad ecological amplitude and high competitiveness, beech (*Fagus sylvatica*) dominates forests at different environmental ranges (Leuschner et al. 2006), and can occur in combination with a broad spectrum of other tree species, like silver fir (*Abies alba*) and spruce (*P. abies*) in harsher climatic conditions and maples (*Acer platanoides*, *A. pseudoplatanus*), hornbeam (*Carpinus betulus*), ash (*Fraxinus excelsior*) and oaks (*Quercus robur*, *Q. petraea*) in milder climate zones (Peters 1997; Standovár and Kenderes 2003).

Temperate broadleaved forests have generally been heavily affected by human activities. Even before the introduction of forestry in the eighteenth and nineteenth centuries, beech forests had been pastured for centuries and selectively cut for timber (Hahn and Fanta 2001). Large areas had been also coppiced for firewood and other purposes, although beech has a relatively low ability to produce vegetative shoots (Peters 1997). With increasing demand for timber in the nineteenth century, many of these forests were cleared and replaced by coniferous plantations. Most of the recent beech forest stands are managed by rotation forestry systems, mainly a shelterwood forestry system using 100–120 years as the rotation period (Hahn and Fanta 2001). This type of management results in even aged monodominant stands with low structural heterogeneity (Brunet et al. 2010). Modern forest management has a serious negative impact on the overall diversity of forest species and thus ecological stability (Larsen 1995; Gamborg and Larsen 2003; Brunet et al. 2010). Tree species and age unification along with a significant reduction of senescent trees and coarse woody debris in forests negatively influence species across different groups (Harmon et al. 1986; Samuelsson et al. 1994; Jonsson et al. 2005; Friedel et al. 2006; Fritz et al. 2008a; Halme et al. 2013). One of the species groups most threatened by the exploitation of temperate forests are epixylic bryophytes (inhabiting decaying wood). Many studies have shown that the diversity of epixylic bryophytes is directly linked to the coarse woody debris of different tree species, volumes and decay stages (e.g. Rambo and Muir 1998; Ódor and Standovár 2001; Ódor and van Hees 2004; Táborská et al. 2015), which is rather scarce in managed forests. Epiphytic bryophytes (inhabiting the trunks of living trees) are also very sensitive to forest management. Many species are associated with large, veteran trees because they can provide the necessary microhabitats and allow a sufficient time for the colonization of dispersal-limited species (Fritz et al. 2008b; Madžule et al. 2011; Király et al. 2013). These assemblages are also very sensitive to forest continuity and fragmentation (Löbel et al. 2006; Ódor et al. 2006; Snäll et al. 2004).

With the greater recent emphasis on nature conservation in Europe, remnants of natural and old-growth forests are often protected by law, and there has been an effort to restore beech forest sites that have been disturbed in the past (e.g. Zerbe 2002; Bauhus et al. 2009; Felton et al. 2010). There have been many studies concluding that once the continuity of a forest is disturbed (including from the point-of-view of certain substrates such as large senescent trees or decaying logs), the full restoration of specialist communities may be long delayed and in some cases is not even possible (Andersson and Hytteborn 1991; Similä et al. 2003; Ódor et al. 2006; Moning and Müller 2009; Heilmann-Clausen et al. 2014). But few of these studies have actually presented results from sites which have current old-growth structure and where the history of disturbances is known (Fritz et al. 2008a).

One way to describe and compare community structures on a gradient of management history is the analysis of beta diversity (Anderson et al. 2011). According to Podani and Schmera (2011) and Carvalho et al. (2013), beta diversity patterns consist of two distinct processes: species replacement and species loss (or gain), the latter being closely related to nestedness. Nestedness refers to the extent that species-poor assemblages are a subset of species-rich ones (Atmar and Patterson 1993) and therefore it can give us valuable information about the distribution of certain species. In the case of fragmented habitats it is usually related to patch size and the level of isolation (Berglund and Jonsson 2003; Hokkanen et al. 2009; Fahrig 2013).

In this paper, we explored the patterns of epiphytic and epixylic bryophyte assemblages in beech dominated forest reserves of different management history in the Czech Republic. Our aim was to contribute to the general knowledge of wood inhabiting (epiphytic and epixylic) bryophyte communities in long-term unmanaged beech-dominated forests. To accomplish this we examined the bryophyte assemblages of beech trunks and logs (for simplicity hereinafter referred to as logs) of large volumes, focusing on the effect of forest history (between sites) and decay stages (within sites) on the community structure (species richness, beta diversity, nestedness, species composition). Our main questions were:

(i) To what extent do management history and decay stage determine the site- and log-level species richness of wood inhabiting bryophytes and the species composition of the communities?
(ii) Are site- and log-level beta diversity and nestedness values of the community different from random (neutral) references?
(iii) Are beta diversity values different between and within sites, and between decay stages within sites?
(iv) How is beta diversity related to the management history and species richness of sites?

Materials and methods

Study sites and sampling

This study comprised seven old-growth mixed forest sites with different management histories in the Czech Republic. All of them are currently protected as nature reserves and excluded from logging and other management activities. All sites have old-growth structure with a long-term absence of human influence, characterized by the presence of old veteran trees, regeneration in naturally created gaps, a fine scale mosaic of forest developmental stages and a high amount of coarse woody debris (Král et al. 2014a). None of these sites has ever been clear-cut, but different human activities in different combinations were performed at every site except one virgin forest site. Based on historical data we divided them into three groups according to the intensity of past management. The general features of the sites along with their environmental characteristics, management history and derived classification are shown in Table 1. Detailed information about the proportion of living trees and dead wood of important tree species in the total volume for each locality are presented in Table 2. Most of these localities are naturally dominated by beech, with the exception of Boubín, where spruce has a similar dominance as beech (Table 2).

For the preselection of appropriate logs we used census datasets from all investigated sites. All standing and downed trees of DBH $\geq$10 cm at these seven sites had previously been mapped and the DBH recorded. In the 1970s, 1990s and 2000s stem-position maps were based on tripod-based theodolite positioning (with sub-meter absolute positional accuracy anticipated). In the 2000s we also used Field-Map technology (http://www.fieldmap.cz). Tree heights were measured on a sample of ca. 10% of trees and fitted using Näslund's height curve (Näslund 1936). Deadwood measurements (incl. lying stem lengths, decay stage determination) were carried out according to the „Deadwood Protocol“ (Král et al. 2014b—supplementary material).

Here we focused on those beech trees with maximum DBH, and selected 35 such logs at each locality. For the purpose of this study we distinguished three decay stages: DS 0—trunks of standing living trees, 10 per each locality; DS 1—dead logs in early decay stages characterized by hard wood and high bark cover (corresponding to decay stage 1 and 2 sensu Heilmann-Clausen 2001), 10 per each locality; DS 2—dead logs in intermediate and late decay stages characterized by soft wood, without bark (corresponding to decay stage 3, 4 and 5 sensu Heilmann-Clausen 2001), 15 per each locality (except for the locality Salajka, where DS 2 was represented by only 12 logs).

In 2015, the presence of bryophytes was surveyed on the whole log surface from the ground to 2 m high in the case of living trees and on the whole surface of dead logs above ground, excluding branches. If the logs included an uprooted part it was not included in the survey. Species were identified in the field or collected for microscopic identification. Voucher specimens are deposited in herbarium of the first and second authors. The species *Hypnum andoi* and *H. cupressiforme* were not distinguished and are here referred to together as *H. cupressiforme*. Nomenclature followed Kučera et al. (2012).

Data analysis

The effect of site and decay stages on log-level species richness was tested by ANOVA with nested error structure (logs of different decay stages were nested within sites, Crawley 2007). The levels of the factors were compared by Tukey multiple comparisons (Zar 1999).

Community diversity structure was explored by the SDR simplex approach proposed by Podani and Schmera (2011). This involves partitioning the relationship between a pair of sample units into three additive components summing up to 1: similarity (S) as measured by the Jaccard index, species replacement (R) and richness difference (D). Beta diversity (also called turnover, T) between pairs was expressed as D+R, and nestedness (nest) as S+D. These functions were calculated between site pairs (using cumulative species lists of the sites) and log pairs. The R script of the studied functions is given in Onine Appendix 1. The mean of the functions were calculated as descriptive statistics, and the position of the pairs were plotted in ternary plot. These measures are dependent on the proportion of the presence records in the matrix (also called matrix fill) as well as on the total number of species in the matrix. The difference of the statistics from randomness was tested by a Monte-Carlo simulation using 999 restricted permutations of the original matrix keeping the size and the presence fill of the matrix as well as the sampling unit species richness fixed. For more details on the method see Podani and Schmera (2011) and Halme et al. (2013).

Table 1 Climatic, structural and historical characteristics of the studied old-growth beech-dominated stands in the Czech Republic. The part of the table evaluating the history of management and the resulting level of human influence in the past is marked in gray background. Human interventions are indicated by red

abbreviation	BO	KO	MI	PO	SA	ZF	ZH
Reserve	Boubínský prales	Kohoutov	Mionší	Polom	Salajka	Žofínský prales	Žákova hora
GPS ("mid-point" of studied area)	48°58'43''N, 13°48'43''E	49°55'26"N, 13°46'18"E	49°32'11''N, 18°39'30''E	49°47'32"N, 15°40'20''E	49°24'07''N, 18°25'17''E	48°39'58''N, 14°42'28''E	49°39'20''N, 15°59'39''E
Elevation (m)	925 – 1105	417 – 568	778 – 890	545 – 625	715 – 820	730 – 837	725 – 800
Total size (ha)	666.4	30.1	170	18	21.9	101.7	38.1
Studied area (ha)	46.6[f]	25.3	9.4	19.3	19	74.2	17.5
Spontaneous development since	ever	1933	1935	1925	1930	1838	1929
Historical management:							
deadwood haulage till	never	1933	1935	1936	1930	1888	1929
deadwood haulage full (f)/ partly, randomized (p)	---	f	p	f	p	p	p
selective felling in the past (yes/no)	n	n	y	y	y	y	y
group felling in the past (yes/no)	n	y	n	y	n	n	n
planting or reforestation in the past (part of the reserve) (yes/no)	n	n	n	y	n	n	y
charcoal burning in the past (yes/no)	n	y	n	n	n	n	y
Level of human influence in the past[a]	**A**	**C**	**B**	**C**	**B**	**B**	**C**
Other common tree species besides beech	*Picea abies*	*Acer platanoides, A. pseudoplatanus, Carpinus betulus, Picea abies, Quercus petraea, Tilia. sp.*	*Abies alba*	*Picea abies*	*Abies alba*	*Abies alba, Picea abies*	*Picea abies*
Living/dead wood ratio	65/35	85/15	69/31	83/17	68/32	60/40	81/19
DBH of dead wood[b]	80 (48, 132)	94 (72, 125)	81 (60, 105)	108 (76, 140)	81 (55, 120)	101 (74, 129)	91 (65, 115)
Bedrock	shist	rhyolite	flysh	migmatite, amphibolite	flysh	granite	migmatite, orthogneiss
T_{ave} (°C)[c]	4.9	7.8	5.2	7.4	6.2	4.3	6.1
Precipitation (mm)[d]	1067	597	1207	774	1142	704	781
References[e]	Vrška et al. 2012	Průša 1985	Vrška et al. 2000	Vrška et al. 2002	Vrška 1998	Pícha 2010, 2012	Vrška et al. 2002

[a] Three levels: A = no human impact, B = only selective felling, C = combination of more activities

[b] Mean diameter at breast height (DBH) based on the investigated dead trees, minimum and maximum are in brackets

[c] Mean annual temperature (*source* Czech Hydrometerological Institute, data interpolation from 1981 to 2011)

[d] Annual precipitation (*source* Czech Hydrometerological Institute, data interpolation from 1981 to 2011)

[e] Historical data were published mostly in regional journals in Czech language. Whenever possible, we refer to literature in English

[f] Core part which has never been managed by man 46.6 ha

Table 2 Proportion of living trees and deadwood (DBH >10 cm) in the total volume for individual tree species calculated according to tree counts, basal area and volume for seven studied old-growth beech-dominated stands in the Czech Republic

Site	BO	KO[a]	MI	PO	SA	ZF	ZH
Proportion of deadwood (% of volume in total)							
F. sylvatica	16.4	88.4	32.8	40.4	15.8	25.5	54.5
A. alba	20.0	4.4	62.2	24.8	79.2	16.4	3.2
P. abies	63.5	0.0	2.7	31.1	4.9	57.7	39.8
Other	0.1	7.2	2.3	3.7	0.1	0.4	2.5
Total	100.0	100.0	100.0	100.0	100.0	100.0	100.0
Proportion of living trees (% of volume in total)							
F. sylvatica	45.7	80.8	78.9	17.0	68.5	62.0	73.9
A. alba	4.3	0.1	5.0	0.6	21.7	3.4	0.0
P. abies	49.8	0.7	0.2	70.7	8.9	33.4	13.5
Other	0.2	18.5	15.9	11.7	0.9	1.2	12.6
Total	100.0	100.0	100.0	100.0	100.0	100.0	100.0

[a] Data from KO (Kohoutov) arte avialable only for trees with DBH >30 cm and calculation is based only on basal area (data about volume are not currently avialable)

The effects of sites and decay stages on the beta diversity of log pairs were then studied in more detail. Within- and between-site beta diversity were compared by a Monte-Carlo simulation (using 999 permutations of the original beta diversity values), and beta diversity between and within decay stages (analyzing only within site pairs) were also studied in a similar way. The effect of sites on within-site beta diversity values and the effect of decay stages on within-site, within-decay stage beta diversity values were tested by F statistics via a Monte-Carlo simulation and Tukey multiple comparisons. In each analysis, site was used as an explanatory factor, but sites of the same management histories were visualized by colors in the boxplots.

The effect of sites and decay stages on species composition was studied by Redundancy Analysis as a direct ordination method (Borcard et al. 2011). The effects of these factors on species composition were also tested by permutational multivariate analysis of variance (Anderson 2001) using the R function "adonis".

All analyses were carried out in the R 3.3.2 environment (RCore Team 2013), with the "vegan" package used for multivariate analyses (Oksanen et al. 2016), and the "multcomp" package for multiple comparisons (Hothorn et al. 2008).

Results

Species richness

We sampled 243 beech logs and found a total 98 bryophyte species (20 of them were liverworts and 78 mosses). Boubín was the richest site (71), Žofín and the reserves with selective felling in the past had intermediate site level richness (60 in average), while reserves with higher levels of past human activities had the lowest values (50 in average; Fig. 1a). Log-level species richness had similar patterns, and the effect of site was significant (nested ANOVA, $F = 5.68$, $p = 0.005$): based on multiple comparisons the sites more influenced by human activities (KO and PO) significantly differed from those less influenced (Fig. 1b). Log-level species richness significantly differed among decay stages (nested ANOVA, $F = 13.63$, $p < 0.001$), with living trunks having the highest species richness, the early decay stage having intermediate values, and the late decay stage the lowest (Fig. 2).

Beta diversity and nestedness

On the site-level, the mean values of similarity and richness differences were higher, while species replacement was lower than the randomized values, which indicated higher nestedness and lower beta diversity than predicted by the null model (Fig. 3; Table 3). The data points in the ternary plot are closer to the S-vertex and side representing richness agreement, and all points are in the lower part of the triangle. This means that on the site-level, the effect of similarity is higher than species replacement in bryophyte communities, which generally indicates low beta diversity. There is a short gradient of nestedness along the bottom side of the ternary plot. The high level of nestedness is also demonstrated by the species list (Online Appendix 2).

On the log-level we found the same patterns as on the site-level (Table 3). In the case of log-level data, matrix fill is much lower than for sites. This results in a high percentage of species replacement and therefore the beta diversity is increased artificially (Podani and Schmera 2011). The resulting beta diversity index is quite high (0.771), but still lower than in a random community of similar matrix fill. On the other hand, nestedness is higher.

Log-level beta diversity was higher between sites than within sites (Fig. 4a, Monte-Carlo simulation $p < 0.001$). In addition, within-site values of beta diversity were higher between decay stages than within decay stages (Fig. 4b, Monte-Carlo simulation $p < 0.001$). Within-site beta diversity was independent of the species richness of the sites ($F = 0.4$, $p = 0.56$, Fig. 5). The effect of site on beta diversity was significant (Fig. 6, $F = 51.7$, $p < 0.001$), but this was not related to forest history. Decay stage also had a

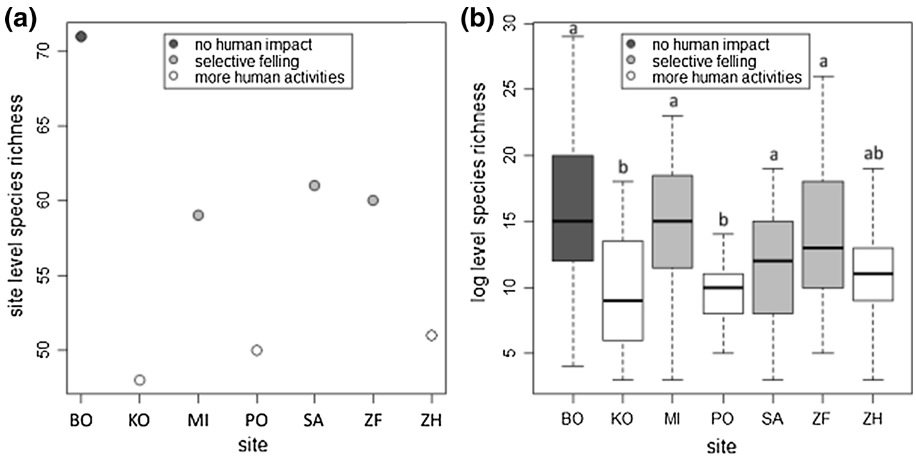


Fig. 1 Site-level (**a**) and log-level (**b**) species richness of old-growth beech-dominated sites in the Czech Republic. On the boxplot (**b**) median, interquartile range and range are indicated. Site name abbreviations are listed in Table 1. Human influence categories are indicated by *different colors*. Significant differences based on Tukey multiple comparisons are marked by *different letters*

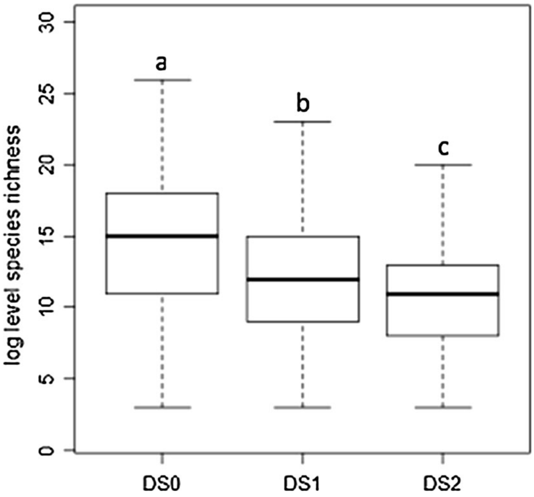


Fig. 2 Boxplot of log-levels species richness of different decay stages. Significant differences based on Tukey multiple comparisons are marked by *different letters*

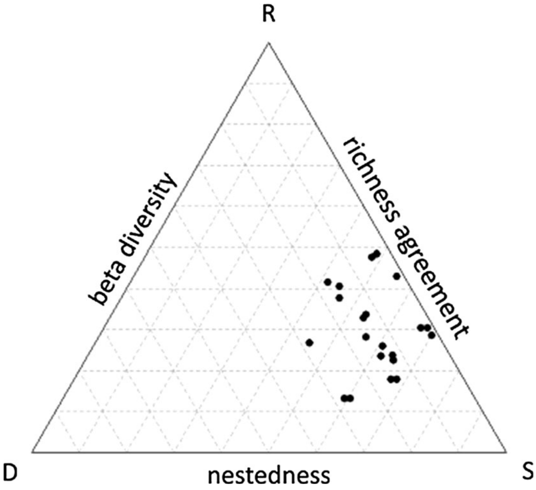


Fig. 3 SDR simplex approach involves partitioning the relationship between pairs of sample units into three additive components: *S* similarity, *R* species replacement, *D* species richness difference. The position of each data point within the ternary plot (the distance from each vertex and site) characterizes the type of difference in community structure measured between each pair of sites. For a more detailed explanation of this type of plotting see Podani and Schmera (2011) and Halme et al. (2013)

significant effect on beta diversity, being higher in the case of decaying logs (DS 1 and 2) than for living trunks (DS 0, Fig. 7, F = 24.23, $p < 0.001$).

Species composition

In the RDA (Fig. 8), constrained axes determined by tree decay stages and seven sites explained 28.3% of total variability (F = 37.7, P = 0.001). The first constrained axis (11.6%) was related to the gradient of decay stages, and the second constrained axis (5.6%) reflected different sites. These results are also supported by the multiresponse

Table 3 Results of the SDR simplex approach, partitioning the relationship between a pair of sample units into three additive components summing up to 1: similarity (S) as measured by the Jaccard index, species replacement (R) and richness difference (D). Beta diversity (also called turnover, T) between pairs was expressed as D+R, and nestedness (Nest) as S+D. These functions were calculated between all site pairs (using cumulative species lists of the sites) and all log pairs. The difference of the statistics from randomness was tested by a Monte–Carlo simulation using 999 restricted permutations of the original matrix keeping the size and the presence fill of the matrix as well as the sampling unit species richness fixed

	Mean value	Confidence interval lower (95%)	Confidence interval upper (95%)	Standard error	Difference from random
Site-level					
S	0.409	0.40838	0.40948	<0.001	Higher
D	0.116	0.11606	0.11616	<0.001	Higher
R	0.475	0.47437	0.47555	<0.001	Lower
Betadiversity	0.591	0.5905	0.59162	<0.001	Lower
Nestedness	0.525	0.52445	0.52563	<0.001	Higher
Log-level					
S	0.064	0.06445	0.06449	<0.001	Higher
D	0.249	0.24866	0.24867	<0.001	Higher
R	0.687	0.68684	0.68689	<0.001	Lower
Betadiversity	0.936	0.93551	0.93555	<0.001	Lower
Nestedness	0.243	0.24304	0.24316	<0.001	Higher

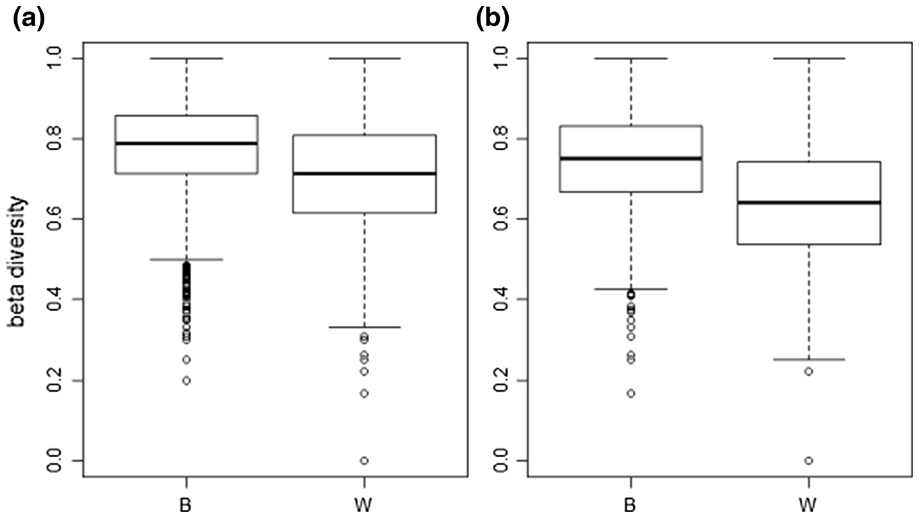


Fig. 4 Boxplots of beta diversity between (B) and within (W) sites (**a**), and beta diversity between (B) and within (W) decay stages within sites (**b**). The differences of median values were significant ($p < 0.001$), based on a Monte-Carlo simulation

permutation test, which confirmed differences in species composition between different decay stages ($R2 = 0.10$, $P < 0.001$) and also between different sites ($R2 = 0.15$, $P < 0.001$).

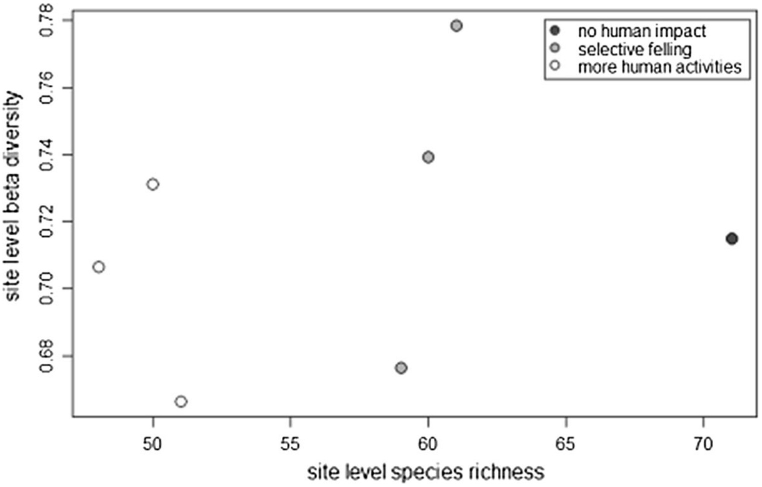


Fig. 5 Relationship between site-level species richness and beta diversity (F = 0.4, p = 0.56). Each site was associated to one of the three levels of human influence in the past according to Table 1

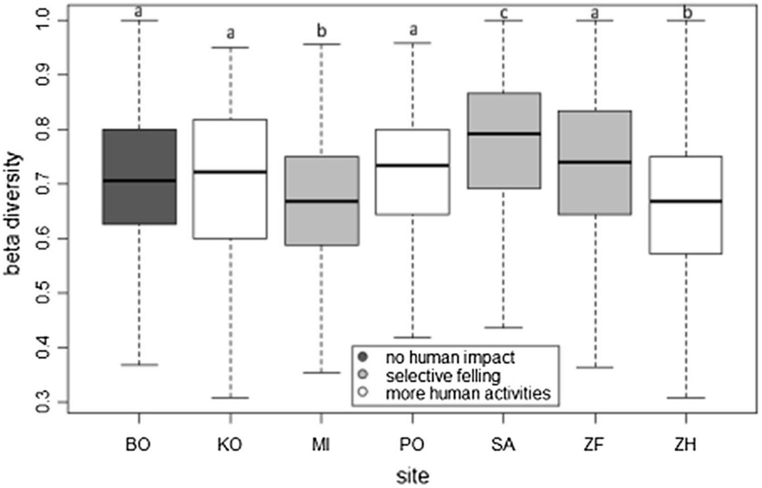


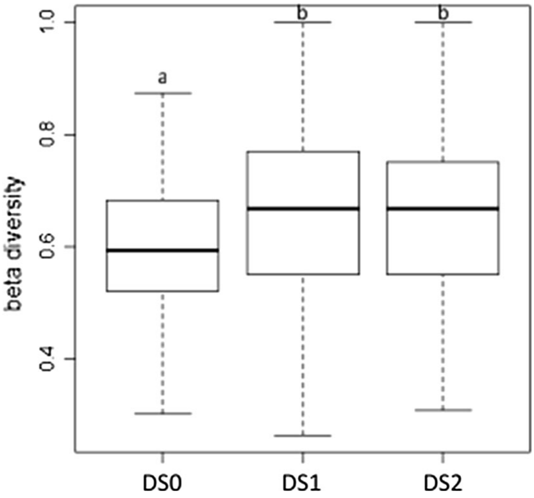
Fig. 6 Boxplot of the beta diversity of sites (F = 51.7, p < 0.001). Significant differences based on Tukey multiple comparisons are marked by *different letters*. Sites are colored based on their human influence categories (Table 1), which were not related to beta diversity

Discussion

Different management history and current species richness and composition

In this paper we present data from beech-dominated forest sites with old-growth structure in terms of the availability of coarse woody debris, the presence of large and senescent trees, and spontaneous development. All of them have remained unmanaged for at least 80 years and have never been clear-cut in the past, but they have had different histories of

Fig. 7 Boxplot of the beta diversity of decay stages (F = 24.23, p < 0.001, permutation test). Beta diversity values were calculated within sites and within decay stages



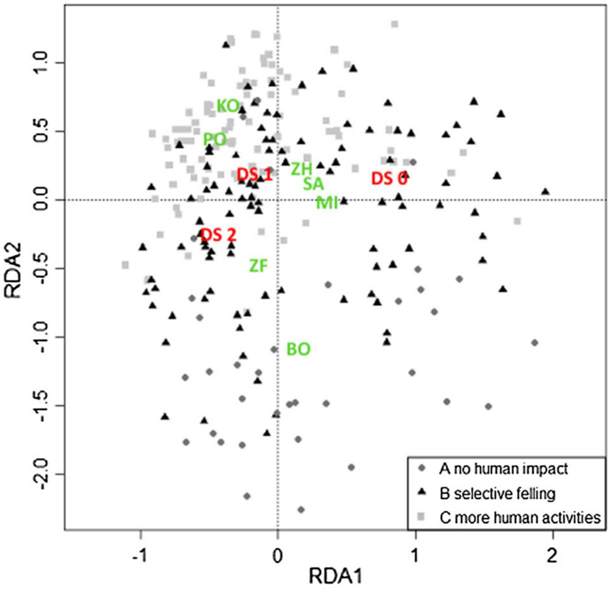


Fig. 8 RDA ordination of logs, marked by different human intervention categories of sites. The explanatory factors are decay stages (*red*) and sites (*green*). (Color figure online)

human activities. Although all these sites currently provide sufficient good-quality substrates for wood inhabiting bryophytes, our results suggest that past human intervention negatively influenced the site and log-level species richness as well as the species composition. In the past, selective felling in combination with full deadwood haulage and/or charcoal burning was focused on the largest trees—living or recently dead—which are the most important substrate for bryophytes (e.g. Ódor et al. 2006; Hofmeister et al. 2015a). This effect was likely apparent long after management had ceased as a result of delay in species colonization. This is consistent with most studies dealing with the diversity of different groups of organisms bound to live trees and dead wood in forest ecosystems (e.g. Brunet et al. 2010; Nordén et al. 2014; Flensted et al. 2016).

Once the continuity of the forest is disturbed, restoration of wood-inhabiting communities is long-lasting process (Andersson and Hytteborn 1991; Ódor et al. 2006; Heilmann-Clausen et al. 2014). One of the main reasons is forest fragmentation, which is common in the European landscape (Kolb and Diekmann 2004; Fritz et al. 2008a; Flensted et al. 2016). In fragmented landscapes with small patches of well-preserved forests often very isolated from each other, recovery is limited by several factors such as dispersal abilities, permeability of the landscape or the availability of suitable microhabitats (Nordén and Appelqvist 2001; Pharo and Zartman 2007; Ódor et al. 2013). The smaller the area of unmanaged stands and the greater the distance to the nearest refuge, the less likely species are to survive (Hofmeister et al. 2015a).

One factor that complicates the interpretation of our results is the fact that in central Europe the intensity of management history is very often correlated with elevation. Forests in lowlands have been influenced by human activities for much longer and more intensively than more inaccessible mountain forests (Kaplan et al. 2009; Chytrý 2012). The positive relationship of the species richness of bryophytes to the rising altitude has been described earlier (Bruun et al. 2006) and these two factors are so closely linked that it is difficult to separate their common influence. This needs to be considered when interpreting the results, however we hope that within one vegetation type this effect could be minor.

The strong effect of decay stage

Decay stage also had a significant effect on both species richness and species composition. The highest species richness was associated with DS 0, i.e. living trees, and decreased with increasing decay stage. The initial high species richness resulted from the high proportion of epiphytic species in the community, which decreases rapidly during the decay process because of gradual bark loss. Late decay stages are represented mostly by generalists, since epixylic specialists prefer the logs of conifers because of more suitable substrate pH and water holding capacity (Táborská et al. 2015).

Considering the beta diversity between decay stages within sites, it was higher on logs (DS 1 and DS 2) than on trunks (DS 0), in contrast to species richness. The higher beta diversity on logs likely resulted from higher habitat diversity. Logs are more heterogeneous, consisting of a mosaic of microhabitats like bark, soft wood, rot holes or humus, while trunks are much more uniform and extreme in terms of microclimatic conditions (desiccation, direct sun shine, abrasion etc.), especially in the case of beech. Generally, beta diversity between trunks is mainly driven by different tree species (Mežaka et al. 2012; Ódor et al. 2013) and tree size (Fritz et al. 2008b; Király et al. 2013), but in our case these factors were excluded by the sampling design.

We found that within-site beta diversity was lower than between-site beta diversity. The site effect was significant, but relatively small. In species composition, decay stage effect overwhelmed the differences between sites. On a larger (continental) scales, regional differences for wood inhabiting bryophyte communities are very strong and more important than local factors (Qian et al. 1998; Ódor et al. 2006; Heilmann-Clausen et al. 2014). Also, within a region the differences among sites are generally more important for species composition than within site factors like decay stage, driven mainly by climatic differences (Ódor and van Hees 2004). In our study we included data not only from lying logs (DS 1 and DS 2) but also from live trunks (DS 0). These two substrates have very different conditions (mainly water holding capacity, surface pH) and there was also a large difference between our DS 0 and DS 1—2 in terms of physical and chemical properties. This could explain why in our case decay stage had a stronger effect on species composition than the site.

Nestedness and beta diversity in old-growth forests with different management histories

Based on the SDR analysis we found that wood-inhabiting bryophyte communities in our studied sites are nested. In other words, the species composition of species-poor plots is a subset of richer plots (Patterson and Atmar 1986). This was true both on the site- and log-levels. The beta diversity of wood-inhabiting bryophytes was lower than random both on the site- and log-levels. These results indicate that there is a significant proportion of shared species present both in species-rich and species-poor communities resulting in small differences in beta diversity; this is typical for organisms with good dispersal ability (Qian 2009). While the long-distance dispersal ability of bryophytes is still under discussion (Laaka-Lindberg et al. 2006; Barbe et al. 2016), on a local scale most bryophytes are considered to be good colonizers due to their microscopic wind-dispersed spores and the generally rich production of propagules (Frahm 2008). In addition to common species, we found a group of rare species that were arranged in a nested pattern (e.g. *Neckera pennata*, *Nowellia curvifolia*, *Pseudoamblystegium subtile*, *Zygodon dentatus*). This group is represented by substrate specialists that tend to increase in number with rising habitat heterogeneity (Brunet et al. 2010) in space and time.

Based on our data we found that beta diversity and site-level species richness are independent of each other. This is consistent with Hofmeister et al. (2015b), who published similar results for bryophytes in their study comparing forests with different current management intensity to nature reserves. Ujházyová et al. (2016) also confirmed that the species richness and beta diversity of beech forest vegetation can be driven by different environmental factors. Moreover, site- and log-level species richness were related to the intensity of management in the past while beta diversity was independent of it. The present lower species richness on sites with broken continuity could be explained by local extinctions caused by a lack of suitable microhabitats in the past. Beta diversity, on the other hand, reflects current local conditions and environmental heterogeneity of the studied substrate independently of the management history.

Implications for nature conservation

Our study confirms that forest conservation activities should be aimed at the protection of natural sites and improvements to their connectivity in fragmented landscapes. This is in line with the conclusion of the review of Nordén et al. (2014) that permanent reserves are still key conservation tool. Dispersal limitation in combination with random extinctions, and possibly also colonization delay, are the strongest factors threatening current wood-inhabiting bryophyte populations and complicating their re-establishment after disturbances (Fritz et al. 2008a). The isolation of natural and old-growth forests could be reduced by retention forestry management, which introduces the inclusion of old-growth attributes in managed forests (Lindenmayer et al. 2012; Fedrowitz et al. 2014). The presence of large senescent trees of different species and coarse woody debris of different volumes and decay stages is crucial for the survival of specialized species (Hofmeister et al. 2015a). However, nature conservation expectations should be realistic with respect to the management history of the site, since as our study demonstrates the quality of old-growth forests is strongly limited by past human impacts, at least within the time period we focused on. We also found that beta diversity indices are good for measuring environmental heterogeneity, but should not be used as indicators of the biodiversity value for bryophyte communities.

Conclusions

In this study we analyzed wood-inhabiting bryophytes in seven beech-dominated old-growth forests with different management intensities in the past. We confirmed an impoverishment in terms of both species richness and composition on sites with previous human intervention. This is consistent with studies describing the influence of forest continuity disruption on different groups of specialized organisms. On the other hand, we found no relationship between management history and site- and log-level beta diversity. Unlike simple species richness, indices of beta diversity give us information about the current habitat heterogeneity. Decay stage had considerable effect on site-level species richness, composition and beta diversity increasing habitat heterogeneity of sites. We included live tree trunks, considered decay stage zero, and distinguished only two decay stages for dead logs. These classes differed significantly from each other from the point of view of their physical and chemical properties, leading to clear differences in all studied parameters. To preserve diverse wood-inhabiting bryophyte communities, protection of current old-growth forests and improvements in their mutual connectivity must be provided.

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