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# Diversity and ecology of epiphytic bryophyte communities on dead wood in forest nature reserves.

Ph. D. Dissertation

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# Abstract

In the Czech Republic, or more generally throughout Central Europe, the biodiversity of saproxylic organisms is mainly related to natural old-growth forests. Such forests are the only biotopes in our landscape where sufficient amounts of the dead wood of a certain quality can be found. Besides its role in many functional processes, dead wood plays a crucial part in the overall biodiversity of a stand. Large pieces of decaying trunks are colonized by crowds of species of bacteria, fungi, plants and animals, which are at least at some point in their life-cycle dependent on dead wood. Their diversity increases with the heterogeneity of this substrate, represented by the diversity of tree species, dead wood types, decay stages and size categories. Various combinations of these factors create specific conditions and niches sought out by specialists or colonized by opportunistic species or generalists. The resulting specific communities show a successional process following the decay of the substrate. Because dead wood is a temporary substrate, the long-term stand-scale continuity of dead wood is crucial for the survival of saproxylic populations.

Among the most significant parts of this system are bryophytes colonizing the surface of decaying trunks. At the beginning of the decay, epiphytic species are still present. As the bark disappears, epixylic specialists colonize the decayed wood substrate. There are many generalists (opportunistic species) that can occur in all decay stages. Epixylic species take advantage of the specific environment of well-decayed logs characterized by relatively stable moisture regime, low spatial competition with forest floor plant species and absence of litter. In this thesis I have focused on three groups of factors influencing species richness and composition of bryophytes inhabiting dead wood. In particular we have studied:

1) The differences between two tree species and different decay stages on one site comparing coniferous (*Abies alba*) and deciduous (*Fagus sylvatica*) decaying logs in terms of epixylic bryophytes.

2) The effect of different histories of human activities in the past on recent bryophyte communities inhabiting both living and dead *Fagus sylvatica* trees in seven currently protected old-growth forests.

3) The effect of a topographically-induced microclimatic gradient on epixylic bryophytes inhabiting logs of similar quality (large *Abies alba* logs in advanced decay stage).

**Paper I.** Táborská M, Přívětivý T, Vrška T, Ódor P (2015) Bryophytes associated with two tree species and different stages of decay in a natural fir-beech mixed forest in the Czech Republic. Preslia 87:387–401.

Species richness and composition of bryophyte communities on two species of trees in different stages of decay were studied on 57 logs of *Abies alba* and *Fagus sylvatica* in the natural montane beech-fir forest reserve Salajka (Czech Republic). There were 68 species of bryophytes. At the stand level, the species richness recorded on *Fagus* was higher than that on *Abies*. This is due to a higher diversity of epiphytic species on *Fagus* in the early stages of decay, when the conditions of logs are more heterogeneous and there are more microhabitats than on *Abies*. The log-level species richness was higher on *Abies* in later stages of decay because it is more favorable for epixylic species occurring on very acid and constantly moist substrates. Both at stand and log level, the highest species richness was recorded in intermediate stages of decay, which constitute a transitional phase in decay succession, in which species associated with all stages of decay overlap and therefore the overall number is relatively high. Species composition differed significantly on the two trees, with two clearly defined groups of

indicator species. In contrast, the different stages of decay were not so sharply distinguished in terms of indicator species. We also found significant differences in pH both between the two trees and stages of decay, which may also affect compositional patterns on the logs studied. In conclusion, the species richness and composition of bryophytes on dead wood is associated with both stage of decay and species of tree and their various combinations, which further increase the total diversity. Therefore, successful bryophyte conservation should focus on the preservation of mixed stands and the continuity of dead wood in the montane beech-fir zone of Europe.

**Paper II.** Táborská M, Procházková J, Lengyel A, Vrška T, Hort L, Ódor P (2017) Wood-inhabiting bryophyte communities are influenced by different management intensities in the past. Biodivers Conserv 26:2893–2909. doi: 10.1007/s10531-017-1395-8

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 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 anthropogenically affected habitats. We found that bryophyte communities in forests with more intensive past management were significantly impoverished in terms of 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 forests and improvements to their connectivity in fragmented landscapes are crucial for the survival and restoration of the diversity of wood-inhabiting bryophytes.

**Paper III.** Táborská M, Kovács B, Németh Cs, Přívětivý T., Ódor P (2018) Microclimate as an important driver of epixylic bryophyte communities. Manuscript

Bryophyte communities inhabiting dead wood are formed by several important factors. Besides the amount, quality and continuity of the substrate, there are also external factors indirectly influencing the structure of bryophyte communities. One of the most important such factors is local microclimate. This fact has been recognized by many previous authors, yet no one has directly demonstrated it by microclimate measurements *in situ.* Based on directly measured values of local temperature and air humidity during three seasons, we explored the effects of microclimate on epixylic bryophyte communities. These relationships were investigated on 62 silver fir logs in an advanced stage of decay in an old-growth mixed forest in the Czech Republic. Our analysis revealed a clear response of the communities to the microclimatic gradient. Total species richness and cover increased with decreasing mean temperature and increasing air humidity. The appearance of sensitive epixylic red-listed specialists (mainly liverworts) was also positively correlated with these microclimatic conditions. On the other hand, species more tolerant to desiccation, which are often found also on the bark of living trees, preferred logs with a drier and warmer microclimate.

# Abstrakt

Diverzita saproxylických organismů v České republice, potažmo napříč celou střední Evropou, je vázána především na pralesovité porosty. Tyto lesy jsou v naší krajině jediným biotopem, ve kterém lze najít dostatečné množství tlejícího dřeva vhodných vlastností. Jendou z celé řady významných funkcí tlejícího dřeva v lese je jeho klíčová role z pohledu celkové biodiverzity na lokalitě. Velké kusy rozkládajících se kmenů jsou kolonizovány celými zástupy druhů bakterií, hub, rostlin a živočichů, které jsou alespoň v některé fázi svého životního cyklu závislé na tlejícím dřevě. Jejich diverzita vzrůstá se zvyšující se heterogenitou tohoto substrátu. Ta se odvíjí především od pestrosti druhů dřevin, typů tlejícího dřeva, stádií rozkladu a různých velikostí tlejícího dřeva. Díky různým kombinacím těchto vlastností vzniká pestrá škála mikrostanovišť a nik, které jsou vyhledávány specialisty či kolonizovány generalisty a oportunistickými druhy. Vznikají tak specifická společenstva, která se postupně proměňují a vyvíjí s pokračujícím rozkladem substrátu. Jelikož tlející dřevo je pouze dočasným substrátem, pro dlouhodobou přítomnost saproxylických organismů je klíčový jeho dlouhodobý nepřetržitý výskyt na lokalitě.

Mechorosty jsou jednou z významných skupin obývající tlející dřevo. V počátečních stádiích rozkladu dominují především epifytické druhy. Postupem času dochází k rozkladu borky a dalšímu tlení a objevují se epixyličtí specialisté. Mnoho generalistů a oportunistických druhů se objevuje napříč všemi fázemi tlení. Specializované epixylické druhy jsou závislé na specifickém prostředí, které jim dřevo v pokročilých stádiích rozkladu může nabídnout. Padlý kmen je většinou vyvýšen nad okolní terén, díky tomu druhy osídlující jeho povrch nemusí bojovat o prostor s vysoce pokryvnými druhy lesního podrostu, ani nejsou zakryty opadem. V této fázi je substrát charakteristický relativně stabilní vlhkostí, která je klíčová pro přežití řady citlivých druhů. V této práci jsem se zaměřila na tři skupiny faktorů ovlivňující druhovou bohatost a složení společenstev mechorostů obývajících tlející dřevo. Konkrétně jsme studovali:

1) Rozdíly mezi dvěma druhy dřevin a různými stádii rozkladu na jedné lokalitě. Sledovali jsme rozdíly ve společenstvech epixylických mechorostů obývajících tlející kmeny jehličnanu (*Abies alba*) a listnáče (*Fagus sylvatica*).

2) Vliv různé intenzity lidské činnosti v minulosti na současnou podobu společenstev mechorostů obývajících živé i tlející kmeny buku (*Fagus sylvatica*) v sedmi pralesovitých rezervacích.

3) Vliv mikroklimatu na společenstva epixylických mechorostů obývajících kmeny podobných fyzických vlastností (velké kmeny jedle (*Abies alba*) v pokročilém stádiu rozkladu) situovaných na topografickém gradientu v rámci studované lokality.

**Článek I.** Táborská M, Přívětivý T, Vrška T, Ódor P (2015) Bryophytes associated with two tree species and different stages of decay in a natural fir-beech mixed forest in the Czech Republic. Preslia 87:387–401.

V rámci práce byla studována druhová bohatost a složení společenstev mechorostů obývajících kmeny dvou druhů dřevin v různých stádiích rozkladu. Ve studii byla použita data z 57 kmenů jedle (*Abies alba*) a buku (*Fagus sylvatica*) nacházejících se v Národní přírodní rezervaci Salajka v České republice, ve které je předmětem ochrany horský buko-jedlový pralesovitý porost. Nalezeno bylo celkem 68 druhů mechorostů. Na úrovni celé lokality bylo více druhů zaznamenáno na kmenech buku. To je způsobeno především rozmanitějšími podmínkami a větším množstvím mikrostanovišť, která kmeny buku

v porovnání s jedlí nabízí v počátečních stádiích rozkladu. Na úrovni jednotlivých kmenů byla vyšší druhová bohatost zaznamenána na jedlích v pokročilejších stádiích rozkladu, kdy na tomto substrátu narůstá počet specializovaných epixylických druhů, vázaných na kyselý substrát se stabilní vlhkostí. Na úrovni lokality i jednotlivých kmenů byly druhově nejbohatší kmeny ve středním stádiu rozkladu, které jsou tvořeny mozaikou substrátů různých vlastností a díky tomu poskytují vhodné podmínky k životu druhů všech sukcesních stádií, kterých se tak na jednom kmenu může vyskytovat relativně mnoho. Druhové složení společenstev epixylických mechorostů bylo výrazně odlišné v závislosti na druhu kolonizované dřeviny. Naopak jednotlivá stádia rozkladu nebyla z hlediska druhového složení mechorostů tak výrazně odlišná. Studované druhy dřevin i jednotlivá stádia rozkladu se také významně lišila z pohledu pH povrchu kmenů, což může mít vliv na složení společenstev mechorostů. Závěrem lze shrnout, že druhová bohatost i složení společenstev epixylických mechorostů jsou závislé jak na druhu dřeviny, tak i na stádiu rozkladu kmene. Různorodé vzájemné kombinace těchto dvou faktorů přispívají ke zvýšení celkové diverzity těchto společenstev. Z pohledu udržení diverzity epixylických mechorostů je klíčová ochrana smíšených porostů s nepřetržitým výskytem tlejícího dřeva.

**Článek II.** Táborská M, Procházková J, Lengyel A, Vrška T, Hort L, Ódor P (2017) Wood-inhabiting bryophyte communities are influenced by different management intensities in the past. Biodivers Conserv 26:2893–2909. doi: 10.1007/s10531-017-1395-8

Řada studií potvrzuje, že pokud dojde k narušení kontinuity lesního porostu, společenstva organismů obývajících dřevo mohou být nenávratně poškozena. Na druhou stranu pouze několik studií toto tvrzení podkládá daty z lokalit, které mají v současné době pralesovitou strukturu, avšak zároveň existují údaje o jich narušení lidskou činností v minulosti. V této práci se zabýváme druhovou bohatostí, zahnízděností (nestedness), beta diverzitou a druhovým složením mechorostů obývajících živé a tlející kmeny buku (*Fagus sylvatica*) v sedmi pralesovitých porostech s různou historií lidské činnosti v České republice. Naše výsledky ukazují, že tato společenstva jsou vzájemně zahnízděná a jejich beta diverzita je nižší než náhodná. Existuje zde významný podíl druhů, které jsou vzájemně sdílené, vzácné druhy se objevují pouze na lokalitách, které byly v minulosti člověkem nejméně ovlivněné a jejichž struktura je značně heterogenní. Společenstva v lesích s intenzivnějším managementem v minulosti jsou i v dnešní době ochuzená z pohledu celkového počtu druhů i druhového složení. Beta diverzita není závislá historii lidských zásahů a odráží současnou heterogenitu porostu. Druhová bohatost a beta diverzita jsou více ovlivněny jednotlivými stádii rozkladu než rozdíly mezi lokalitami. Naše výsledky poukazují na význam ochrany stávajících pralesovitých porostů s dominancí buku a důležitost zlepšení jejich vzájemného propojení v krajině. Tyto kroky jsou klíčové pro přežití a obnovu pestrosti společenstev epixylických mechorostů.

**Článek III.** Táborská M, Kovács B, Németh Cs, Přívětivý T., Ódor P (2018) Microclimate as an important driver of epixylic bryophyte communities. Manuscript.

Struktura společenstev obývajících tlející dřevo je závislá na několika důležitých faktorech. Kromě množství, kvality a kontinuity výskytu tlejícího dřeva jsou to také externí faktory, které mají na společenstva nepřímý vliv. Jedním z nejdůležitějších je mikroklima v bezprostředním okolí tlejícího kmene. Jeho význam byl již zdůrazněn celou řadou autorů, dosud však žádný z nich nepřinesl přímý důkaz prostřednictvím měření a zachycení vztahu mikroklimatu a společenstev epixylických mechorostů v terénu. V této práci jsme se zaměřili na přímé měření teploty a vzdušné vlhkosti během tří ročních období. Na základě takto získaných dat popisujeme vliv mikroklimatu na společenstva mechorostů. Tento vztah byla zkoumán v pralesovitém smíšeném lese v České republice na 62 tlejících kmenech jedle v pokročilém stádiu rozkladu. Naše analýza odhalila přímý vliv mikroklimatického gradientu na strukturu společenstev mechorostů. Celková bohatost společenstev a pokryvnost mechorostů stoupala se snižující se teplotou a rostoucí vzdušnou vlhkostí. Stejně tak výskyt vzácných specializovaných epixylických druhů (především játrovek) byl pozitivně korelován s těmito mikroklimatickými podmínkami. Naopak druhy s vyšší tolerancí vůči suchu, které můžeme často nalézt i na borce živých stromů, vyhledávali kmeny se sušším a teplejším mikroklimatem.

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In last six years, I spent hundreds of days in the field working on various projects mostly in forests. These have been a great pleasure, for the most part, thanks to my colleagues and friends who shared these with me. Thanks to all of them for great help, inspiration and good company. Special thanks to Malu, Evča Mikulášková, Bence, and Csaba! For help with some critical bryophyte species determination many thanks to Svatka Kubešová, Honza Kučera, and Evča again. Also thanks to Péter Szabo for correcting my English.

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„Potřebovali bychom opadat jako stromy,

potřebovali bychom ten vegetační klid,

kdy život v našich kmenech by byl jen tušit.

Němě se kývat ve větru několik měsíců a nevědět o tom.“

Jan Balabán

## Content

## List of original publications

The thesis is based on three papers (two published and one submitted manuscript) that are referred to in the text by Roman numerals as follows:

**Paper I** Táborská M, Přívětivý T, Vrška T, Ódor P (2015) Bryophytes associated with two tree species and different stages of decay in a natural fir-beech mixed forest in the Czech Republic. Preslia 87:387–401.

MT and PÓ designed the study; MT did the field sampling and prepared the dataset; MT and PÓ performed all analyses; all authors participated in manuscript writing, which was led by MT.

**Paper II** Táborská M, Procházková J, Lengyel A, Vrška T, Hort L, Ódor P (2017) Wood-inhabiting bryophyte communities are influenced by different management intensities in the past. Biodivers Conserv 26:2893–2909. doi: 10.1007/s10531-017-1395-8

MT and JP designed the study, did the field sampling and prepared the dataset; MT and PÓ developed the methods of data analyses and performed all analyses except SDR simplex, which was performed by AL; all authors participated in manuscript writing, which was led by MT.

**Paper III** Táborská M, Kovács B, Németh Cs, Přívětivý T, Ódor P (2018) Microclimate as an important driver of epixylic bryophyte communities. *Submitted manuscript.*

MT and PÓ developed the research idea and methodology, all authors were involved in data collection and manuscript writing, which was led by MT; MT, PÓ and BK did the data analysis.

# Introduction

*Natural old-growth forests and their role in the cultural landscape of the 21st century*

If we want to study the dynamics of decaying wood and dependent biodiversity in the context of the temperate forest zone, our attention will be inevitably attracted to natural old-growth forests. In the Czech landscape of the 21st century defining this type of biotope could be quite tricky. Sooner or later we have to resign on the idea of a pristine forest and take into account also sites which have been influenced by human activities. At least indirect effects – such as industrial air pollution or overpopulation of deer – have influenced probably every forest in our territory. Nonetheless, there are fragments of well-preserved forests that meet the requirements to be classified as natural and near-natural forests (based on the Amendment to the Nature and Landscape Protection Act n. 114/1992 coll. from the year 2017). About 1.15 % of all forests in the Czech Republic still have old-growth structure with a long-term absence of human influence. They are characterized by the presence of 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). These remnants are mostly concentrated in places difficult to access, such as remote areas in higher mountains, steep rocky slopes or deep valleys (Vrška et al. 2018).

It is obvious from this definition how these small fragments of natural forests differ from the remaining nearly 99% of usually heavily managed forests. There are many aspects that could be discussed but from the point of view of the field of my study, I will focus on the major differences in the amount and quality of the available decaying wood. Standard forest management entails that only negligible amounts of woody debris are left in the forest. This usually involves only small branches with diameter less than 10 cm. This category of dead wood can partly compensate for the absence of larger pieces, but for many groups of saproxylic and epiphytic (in the case of dead wood "epixylic" is a more adequate category, therefore it will be used in the text) organisms this is not a substrate adequate enough for colonization and/or the establishment of viable populations. Especially rare and highly specialized species are directly dependent on the availability of large decaying logs, standing snags or living trees with heartrot and dying branches. For these species the role of the natural old-growth forests is irreplaceable (Ódor and Standovár 2001; Lonsdale et al. 2007; Hofmeister et al. 2015).

*Dead wood as a substrate*

In addition to volume, the quality of dead wood also belongs among the factors driving saproxylic and epixylic biodiversity in forests. The death and decay of a tree is a dynamic process characterized by continuous changes in the physical and chemical properties of the log. The first factor determining the whole process of decay is the cause of death of a tree. There are major differences between trees which had been in perfect physical condition and their death was caused by some abrupt event like windthrow, heavy snow or desiccation, and trees whose death was a complex and gradual process including colonization by pathogens during the last phases of life (Harmon et al. 1986; Bobiec et al. 2005). There are many processes in forest ecosystems which are influenced by the way in which a tree dies. Here I focus only on potential decay pathways driving the ecological succession on the logs.

The first colonizers are usually saproxylic bacteria and fungi which can already be present at the time of death or can colonize the log once the decay process is accelerated due to the increased moisture of the wood tissues. The species composition of saproxylic bacteria and fungi differs depending on the initial health condition of the log and they basically determine the decay processes due to their interspecific interactions. It is important to distinguish physiologically white rot fungi (decomposing both lignin and cellulose) and brown rot fungi (decomposing only cellulose and hemicellulose) as they create different environments and niches for other wood-inhabiting organisms (Boddy 2001).

The log is gradually populated by other groups of organisms, among which the most active in the decay process are saproxylic insects. These depend either on the dead wood itself or on saproxylic fungi and other insects inhabiting this substrate. Similarly to fungi, saproxylic insects play an irreplaceable role in the decomposition and mineralization of the organic woody material. With time, the previously smooth surface of the log changes, the log loses its bark, cracks and hollows appear on the surface, which is colonized by desiccation tolerant species of bryophytes, lichens and flowering plants. As the wood gets softer, species sensitive to moisture appear, as they are supported by the stable microclimate and humidity of the decaying wood. For all of these groups, high diversity of the species bound to dead wood is typical, reflecting the variability, heterogeneity and historical significance of this substrate (Bobiec et al. 2005; Stokland et al. 2012).

Many studies repeatedly demonstrated that only sites with sufficient amounts of coarse woody debris in all decay stages can provide high quality substrate for specialized species of bryophytes, lichens, invertebrates and fungi (e.g. Harmon et al. 1986; Berg et al. 2002; Grove 2002; Botting and DeLong 2009). Species richness in these groups of organisms increases also with the diversity of tree species on the site. In the temperate forest zone, major difference could be recognized in bryophyte communities inhabiting coniferous and deciduous trees, both live and dead (Ódor et al. 2013). Fungi or invertebrates are often even more specialized and there are many species surviving only on a specific tree species (Grove 2002; Heilmann-Clausen et al. 2005).

The presence of good quality substrate increases saproxylic biodiversity. However, it cannot guarantee the presence of specialized, dispersal limited and rare species. For their occurrence, the continuity of convenient conditions on the site is a crucial factor. Not only the continuous presence of the forest itself, but also a stable supply of all kinds of dead wood substrates is necessary for the survival of these sensitive species, which are often dispersal-limited or poorly regenerating (e.g. Fritz et al. 2008; Nordén et al. 2014; Flensted et al. 2016). Their ability to survive in fragmented cultural landscapes is therefore limited only to historically well-preserved localities and their restoration on sites with previously broken continuity may take a long time or in some cases may even be impossible (Andersson and Hytteborn 1991; Heilmann-Clausen et al. 2014).

### *Epixylic bryophytes – one of the major groups of dead wood inhabiting organisms*

There are many groups of organisms that depend on dead wood at least in a certain phase of their life cycle. Decaying logs can provide nutrients, water, substrate or shelter for functionally different organisms, which produce complex saproxylic food chains dependent on dead wood (Stokland et al. 2012). Bryophytes are one of the most significant groups in this microcosm. Generally we refer to this group as epixylics, because they colonize the surface of dead wood without taking part in the decomposition (unlike saproxylic organisms). Decaying wood is a substrate with relatively stable microclimatic conditions (especially large logs in later decay stages) and lower competition by robust forest-floor species (Ódor et al. 2006) . These parameters are crucial for the occurrence of specialized species, which are often represented by very small, humidity-sensitive liverworts creating single-layered mats on the wood surface (Söderström 1988; Jansová and Soldán 2006).

During the decaying process of the log, the composition of bryophyte communities also changes along a well-described successional pattern. At the beginning of the process mainly epiphytic species are present, which survive as long as the bark remains. Most species occur in the transition stage between early and late stages of decay when there are various microhabitats, including both hard wood with remnants of bark and very soft, often spongy, well-decayed wood. These can be colonized concurrently by species with different demands – epiphytes, opportunistic species, generalists and epixylic specialists. In the later stages of decay, epixylic specialists dominate and are gradually replaced by robust species of the forest floor as the substrate is completely decomposed and the log slowly sink into the ground (Söderström 1988b; Kruys et al. 1999; Ódor and van Hees 2004, Heilmann-Clausen et al. 2005). This pattern applies both to deciduous and coniferous trees with some variations. For deciduous trees, the diversity of the first successional stage is higher compared to conifers because of the high numbers of epiphytes. Diversity decreases during decay (Király and Ódor 2010; Mežaka et al. 2012). In contrast, in the case of conifers later decay stages are richer, especially in terms of specialized epixylic species represented mostly by liverworts (Jansová and Soldán 2006; Ódor et al. 2006).

*From the beginning to the present – 70 years of the research*

One of the facts that attracted the attention of scientists from the beginning was this obvious successional series resulting in very high species diversity on natural sites with high-quality dead wood. Probably the first international paper dealing with this topic was published in *Ecology* 70 years ago (McCullough 1948) and can be considered as the corner stone of a modern epixylic bryophyte ecology research. McCullough came up with the first decay stage classification distinguishing 8 decay stages and characterized the typical vegetation (considering bryophytes, lichens and vascular plants) for each. The first complex publication summarizing current knowledge about the ecology of coarse woody debris in the temperate zone appeared almost 40 years later (Harmon et al. 1986) and to this day it is probably the most cited source in this field. This publication was created primarily for the purposes of forest management, so it mostly focused on trees and the decomposition process *per se*, but there are also extensive chapters discussing biodiversity connected to this substrate.

Since then, more intensive research focusing directly on epixylic bryophyte communities began to expand. Scandinavia has become, and to some extent still remains, its cradle. Except detailed studies on succession in natural forests (Söderström 1988b; Söderström 1988c), scholars began to pay attention to other topics, such as the diversity of bryophytes in managed forests (Gustafsson and Hallingbäck 1988; Söderström 1988a; Andersson and Hytteborn 1991) and the attributes determining the structure of epixylic communities (e.g. Kimmerer and Young 1996; Ohlson et al. 1997; Aude and Lawesson 1998). Over time, these research questions have been deepened and broadened, new opportunities have appeared with advanced statistical methods, larger data sets and data availability. Interesting findings arose from interdisciplinary studies and reviews (Berg et al. 2002; Lonsdale et al. 2007; Paillet et al. 2010; Nordén et al. 2014; Heilmann-Clausen et al. 2014). Generally these concluded that the carriers of overall biodiversity are the attributes of natural forests: the presence of the dead wood and large trees as well as the continuity of dead wood and forest cover are crucial.

Even after decades of intensive research, many questions remain unexplored. With the papers included in this thesis, we tried to fill some of the gaps in the general knowledge on the ecology of epixylic bryophytes. According to my view, the results of a recent study (**Paper III**) make the most important contribution to the topic. This study describes the influence of microclimate on epixylic bryophyte communities on dead wood. Using the data about temperature and air humidity directly measured close to the surface of all surveyed logs, we obtained precise data and original results. To the best of our knowledge, this is the first such a study for epixylic bryophytes in the temperate forest zone. The importance of humid and cool microclimate in the biodiversity of epixylic bryophytes is a general experience of field bryologist, but this hypothesis was not proven scientifically by direct microclimate measurements. The case of the **Paper II** is similar. In this paper we studied seven currently protected old-growth forests with different histories of human activities in the past and their effect on recent bryophyte communities inhabiting both living and dead *Fagus* trees. **Paper I**, in which we compared communities inhabiting logs of *Abies* a *Fagus* in three decay stages, is particularly helpful in analyzing the indicator species which characterize individual tree species and decay stages. This study is exceptional in comparing two tree species which are co-dominant on one site – most existing studies focused only on one dominant tree species.

## Study questions of the Ph. D. thesis

In all three presented papers we studied the effects of different factors on species richness and composition of epixylic bryophyte communities.

1. **Paper I – The effect of substrate:** What are the differences between bryophyte communities inhabiting decaying logs of *Abies* and *Fagus*:
    a. Is the species richness recorded on these two tree species similar?
    b. Is the species richness the highest in the intermediate decay stage?
    c. Does the species composition on the two trees and at different stages of decay differ significantly?
    d. Is the effect of species of tree on species composition stronger than that of stage of decay?
    e. Is *Fagus* characterized by epiphytic and opportunistic species, and *Abies* by epixylics (mainly liverworts)?
    f. What are the differences in pH of the surface between these two tree species and does pH change during the decay?

2. **Paper II – The effect of site history:** To what extent are wood-inhabiting bryophytes influenced by different management intensities in the past?
    a. 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?
    b. Are site- and log-level beta diversity and nestedness values of the community different from random (neutral) references?
    c. Are beta diversity values different between and within sites, and between decay stages within sites?
    d. How is beta diversity related to the management history and species richness of sites?

3. **Paper III – The effect of microclimate:** What is the effect of microclimate on epixylic bryophyte communities?
    a. What are the seasonal differences in microclimate and which periods are the most important in terms of the regulation of bryophyte communities?
    b. What is the relationship between total species richness, cover and microclimate?
    c. How do the assemblage and single species respond to microclimatic conditions? Do epixylic specialists prefer logs with more humid conditions?

## Material and methods

Detailed descriptions of the study sites, data sampling and processing can be found in the relevant chapters of the individual papers. Here I present only a general overview of the field sampling and data analyses.

*Study sites*

For all three presented papers we used data about epixylic bryophytes from seven old-growth mixed forest sites in the Czech Republic, which are nowadays protected as nature reserves. The flagship of our research was the locality Salajka in Moravskoslezské Beskydy Mts. (GPS 49.401°N, 18.418°E) (**Paper I, II, III**). The total area of the forest reserve is 22 ha, where elevation ranges from 715 to 815 m above sea level. The forest is dominated by European beech *Fagus sylvatica* L. (60.9% of standing volume, hereafter referred to as *Fagus*) and silver fir *Abies alba* Mill. (29.2% of standing volume, hereafter referred to as *Abies*); the two most common admixture tree species are Norway spruce *Picea abies* L. (8.9% of standing volume) and sycamore *Acer pseudoplatanus* L. (0.9% of standing volume) (Král et al. 2014b). The forest has an old-growth structure characterized by veteran trees, regeneration in gaps and a fine-scale mosaic of patches of various forest developmental stages (Král et al. 2014a). The amount of the dead wood is high, representing 40.3% of the total timber volume. In contrast to the standing trees, dead wood is dominated by *Abies* (84.4% of the total dead wood), followed by *Fagus* (11.9% of the total dead wood) and *Picea* (3.7% of the total dead wood) (Král et al. 2014b). The high proportion of *Abies* in the dead wood is exceptional in the context of Czech old-growth forests and here it is a sort of historical heritage (Janík et al. 2014). The dead wood of *Abies* is not widely studied due to its rarity, which is why we explored the bryophyte biodiversity of this substrate and compared it to the second most common species on the locality, *Fagus,* in **Paper I**.

The site has been under protection and unmanaged since 1937. The forest stand occurs here on two opposite-facing slopes, one facing south and the other facing north. Between them there is a small creek with several parallel tributaries mostly originating on the northern slope. This site was chosen for the microclimatic study because of its topography: to test whether the opposing aspects under closed forest canopy have a microclimate-driven impact on bryophyte assemblages (**Paper III**). The bedrock in the area is flysch rocks of the Solan system made up of sandstone, clay stone and argillaceous shale layers (Menčík 1979), the soil is silt-loam, loam and clay-loam Haplic Cambisols (Driessen et al. 2001). The site has a temperate montane climate, mean annual temperature is 5.4 °C and annual precipitation is 1144 mm (Tolasz et al. 2007).

In **Paper II** we compared data from seven old-growth mixed forest sites. 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. Detailed information about the study sites is provided in **Paper II**, Table 1. Based on historical data we divided the sites into three groups according to the intensity of past management and examined the difference in present epixylic bryophyte communities in relation to this historical human influence.

*Data sampling and data analyses*

For the three presented studies, data were collected as three separate datasets. We had different criteria for the selection of sampled logs in each case. Based on these criteria, in the first step we made a pre-selection of the logs using the stem database for each locality. These databases have been periodically updated since the 1970s. Each database contains among other things information about the position, tree species, live status, diameter at breast height (DBH) and also the decay stage of the dead trees. All these data are also processed in the stem position map. For more details on dead wood measurements and volume calculations see the 'Deadwood protocol' in Supplementary Materials published by (Král et al. 2014b).

In **Paper I** we compared differences in the structure of bryophyte communities inhabiting *Fagus* and *Abies*, for this study we sampled 57 dead trees with DBH 60 to 90 cm, evenly distributed in the three decay stages (DS): DS1 – earliest stage of decay: the species is still recognizable, the stem is usually covered with bark and relatively healthy, and the wood still hard – which is the distinctive feature –, and branches are still present; DS2 – intermediate stage of decay: the species can usually still be identified, the wood is not hard along the entire length of the stem with the core or outer mantle subjected to rot, bark is missing (or negligible); DS3 – late stage of decay: the wood is in an advanced stage of rot, species cannot be identified, log is often broken, its outline uncertain and is partly sunk in the soil. This classification simplifies the six levels classification of decay of Ódor and van Hees (2004). On these selected logs we recorded all bryophytes along a 5 m long section of the logs from their base. The whole surface of the log above ground was surveyed (including the top and the sides). The length of the sample was based on the authors' field experience and is considered to be sufficient for recording most of the species present. It was set to standardize the size of the plots sampled. If the logs included an uprooted part, this part was not included in the survey. In addition to the physical properties of the logs, surface pH was also measured for a subset (altogether 38 logs).

In **Paper II** we compared bryophyte communities on *Fagus* in seven different localities. We focused on dead trees of maximum DBH, and for each locality we selected 35 logs. For the purposes of this study we distinguished three decay stages (DS): DS0— trunks of standing living trees, 10 per each locality; DS1—dead logs in early decay stages characterized by hard wood and high bark cover (corresponding to decay stages 1 and 2 *sensu* Heilmann-Clausen 2001), 10 per each locality; DS2—dead logs in intermediate and late decay stages characterized by soft wood without bark (corresponding to decay stages 3, 4 and 5 *sensu* Heilmann-Clausen 2001), 15 per each locality (except for Salajka, where DS2 was represented by only 12 logs). On these selected trees and logs the presence of bryophytes was surveyed on the whole log surface from the ground to 2 m in height 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, this part was not included in the survey.

In **Paper III** our aim was to capture the effect of microclimate on bryophyte communities inhabiting decaying logs of *Abies*. To eliminate the effect of the substrate itself, we selected only logs with diameter 60–90 cm in an advanced decay stage. Advanced decay stage was defined by wood rot, missing bark, wood being soft, and the log often broken with its outline deformed. Such logs were often partly sunk in the soil (decay stages 4 and 5 based on Ódor and van Hees 2004). The reason for the selection of this type of logs was their great availability on the site and also the presence of epixylic specialists, which are significantly less present on the dead wood of deciduous species. On each log, a

5 m long segment measured from the stem base was examined for bryophytes. The uprooted parts of logs were not included in the survey. Species presence and percentage cover were recorded. The selected logs occurred along a topographic gradient including a north facing slope, valley bottom with a small creek and a south facing slope. We supposed that this topographic gradient provided high microclimatic heterogeneity for the selected logs. Microclimate was measured in three periods of the year 2017, each period lasted 8 days. In spring it was 29 March – 5 April, in summer 8-15 August, in autumn 9-16 November. MCC USB-502 combined air temperature and humidity loggers (Measurement Computing Corp., Norton, MA) were used for microclimate measurements on each log, recording air temperature and humidity in 5-minute intervals. They were temporarily installed on the surface of the logs, at approximately the middle point of each sampled segment.

In all presented papers we studied the effects of different external factors on the diversity and species richness of epixylic bryophyte communities (**Paper I**: tree species, decay stage; **Paper II**: management history of the site, decay stage; **Paper III**: microclimatic gradient). We tried to use the most appropriate and up-to date statistical methods tailor-made to our research questions. This led to different statistical approaches in each paper – detailed descriptions of methods are included in the relevant chapters of the individual papers. However, in each paper the relationships between the dependent variables (species richness, cover, beta diversity etc.) and the investigated factors (tree species, decay stages, forest stands etc.) were explored by general linear models (Faraway 2005, 2006) and mixed models (Zuur et al. 2009). The relationship between multivariate species composition and explanatory variables were analyzed by indirect and direct ordination methods (principal component analysis – PCA, redundancy analysis – RDA, canonical correspondence analysis – CCA, Borcard et al. 2011). In **Paper II** a new simplex method was used for the description of meta-community structure of the studied assemblages (Podani and Schmera 2011). R statistical environment was used in all analyses (R Core Team 2017).

## Main Results

### Paper I

*Species richness*

Altogether we sampled 57 logs, on which we found 68 species (19 liverworts and 49 mosses). The general stand-level species richness recorded for *Fagus* was higher than that for *Abies*. The highest stand-level species richness was recorded for the intermediate stage of decay (DS2) and the values for DS1 and DS3 were similar. The log-level species richness of both liverworts and mosses combined was significantly associated with the stage of decay ($p = 0.0002$, quasi $R^2 = 0.237$). Neither tree species ($p = 0.67$) nor the interaction of tree species and decay stage ($p = 0.39$) had significant effects. The species richness associated with DS2 was significantly higher than that of DS1 and DS3.

*Species composition*

The two explanatory factors of CCA explained 20.4% of the total variance ($F = 4.5$, $P = 0.005$, Fig. 2). Tree species explained 11.5% ($p = 0.005$) and decay stage 5.4% ($p = 0.005$) of the species variance, and the joint variance was zero. The first CCA axis (15.6%, $F = 10.4$, $p = 0.005$) was related to tree species with *Abies* dominant on the negative and *Fagus* on the positive side. The second CCA axis (3.7%, $F = 2.5$, $p = 0.005$) represented an increasing effect of DS. These results are supported by the indicator value analysis. Many epixylic liverwort and also bryophyte species were associated with *Abies.* On the other hand, most of the species associated with *Fagus* are epiphytes or opportunistic species. Only three species were associated with DS2, strict epixylic species were associated with DS3.

*Tree surface pH*

The surface pH of the trees sampled was significantly different for species of tree ($F = 67.4$, $p < 0.001$) and stage of decay ($F = 7.7$, $p = 0.002$). The effect of tree species on surface pH was stronger than that of decay stage (the explained variance was 57.7% and 13.1%, respectively). The pH recorded for *Abies* (mean = 3.6, SD ± 0.30) was significantly lower with a smaller variance than that of *Fagus* (mean = 4.6, SD ± 0.52) ($p < 0.001$). For decay stages, the pH recorded for DS3 was significantly lower than that recorded for DS1 and DS2 (DS1-2, $p = 0.803$; DS1-3, $p = 0.004$; DS2-3, $p = 0.014$).

### Paper II

*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 on average), while reserves with higher levels of past human activities had the lowest values (50 on average). Log-level species richness had similar patterns, and the effect of site was significant (nested ANOVA, $F = 5.68$, $p = 0.005$). 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 values.

*Beta diversity and nestedness*

On the site level, the effect of similarity was higher than species replacement in bryophyte communities, which generally indicated low beta diversity and high nestedness. On the log level, we found the same patterns as on the site level. Log-level beta diversity was higher between sites than within sites. In addition, within-site values of beta diversity were higher between decay stages than within decay stages. The effect of site on beta diversity was significant, but this was not related to forest history. Decay stage also had a significant effect on beta diversity, being higher in the case of decaying logs (DS 1 and 2) than for living trunks (DS 0, $F = 24.23$, $p < 0.001$).

*Species composition*

In the RDA, constrained axes determined by decay stages and sites explained 28.3% of total variance ($F = 37.7$, $p = 0.001$). The first RDA axis (11.6%) was related to the gradient of decay stages, and the second axis (5.6%) reflected sites. These results were also supported by the multiresponse permutation test, which confirmed differences in species composition between different decay stages ($R^2 = 0.10$, $p < 0.001$) and also between different sites ($R^2 = 0.15$, $p < 0.001$).

**Paper III**

*VPD during the vegetation season*

The mean vapor pressure deficit (VPD) values of the investigated periods were significantly different ($F = 50.7$, $p < 0.001$). VPD was significantly lower in autumn than in spring and summer. VPD values clearly showed differences among the periods, in autumn the VPD was close to zero (very low evaporation), while it was between 0.2-0.4 kPa in spring and 0.45-0.6 kPa in summer. Topography considerably influenced VPD in summer and spring. VPD was higher on the south facing slope and on the top of the hills than in the valley and on the bottom part of the north facing slope.

*Effect of microclimate on bryophytes*

Altogether we sampled 62 logs and found 42 species of bryophytes, of which 20 were liverworts and 22 mosses. The combined effect of the spring and summer VPD values were extracted by PCA. The generalized first PCA axis, which we can call microclimate gradient, explained 77% of the variance of the two significant VPD variables. The microclimate gradient in a separate CCA analysis explained 8.66% of the species variance ($F = 5.40$, $p < 0.001$). High microclimate scores represented low VPD values (high humidity, low temperature), while low microclimate scores had the opposite effect. Bryophyte cover ($R^2 = 0.31$, $F = 27.11$, $p<0.001$) and species richness ($R^2 = 0.16$, $F = 11.65$, $p = 0.0012$) were positively related to the microclimate scores, which increased with more humid and cool microclimate (low VPD values). Based on the CCA, species showed a clear separation along microclimate, which was strongly related to the individual response of the species. On the positive side of the microclimate gradient the cover of epixylic and humidity sensitive species exponentially increased or had a unimodal positive response. In the middle part of the gradient there were opportunistic species that did not respond to microclimate. The negative side of the gradient was represented by higher VPD and therefore more dry and warm microclimate was correlated mostly with species with exponentially decreasing response or a linear decreasing response. These were pleurocarpic and acrocarpic mosses, which could occur not only on dead wood but often on the bark of standing trees as epiphytic species.

# Discussion

### *Differences in epixylic bryophyte communities inhabiting two tree species* (**Paper I**)

While the effect of tree species is widely accepted for epiphytes (Slack 1976; Smith 1982; Nascimbene et al. 2013), it is less well studied for epixylic bryophyte assemblages. As we hypothesized, the species richness of the two studied tree species (*Abies* and *Fagus*) was similar at the log level and the most species rich communities occurred in DS2 for both. Both tree species and decay stage had a significant effect on species composition, but this effect was greater for tree species. Epiphytic and opportunistic species were characteristically associated with *Fagus*, while epixylics, mainly liverworts, with *Abies*. Epiphytic species are generally much more common on deciduous trees in early decay stages. This is in part due to the more favorable structure and higher pH of their bark (Löbel et al. 2006; Mežaka et al. 2012) and the more open canopy of *Fagus*, which results in there being more light for epiphytic species (Király and Ódor 2010; Király et al. 2013). For *Abies*, the higher diversity of liverworts was confirmed, represented partly by epixylic specialists occurring typically on conifers in later decay stages due to their lower pH and stable water regime (Ódor et al. 2006; Jansová 2006). These species are usually not present on *Fagus*, which is very often decomposed by *Pyrenomycetes*. This results in a relatively dry well-decayed wood, which is not so suitable for the establishment and survival of epixylic species. It is likely that processes driven by fungi could have a major influence on the bryophyte communities occurring on the surface of logs (Ódor and van Hees 2004).

The pH recorded for *Fagus* was higher than that for *Abies* and decreased during decay. Higher variance in the values for *Fagus* is because there was a greater decrease in pH during decay and also because there were big differences between the pH of bark and decayed wood. In the case of *Abies*, the bark is very acid and the pH does not change dramatically during decay. McAlister (1997) also recorded that the difference between the pH of the bark and wood of pine is much smaller than that recorded for deciduous trees, which accounts for the fewer compositional changes of bryophytes on pine during decay. This observation supports our interpretation of the differences in species richness and composition associated with the two trees and their stages of decay.

### *Human activities in the past and their effect on current epixylic bryophyte communities* (**Paper II**)

All seven study sites nowadays have old-growth structure, have never been clear-cut in the past and remain unmanaged for at least 80 years, but they have had different histories of 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 dead wood haulage and/or charcoal burning was focused on the largest trees—living or recently dead—which are the most important substrate for bryophytes (Ódor et al. 2006; Hofmeister et al. 2015). This effect was likely apparent long after management had ceased as a result of delay in species colonization, which becomes more and more complicated in a fragmented cultural landscape.

Decay stage of the studied logs of *Fagus* also had a significant effect on both species richness and species composition. The highest species richness was associated with DS0, 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. Considering the beta diversity between decay stages within sites, it was higher on logs (DS1 and DS2) than on trunks (DS0), in contrast to species richness resulting from their higher habitat heterogeneity.

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. The reason for this was the relatively small size of the study area. Differences between regions become manifest on a larger (continental) scale (Qian et al. 1998; Heilmann-Clausen et al. 2014). Moreover, in our study we included data not only from lying logs (DS1 and DS2) but also from living trunks (DS0). These two substrates have very different conditions (mainly water holding capacity, surface pH) and there was also a large difference between our DS0 and DS1—2 in terms of physical and chemical properties. Based on the SDR analysis we found that the species composition of species-poor plots is a subset of richer plots. 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). Specialized species tend to increase in number with rising habitat heterogeneity in space and time (Brunet et al. 2010).

### *Microclimate as an important driver of epixylic bryophyte communities* (**Paper III**)

Our results showed that the variability in microclimate in spring and summer is much higher than in autumn. Mean VPDs in these two periods are much higher and this could be a limiting factor for species growth or even survival. In these two periods the differences between studied logs reflect the topography of the site. Epixylic bryophyte communities significantly responded to the microclimatic gradient. As expected, total species richness and cover increased with positive microclimatic scores, which represent decreasing temperature and increasing humidity. In these conditions, bryophyte communities are enriched with humidity sensitive specialized species. This fact is clearly reflected in the analysis of species composition. Species that are classified as epixylic specialists (according to Hill et al. 2007) (*Liochlaena lanceoloata, Calypogeia suecica, Harpanthus scutatus, Callicladium haldanianum, Syzygiella autumnalis* and *Cephalozia catenulata*) were all positively correlated with higher microclimatic scores increasing in their cover along the gradient. Species not responding to the microclimatic gradient (e.g. *Dicranodontium denudatum, Chiloscyphus polyanthos, Tetraphis pellucida, Herzogiella seligeri*) are the dominant species of decayed logs independently from their topographic positions. The last group of species which were negatively related to microclimatic scores (e.g. *Hypnum andoi, Hypnum pallescens, Dicranum montanum, Chiloscyphus profundus*) can often occur on the bark of living trees. Obviously, water availability is not a limiting factor for them and on dead wood they just use niches which have not been suitable for more demanding species.

### *Implications for conservation and management*

In our studies we once again demonstrated that the preservation of natural sites and improvements to their connectivity in fragmented landscapes is crucial for the survival of specialized bryophyte species. 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. 2008). The presence of large senescent trees of different species and coarse woody debris of different volumes and decay stages on larger areas with heterogeneous topography is crucial for the survival of specialized species (Hofmeister et al. 2015). 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.

## Conclusions

The presented studies improved our knowledge about the ecology of epixylic bryophytes. In **Paper I** we proved that on the site level there are major differences between species richness and composition in bryophyte communities inhabiting logs of *Abies* and *Fagus* in different decay stages. While *Fagus* is characterized by high diversity of epiphytic species in initial decay stages, *Abies* is distinguished by its high diversity of epixylic specialists colonizing well-decayed logs with a relatively stable microclimate. We focused on this issue more in detail in **Paper III**, where we studied the topographically-induced microclimatic gradient and its influence on the occurrence of these specialized species on large *Abies* logs in advanced decay stages. These species were scattered along the whole gradient, but their cover increased significantly with more humid and cooler microclimate. In this study we demonstrated that the generally presumed buffering ability of this type of logs is limited and is related to microclimate.

Both **Paper I** and **Paper III** were conducted in a natural old-growth forest with low levels of recorded history of tree or dead wood exploitation. To find out to what extent the human intervention in the past could be apparent in currently protected forests with old-growth structure, we compared seven natural sites with different historis in **Paper II**. Our results indicated that even after more than 80 years of protection, the impact of continuity disruption is still reflected in species impoverishment on these sites.

Through our studies we both directly and indirectly supported the general opinion held by many scientists from different fields that the heterogeneity of conditions in forests must be preserved and improved to conserve overall biodiversity. It is crucial to at least maintain current levels of protection in natural sites and to improve their connectivity in the landscape to support the survival rate of specialized species.

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# Paper I

Táborská M, Přívětivý T, Vrška T, Ódor P (2015) **Bryophytes associated with two tree species and different stages of decay in a natural fir-beech mixed forest in the Czech Republic.** Preslia 87:387–401.

# Dead wood inhabiting bryophytes and their relationship to tree species and decay stages in natural fir-beech mixed forest in Czech Republic.

## Mechorosty tlejícího dřeva a jejich vztah ke druhu stromu a stádiu rozkladu v přirozeném jedlo-bukovém lese v České Republice.

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### Abstract

Species richness and composition of bryophyte communities in relation to two tree species and decay stage were explored on 57 logs of *Abies alba* and *Fagus sylvatica* in natural montane beech-fir forest reserve Salajka (Czech Republic). Bryophytes were represented by 68 species. At the stand level, the species richness of *Fagus* was higher than that of *Abies*. It is explained by higher diversity of epiphytic species on *Fagus* in earlier decay stages, when the conditions of logs are heterogeneous and they provide more microhabitats than *Abies.* The log level species richness was higher on *Abies* in later decay stages because it is more favourable for epixylic species occurring on very acid and constantly moist substrates. Both at the stand and log level, the intermediate decay stage had the highest species richness. It is a transitional phase in the decay succession, where species from all stages overlap and therefore overall number is relatively high.

Species composition differed significantly between the hosts, with two clearly defined groups of indicator species. On the contrary, individual decay stages were not so sharply distinguished from the point of view of indicator species. We also found significant differences in pH both between studied tree species and decay stages, which may also affect compositional patterns on the studied logs. In conclusion both decay stage and tree species influence the species richness and composition of bryophytes on dead wood and their various combinations increase the total diversity. Therefore, successful bryophyte conservation should be focused on the preservation of mixed stands and the continuity of dead wood in the montane beech-fir zone of Europe.

**Key words:** *Abies alba*; bryophytes; conservation; dead wood; decay stage; *Fagus sylvatica*; management; species diversity

## Introduction

It has been proved many times, that sufficient amount of the high-quality dead wood in all decay stages is crucial for many groups of organisms, including arthropods, birds, small mammals, fungi, lichens and bryophytes (Maser and Trappe 1984; Harmon et al. 1986; Samuelsson et al. 1994; Jonsson et al. 2005). This habitat is a biodiversity hot-spot within forests providing food, substrates or shelter to many specialists with strict preferences (e.g. Christensen et al. 2005; Ódor et al. 2006; Stokland et al. 2012). In old-growth forests the proportion of dead wood in different volumes, decay stages and microclimatic conditions is much higher than in managed forests (Siitonen 2001; Jonsson et al. 2005). Therefor these unmanaged forests are more diverse in terms of saproxylic organisms (Söderström 1988; Grove 2002; Müller et al. 2007; Paillet et al. 2010).

During decay the physical and chemical quality of logs change, which drives a succession in bryophyte communities. At the beginning of the process there are mainly epiphytic species present which can survive until the bark is missing. In this stage the bryophyte assemblages vary between tree species because the bark of tree species differs in many factors (Schmitt and Slack 1990; Lewis and Ellis 2010; Mežaka et al. 2012; Király et al. 2013). In later stages, the decaying wood is less species specific than bark, but there are remarkable differences between coniferous and deciduous trees in terms of chemical compounds, physical structure and decay processes (e.g. Harmon et al. 1986). The effect of tree species on epixylic bryophytes is less explored than for epiphytes (McAlister 1995; Jansová and Soldán 2006).

The most species occur in the mid-stage, which is a transition stage between the early and late decay types and therefore rich in different microhabitats which can be colonized by species with various demands (Söderström 1988; Kruys and Jonsson 1999; Heilmann-Clausen et al. 2005). In this stage the community is a mixture of epiphytic, opportunistic and strictly epixylic species. The strict epixylics are represented mostly by small liverworts very sensitive to desiccation, and with high substrate specificity (Lesica et al. 1991; Ódor et al. 2006).

In later decay stages epixylic specialists dominate, which are gradually replaced by species of the forest floor as the substrate is completely decomposed. These forest floor species are mainly bryophytes in the boreal zone (Söderström 1988) and mainly vascular plants in temperate deciduous forests (Ódor and van Hees 2004). This succession pattern and changes in community composition has been described in several studies (McCullough 1948; Söderström 1988; Ódor and van Hees 2004; Ódor et al. 2005; Jansová and Soldán 2006; Heilmann-Clausen et al. 2014), but there are not many papers dealing with the connection between decay stage and species richness (Ódor et al. 2006).

One of the important factor changing during succession and influencing the germination of the propagules, growth survival and nutrient availability is the pH of the colonized substrate (Bates 2009; Goffinet and Shaw 2009). The bark pH and also the pH of decayed logs of various tree species differs ( Barkman 1958; Bates & Brown 1981; Harmon et al. 1986). During decay the pH changes, bark pH is usually higher than that of decayed wood of the same species. We compare the pH of bark and wood in different decay stages of the studied species as a potentially important background variable influencing bryophytes.

In this study we investigate the bryophyte species composition of *Fagus* and *Abies* in different decay stages and the change of substrate pH. We hypothesize that (1) the species richness of the two hosts are similar; (2) the species richness is the highest in intermediate decay stage; (3) the species composition significantly differ both between the two hosts and decay stages; (4) the effect of hosts on species composition is stronger than that of decay stages; (5) *Fagus* is characterized by epiphytic and opportunistic species, while *Abies* by epixylics (mainly liverworts); (6) the pH of *Fagus* is higher than *Abies*; and (7) the pH decreases during decay.

## Materials and Methods

### *Study area*

The study was carried out in the national nature reserve Salajka in Moravskoslezské Beskydy Mountains in the Czech Republic (49.401°N, 18.418°E). The forest occurs between 715 to 815 m elevation range, it is situated on two opposite-facing slopes, with a small creek between them. The bedrock of the area is flysch rocks of the Solan system made up of sandstone, clay stone and argillaceous shale layers (Menčík 1979), the soil belongs to silt-loam, loam and clay-loam Haplic Cambisols (Driessen et al. 2001). It has a temperate montane climate, mean annual temperature is 5.4 °C, and annual precipitation is 1144 mm (Tolasz et al. 2007). The size of the reserve is 22 ha, it is dominated by European beech Fagus sylvatica L. (60.9% of standing volume) and silver fir Abies alba Mill. (29.2% of standing volume), Norway spruce Picea abies L. (8.9% of standing volume) and sycamore maple Acer pseudoplatanus L. (0.9% of standing volume) are also present (Král et al. 2014b). The site has been protected since 1937 without any management activities. It has an old-growth stand structure characterized by veteran trees, regeneration patches in gaps and a fine scale mosaic of forest developmental stages (Král et al. 2014a), the timber volume is 556 m3/ha (Vrška et al., unpublished data). The amount of dead wood is high – 40.3% of the timber volume. While deciduous trees (mainly Fagus) dominate the living volume, there is an opposite situation in dead wood: 84.4% of the dead wood consists of Abies, 3.7% of Picea and 11.9% of Fagus (Král et al. 2014b). The cover of the herb layer is low, it is dominated by Dentaria enneaphyllos L. and D. bulbifera L., other dominant species are Galeobdolon montanum (Pers.) Rchb., Carex sylvatica Huds. and Galium odoratum (L.) Scop. (Šamonil and Vrška 2007).

### *Data collection*

For the pre-selection of appropriate logs we used the stem geographic database of the Salajka reserve which is periodically updated since 1970´s. This map contains among others information about tree species and diameter at breast height (DBH) of each living or dead tree and also about decay stage of the dead logs. For more details on dead wood measurements and volume calculations see the 'Deadwood protocol' in Supplementary Materials published by Král et al. (2014b). Based on this data we were able to select and distinguish 57 logs with DBH from 60 to 90 cm (Tab. 1) classified into three decay stages (DS) as DS1 – early: the species is still recognizable, the stem usually has bark and relatively healthy and hard wood (hard wood is the distinctive feature), branches present; DS2 – intermediate: the species can usually still be identified, the wood is not compact any more along the entire stem length with the core or outer mantle subjected to rot. Bark is missing (or negligible); DS3 – late: the wood is at a stage of advanced rot, the species cannot be identified any more, log outline is undecided, log is broken, partly sank to the soil. This classification follows the six level classes of Ódor and van Hees (2004) merging their 1-2, 3-4 and 5-6 categories. The proportion of *Fagus* and *Abies* as well as decay stages was balanced in the sample (Tab. 1).

Bryophytes were recorded in a 5 m long section of the logs from their base. The whole area of the log section (not sinked into the soil) was surveyed (including the top and the sides). We chose a relatively large sampling unit size, because we wanted to approximate the species pool and the species richness of the logs surveying a similar sized area. The length of the sample was set based on authors´ filed experience and it is considered to be sufficient for catching most species. It was set to standardize the size of sampled plots. If the logs had uprooting part it was excluded from the survey. Along the 5 meters section presence of the species was recorded. Species were identified in the field or transported into the laboratory for microscopic identification. From all species voucher specimens are deposited in the herbarium of the first author. *Orthotrichum* spp. were identified to genus only because they were mostly sterile and impossible to determine (all the fertile plants were *O. stramineum*). The nomenclature followed Kučera et al. (2012). The species were classified as strict epixylic, epiphytic, epilithic, terricolous and opportunistic (occurring on many substrates as rock-bark, bark-dead wood, dead wood-soil etc.) following the classification of Heilmann-Clausen et al. (2014) and Jansová and Soldán (2006). The recorded bryophyte species and substrate categories are listed in Supplementary Material (Appendix 1). The sampling was done in the season 2013.

pH of the log surface was measured in 38 logs (subsample of the 57 logs studied for bryophytes). In each log 3 measurements were made along the studied section with a Vario pH meter. Depending on the log´s condition we measured pH of the present bark or bare wood. If it was partly bare wood and partly covered by bark we made these 3 measurements approximately in the ratio of this parts. pH measurements were carried out within one day on all logs, the weather conditions were homogenous.

Tab 1. The number of sampled logs according to the tree species and the decay stage proportions. DS1 = early decay stage, DS2 = intermediate decay stage, DS3 = late decay stage.

|  | DS1 | DS2 | DS3 | **Sum** |
|---|---|---|---|---|
| *Abies alba* | 8 | 10 | 10 | **28** |
| *Fagus sylvatica* | 9 | 11 | 9 | **29** |
| **Sum** | 17 | 21 | 19 | **57** |

*Data analysis*

The effect of tree species (*Fagus* and *Abies*) and decay stages (DS1-3) at the stand level and log level on species richness were studied separately. At the log level species richness and the effect of the explanatory factors were analyzed by general linear models using Poisson error structure and log link function (Faraway 2006). During this analysis model selection was based on maximum likelihood methods, it was tested by Chi square statistics, the explained variance was estimated by pseudo R square. The difference among decay stage levels were tested by Tukey HSD test (Zar 1999).

Species composition of the logs was studied by multivariate methods (Podani 2000). For these analyses we used only species with 5 or more occurrences. The species data had been square root transformed. Detrended correspondence analysis was made as a preliminary indirect method for exploring the gradient length of the species variance (Lepš and Šmilauer 2003). Because the gradient length was quite long along the first DCA axis (4.5 SD unit) canonical correspondence analysis (CCA) was used as direct ordination for the exploration of the relationships between species and environmental factors (tree species and decay stages). Their explained variance was tested by variation partitioning (Peres-

Neto et al. 2006). During the CCA analysis the effect of explanatory variables was tested by F-statistics via Monte-Carlo simulation with 1000 permutations, the significance of the constrained axes and the whole CCA model was tested by similar way (Borcard et al. 2011). Preference of bryophyte species to tree species and decay stage was tested by indicator species analysis (Dufrene and Legendre 1997; Legendre and Legendre 1998). The difference of pH between tree species and decay stages was tested by linear model (Faraway 2005), Tukey HSD test was made for multiple comparison.

All analyses was carried out in R 3.0.2 environment (R Core Team 2013), vegan package was used for multivariate analyses (Oksanen et al. 2013), labdsv package for indicator species analysis (Roberts 2012).

## Results

### *Species richness*

Altogether we sampled 57 logs on which we found 68 species (19 liverworts and 49 mosses) (Tab. 2). The general stand level species richness of *Fagus* was higher than that of *Abies*. This was also true separately for mosses, but in case of liverworts the stand level species richness of both tree species was similar. Intermediate decay stage (DS2) had the highest stand level species richness, while this value was similar in DS1 and DS3. Again this pattern was the same in case of mosses but for liverworts DS1 had the lowest stand level species richness and DS2 the highest.

Tab 2. Stand and log level species richness of tree species and decay stages and their combinations. For log level species richness the significant differences are marked by uppercase letters (ns: non-significant).

| | **Stand level species richness** | **Log level species richness** |
|---|---|---|
| **Total** | 68 | 10.3 ± 3.61 |
| **Tree species** | | |
| *Abies alba* | 42 | 10.1 ± 3.49$^{ns}$ |
| *Fagus sylvatica* | 59 | 10.5 ± 3.72$^{ns}$ |
| **Decay stages** | | |
| DS1 | 38 | 8.2 ± 2.68$^{a}$ |
| DS2 | 56 | 12.4 ± 3.47$^{b}$ |
| DS3 | 41 | 9.8 ± 3.18$^{a}$ |
| | **Stand level species richness** | **Log level species richness** |
| **Combination** | | |
| *Abies* DS1 | 21 | 7.4 ± 1.32$^{ns}$ |
| *Abies* DS2 | 40 | 11.9 ± 3.7$^{ns}$ |
| *Abies* DS3 | 26 | 10.5 ± 3.11$^{ns}$ |
| *Fagus* DS1 | 30 | 8.9 ± 3.32$^{ns}$ |
| *Fagus* DS2 | 43 | 12.9 ± 3.18$^{ns}$ |
| *Fagus* DS3 | 30 | 9.1 ± 3.11$^{ns}$ |

The log level species richness of liverworts and mosses together was only significantly influenced by decay stage (p=0.0002, quasi $R^2$=0.237). Neither tree species (p = 0.67) nor the tree species and decay stage interaction (p=0.39) had significant effects. The species richness of DS2 was significantly higher than DS1 and DS3 (Tab. 2, Fig. 1). However, analyzing separately liverworts and mosses both tree species and decay stage had significant effects (see Appendix 2). For liverworts species richness of Abies was higher than that of mosses, and the species richness of DS1 was lower than that of DS2 and DS3. For mosses the richness of Fagus was higher, and DS2 had higher species richness than DS1 and DS3.

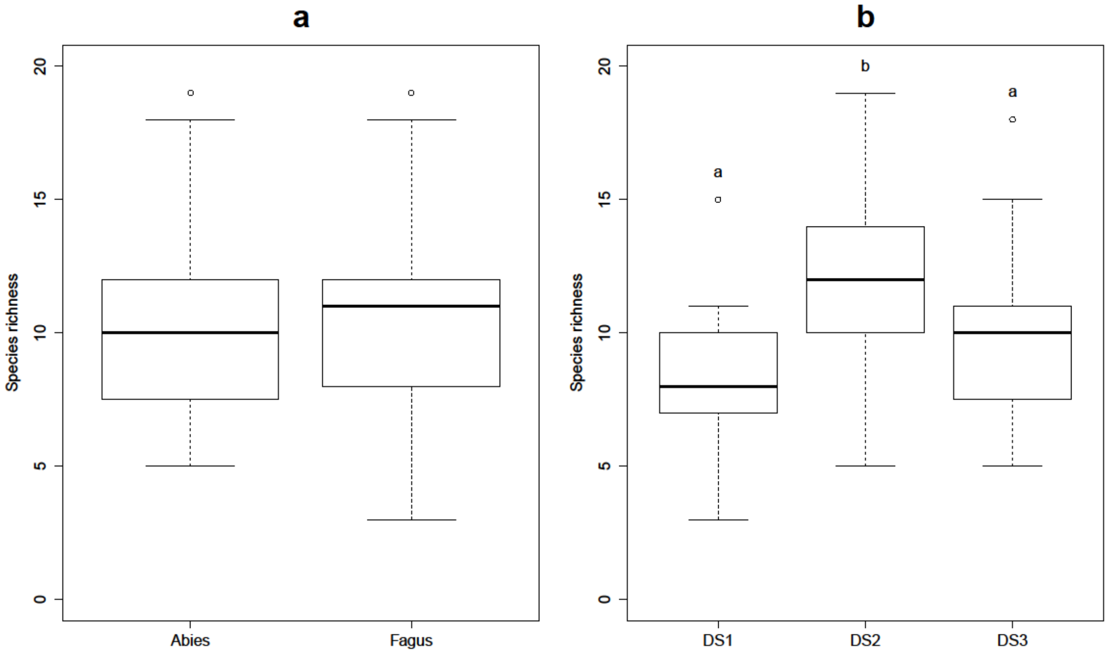

Fig 1. Log level species richness of the different tree species (a) and the decay stages (DS1, DS2, DS3, b). Significant differences based on Tukey HSD test are marked by different letters.

*Species composition*

The two explanatory factors explained 20.4% of the total variance (F = 4.5, p = 0.005, Fig. 2). Tree species explained 11.5% (p = 0.005), decay stage 5.4% (p = 0.005) of the species variance, the joint variance was zero.

The first axis (15.6%, F = 10.4, p = 0.005) was related to tree species with dominance of *Abies* on the negative and *Fagus* on the positive side. The second axis (3.7%, F = 2.5, p = 0.005) represented an increasing DS effect. Species with negative CCA1 values showed preference to *Abies* (*Calypogeia suecica, Cephalozia bicuspidata, Cephalozia catenulata, Herzogiella seligeri, Nowellia curvifolia, Plagiothecium curvifolium*), while species on the positive side of CCA1 preferred *Fagus* (*Brachytheciastrum velutinum, Bryum moravicum, Pterigynandrum filiforme, Radula complanata, Sciuro-hypnum reflexum*).

These visual results are supported by indicator value analysis (Tab. 3, Tab. 4). Many epixylic liverwort species were related to *Abies* (*Blepharostoma trichophyllum, Calypogeia suecica, C. lunulifolia, Nowellia curvifolia*). Most of the bryophytes preferring *Abies* were also epixylic species (*Herzogiella *seligeri, Tetraphis pellucida, Dicranodontium denudatum*), but exception were the epiphytic *Dicranum montanum* and opportunistic *Dicranum scoparium* and *Plagiothecium curvifolium*. On the other hand, most of the species preferring *Fagus* are epiphytes (*Bryum moravicum, Metzgeria furcata, Pterigynandrum filiforme, Radula complanata, Orthotrichum* species) or opportunistic species for decay (like *Brachythecium rutabulum, Brachytheciastrum velutinum*).

Only three species, *Sanionia uncinata, Dicranum montanum* and *Brachythecium salebrosum*, preferred DS2. The DS3 was preferred by strict epixylic species like *Blepharostoma trichophyllum, Cephalozia lunulifolia, C. catenulata, Herzogiella seligeri* and *Tetraphis pellucida*. For DS3 there is also one indicator species classifies as opportunistic, *Lepidozia reptans* (Tab. 4).

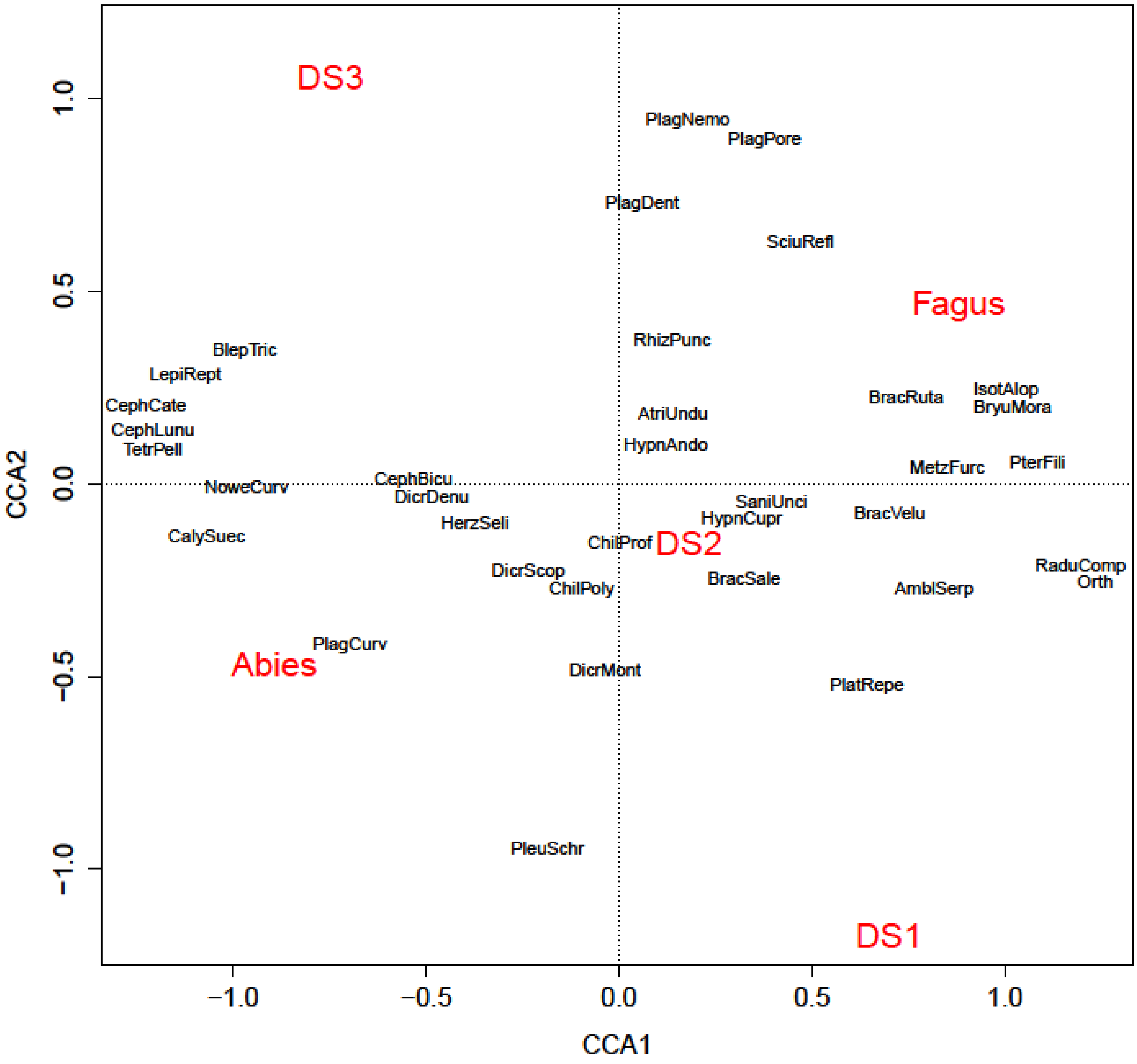

Fig 2. Canonical correspondence analysis biplot of species and environmental factors. The levels of tree species are *Abies alba* (Abies) and *Fagus sylvatica* (Fagus), the increasing degree of decay stages were DS1, DS2 and DS3, respectively. Full names of the species are listed in Appendix 1.

### *Tree surface pH*

The surface pH of the sampled trees was significantly different for both the tree species (F = 67.4, p < 0.001) and decay stages (F = 7.7, p = 0.002, Fig. 3). The effect of tree species on surface pH is stronger than that of decay stages (the explained variance is 57.7% and 13.1%, respectively). The pH of *Abies* (mean = 3.6, SD ± 0.30) is significantly lower with a smaller variance than *Fagus* (mean = 4.6, SD ± 0.52) (p < 0.001). In case of DS, the DS3 pH is significantly lower than DS1 and DS2 (DS1-2 p = 0.803, DS1-3 p = 0.004, DS2-3 p = 0.014).

Tab 3. Species with significant indicator values for tree species (A: *Abies alba*, F: *Fagus sylvatica*). Probability = the significance that the indicator value is different from 0 (probability of first type error).

| **Bryophyte species** | **Tree species A/F** | **Indicator value** | **Probability** | **Frequency on A/F** | **Occurrence (%) on A – F** |
|---|---|---|---|---|---|
| *Herzogiella seligeri* | A | 0.6905 | 0.001 | 28 | 100 – 45 |
| *Tetraphis pellucida* | A | 0.5357 | 0.001 | 15 | 54 – 0 |
| *Dicranum scoparium* | A | 0.4981 | 0.009 | 21 | 75 – 38 |
| *Dicranum montanum* | A | 0.4523 | 0.044 | 20 | 71 – 41 |
| *Dicranodontium denudatum* | A | 0.4344 | 0.009 | 17 | 61 – 24 |
| *Lepidozia reptans* | A | 0.4322 | 0.001 | 13 | 46 – 3 |
| *Nowellia curvifolia* | A | 0.4322 | 0.001 | 13 | 46 – 3 |
| *Blepharostoma trichophyllum* | A | 0.3342 | 0.003 | 11 | 39 – 7 |
| *Cephalozia lunulifolia* | A | 0.3214 | 0.003 | 9 | 32 – 0 |
| *Cephalozia bicuspidata* | A | 0.2908 | 0.038 | 11 | 39 – 14 |
| *Plagiothecium curvifolium* | A | 0.2903 | 0.004 | 9 | 32 – 3 |
| *Calypogeia suecica* | A | 0.25 | 0.006 | 7 | 25 – 0 |
| *Cephalozia catenulata* | A | 0.25 | 0.007 | 7 | 24 – 0 |
| *Bryum moravicum* | F | 0.5172 | 0.001 | 15 | 0 – 52 |
| *Pterigynandrum filiforme* | F | 0.5172 | 0.001 | 15 | 0 – 52 |
| *Metzgeria furcata* | F | 0.4885 | 0.001 | 16 | 7 – 55 |
| *Brachythecium rutabulum* | F | 0.4545 | 0.002 | 15 | 7 – 52 |
| *Brachytheciastrum velutinum* | F | 0.3287 | 0.015 | 12 | 11 – 41 |
| *Orthotrichum* species | F | 0.2414 | 0.013 | 7 | 0 – 24 |
| *Radula complanata* | F | 0.2414 | 0.011 | 7 | 0 – 24 |
| *Plagiochila porelloides* | F | 0.2103 | 0.043 | 7 | 4 – 24 |

Tab 4. Species with significant indicator values for decay stages (DS1, DS2, DS3). Probability = the significance that the the indicator value is different from 0 (probability of first type error).

| **Bryophyte species** | **Decay stage (1, 2, 3)** | **Indicator value** | **Probability** | **Frequency (DS2, DS3)** | **Occurrence (%) in DS1 – DS2 – DS3** |
|---|---|---|---|---|---|
| *Sanionia uncinata* | 2 | 0.3817 | 0.01 | 15 | 41 – 71 – 21 |
| *Dicranum montanum* | 2 | 0.3472 | 0.041 | 16 | 65 – 76 – 26 |
| *Brachythecium salebrosum* | 2 | 0.259 | 0.049 | 10 | 29 – 48 – 11 |
| *Lepidozia reptans* | 3 | 0.3865 | 0.002 | 10 | 0 – 19 – 53 |
| *Herzogiella seligeri* | 3 | 0.3724 | 0.048 | 17 | 59 – 67 – 89 |
| *Tetraphis pellucida* | 3 | 0.3624 | 0.001 | 10 | 0 – 24 – 53 |
| *Blepharostoma trichophyllum* | 3 | 0.3378 | 0.004 | 9 | 0 – 19 – 47 |
| *Cephalozia lunulifolia* | 3 | 0.2174 | 0.035 | 6 | 0 – 14 – 32 |
| *Cephalozia catenulata* | 3 | 0.1932 | 0.03 | 5 | 0 – 10 – 26 |

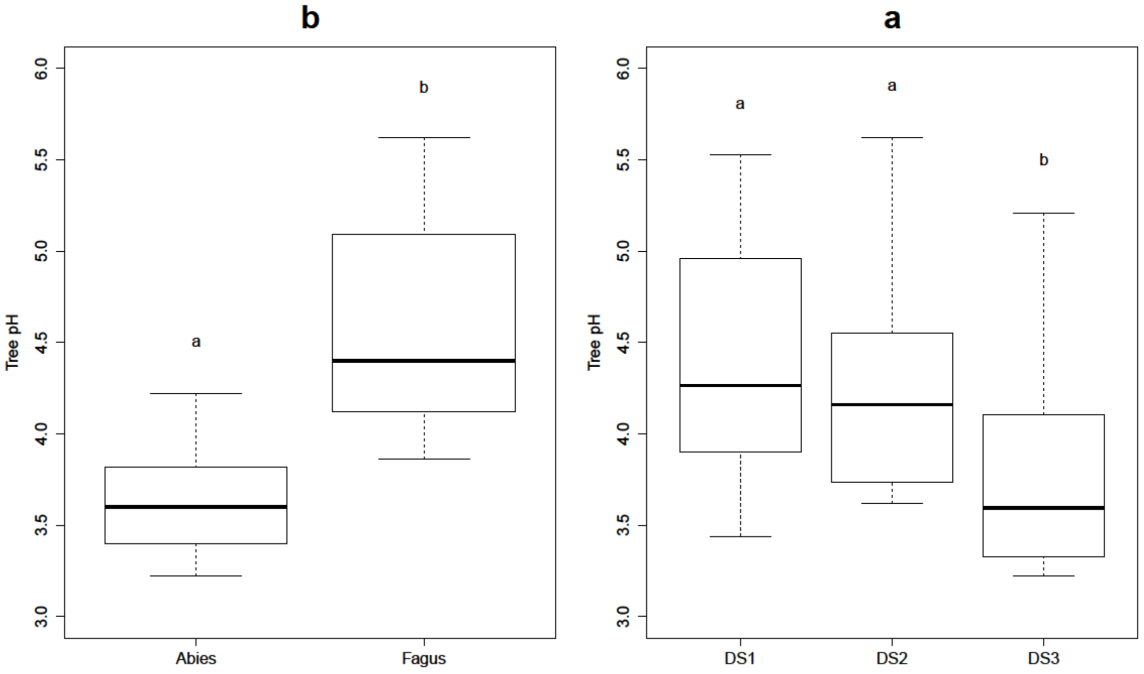

Fig 3. Tree surface pH of different tree species (a) and decay stages (DS1, DS2, DS3; b). Significant differences are marked by different letters.

## Discussion

*Hypotheses 1-2: The species richness of the two hosts is similar, intermediate decay stage maintain the highest species richness.*

At a stand level the species richness of *Fagus* was higher than that of *Abies* (statistically not tested), but the log level species richness was the same for the two hosts. Both at the stand and log level, DS2 had the highest species richness. Higher stand level species richness of *Fagus* can be caused by higher diversity of epiphytes on *Fagus* in early decay stages that increases the total diversity for this tree species. These species are mostly mosses which is confirmed by separate analysis of the two groups. Generally epiphytic species are much more common on deciduous trees. This is caused in part by the more favorable structure and higher pH values of the bark (Löbel et al. 2006; Mežaka et al. 2012) and the more open canopy of *Fagus* that provides more light for sensitive epiphytic species (Király and Ódor 2010; Király et al. 2013). At the log level this difference disappears, the general diversity of *Abies* and *Fagus* logs is similar. It means, that heterogeneity of *Fagus* logs is higher than that of *Abies*. This is given by higher species diversity on *Fagus* in earlier decay stages, when the conditions of logs are heterogeneous and they provide more microhabitats than *Abies.* Higher diversity of liverworts on *Abies* is given by presence of the group of epixylic specialists which occurs mostly on coniferous trees. DS2 represents a transitional phase in the decay succession, where species from all stages are overlapping and therefore the overall number of them is relatively high (Söderström 1988; Crites and Dale 1998; Kruys and Jonsson 1999; Heilmann-Clausen et al. 2005). In case of liverworts DS3 is as rich as DS2. These two stages represent the part of the decay process when the epixylic specialists are present (Söderström 1988; Jansová and Soldán 2006; Ódor et al. 2006).

*Hypotheses 3-5: The species composition significantly differs both between the two hosts and decay stages, the effect of hosts on species composition is stronger than that of decay stages. Fagus is characterized by epiphytic and opportunistic species, while Abies by epixylics (mainly liverworts).*

The study supported all of the hypotheses. There are many studies from different parts of the temperate and boreal zone that support the effect of decay on bryophyte species composition, as a main drivers of the succession (McCullough 1948; Söderström 1988; Ódor and van Hees 2004; Kushnevskaya et al. 2007). However, on a continental scale the determining local effect of decay stage is impacted by regional factors (like climate and land use history), which is not true for another well studied organism group: saproxylic fungi (Heilmann-Clausen et al. 2014). While the effect of host is widely declared for epiphytes (Barkman 1958; Slack 1976; Smith 1982; Nascimbene et al. 2013), it is less explored for epixylic bryophyte assemblages. Jansová and Soldán (2006) found a similar effect, the importance of tree species was higher on epixylic bryophyte assemblage than decay stage in a beech-fir-spruce mixed forest. It can be hypothesized that the extremely high epixylic bryophyte diversity of the montane beech-fir forest zone can be explained by the mixture of deciduous and coniferous trees compared to the temperate pure beech or boreal spruce zone of Europe (Ódor pers. com.). The representation of different functional groups is very different for the studied tree species. On *Fagus* there are mostly epiphytes, appearing on bark and its remnants during the decay process, or opportunistic species, preferring moderately acid environment, for which the dead wood is just one of the suitable substrates. On the contrary, well decayed *Abies* logs provide usually constantly humid substrate necessary for sensitive epixylic species (Lesica et al. 1991). Therefore species typical for *Abies* are mostly specialists, with high representation of epixylic liverworts occurring on very acid and constantly moist substrates (according to their Ellenberg indicator values, Hill et al. 2007). *Fagus*, on the other hand, is very often decomposed by *Pyrenomycetes*, which make a relatively dry well-decayed wood, which is not so suitable for the establishment and survival of epixylic species. We suppose that processes driven by fungi could have a major influence on the bryophyte communities occurring on the surface of the logs and therefore they should be given special attention in further research (Ódor and van Hees 2004). The occurrence of the species is limited both by the acidity and the water holding capacity of the substrate, which considerably depends on the decay stage of the log.

DS1 and DS2 are not very specific in terms of species composition and they are more or less overlapping. At the beginning of the decay and in the middle stages the conditions provided by the substrate to bryophytes are still quite similar – there are at least remnants of the bark, the wood is still quite hard and therefore it doesn't have sufficient water holding capacity necessary for epixylic specialists. DS1 and DS2 are dominated mainly by epiphytic and opportunistic species. In later decay stages the wood becomes softer, the bark is gone and the substrate is usually constantly wet (at least for *Abies*) providing stable microclimate for sensitive epixylic liverworts.

*Hypotheses 6-7: The pH of Fagus is higher than Abies and the pH is decreasing during decay.*

Both hypotheses were supported. It is a general phenomenon that the bark of deciduous trees has higher pH than coniferous trees (Barkman 1958) and it is also emphasized that bark pH is a determining driver of epiphytic communities (Löbel et al. 2006). Other studies also support hypothesis 7, that the pH of the decaying wood decreasing during decay, but in the latest stage it can increase again because of nutrient and humus accumulation (Harmon et al. 1986). Higher variance of the measured values for *Fagus* is explained by larger decrease of the pH during the decay of the log and bigger differences between bark and the decayed wood. In the case of *Abies*, the bark is also very acid and the pH doesn´t change dramatically during decay. McAlister (1995) also found that the difference between bark and wood pH of pine is much smaller than that of deciduous trees, which lead to lower compositional changes of bryophytes during decay.

At the beginning the difference between the two tree species is large, therefore the variance of the pH values in DS1 is very large. During the decay process the log surface acidity decreases and at the end of decay (DS3) pH values are quite low for both types of substrate, moreover significantly different from the previous decay stages. Generally, the combination of chemical and physical changes of the wood and the period for which the log is decaying provide specific conditions convenient for epixylic specialists (Crites and Dale 1998).

This observation supports our interpretation of the differences in species richness and composition depending on tree species and the decay stage. But it is presumed, that pH is only one of the many potentially limiting variables that determine the succession of bryophytes during decay. However, practically all of the studies relating bryophyte composition of different hosts and decay stages to environmental conditions are correlative. An experimental study of bryophyte spore germination under different conditions also proved, that a specialist epixylic species has lower pH optima than an epiphytic one, but pH is more limiting for germination under dry conditions than on high water holding capacity substrates (Wiklund and Rydin 2004).

*Implications for conservation and management*

In this study we showed that tree species diversity is important not only for epiphytes but also for epixylic species. The specialists are not obligatorily associated to a single tree species but there are definitely differences between bryophyte communities on deciduous and coniferous trees. Many studies have emphasized the importance of tree species diversity on the diversity of epiphytic bryophytes (Király and Ódor 2010; Ellis 2012; Mežaka et al. 2012; Király et al. 2013), but it is also true for the assemblages of decaying logs. Not only the diversity, but also continuity of the substrate is important (Söderström 1989; Löbel et al. 2006; Ellis 2012). Only permanently available amount of well decayed logs with large diameter provide good conditions for this life strategy.

Not just the conservation of natural forests is needed but also the improvement of the connectivity between these localities. One of the tools of forest management is to increase the amount of the dead wood also in managed forests and provide enough substrate for saproxylic and epixylic species with stepping-stone life strategy (Glime 2014) in all management phases. This can be achieved by nature-based forest management (like continuous forest cover forestry), providing an uneven-aged forest structure, mixed stands, prevailing use of natural regeneration and group selection system, providing greater abundance of standing and lying dead wood and large old trees representing habitats for sensitive species(Franklin et al. 2002; Gamborg and Larsen 2003; Larsen and Nielsen 2007; Burger 2009; Brunet et al. 2010).

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## Souhrn

V předložené práci se věnujeme druhové bohatosti a složení společenstev epixylických mechorostů ve vztahu k druhu dřeviny a stádiu rozkladu padlých kmenů. Data pro tuto studii pochází z 57 kmenů jedle bělokoré (*Abies alba*) a buku lesního (*Fagus sylvatica*) z přirozeného jedlo – bukového smíšeného lesa národní přírodní rezervace Salajka (Moravskoslezské Beskydy, Česká republika). Na studovaném substrátu bylo nalezeno 68 druhů mechorostů. Na dřevě buků rostlo celkově více druhů mechorostů než na dřevě jedlí. Z pohledu jednotlivých kmenů byly však počty druhů podobné. Lze tedy říci, že beta heterogenita mechorostů na kmenech buků je vyšší než na kmenech jedlí. To je dáno především větší rozmanitostí epifytických druhů v počátečních stádiích rozkladu, kdy kmeny buků poskytují mechorostům různorodější podmínky a více mikrostanovišť. Pro jedle je naopak typická vyšší diverzita v pokročilých stádiích rozkladu, reprezentovaná především epixylickými specialisty, rostoucími na velmi kyselém a trvale vlhkém substrátu. Celkový počet druhů této skupiny je ale nižší. Nejvyšší diverzitou mechorostů se vyznačoval střední stupeň stádia rozkladu, a to jak z pohledu celého studovaného porostu, tak z pohledu jednotlivých kmenů. Střední stádium rozkladu tvoří přechod mezi počátkem a koncem tohoto procesu a proto se v něm potkávají druhy všech stádií a jejich celkový počet je tedy relativně vysoký.

Druhová složení společenstev mechorostů na studovaných dřevinách se vzájemně průkazně lišila dvěma jasně vymezenými skupinami indikačních druhů. Na druhou stranu jednotlivá stádia rozkladu nebyla z pohledu indikačních druhů příliš rozdílná. Studované druhy dřevin i jednotlivá stádia rozkladu se také průkazně lišily z hlediska pH povrchu stromu, které ovlivňuje strukturu společenstev mechorostů na tlejících kmenech. Lze tedy říci, že druh stromu i stádium rozkladu mají vliv na druhovou bohatost i složení těchto společenstev a jejich různé vzájemné kombinace přispívají k nárůstu celkové diverzity mechorostů. Z hlediska ochrany mechorostů v zóně evropských horských jedlo-bučin je tedy důležité zachování smíšených porostů a stálá přítomnost mrtvého dřeva v různých stádiích rozkladu.

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## Supplementary material, Paper I

### Appendix 1

**Reference:** Kučera J, Váňa J, Hradílek Z (2012) Bryophyte flora of the czech republic: Updated checklist and red list and a brief analysis. Preslia 84:813–850.

Status – Categories (Kučera et al. 2012):
EN = (very) endangered
VU = vulnurable
LR-nt = near threat
LC-att = least concern (requiring attention)
LC = least concern

Substrate classification categories:
E = epiphytic
L = epilytic
O = oportunistic
T = terricolous
X = epixylic

| NO of Sample | | | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Decay Stage | | | | DS3 | DS2 | DS3 | DS3 | DS3 | DS2 | DS2 | DS2 | DS3 | DS3 | DS2 | DS3 | DS3 |
| Tree Species (A = *Abies* , F = *Fagus* ) | | | | A | A | F | F | A | A | A | F | A | A | A | A | F |
| Tree Surface pH - 1st measurement | | | | 3.8 | 3.92 | 4.72 | 3.75 | 3.24 | 3.78 | 3.61 | 4.18 | 3.34 | 3.56 | 3.57 | 3.36 | 3.52 |
| Tree Surface pH - 2nd measurement | | | | 3.57 | 4.16 | 6.03 | 4.02 | 3.08 | 3.98 | 3.65 | 4.04 | 3.12 | 3.16 | 3.68 | 3.9 | 3.82 |
| Tree Surface pH - 3rd measurement | | | | 3.53 | 4.38 | 4.87 | 4.58 | 3.65 | 3.7 | 3.69 | 4.29 | 3.27 | 3.28 | 3.6 | 3.55 | 4.24 |
| **Tree Surface pH - Average** | | | | **3.63** | **4.15** | **5.21** | **4.12** | **3.32** | **3.82** | **3.65** | **4.17** | **3.24** | **3.33** | **3.62** | **3.60** | **3.86** |
| Bryophyte Species (Kučera et al. 2012) | Species abrevation | Status | Substrate | Presence (1) / Absence (0) | | | | | | | | | | | | |
| *Alleniella complanata* | AlleComp | LC | **E** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Amblystegium serpens* | AmblSerp | LC | **O** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Anomodon attenuatus* | AnomAtte | LC | **E** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Atrichum undulatum* | AtriUndu | LC | **O** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *Blepharostoma trichophyllum* | BlepTric | LC | X | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 |
| *Brachytheciastrum velutinum* | BracVelu | LC | **O** | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Brachythecium rutabulum* | BracRuta | LC | **O** | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Brachythecium salebrosum* | BracSale | LC | O | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Bryum moravicum* | BryuMora | LC | E | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Buxbaumia viridis* | BuxbViri | **VU** | **X** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Calypogeia suecica* | CalySuec | **LR-nt** | **X** | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 |
| *Cephalozia bicuspidata* | CephBicu | LC | **O** | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 |
| *Cephalozia catenulata* | CephCate | **LR-nt** | **X** | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 |
| *Cephalozia lunulifolia* | CephLunu | LC | **X** | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 |
| *Ceratodon purpureus* | CeraPurp | LC | **O** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Dicranella heteromalla* | DcrlHete | LC | **O** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Dicranodontium denudatum* | DcrnDenu | LC | **X** | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 |
| *Dicranum montanum* | DicrMont | LC | **E** | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 |
| *Dicranum scoparium* | DicrScop | LC | **O** | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 |
| *Eurhynchium angustirete* | EurhAngu | LC | T | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Exsertotheca crispa* | ExseCris | LC | **E** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Frullania dilatata* | FrulDila | LC | **E** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Harpanthus scutatus* | HarpScut | **EN** | **X** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *Herzogiella seligeri* | HerzSeli | LC | X | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 |
| *Homalia trichomanoides* | HomaTric | LC | E | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Homalothecium sericeum* | HomtSeri | LC | E | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Hylocomium splendens* | HyloSple | LC | T | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Hypnum andoii* | HypnAndo | LC | E | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 |
| *Hypnum cupressiforme* | HypnCupr | LC | **O** | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 |
| *Hypnum pallescens* | HypnPall | **LC-att** | **E** | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| *Chiloscyphus coadunatus* | ChilCoad | LC | **T** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Chiloscyphus polyanthos* | ChilPoly | LC | **X** | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Chiloscyphus profundus* | ChilProf | LC | **X** | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 |
| *Isothecium alopecuroides* | IsotAlop | LC | **E** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

| NO of Sample | | | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Decay Stage | | | | DS3 | DS2 | DS3 | DS3 | DS3 | DS2 | DS2 | DS2 | DS3 | DS3 | DS2 | DS3 | DS3 |
| Tree Species (A = *Abies* , F = *Fagus* ) | | | | A | A | F | F | A | A | A | F | A | A | A | A | F |
| Tree Surface pH - 1st measurement | | | | 3.8 | 3.92 | 4.72 | 3.75 | 3.24 | 3.78 | 3.61 | 4.18 | 3.34 | 3.56 | 3.57 | 3.36 | 3.52 |
| Tree Surface pH - 2nd measurement | | | | 3.57 | 4.16 | 6.03 | 4.02 | 3.08 | 3.98 | 3.65 | 4.04 | 3.12 | 3.16 | 3.68 | 3.9 | 3.82 |
| Tree Surface pH - 3rd measurement | | | | 3.53 | 4.38 | 4.87 | 4.58 | 3.65 | 3.7 | 3.69 | 4.29 | 3.27 | 3.28 | 3.6 | 3.55 | 4.24 |
| **Tree Surface pH - Average** | | | | **3.63** | **4.15** | **5.21** | **4.12** | **3.32** | **3.82** | **3.65** | **4.17** | **3.24** | **3.33** | **3.62** | **3.60** | **3.86** |
| Bryophyte Species (Kučera et al. 2012) | Species abrevation | Status | Substrate | Presence (1) / Absence (0) | | | | | | | | | | | | |
| *Lejeunea cavifolia* | LejeCavi | LC | **E** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Lepidozia reptans* | LepiRept | LC | **O** | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Metzgeria furcata* | MetzFurc | LC | E | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Nowellia curvifolia* | NoweCurv | **LC-att** | **X** | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 |
| *Orthotrichum* sp. | Orth | LC | **E** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Paraleucobryum longifolium* | ParaLong | LC | **L** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Pellia neesiana* | PellNees | LC | **T** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Plagiochila porelloides* | PlagPore | LC | **O** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Plagiomnium affine* | PlgmAffi | LC | O | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Plagiomnium cuspidatum* | PlgmCusp | LC | **O** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Plagiothecium curvifolium* | PlagCurv | LC | **O** | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Plagiothecium denticulatum* | PlagDent | LC | **O** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| *Plagiothecium laetum* | PlagLaet | LC | O | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Plagiothecium nemorale* | PlagNemo | LC | O | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *Plagiothecium succulentum* | PlagSucc | LC | O | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Platygyrium repens* | PlatRepe | LC | **E** | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Pleurozium schreberi* | PleuSchr | LC | T | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Pogonatum aloides* | PogoAloi | LC | **T** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Pohlia nutans* | PohlNuta | LC | **O** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Polytrichum formosum* | PolyForm | LC | **T** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *Pseudoleskeella nervosa* | PseuNerv | LC | **E** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Pterigynandrum filiforme* | PterFili | LC | **E** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Ptilidium pulcherrimum* | PtilPulc | LC | O | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Pylaisia polyantha* | PylaPoly | LC | E | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Radula complanata* | RaduComp | LC | **E** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Rhizomnium punctatum* | RhytLore | LC | **X** | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 |
| *Rhytidiadelphus loreus* | RhizPunc | LC | **T** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Rhytidiadelphus triquetrus* | RiccLati | LC | T | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Riccardia latifrons* | RhytSqua | **LC-att** | **X** | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 |
| *Sanionia uncinata* | SaniUnci | LC | X | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Sciuro-hypnum populeum* | SciuPopu | LC | O | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Sciuro-hypnum reflexum* | SciuRefl | LC | **O** | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Tetraphis pellucida* | TetrPell | LC | **X** | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 |
| *Tritomaria quinquedentata* | TritQuin | LC | **O** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

| NO of Sample | | | | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Decay Stage | | | | DS3 | DS2 | DS3 | DS1 | DS2 | DS2 | DS2 | DS2 | DS1 | DS2 | DS3 | DS1 | DS3 |
| Tree Species (A = *Abies* , F = *Fagus* ) | | | | A | A | A | F | A | F | F | F | F | F | A | F | F |
| Tree Surface pH - 1st measurement | | | | 3.13 | 3.94 | 3.75 | 5.61 | 3.59 | 4.72 | 4.69 | 5.26 | 5.08 | 4.36 | 3.31 | 3.72 | 4.12 |
| Tree Surface pH - 2nd measurement | | | | 3.26 | 3.7 | 3.51 | 5.77 | 3.61 | 4.35 | 4.54 | 5.48 | 5.05 | 4.3 | 3.78 | 4.53 | 4.4 |
| Tree Surface pH - 3rd measurement | | | | 3.28 | 3.96 | 3.52 | 5.2 | 3.68 | 4.33 | 4.65 | 6.11 | 5.19 | 4.54 | 3.2 | 4.67 | 3.78 |
| **Tree Surface pH - Average** | | | | **3.22** | **3.87** | **3.59** | **5.53** | **3.63** | **4.47** | **4.63** | **5.62** | **5.11** | **4.40** | **3.43** | **4.31** | **4.10** |
| Bryophyte Species (Kučera et al. 2012) | Species abrevation | Status | Substrate | | | | | | | | | | | | | |
| *Alleniella complanata* | AlleComp | LC | **E** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| *Amblystegium serpens* | AmblSerp | LC | **O** | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Anomodon attenuatus* | AnomAtte | LC | **E** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Atrichum undulatum* | AtriUndu | LC | **O** | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Blepharostoma trichophyllum* | BlepTric | LC | X | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Brachytheciastrum velutinum* | BracVelu | LC | **O** | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *Brachythecium rutabulum* | BracRuta | LC | **O** | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 |
| *Brachythecium salebrosum* | BracSale | LC | O | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Bryum moravicum* | BryuMora | LC | E | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 |
| *Buxbaumia viridis* | BuxbViri | **VU** | **X** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Calypogeia suecica* | CalySuec | **LR-nt** | **X** | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| *Cephalozia bicuspidata* | CephBicu | LC | **O** | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| *Cephalozia catenulata* | CephCate | **LR-nt** | **X** | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Cephalozia lunulifolia* | CephLunu | LC | **X** | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| *Ceratodon purpureus* | CeraPurp | LC | **O** | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Dicranella heteromalla* | DcrlHete | LC | **O** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Dicranodontium denudatum* | DcrnDenu | LC | **X** | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 |
| *Dicranum montanum* | DicrMont | LC | **E** | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Dicranum scoparium* | DicrScop | LC | **O** | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 |
| *Eurhynchium angustirete* | EurhAngu | LC | T | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Exsertotheca crispa* | ExseCris | LC | **E** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Frullania dilatata* | FrulDila | LC | **E** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *Harpanthus scutatus* | HarpScut | **EN** | **X** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Herzogiella seligeri* | HerzSeli | LC | X | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 |
| *Homalia trichomanoides* | HomaTric | LC | E | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Homalothecium sericeum* | HomtSeri | LC | E | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Hylocomium splendens* | HyloSple | LC | T | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Hypnum andoii* | HypnAndo | LC | E | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 |
| *Hypnum cupressiforme* | HypnCupr | LC | **O** | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| *Hypnum pallescens* | HypnPall | **LC-att** | **E** | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Chiloscyphus coadunatus* | ChilCoad | LC | **T** | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Chiloscyphus polyanthos* | ChilPoly | LC | **X** | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 |
| *Chiloscyphus profundus* | ChilProf | LC | **X** | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 |
| *Isothecium alopecuroides* | IsotAlop | LC | **E** | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |

| NO of Sample | | | | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Decay Stage | | | | DS3 | DS2 | DS3 | DS1 | DS2 | DS2 | DS2 | DS2 | DS1 | DS2 | DS3 | DS1 | DS3 |
| Tree Species (A = *Abies* , F = *Fagus* ) | | | | A | A | A | F | A | F | F | F | F | F | A | F | F |
| Tree Surface pH - 1st measurement | | | | 3.13 | 3.94 | 3.75 | 5.61 | 3.59 | 4.72 | 4.69 | 5.26 | 5.08 | 4.36 | 3.31 | 3.72 | 4.12 |
| Tree Surface pH - 2nd measurement | | | | 3.26 | 3.7 | 3.51 | 5.77 | 3.61 | 4.35 | 4.54 | 5.48 | 5.05 | 4.3 | 3.78 | 4.53 | 4.4 |
| Tree Surface pH - 3rd measurement | | | | 3.28 | 3.96 | 3.52 | 5.2 | 3.68 | 4.33 | 4.65 | 6.11 | 5.19 | 4.54 | 3.2 | 4.67 | 3.78 |
| **Tree Surface pH - Average** | | | | **3.22** | **3.87** | **3.59** | **5.53** | **3.63** | **4.47** | **4.63** | **5.62** | **5.11** | **4.40** | **3.43** | **4.31** | **4.10** |
| Bryophyte Species (Kučera et al. 2012) | Species abrevation | Status | Substrate | | | | | | | | | | | | | |
| *Lejeunea cavifolia* | LejeCavi | LC | **E** | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Lepidozia reptans* | LepiRept | LC | **O** | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| *Metzgeria furcata* | MetzFurc | LC | E | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 |
| *Nowellia curvifolia* | NoweCurv | **LC-att** | **X** | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Orthotrichum* sp. | Orth | LC | **E** | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 |
| *Paraleucobryum longifolium* | ParaLong | LC | **L** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *Pellia neesiana* | PellNees | LC | **T** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Plagiochila porelloides* | PlagPore | LC | **O** | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 |
| *Plagiomnium affine* | PlgmAffi | LC | O | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Plagiomnium cuspidatum* | PlgmCusp | LC | **O** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Plagiothecium curvifolium* | PlagCurv | LC | **O** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Plagiothecium denticulatum* | PlagDent | LC | **O** | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 |
| *Plagiothecium laetum* | PlagLaet | LC | O | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Plagiothecium nemorale* | PlagNemo | LC | O | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Plagiothecium succulentum* | PlagSucc | LC | O | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Platygyrium repens* | PlatRepe | LC | **E** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Pleurozium schreberi* | PleuSchr | LC | T | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Pogonatum aloides* | PogoAloi | LC | **T** | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Pohlia nutans* | PohlNuta | LC | **O** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Polytrichum formosum* | PolyForm | LC | **T** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Pseudoleskeella nervosa* | PseuNerv | LC | **E** | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Pterigynandrum filiforme* | PterFili | LC | **E** | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Ptilidium pulcherrimum* | PtilPulc | LC | O | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *Pylaisia polyantha* | PylaPoly | LC | E | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| *Radula complanata* | RaduComp | LC | **E** | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 |
| *Rhizomnium punctatum* | RhytLore | LC | **X** | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 |
| *Rhytidiadelphus loreus* | RhizPunc | LC | **T** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Rhytidiadelphus triquetrus* | RiccLati | LC | T | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Riccardia latifrons* | RhytSqua | **LC-att** | **X** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Sanionia uncinata* | SaniUnci | LC | X | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 |
| *Sciuro-hypnum populeum* | SciuPopu | LC | O | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Sciuro-hypnum reflexum* | SciuRefl | LC | **O** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| *Tetraphis pellucida* | TetrPell | LC | **X** | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| *Tritomaria quinquedentata* | TritQuin | LC | **O** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

| NO of Sample | | | | 27 | 28 | 29 | 30 | 31 | 32 | 33 | 34 | 35 | 36 | 37 | 38 | 39 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Decay Stage | | | | DS2 | DS1 | DS3 | DS1 | DS3 | DS3 | DS1 | DS1 | DS3 | DS1 | DS1 | DS1 | DS2 |
| Tree Species (A = *Abies* , F = *Fagus* ) | | | | F | A | F | A | F | A | A | F | A | A | A | F | A |
| Tree Surface pH - 1st measurement | | | | 5.17 | 3.34 | 4.4 | 3.28 | 4.02 | 3.24 | 4.33 | 3.9 | 3.64 | 4.25 | 3.86 | 4.62 | |
| Tree Surface pH - 2nd measurement | | | | 5.35 | 3.48 | 3.9 | 3.74 | 4.13 | 3.2 | 4.05 | 4.46 | 3.3 | 4.06 | 3.98 | 5.12 | |
| Tree Surface pH - 3rd measurement | | | | 4.74 | 3.49 | 4.07 | 3.78 | 4.19 | 3.47 | 4.02 | 4.81 | 3.26 | 4.35 | 3.85 | 5.14 | |
| **Tree Surface pH - Average** | | | | **5.09** | **3.44** | **4.12** | **3.60** | **4.11** | **3.30** | **4.13** | **4.39** | **3.40** | **4.22** | **3.90** | **4.96** | |
| Bryophyte Species (Kučera et al. 2012) | Species abrevation | Status | Substrate | | | | | | | | | | | | | |
| *Alleniella complanata* | AlleComp | LC | **E** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Amblystegium serpens* | AmblSerp | LC | **O** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *Anomodon attenuatus* | AnomAtte | LC | **E** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Atrichum undulatum* | AtriUndu | LC | **O** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Blepharostoma trichophyllum* | BlepTric | LC | X | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Brachytheciastrum velutinum* | BracVelu | LC | **O** | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 |
| *Brachythecium rutabulum* | BracRuta | LC | **O** | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 |
| *Brachythecium salebrosum* | BracSale | LC | O | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 |
| *Bryum moravicum* | BryuMora | LC | E | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Buxbaumia viridis* | BuxbViri | **VU** | **X** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Calypogeia suecica* | CalySuec | **LR-nt** | **X** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Cephalozia bicuspidata* | CephBicu | LC | **O** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 |
| *Cephalozia catenulata* | CephCate | **LR-nt** | **X** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| *Cephalozia lunulifolia* | CephLunu | LC | **X** | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Ceratodon purpureus* | CeraPurp | LC | **O** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Dicranella heteromalla* | DcrlHete | LC | **O** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Dicranodontium denudatum* | DcrnDenu | LC | **X** | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 |
| *Dicranum montanum* | DicrMont | LC | **E** | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Dicranum scoparium* | DicrScop | LC | **O** | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| *Eurhynchium angustirete* | EurhAngu | LC | T | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Exsertotheca crispa* | ExseCris | LC | **E** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Frullania dilatata* | FrulDila | LC | **E** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Harpanthus scutatus* | HarpScut | **EN** | **X** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Herzogiella seligeri* | HerzSeli | LC | X | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 |
| *Homalia trichomanoides* | HomaTric | LC | E | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Homalothecium sericeum* | HomtSeri | LC | E | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Hylocomium splendens* | HyloSple | LC | T | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Hypnum andoii* | HypnAndo | LC | E | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Hypnum cupressiforme* | HypnCupr | LC | **O** | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| *Hypnum pallescens* | HypnPall | **LC-att** | **E** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Chiloscyphus coadunatus* | ChilCoad | LC | **T** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Chiloscyphus polyanthos* | ChilPoly | LC | **X** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Chiloscyphus profundus* | ChilProf | LC | **X** | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 |
| *Isothecium alopecuroides* | IsotAlop | LC | **E** | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

| NO of Sample | | | | 27 | 28 | 29 | 30 | 31 | 32 | 33 | 34 | 35 | 36 | 37 | 38 | 39 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Decay Stage | | | | DS2 | DS1 | DS3 | DS1 | DS3 | DS3 | DS1 | DS1 | DS3 | DS1 | DS1 | DS1 | DS2 |
| Tree Species (A = *Abies* , F = *Fagus* ) | | | | F | A | F | A | F | A | A | F | A | A | A | F | A |
| Tree Surface pH - 1st measurement | | | | 5.17 | 3.34 | 4.4 | 3.28 | 4.02 | 3.24 | 4.33 | 3.9 | 3.64 | 4.25 | 3.86 | 4.62 | |
| Tree Surface pH - 2nd measurement | | | | 5.35 | 3.48 | 3.9 | 3.74 | 4.13 | 3.2 | 4.05 | 4.46 | 3.3 | 4.06 | 3.98 | 5.12 | |
| Tree Surface pH - 3rd measurement | | | | 4.74 | 3.49 | 4.07 | 3.78 | 4.19 | 3.47 | 4.02 | 4.81 | 3.26 | 4.35 | 3.85 | 5.14 | |
| **Tree Surface pH - Average** | | | | **5.09** | **3.44** | **4.12** | **3.60** | **4.11** | **3.30** | **4.13** | **4.39** | **3.40** | **4.22** | **3.90** | **4.96** | |
| Bryophyte Species (Kučera et al. 2012) | Species abrevation | Status | Substrate | | | | | | | | | | | | | |
| *Lejeunea cavifolia* | LejeCavi | LC | **E** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Lepidozia reptans* | LepiRept | LC | **O** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| *Metzgeria furcata* | MetzFurc | LC | E | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Nowellia curvifolia* | NoweCurv | **LC-att** | **X** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| *Orthotrichum* sp. | Orth | LC | **E** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Paraleucobryum longifolium* | ParaLong | LC | **L** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Pellia neesiana* | PellNees | LC | **T** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Plagiochila porelloides* | PlagPore | LC | **O** | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Plagiomnium affine* | PlgmAffi | LC | O | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Plagiomnium cuspidatum* | PlgmCusp | LC | **O** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Plagiothecium curvifolium* | PlagCurv | LC | **O** | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| *Plagiothecium denticulatum* | PlagDent | LC | **O** | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Plagiothecium laetum* | PlagLaet | LC | O | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Plagiothecium nemorale* | PlagNemo | LC | O | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Plagiothecium succulentum* | PlagSucc | LC | O | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Platygyrium repens* | PlatRepe | LC | **E** | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Pleurozium schreberi* | PleuSchr | LC | T | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 |
| *Pogonatum aloides* | PogoAloi | LC | **T** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Pohlia nutans* | PohlNuta | LC | **O** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Polytrichum formosum* | PolyForm | LC | **T** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Pseudoleskeella nervosa* | PseuNerv | LC | **E** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Pterigynandrum filiforme* | PterFili | LC | **E** | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Ptilidium pulcherrimum* | PtilPulc | LC | O | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Pylaisia polyantha* | PylaPoly | LC | E | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Radula complanata* | RaduComp | LC | **E** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Rhizomnium punctatum* | RhytLore | LC | **X** | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 |
| *Rhytidiadelphus loreus* | RhizPunc | LC | **T** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Rhytidiadelphus triquetrus* | RiccLati | LC | T | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Riccardia latifrons* | RhytSqua | **LC-att** | **X** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Sanionia uncinata* | SaniUnci | LC | X | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Sciuro-hypnum populeum* | SciuPopu | LC | O | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Sciuro-hypnum reflexum* | SciuRefl | LC | **O** | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Tetraphis pellucida* | TetrPell | LC | **X** | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| *Tritomaria quinquedentata* | TritQuin | LC | **O** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |

| NO of Sample | | | | 40 | 41 | 42 | 43 | 44 | 45 | 46 | 47 | 48 | 49 | 50 | 51 | 52 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Decay Stage | | | | DS1 | DS2 | DS2 | DS2 | DS1 | DS3 | DS2 | DS2 | DS1 | DS2 | DS3 | DS3 | DS2 |
| Tree Species (A = *Abies* , F = *Fagus* ) | | | | A | F | F | F | A | F | F | A | A | F | F | F | A |
| Tree Surface pH - 1st measurement | | | | | | | | | | | | | | | | |
| Tree Surface pH - 2nd measurement | | | | | | | | | | | | | | | | |
| Tree Surface pH - 3rd measurement | | | | | | | | | | | | | | | | |
| **Tree Surface pH - Average** | | | | | | | | | | | | | | | | |
| Bryophyte Species (Kučera et al. 2012) | Species abrevation | Status | Substrate | | | | | | | | | | | | | |
| *Alleniella complanata* | AlleComp | LC | **E** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Amblystegium serpens* | AmblSerp | LC | **O** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Anomodon attenuatus* | AnomAtte | LC | **E** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Atrichum undulatum* | AtriUndu | LC | **O** | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Blepharostoma trichophyllum* | BlepTric | LC | X | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Brachytheciastrum velutinum* | BracVelu | LC | **O** | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 |
| *Brachythecium rutabulum* | BracRuta | LC | **O** | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Brachythecium salebrosum* | BracSale | LC | O | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 |
| *Bryum moravicum* | BryuMora | LC | E | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Buxbaumia viridis* | BuxbViri | **VU** | **X** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Calypogeia suecica* | CalySuec | **LR-nt** | **X** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Cephalozia bicuspidata* | CephBicu | LC | **O** | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 |
| *Cephalozia catenulata* | CephCate | **LR-nt** | **X** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Cephalozia lunulifolia* | CephLunu | LC | **X** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Ceratodon purpureus* | CeraPurp | LC | **O** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Dicranella heteromalla* | DcrlHete | LC | **O** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Dicranodontium denudatum* | DcrnDenu | LC | **X** | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Dicranum montanum* | DicrMont | LC | **E** | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 |
| *Dicranum scoparium* | DicrScop | LC | **O** | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 |
| *Eurhynchium angustirete* | EurhAngu | LC | T | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Exsertotheca crispa* | ExseCris | LC | **E** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Frullania dilatata* | FrulDila | LC | **E** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Harpanthus scutatus* | HarpScut | **EN** | **X** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Herzogiella seligeri* | HerzSeli | LC | X | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| *Homalia trichomanoides* | HomaTric | LC | E | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Homalothecium sericeum* | HomtSeri | LC | E | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Hylocomium splendens* | HyloSple | LC | T | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Hypnum andoii* | HypnAndo | LC | E | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 |
| *Hypnum cupressiforme* | HypnCupr | LC | **O** | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Hypnum pallescens* | HypnPall | **LC-att** | **E** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Chiloscyphus coadunatus* | ChilCoad | LC | **T** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Chiloscyphus polyanthos* | ChilPoly | LC | **X** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Chiloscyphus profundus* | ChilProf | LC | **X** | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 |
| *Isothecium alopecuroides* | IsotAlop | LC | **E** | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

| NO of Sample | | | | 40 | 41 | 42 | 43 | 44 | 45 | 46 | 47 | 48 | 49 | 50 | 51 | 52 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Decay Stage | | | | DS1 | DS2 | DS2 | DS2 | DS1 | DS3 | DS2 | DS2 | DS1 | DS2 | DS3 | DS3 | DS2 |
| Tree Species (A = *Abies* , F = *Fagus* ) | | | | A | F | F | F | A | F | F | A | A | F | F | F | A |
| Tree Surface pH - 1st measurement | | | | | | | | | | | | | | | | |
| Tree Surface pH - 2nd measurement | | | | | | | | | | | | | | | | |
| Tree Surface pH - 3rd measurement | | | | | | | | | | | | | | | | |
| **Tree Surface pH - Average** | | | | | | | | | | | | | | | | |
| Bryophyte Species (Kučera et al. 2012) | Species abrevation | Status | Substrate | | | | | | | | | | | | | |
| *Lejeunea cavifolia* | LejeCavi | LC | **E** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Lepidozia reptans* | LepiRept | LC | **O** | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Metzgeria furcata* | MetzFurc | LC | E | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 |
| *Nowellia curvifolia* | NoweCurv | **LC-att** | **X** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Orthotrichum* sp. | Orth | LC | **E** | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Paraleucobryum longifolium* | ParaLong | LC | **L** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Pellia neesiana* | PellNees | LC | **T** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Plagiochila porelloides* | PlagPore | LC | **O** | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *Plagiomnium affine* | PlgmAffi | LC | O | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Plagiomnium cuspidatum* | PlgmCusp | LC | **O** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *Plagiothecium curvifolium* | PlagCurv | LC | **O** | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| *Plagiothecium denticulatum* | PlagDent | LC | **O** | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 |
| *Plagiothecium laetum* | PlagLaet | LC | O | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Plagiothecium nemorale* | PlagNemo | LC | O | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 |
| *Plagiothecium succulentum* | PlagSucc | LC | O | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Platygyrium repens* | PlatRepe | LC | **E** | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Pleurozium schreberi* | PleuSchr | LC | T | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Pogonatum aloides* | PogoAloi | LC | **T** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Pohlia nutans* | PohlNuta | LC | **O** | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Polytrichum formosum* | PolyForm | LC | **T** | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Pseudoleskeella nervosa* | PseuNerv | LC | **E** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Pterigynandrum filiforme* | PterFili | LC | **E** | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 |
| *Ptilidium pulcherrimum* | PtilPulc | LC | O | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Pylaisia polyantha* | PylaPoly | LC | E | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Radula complanata* | RaduComp | LC | **E** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Rhizomnium punctatum* | RhytLore | LC | **X** | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 |
| *Rhytidiadelphus loreus* | RhizPunc | LC | **T** | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Rhytidiadelphus triquetrus* | RiccLati | LC | T | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Riccardia latifrons* | RhytSqua | **LC-att** | **X** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Sanionia uncinata* | SaniUnci | LC | X | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 |
| *Sciuro-hypnum populeum* | SciuPopu | LC | O | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Sciuro-hypnum reflexum* | SciuRefl | LC | **O** | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 |
| *Tetraphis pellucida* | TetrPell | LC | **X** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Tritomaria quinquedentata* | TritQuin | LC | **O** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

| NO of Sample | | | | 53 | 54 | 55 | 56 | 57 |
|---|---|---|---|---|---|---|---|---|
| Decay Stage | | | | DS2 | DS1 | DS1 | DS1 | DS1 |
| Tree Species (A = *Abies* , F = *Fagus* ) | | | | A | F | F | F | F |
| Tree Surface pH - 1st measurement | | | | | | | | |
| Tree Surface pH - 2nd measurement | | | | | | | | |
| Tree Surface pH - 3rd measurement | | | | | | | | |
| **Tree Surface pH - Average** | | | | | | | | |
| Bryophyte Species (Kučera et al. 2012) | Species abrevation | Status | Substrate | | | | | |
| *Alleniella complanata* | AlleComp | LC | **E** | 0 | 0 | 0 | 0 | 0 |
| *Amblystegium serpens* | AmblSerp | LC | **O** | 0 | 1 | 0 | 0 | 0 |
| *Anomodon attenuatus* | AnomAtte | LC | **E** | 0 | 1 | 0 | 0 | 0 |
| *Atrichum undulatum* | AtriUndu | LC | **O** | 0 | 0 | 0 | 0 | 0 |
| *Blepharostoma trichophyllum* | BlepTric | LC | X | 1 | 0 | 0 | 0 | 0 |
| *Brachytheciastrum velutinum* | BracVelu | LC | **O** | 0 | 1 | 0 | 1 | 0 |
| *Brachythecium rutabulum* | BracRuta | LC | **O** | 0 | 0 | 0 | 0 | 0 |
| *Brachythecium salebrosum* | BracSale | LC | O | 0 | 1 | 0 | 0 | 0 |
| *Bryum moravicum* | BryuMora | LC | E | 0 | 1 | 0 | 1 | 1 |
| *Buxbaumia viridis* | BuxbViri | **VU** | **X** | 0 | 0 | 0 | 0 | 0 |
| *Calypogeia suecica* | CalySuec | **LR-nt** | **X** | 0 | 0 | 0 | 0 | 0 |
| *Cephalozia bicuspidata* | CephBicu | LC | **O** | 1 | 0 | 0 | 0 | 0 |
| *Cephalozia catenulata* | CephCate | **LR-nt** | **X** | 0 | 0 | 0 | 0 | 0 |
| *Cephalozia lunulifolia* | CephLunu | LC | **X** | 1 | 0 | 0 | 0 | 0 |
| *Ceratodon purpureus* | CeraPurp | LC | **O** | 0 | 0 | 0 | 0 | 0 |
| *Dicranella heteromalla* | DcrlHete | LC | **O** | 0 | 0 | 0 | 0 | 0 |
| *Dicranodontium denudatum* | DcrnDenu | LC | **X** | 1 | 0 | 0 | 0 | 0 |
| *Dicranum montanum* | DicrMont | LC | **E** | 1 | 1 | 1 | 0 | 0 |
| *Dicranum scoparium* | DicrScop | LC | **O** | 1 | 1 | 0 | 0 | 0 |
| *Eurhynchium angustirete* | EurhAngu | LC | T | 0 | 0 | 0 | 0 | 0 |
| *Exsertotheca crispa* | ExseCris | LC | **E** | 0 | 0 | 0 | 0 | 1 |
| *Frullania dilatata* | FrulDila | LC | **E** | 0 | 0 | 0 | 0 | 1 |
| *Harpanthus scutatus* | HarpScut | **EN** | **X** | 0 | 0 | 0 | 0 | 0 |
| *Herzogiella seligeri* | HerzSeli | LC | X | 1 | 0 | 0 | 1 | 0 |
| *Homalia trichomanoides* | HomaTric | LC | E | 0 | 0 | 0 | 0 | 0 |
| *Homalothecium sericeum* | HomtSeri | LC | E | 0 | 0 | 0 | 0 | 0 |
| *Hylocomium splendens* | HyloSple | LC | T | 0 | 0 | 0 | 0 | 0 |
| *Hypnum andoii* | HypnAndo | LC | E | 0 | 0 | 0 | 1 | 1 |
| *Hypnum cupressiforme* | HypnCupr | LC | **O** | 1 | 1 | 1 | 0 | 1 |
| *Hypnum pallescens* | HypnPall | **LC-att** | **E** | 0 | 0 | 0 | 0 | 0 |
| *Chiloscyphus coadunatus* | ChilCoad | LC | **T** | 0 | 0 | 0 | 0 | 0 |
| *Chiloscyphus polyanthos* | ChilPoly | LC | **X** | 0 | 0 | 0 | 0 | 0 |
| *Chiloscyphus profundus* | ChilProf | LC | **X** | 1 | 1 | 0 | 1 | 0 |
| *Isothecium alopecuroides* | IsotAlop | LC | **E** | 0 | 0 | 0 | 0 | 1 |

| NO of Sample | | | | 53 | 54 | 55 | 56 | 57 |
|---|---|---|---|---|---|---|---|---|
| Decay Stage | | | | DS2 | DS1 | DS1 | DS1 | DS1 |
| Tree Species (A = *Abies* , F = *Fagus* ) | | | | A | F | F | F | F |
| Tree Surface pH - 1st measurement | | | | | | | | |
| Tree Surface pH - 2nd measurement | | | | | | | | |
| Tree Surface pH - 3rd measurement | | | | | | | | |
| **Tree Surface pH - Average** | | | | | | | | |
| Bryophyte Species (Kučera et al. 2012) | Species abrevation | Status | Substrate | | | | | |
| *Lejeunea cavifolia* | LejeCavi | LC | **E** | 0 | 0 | 0 | 0 | 0 |
| *Lepidozia reptans* | LepiRept | LC | **O** | 1 | 0 | 0 | 0 | 0 |
| *Metzgeria furcata* | MetzFurc | LC | E | 0 | 1 | 0 | 0 | 1 |
| *Nowellia curvifolia* | NoweCurv | **LC-att** | **X** | 1 | 0 | 0 | 0 | 0 |
| *Orthotrichum* sp. | Orth | LC | **E** | 0 | 1 | 1 | 0 | 0 |
| *Paraleucobryum longifolium* | ParaLong | LC | **L** | 0 | 0 | 0 | 0 | 0 |
| *Pellia neesiana* | PellNees | LC | **T** | 0 | 0 | 0 | 0 | 0 |
| *Plagiochila porelloides* | PlagPore | LC | **O** | 0 | 0 | 0 | 0 | 0 |
| *Plagiomnium affine* | PlgmAffi | LC | O | 0 | 0 | 0 | 0 | 0 |
| *Plagiomnium cuspidatum* | PlgmCusp | LC | **O** | 0 | 0 | 0 | 0 | 0 |
| *Plagiothecium curvifolium* | PlagCurv | LC | **O** | 0 | 0 | 0 | 0 | 0 |
| *Plagiothecium denticulatum* | PlagDent | LC | **O** | 0 | 0 | 0 | 0 | 0 |
| *Plagiothecium laetum* | PlagLaet | LC | O | 1 | 0 | 0 | 0 | 0 |
| *Plagiothecium nemorale* | PlagNemo | LC | O | 0 | 0 | 0 | 0 | 0 |
| *Plagiothecium succulentum* | PlagSucc | LC | O | 0 | 0 | 0 | 0 | 0 |
| *Platygyrium repens* | PlatRepe | LC | **E** | 0 | 1 | 0 | 1 | 0 |
| *Pleurozium schreberi* | PleuSchr | LC | T | 1 | 0 | 0 | 0 | 0 |
| *Pogonatum aloides* | PogoAloi | LC | **T** | 0 | 0 | 0 | 0 | 0 |
| *Pohlia nutans* | PohlNuta | LC | **O** | 0 | 0 | 0 | 0 | 0 |
| *Polytrichum formosum* | PolyForm | LC | **T** | 0 | 0 | 0 | 0 | 0 |
| *Pseudoleskeella nervosa* | PseuNerv | LC | **E** | 0 | 0 | 0 | 0 | 0 |
| *Pterigynandrum filiforme* | PterFili | LC | **E** | 0 | 1 | 0 | 1 | 1 |
| *Ptilidium pulcherrimum* | PtilPulc | LC | O | 0 | 0 | 0 | 0 | 0 |
| *Pylaisia polyantha* | PylaPoly | LC | E | 0 | 0 | 0 | 0 | 0 |
| *Radula complanata* | RaduComp | LC | **E** | 0 | 1 | 0 | 0 | 1 |
| *Rhizomnium punctatum* | RhytLore | LC | **X** | 0 | 0 | 0 | 0 | 0 |
| *Rhytidiadelphus loreus* | RhizPunc | LC | **T** | 0 | 0 | 0 | 0 | 0 |
| *Rhytidiadelphus triquetrus* | RiccLati | LC | T | 0 | 0 | 0 | 0 | 0 |
| *Riccardia latifrons* | RhytSqua | **LC-att** | **X** | 0 | 0 | 0 | 0 | 0 |
| *Sanionia uncinata* | SaniUnci | LC | X | 1 | 1 | 0 | 1 | 0 |
| *Sciuro-hypnum populeum* | SciuPopu | LC | O | 0 | 0 | 0 | 0 | 0 |
| *Sciuro-hypnum reflexum* | SciuRefl | LC | **O** | 0 | 0 | 0 | 0 | 0 |
| *Tetraphis pellucida* | TetrPell | LC | **X** | 1 | 0 | 0 | 0 | 0 |
| *Tritomaria quinquedentata* | TritQuin | LC | **O** | 0 | 0 | 0 | 0 | 0 |

## Appendix 2

### Log level species richness analysis of liverwort and mosses (separately).

The effect of tree species (Abies, Fagus), decay stages (DS1, DS2, DS3) and their interaction was tested by general linear models using Poisson error structure and log link function. The model selection was based on deviance analysis using Chi square statistics. The differences among the levels of decay stages were tested by Tukey multiple comparisons.

For liverworts both tree species and decay stages were included in the final model (quasi R2=0.265, deviance=19.34, df=3, p=0.0002). The species richness of Abies was higher than that of Fagus (Table A2.1, deviance=8.09, df=2, p=0.0044). The effect of decay stages was also significant (deviance 11.25, df=2, p=0.0036), the species richness of DS2 and DS3 were significantly higher than that of DS1 (Table A2.1, DS2-DS1 p=0.0475; DS3-DS1 p=0.0207; DS2-DS3 p=0.9107).

For mosses similarly to liverworts both tree species and decay stages were included in the final model (quasi R2=0.282, deviance=19.083, df=3, p=0.0002). However in their case Fagus had higher species richness (Table A2.2, deviance=5.25, df=1, p=0.0219) and DS2 had higher species richness than DS1 and DS3 (Tale A2.2, deviance 13.83, df=2, p=0.0010, multiple comparisons: DS2-DS1 p=0.0091; DS2-DS3 p=0.0062, DS3-DS1 p=0.9991).

Table A2.1 Stand and log level species richness of liverworts. Different letters means significant differences.

| | Stand level species richness | Log level species richness |
|---|---|---|
| Total | 20 | 2.9 ± 1.95 |
| Tree species | | |
| *Abies alba* | 14 | 3.6 ± 2.23$^{a}$ |
| *Fagus sylvatica* | 15 | 2.3 ± 1.39$^{b}$ |
| Decay stages | | |
| DS1 | 10 | 1.8 ± 1.33$^{a}$ |
| DS2 | 15 | 3.3 ± 1.90$^{b}$ |
| DS3 | 13 | 3.5 ± 2.14$^{b}$ |
| Combination | | |
| *Abies* DS1 | 7 | 1.8 ± 1.16$^{b}$ |
| *Abies* DS2 | 12 | 3.9 ± 2.38$^{ns}$ |
| *Abies* DS3 | 10 | 4.8 ± 1.87$^{a}$ |
| *Fagus* DS1 | 6 | 1.9 ± 1.54$^{b}$ |
| *Fagus* DS2 | 9 | 2.7 ± 1.19$^{ns}$ |
| *Fagus* DS3 | 7 | 2.1 ± 1.45$^{b}$ |

Table A2.2 Stand and log level species richness of mosses. Different letters means significant differences.

|  | Stand level species richness | Log level species richness |
|---|---|---|
| Total | 48 | 7.4 ± 3.06 |
| Tree species |  |  |
| *Abies alba* | 28 | 6.5 ± 2.78$^{a}$ |
| *Fagus sylvatica* | 44 | 8.2 ± 3.12$^{b}$ |
| Decay stages |  |  |
| DS1 | 28 | 6.4 ± 2.32$^{a}$ |
| DS2 | 41 | 9.1 ± 3.41$^{b}$ |
| DS3 | 28 | 6.3 ± 2.36$^{a}$ |
| Combination |  |  |
| *Abies* DS1 | 14 | 5.6 ± 1.60$^{a}$ |
| *Abies* DS2 | 28 | 8.0 ± 3.71$^{ns}$ |
| *Abies* DS3 | 16 | 5.7 ± 1.89$^{a}$ |
| *Fagus* DS1 | 24 | 7.0 ± 2.74$^{ns}$ |
| *Fagus* DS2 | 34 | 10.2 ± 2.89$^{b}$ |
| *Fagus* DS3 | 23 | 7.0 ± 2.74ns |

## Paper II

Táborská M, Procházková J, Lengyel A, Vrška T, Hort L, Ódor P (2017) **Wood-inhabiting bryophyte communities are influenced by different management intensities in the past.** Biodivers Conserv 26:2893–2909. doi: 10.1007/s10531-017-1395-8

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

**Key words:** 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 (Picea 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 18th and 19th 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 19th 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. 2008b; 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. 2008a; Madžule et al. 2011; Király et al. 2013). These assemblages are also very sensitive to forest continuity and fragmentation (Snäll et al. 2004; Löbel et al. 2006; Ódor et al. 2006).

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. 2008b).

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?

## Material and Methods

### *Study sites and sampling*

This study comprised 7 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 (CWD) (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).

Tab 1. Climatic, structural and historical characteristics of the studied old-growth beech-dominated stands in the Czech Republic.

| **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,<br>13°48'43''E | 49°55'26''N,<br>13°46'18''E | 49°32'11''N,<br>18°39'30''E | 49°47'32''N,<br>15°40'20''E | 49°24'07''N,<br>18°25'17''E | 48°39'58''N,<br>14°42'28''E | 49°39'20''N,<br>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:** | | | | | | | |
| *dead wood haulage till* | never | 1933 | 1935 | 1936 | 1930 | 1888 | 1929 |
| *dead wood 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,*<br>*Quercus petraea , Acer pseudoplatanus,*<br>*Carpinus betulus, Tilia* sp.*, Picea abies* | *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 1981-2011).

[d] Annual precipitation (source: Czech Hydrometerological Institute, data interpolation from 1981-2011).

[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.

Tab 2. Proportions of living trees and dead wood (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* | MI | PO | SA | ZF | ZH |
|---|---|---|---|---|---|---|---|
| proportion of dead wood (% of volume in total) | | | | | | | |
| *Fagus sylvatica* | 16.4 | 88.4 | 32.8 | 40.4 | 15.8 | 25.5 | 54.5 |
| *Abies alba* | 20.0 | 4.4 | 62.2 | 24.8 | 79.2 | 16.4 | 3.2 |
| *Picea 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) | | | | | | | |
| *Fagus sylvatica* | 45.7 | 80.8 | 78.9 | 17.0 | 68.5 | 62.0 | 73.9 |
| *Abies alba* | 4.3 | 0.1 | 5.0 | 0.6 | 21.7 | 3.4 | 0.0 |
| *Picea 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 |

For the preselection of appropriate logs we used census datasets from all investigated sites. All standing and downed trees of DBH≥10 cm at these seven sites had previously been mapped and the DBH recorded. In the 1970`s, 1990`s and 2000`s stem-position maps were based on tripod-based theodolite positioning (with sub-meter absolute positional accuracy anticipated). In the 2000`s 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). Dead wood 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 meters 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 Appendix 1. The mean of the functions were calculated as descriptive statistics, and the position of the pairs were plotted in ternary plots. 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).

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. 2013), 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, Tab. 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 (Appendix 2).

On the log level we found the same patterns as on the site level (Tab. 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 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).

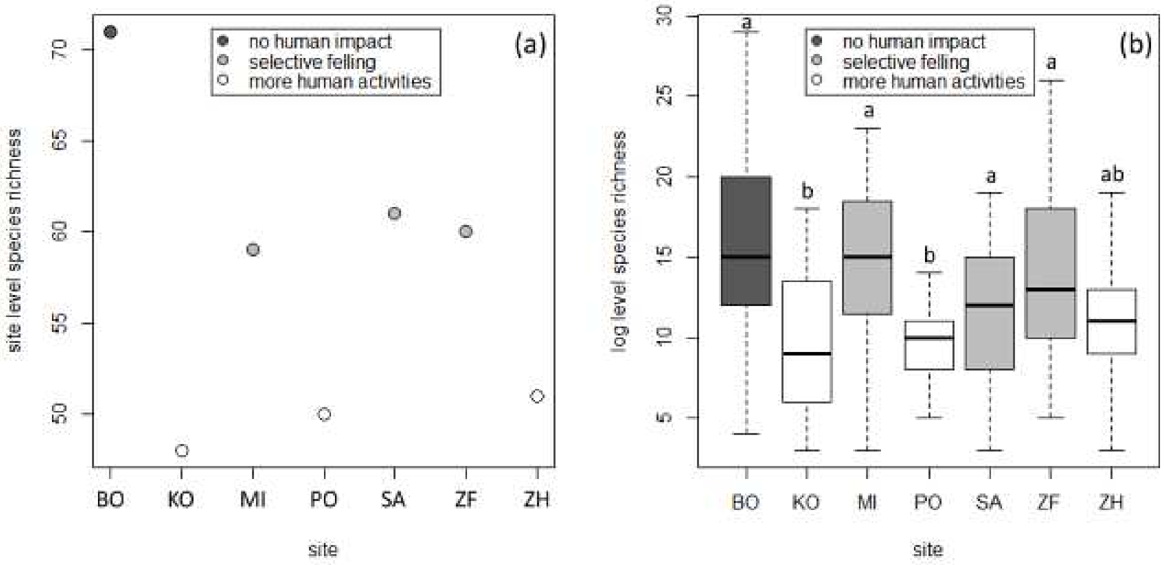

Fig 1. Site level (a) and log level (b) species richness of old-growth beech-dominated sites in the Czech Republic. On the boxplot (Fig. 1b) median, interquartile range and range are indicated. Site name abbreviations are listed in Table 1. Human influence categories are indicated by different colors.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

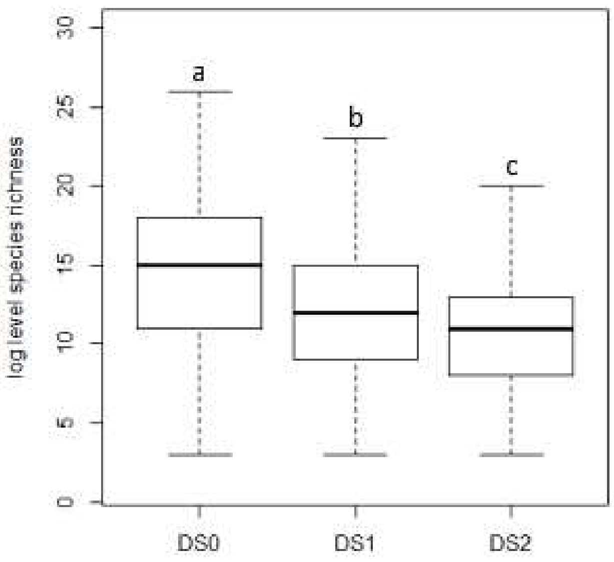

Fig 2. Boxplot of log levels species richness of different decay stages. Significant differences based on Tukey multiple comparisons are marked by different letters.

*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 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).

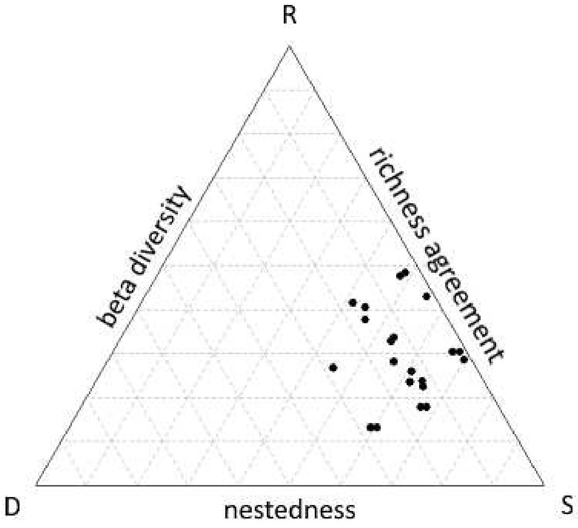

Fig 3. SDR simplex approach involves partitioning the relationship between pairs of sample units into three additive components: S = similarity, R = species replacement, D = species richness difference. The position of each data point within the ternary plot (the distance from each vertex and site) characterizes 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).

Tab 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.

| **Site level** | **Mean value** | **Confidence interval lower (95 %)** | **Confidence interval upper (95 %)** | **Standard error** | **Difference from random** |
|---|---|---|---|---|---|
| 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** | **Mean value** | **Confidence interval lower (95 %)** | **Confidence interval upper (95 %)** | **Standard error** | **Difference from random** |
| 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 |

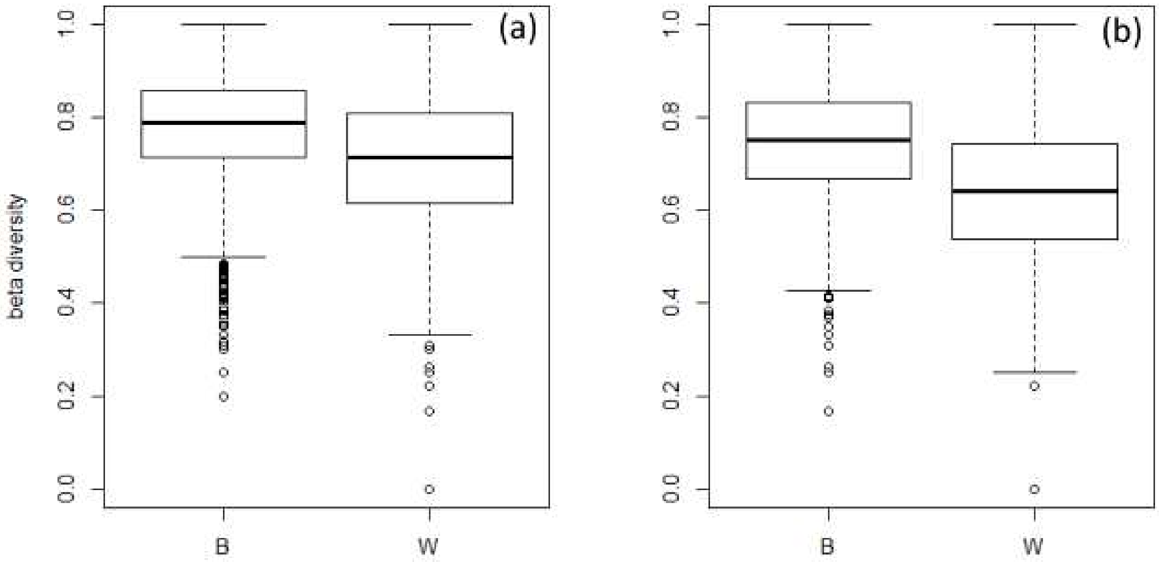

Fig 4. Boxplots of beta diversity between (B) and within (W) sites (a), and beta diversity between (B) and within (W) decay stages within sites (b). The differences of median values were significant ($p<0.001$), based on a Monte-Carlo simulation.

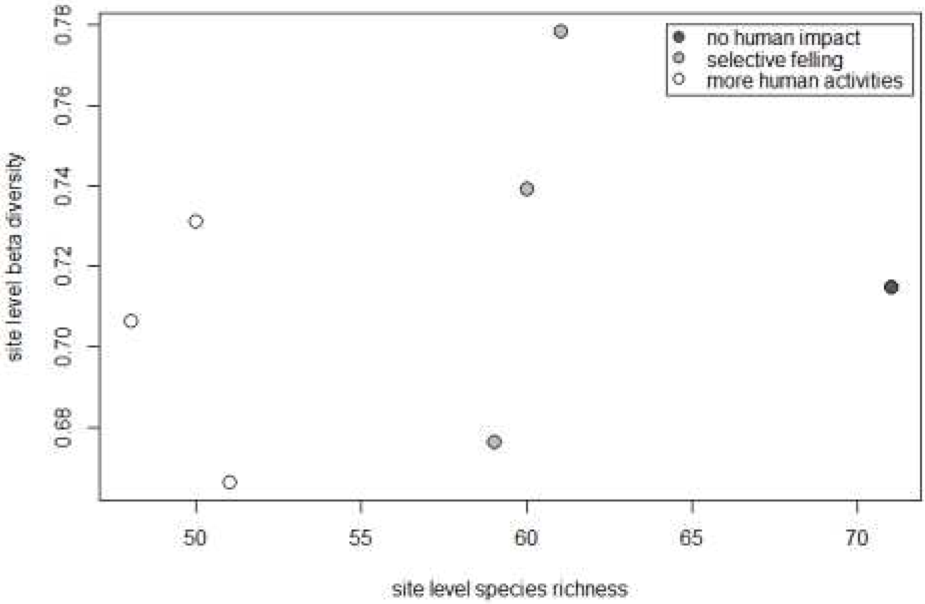

Fig 5. Relationship between site level species richness and beta diversity (F = 0.4, p = 0.56). Each site was associated to one of the three levels of human influence in the past according to Table 1.

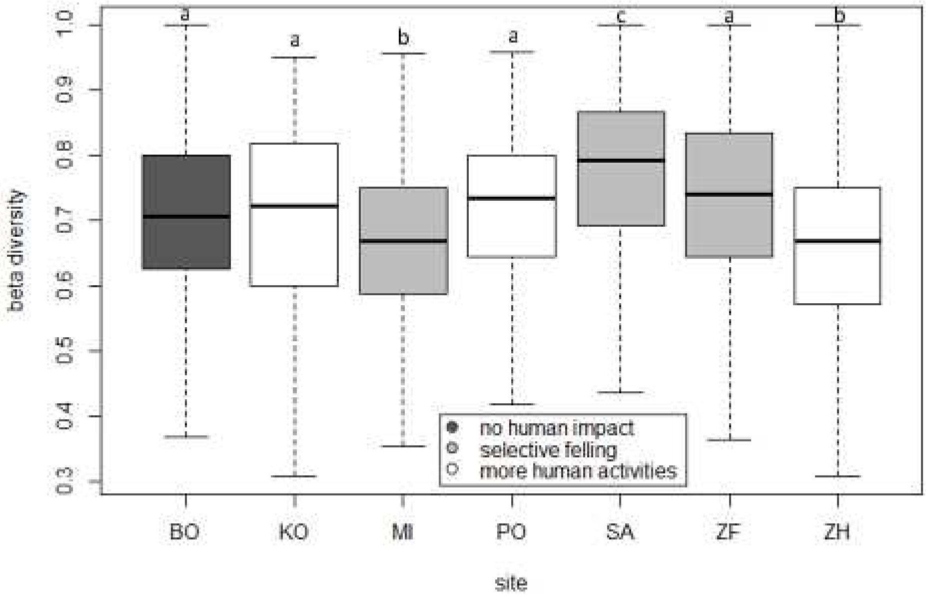

Fig 6. Boxplot of the beta diversity of sites (F = 51.7, p < 0.001). Significant differences based on Tukey multiple comparisons are marked by different letters. Sites are colored based on their human influence categories (Table 1), which were not related to beta diversity.

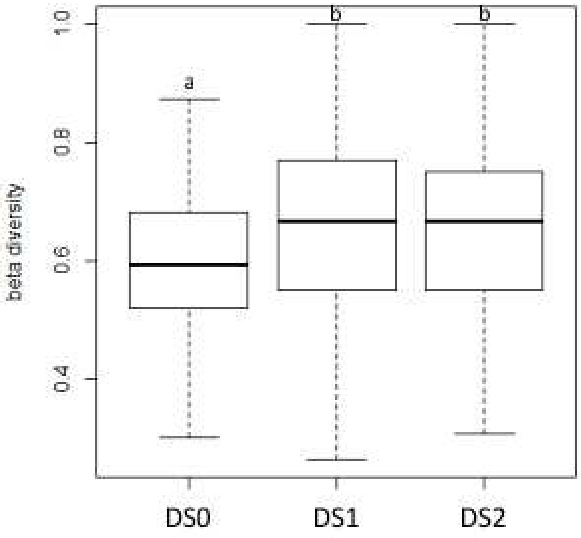

Fig 7. Boxplot of the beta diversity of decay stages (F=24.23, p<0.001, permutation test). Beta diversity values were calculated within sites and within decay stages.

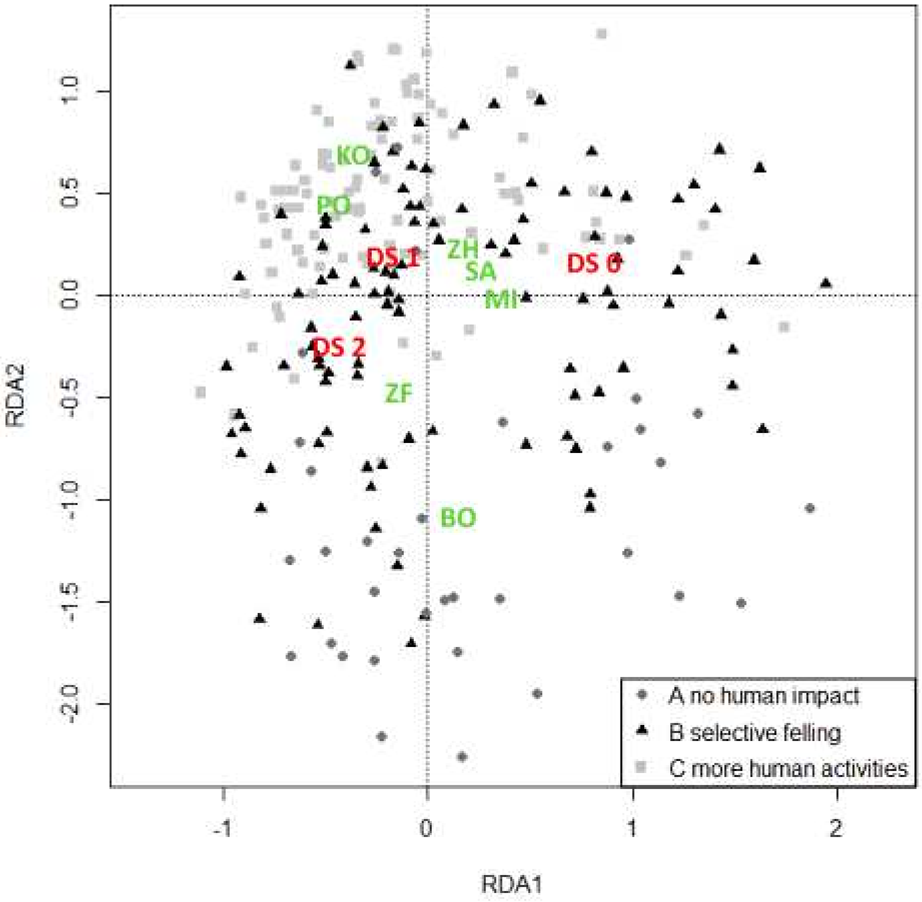

Fig 8. RDA ordination of logs, marked by different human intervention categories of sites. The explanatory factors are decay stages (red) and sites (green).

## 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 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 dead wood haulage and/or charcoal burning was focused on the largest trees - living or recently dead – which are the most important substrate for bryophytes (eg. Ódor et al. 2006; Hofmeister et al. 2015). 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. 2008b; 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. 2008a; 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 (eg. *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. 2008b). 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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Supplementary material, Paper II

## Appendix 1

```
#Analysis for SDR simplex (Podani and Schmera 2006)
#Made by Attila Lengyel, 6/Jan/2017., version 2.2.
#A, B and C components are calculated first for each pair of sites
ABCmat<-function(comm) { #comm is the communitry matrix
comm[comm>0]<-1
N<-nrow(comm)
Amat<-Bmat<-Cmat<-matrix(NA, N,N)
rownames(Amat)<-rownames(Bmat)<-rownames(Cmat)<-colnames(Amat)<-
colnames(Bmat)<-colnames(Cmat)<-rownames(comm)
o<-1
oo<-N*(N-1)/2
pb<-txtProgressBar(1/oo,1,1/oo, style=3)
for(i in 1:(N-1)) {
rel1<-as.numeric(comm[i,])
for(j in (i+1):N) {
rel2<-as.numeric(comm[j,])
a<-sum(rel1==rel2 & rel1==1) #shared species
b<-sum(rel1-rel2==1) #unshared species for first site
ci<-sum(rel1-rel2==-1) #unshared species for second
site
Amat[i,j]<-Amat[j,i]<-a
Bmat[i,j]<-Bmat[j,i]<-b
Cmat[i,j]<-Cmat[j,i]<-ci
o<-o+1
setTxtProgressBar(pb,o/oo)
}
}
diag(Amat)<-rowSums(comm)
diag(Bmat)<-diag(Cmat)<-0
ABC<-structure(list(A=Amat,B=Bmat,C=Cmat))
return(ABC)
}
#simplexABC calculates SDR indices from A, B and C components
simplexABC<-function(A,B,C,relative=T) { #relative=TRUE returns
index values to sum up to 1,
#if relative=FALSE,
returned values are species numbers without standardization
tot<-A+B+C
if(any(tot==0)) {print("At least two sites have no species! Unable to
calculate relative index values!", quote=F)
relative=F
}
ifelse(relative==T, sim<-A/tot, sim<-A)
ifelse(relative==T, repl<-2*pmin(B,C)/tot,repl<-2*pmin(B,C))
ifelse(relative==T, rich<-abs(B-C)/tot, rich<-abs(B-C))
SDR<-
structure(list(similarity=sim,richness.difference=rich,replacement=repl))
return(SDR)
}
#the nestedness function
nestABC<-function(A,B,C, strict=T, relative=T) { #relative=TRUE
standardizes with total species number in the pair of plots, as in
simplexABC
tot<-A+B+C
if(any(tot==0)) {print("At least two sites have no species! Unable to
calculate relative nestedness!", quote=F)
relative=F
```

```
}
nn<-(A+abs(B-C))
nn[A<=0]<-0
if(strict==T) { nn[B==C]<-0 } #'strict' nestedness
ifelse(relative==T, nest<-nn/tot, nest<-nn)
return(nest)
}
######Example######
require(vegan)
data(dune)
x<-ABCmat(dune)
sdr<-simplexABC(A=x$A, B=x$B, C=x$C, relative=T) #for the three basic
components
nest<-nestABC(A=x$A, B=x$B, C=x$C, strict=F, relative=T) #for
absolute nestedness
#Similarity matrix:
sdr$similarity
#Replacement matrix:
sdr$replacement
#Richness difference matrix:
sdr$richness.difference
sdr$similarity+sdr$replacement+sdr$richness.difference #sums up to 1,
if relative=T
#simple handling as distance matrices, different ways of indexing
S<-as.dist(sdr[[1]])
D<-as.dist(sdr[[2]])
R<-as.dist(sdr$replacement)
#triangle plot
require(klaR)
triplot(D,R,S, label=c("D","R","S")) #note the order of components
which is now according to the conventional way by Podani, Schmera et al.
#see klaR package functions
triplot, trilines, tripoints, etc. for more graphical options
```

## Appendix 2

Appendix 2 contains large original species and environmental data set used in all performed analyses. It can be found as a supplementary material on the Publisher´s web sites in a form of an Excel table.

## Paper III

Táborská M, Kovács B, Németh Cs, Přívětivý T, Ódor P (2018) **Microclimate as an important driver of epixylic bryophyte communities.** *Manuscript.*

# Microclimate as an important driver of epixylic bryophyte communities.

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## Abstract

The bryophyte communities inhabiting dead wood are formed by several important factors. Besides the amount, quality and continuity of the substrate, there are also external factors indirectly influencing their structure. One of the most important is local microclimate. This fact has been recognized by many previous authors, yet no one has directly demonstrated it by microclimate measurements *in situ.* Based on directly measured values of local temperature and air humidity during three seasons, we explored the microclimate effect on epixylic bryophyte communities. These relationships were investigated on 62 silver fir logs in an advanced stage of decay in an old-growth mixed forest in the Czech Republic. Our analysis revealed a clear response of the communities to the microclimatic gradient. Total species richness and cover increased with decreasing mean temperature and increasing air humidity. Also, the appearance of sensitive epixylic red-listed specialists (mainly liverworts) was positively correlated with these microclimatic conditions. On the other hand, species more tolerant to desiccation that are often also found on the bark of living trees preferred logs with a dryer and warmer microclimate.

**Key words:** bryophytes; Central Europe; dead wood; fir; microclimate; natural forest; Red List; species response

## Introduction

Many studies have demonstrated the importance of decaying wood as a key substrate for bryophyte diversity in forests (e.g. Berg, Gärdenfors, Hallingback, & Norén, 2002; Hofmeister, Hošek, Holá, & Novozámská, 2015; Söderström, 1993). Some properties of decaying wood have a major influence on the structure and quality of the bryophyte communities. In particular, the total amount of dead wood available in the forest and the presence of all decay stages are crucial for the continuous occurrence of species with specific site requirements (Kruys et al. 1999; Ódor and van Hees 2004). Different combinations of these two factors create a wide spectrum of microhabitats that can be colonized. The size of the logs, stumps, branches and other types of dead wood present is one of the determining factors (Ódor et al. 2006). Larger pieces tend to decay longer and give species with dispersal limitations a better chance to colonize them. They usually consist of a mosaic of different decay stages, and their heterogeneous surface can host many species with different ecological demands. Because of their size, they are also prevented from being overgrown by forest floor generalists (Ódor and van Hees 2004; Jansová and Soldán 2006). Their water holding capacity is generally higher, which is especially important for desiccation-sensitive epixylic specialists, mainly small liverworts (Rambo and Muir 1998; Botting and DeLong 2009). Another factor directly determining bryophyte community structure is tree species composition. In the temperate forest zone, there is a major difference between bryophyte species colonizing deciduous and coniferous trees, mostly because of differences in the pH of these substrates, bark properties and also methods of decay mostly by saproxylic fungi that are often tree species-specific (Heilmann-Clausen et al. 2005). Therefore, the mutual presence of both deciduous and coniferous species increases the total bryophyte species richness (Táborská et al. 2015).

In addition to the direct influence of dead wood and its quality, there are also external factors shaping bryophyte communities. One of the most important background variables is the habitat quality and continuity of the forest. Many recent studies have focused on comparisons of natural and managed forest stands, and have found that species richness and the quality of the community both increase with decreasing human influence, not only in the present but also in the past (Ódor and Standovár 2001; Brunet et al. 2010; Hofmeister et al. 2015a; Táborská et al. 2017). In particular, rare and endangered species are dependent on the continuous presence of sufficient amounts and quality of dead wood, which is very often completely missing in managed forests. There is also a known relationship between bryophyte species richness and regional climatic factors on a larger geographical scale. Heilmann-Clausen et al. (2014) showed that site and landscape filters such as forest naturalness and climate are more important drivers than local filters, represented mostly by available decay stages, on a gradient from Central to Western Europe.

Furthermore, microclimate has repeatedly been pronounced as an important factor driving the total species richness of a site and the local distribution of species in a forest, but studies demonstrating this are quite rare. So far, substitute variables have usually been used, such as macroclimatic variables (Raabe et al. 2010), elevation (Spitale 2016), aspect (Dahlberg et al. 2014), and estimates of moisture (Chmura et al. 2018). Ódor and van Hees (2004) showed that ravines have higher epixylic bryophyte diversity than zonal beech forests, which could be explained by microclimatic conditions. Lately, with the development of technical possibilities, the first studies have begun to emerge in which the attributes of the microclimate of logs are actually measured. The authors mostly define microclimatic conditions based on temperature and air humidity measured on the surface or in the sub-surface of the logs. These methods have been used to answer various questions involving a diversity of colonizing species (Dahlberg et al. 2014; Pouska et al. 2016), tree regeneration on decaying logs (Pichlerová and Homolák 2013) and drivers of local microclimate themselves (Haughian and Frego 2017; Kovács et al. 2017).

The microclimate of a specific spot is a result of interactions between regional climate, topography, vegetation composition and stand structure (Kovács et al. 2017), which has a direct influence on the presence of inhabiting organisms. Bryophytes, as poikilohydric organisms, are especially sensitive to moisture and air humidity (Proctor, 2009). Different species have different water management strategies, with some being water-stress tolerant, and others rather dependent on a stable water supply. Many epixylic specialists belong to the latter category, creating humidity-sensitive, tiny, single-layer mats on the wood surface. Their occurrence is therefore bound to stable moisture conditions

(Söderström 1988; Jansová and Soldán 2006). However, no study has yet demonstrated the preferences of different species by direct field measurements of microclimatic factors.

In this paper, we explore the epixylic bryophyte response to a microclimatic gradient on a local scale in a mixed beech-fir natural forest in the Czech Republic. We address the following questions:

(i) What are the seasonal differences in microclimate, and which periods are most important in terms of the regulation of bryophyte communities?
(ii) What is the relationship between total species richness, cover and microclimate?
(iii) How do the assemblage and single species respond to microclimatic conditions? Do epixylic specialists prefer logs with more humid conditions?

## Material and methods

### *Study area*

The study was conducted in the national nature forest reserve Salajka in the Moravskoslezské Beskydy Mts. in the Czech Republic (49.401°N, 18.418°E). The total area of the forest reserve is 21.86 ha, where elevation ranges from 715 to 820 m above sea level. The forest is dominated by European beech (*Fagus sylvatica* L., 60.9% of standing volume) and silver fir (*Abies alba* Mill., 29.2% of standing volume); the two most common admixing tree species are Norway spruce (*Picea abies* (L.) Karst., 8.9% of standing volume) and sycamore maple (*Acer pseudoplatanus* L., 0.9% of standing volume, (Král et al. 2014b). The forest has an old-growth structure characterized by veteran trees, regeneration in gaps and a fine-scale mosaic of patches of various forest developmental stages (Král et al. 2014a). The amount of the dead wood is high, representing 40.3% of the live standing volume. In contrast to the standing trees, the dead wood is dominated by *Abies* (84.4% of the total dead wood volume), followed by *Fagus* (11.9% of the total dead wood volume) and *Picea* (3.7% of the total dead wood volume) (Král et al. 2014b). The site is under protection and has been unmanaged since 1937.

This site was chosen for a microclimatic study because of its topography: the forest stand occurs on two opposite-facing slopes, one facing south-east and the other facing north-east. This makes it possible to test whether the opposing aspects under a closed forest canopy have a microclimate-driven impact on bryophyte assemblages. Between the two slopes there is a small creek with several parallel tributaries mostly originating on the northern slope (Fig. 1). The bedrock in the area is flysch rock of the Solan system made up of sandstone, clay stone and argillaceous shale layers (Menčík 1979), the soil is silt-loam, loam and clay-loam Haplic Cambisols (Driessen et al. 2001). The area has a temperate montane climate, with a mean annual temperature of 6.2 °C and annual precipitation of 1142 mm.

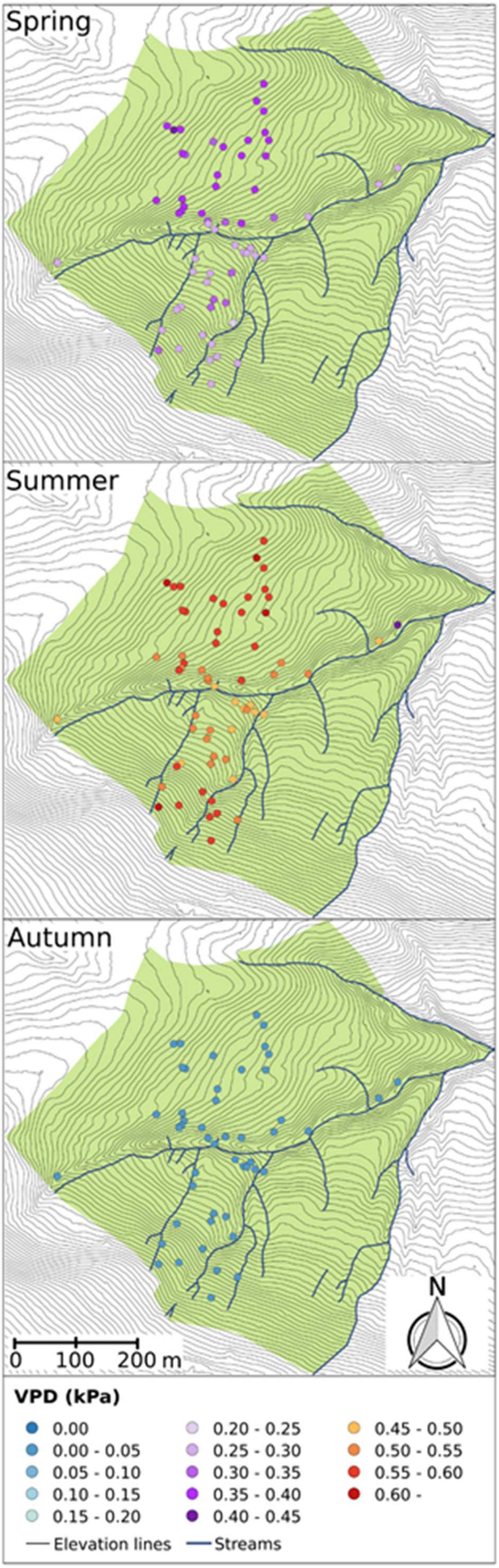


Fig 1. Topographic map of the locality with positions of studied logs. Different colors show seasonal mean vapor pressure deficit (VPD) in kPa for each log.

### *Study design and data collection*

This study focused on the direct effects of microclimate on bryophyte communities on dead wood. To eliminate the effects of other environmental variables like tree species, decay stage and dead wood volume, logs of similar properties were selected for the study. For the pre-selection of appropriate logs a stem database of the Salajka reserve a used. This database has been periodically updated since 1974, with repeated measurements taking place over the years 1974, 1994, 2007 and 2014 (Přívětivý et al. 2016). The database contains among other things information about the tree species, live status, diameter at breast height (DBH) and also the decay stage of the dead trees. All information is also processed in the form of a stem position map. For more details on deadwood measurements and volume calculations see the 'Deadwood protocol' in Supplementary Materials published by Král et al. (2014b). Only logs of *Abies* with diameter 60–90 cm in an advanced decay stage were selected. This was defined as being in an advanced stage of wood rot, with bark missing, soft wood, the log often broken, the outline deformed and the log partly sunk in the soil (decay stage 4 and 5 based on Ódor and van Hees 2004). The reason for this selection of logs was their high availability at the site, and the presence of epixylic specialists that were the subject of interest and that are significantly less frequently present on the dead wood of deciduous species (Táborská et al. 2015). On each log, a 5 m long segment measured from the stem base was examined for bryophytes. Uprooted parts of the logs were not included in the survey. The presence of species and their percentage cover were recorded. Species were identified in the field or transported to the laboratory for microscopic identification. Voucher specimens of all the species are deposited in the herbarium of the first author. The nomenclature follows Kučera et al. (2012).

Microclimate was measured in three periods of the year 2017, each lasting 8 days. The first period was in spring from 29 March – 5 April, then in summer from 8-15 August, and in autumn from 9-16 November. MCC USB-502 combined air temperature and humidity loggers (Measurement Computing Corp., Norton, MA) were used for microclimate measurements, recording air temperature and humidity at 5 minutes intervals. All the loggers were covered by passively ventilated plastic shields to prevent the direct solar radiation on the sensors. They were temporarily installed on the surface of the logs, approximately in the middle of the sampled segment.

### *Data analysis*

Vapor pressure deficit (VPD; kPa) values were calculated from the recorded air temperature (T) and relative humidity (RH) data for every record following the guidelines of Allen et al. (1998): $VPD=(0.6108)\{\exp[17.27\cdot T/(237.3+T)]\}\cdot(1-RH/100)$. VPD directly indicates the atmospheric moisture conditions independently of the actual temperature determining evaporation conditions (Anderson 1936). VPD is a useful microclimate variable describing the drying capacity of the air; generally, the higher the VPD the more intensive is the evaporation rate.

Daily mean VPD values for each log were calculated. The mean VPD values of the three periods were compared by ANOVA and Tukey multiple comparisons using the days within a period as replicates (Zar 1999). The spatial heterogeneity of VPD values was expressed as the standard deviation of the log level VPD values within the measured days, which was also compared between the periods. The log-level mean VPD values of the periods were visualized by Q-GIS 2.18.15 (QGIS Development Team 2017).

The effect of VPD on the species composition of logs was explored by canonical correspondence analysis (CCA, Borcard et al. 2011). The cover values of the species were log-transformed before the analysis. Separate CCA were performed for the VPD values of the three periods, and the explained variance of the VPD variables was tested by Monte-Carlo simulations. The two significant VPD variables found (spring and summer) were combined by principle component analysis (PCA), and this derived variable (called microclimate) was used for further analyses. An improved CCA was then done using microclimate as the explanatory variable, with the position of the species along the microclimate gradient shown. The individual response of the species (with frequency higher than 4) was evaluated and classified qualitatively using simple scatterplots between species cover and microclimate variable, with non-parametric loess smoothing on the observed data (Zuur et al. 2009), and calculating linear correlation coefficients among them. The effect of microclimate on total cover and species richness was analyzed by linear models, since the non-transformed data and Gaussian error structure had the highest explained variance and the best model diagnostics.

All analyses were performed in the R.3.4.1 statistical environment (R Core Team 2017); for CCA the package "vegan" (Oksanen et al. 2017), and for multiple comparison the package "multcomp" (Hothorn et al. 2008) were used.

## Results

### *VPD during the vegetation season*

The mean VPD values of the investigated periods were significantly different (F=50.7, p<0.001), being significantly lower in autumn than in spring and summer (Fig. 2a). The mean and median values were higher in summer than spring, but this difference was not significant. However, the spatial heterogeneity of VPD (expressed as the standard deviation between logs) was much higher in summer than in autumn and spring (F=10.569, p=0.001, Fig. 2b).

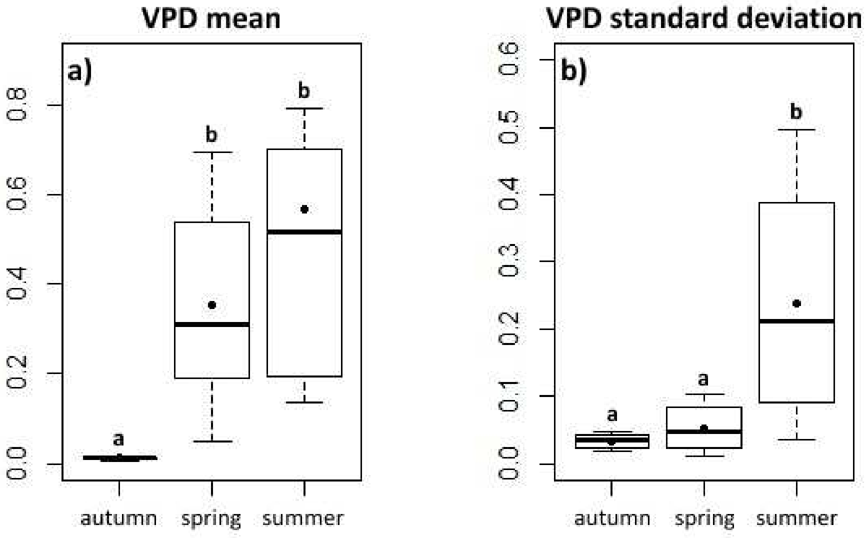


Fig 2. Mean vapor pressure deficit (VPD) and its standard deviation for 62 studied logs during three periods in different seasons of the year.

The visualized VPD values clearly show differences among the periods: in autumn the VPD was close to zero (very low evaporation), while it was between 0.2-0.4 kPa in spring and 0.45-0.6 kPa in summer.

Topography considerably influenced VPD in summer and spring, being higher on the south facing slope and on the top of the hills than in the valley and on the bottom part of the north facing slope (Fig. 1).

*Effect of microclimate on bryophytes*

Altogether we sampled 62 logs and found 42 species of bryophytes, of which 20 were liverworts and 22 mosses. Based on CCA models, the mean VPD values of the logs during the three periods had varying effects on the species composition. While in the autumn the effect of VPD was not significant, its effect in spring and summer was influential, explaining 7.19% and 6.93% of the total species variance, respectively (Table 1). The combined effect of spring and summer VPD values were extracted by PCA. The generalized first PCA axis, which we call a microclimate gradient, explained 77% of the variance of the two significant VPD variables. Using the microclimate gradient in a separate CCA analysis, microclimate explained 8.66% of the species variance (Table 1).

Tab 1. Results of the CCA analysis using mean vapor pressure deficit (VPD) values of three seasons as an explanatory variable. Different seasons had varying effects on the composition of epixylic bryophyte communities.

| **model** | **explained variance (%)** | **F** | **p** |
|---|---|---|---|
| autumn | 2.07 | 0.99 | 0.525 |
| spring | 7.19 | 4.49 | 0.001 |
| summer | 6.93 | 4.32 | 0.001 |
| microclimate gradient | 8.66 | 5.40 | 0.001 |

The high microclimate scores represent low VPD values (high humidity, low temperature), while low microclimate scores have the opposite effect. Bryophyte cover ($R^2$=0.31, F=27.11, p<0.001) and species richness ($R^2$=0.16, F=11.65, p=0.0012) were positively related to the microclimate scores, that is they increased with more humid and cool microclimate (low VPD values, Fig. 3). Based on the CCA, species showed a clear separation along the microclimate gradient (Fig. 4), which was strongly related to the individual response of the species (Fig. 5). On the positive side of the microclimate gradient the cover of epixylic and humidity sensitive species exponentially increase (*Liochlaena lanceolata, Riccardia latifrons, Rhizomnium punctatum, Calypogeia suecica*, *Harpanthus scutatus, Cephalozia bicuspidata*) or have a unimodal positive response (*Syzygiella autumnalis, Lepidozia reptans*). Most of these species are tiny liverworts creating smooth mats on the log surface. In the middle part of the gradient are opportunistic species that did not respond to the microclimate (eg. *Cephalozia lunulifolia, Dicranodontium denudatum, Chiloscyphus polyanthos, Tetraphis pellucida, Herzogiella seligeri*). This is a structurally heterogeneous groups including liverworts, and acrocarpic and pleurocarpic mosses. The negative side of the gradient represented by higher VPD and therefore a drier and warmer microclimate is correlated mostly with species with an exponentially decreasing response (*Hypnum andoi, Hypnum pallescens, Dicranum scoparium*) or a linearly decreasing response (*Dicranum montanum*). These are pleurocarpic and acrocarpic mosses, which can occur not only on dead wood but often on the bark of standing trees as epiphytic species.

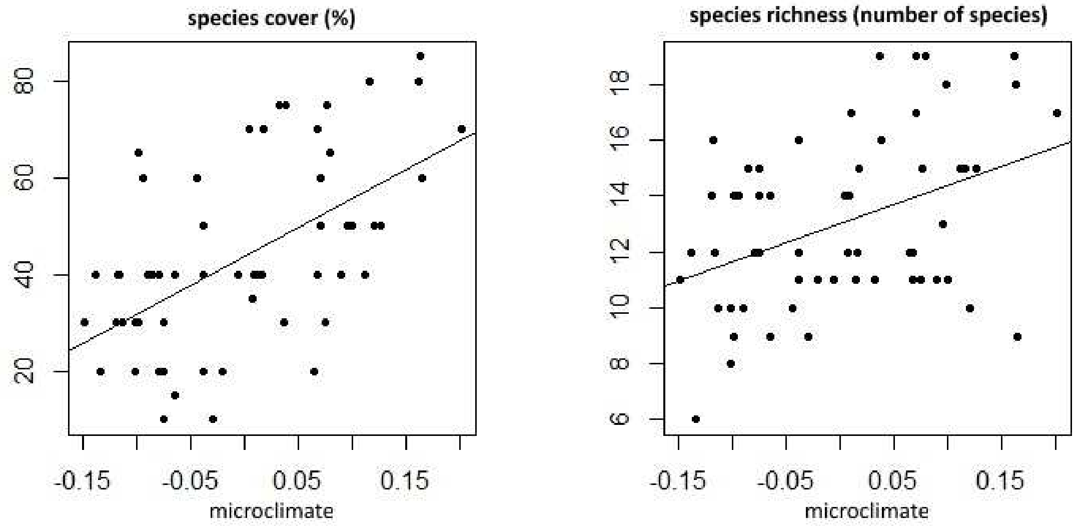


Fig 3. Total species cover (F=27.11, p<0.001) and species richness (F=11.65, p=0.0012) were positively correlated with increasing microclimate scores, representing logs with lower mean temperatures and higher mean air humidity.

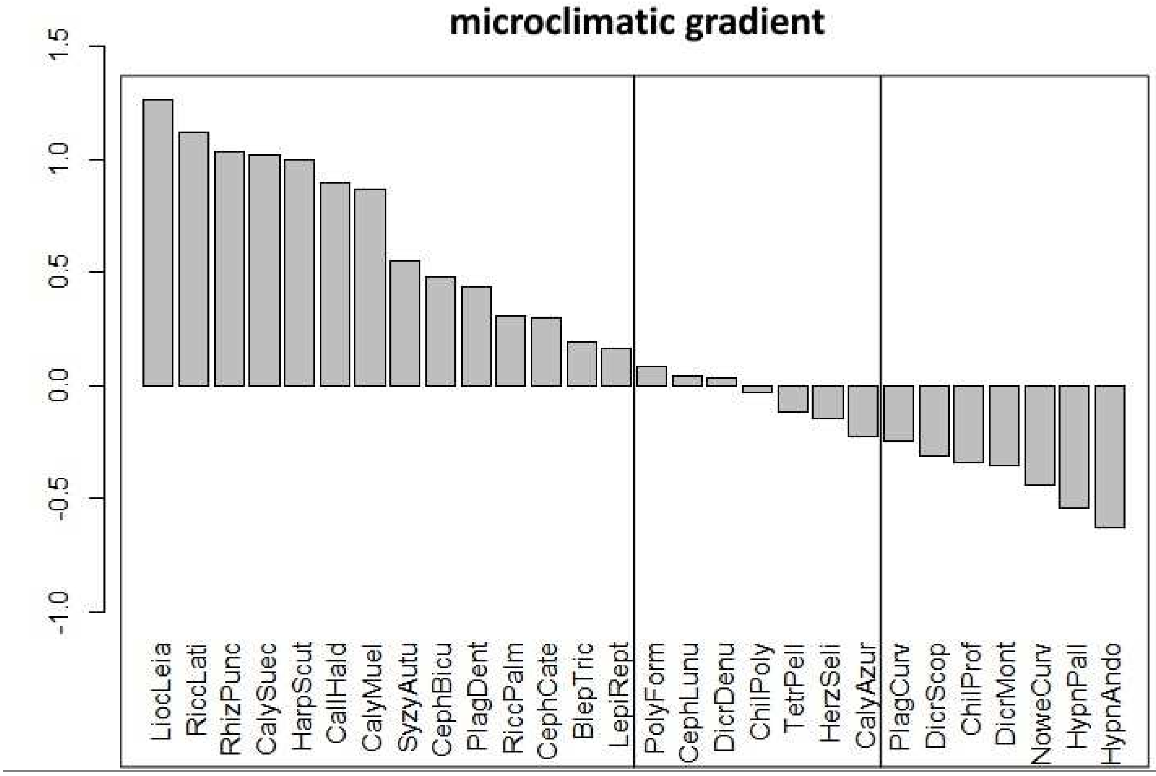
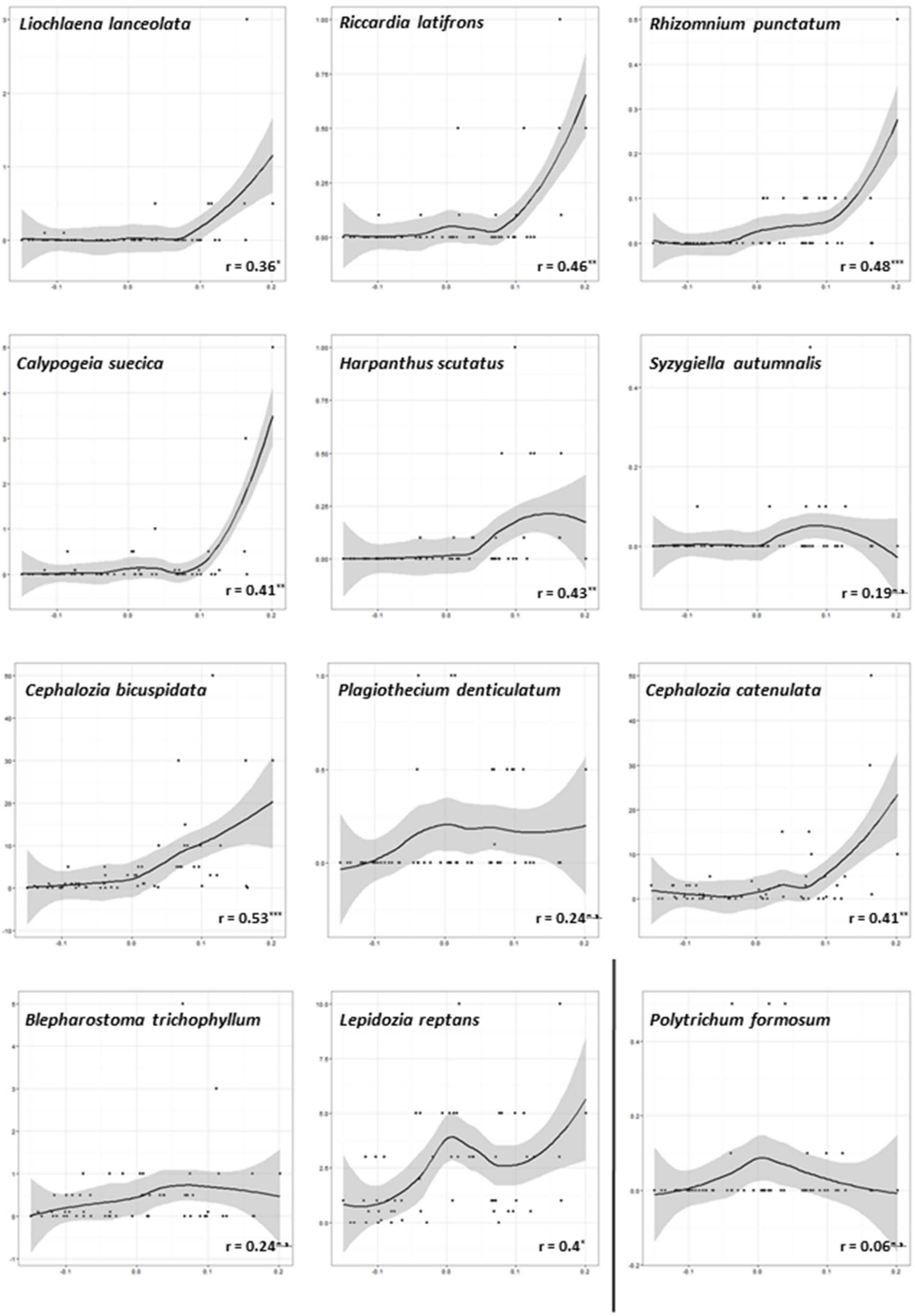


Fig 4. Species distribution along the microclimatic gradient ordered according to their first axis species scores in the CCA based on spring and summer mean vapor pressure deficit (VPD) values. The boxes represent three ecological groups of bryophyte species. For details see Results. Full names of species are listed in Appendix 1.


Liochlaena lanceolata
r = 0.36*
Riccardia latifrons
r = 0.46**
Rhizomnium punctatum
r = 0.48***
Calypogeia suecica
r = 0.41**
Harpanthus scutatus
r = 0.43**
Syzygiella autumnalis
r = 0.19n.s.
Cephalozia bicuspidata
r = 0.53***
Plagiothecium denticulatum
r = 0.24n.s.
Cephalozia catenulata
r = 0.41**
Blepharostoma trichophyllum
r = 0.24n.s.
Lepidozia reptans
r = 0.4*
Polytrichum formosum
r = 0.06n.s.
-0.1
0.0
0.1
0.2

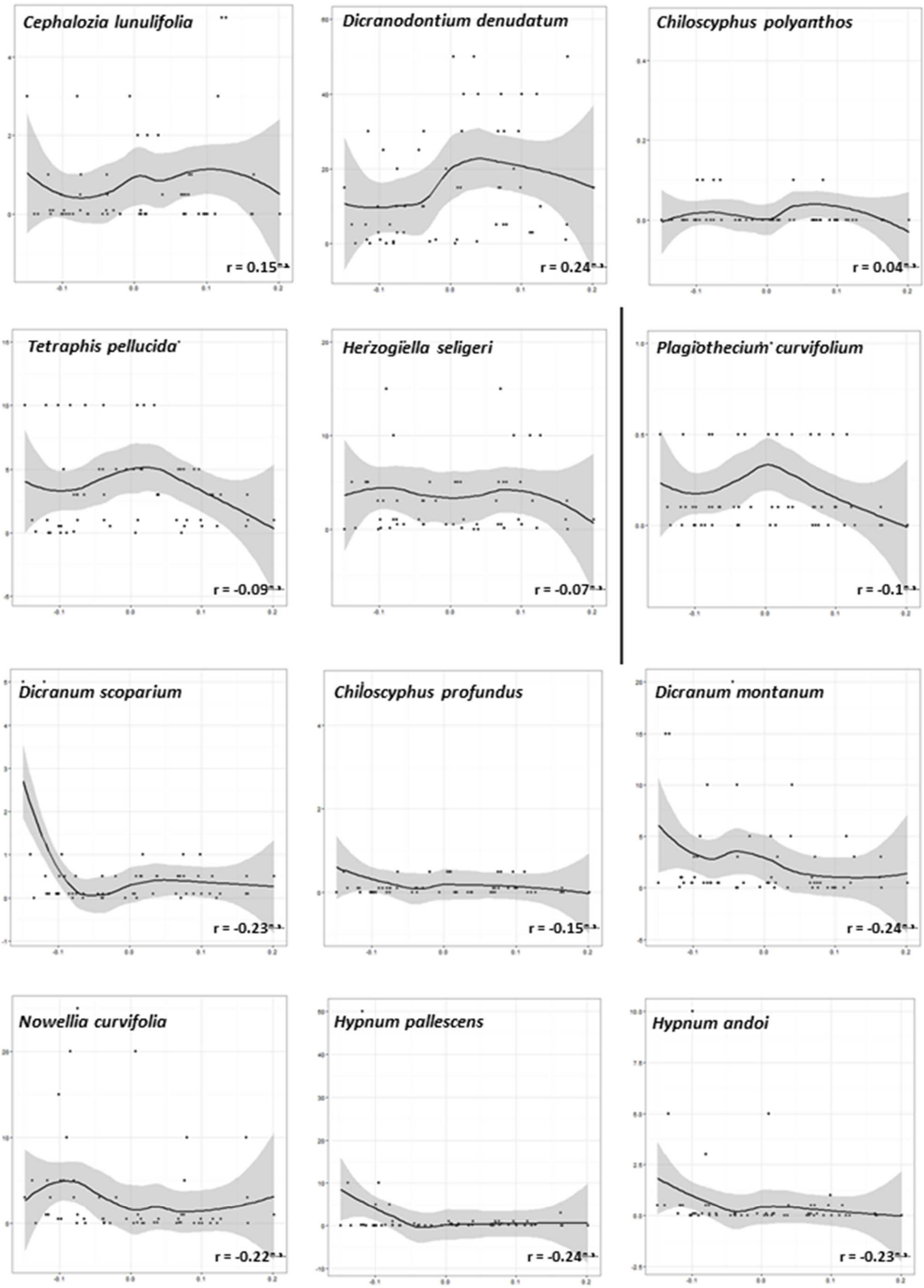


Fig 5. Species response to a microclimatic gradient represented by generalized first PCA axis scores for the studied logs. The order of the species is determined by their decreasing score along the microclimate gradient (first CCA axis), similarly as in Fig. 4. The three response groups are separated by vertical lines.

*Epixylic bryophyte response to microclimatic gradient*

Epixylic bryophyte communities significantly responded to the microclimatic gradient. As expected, total species richness and cover increased with positive microclimatic scores, which reflect decreasing temperature and increasing humidity. In these conditions, bryophyte communities are enriched with humidity sensitive specialized species. These prefer late decay stages in which the soft wood can buffer changes in humidity and temperature thanks to its high water-holding capacity (Ódor and Standovár 2001; Táborská et al. 2015). However, our study indicates that this buffering ability of the logs is limited and the occurrence of these species is also determined by microclimate. It has been demonstrated that for fungi, microclimate can modify successional pathways in otherwise similar logs (Pouska et al. 2016); this may also be true for bryophyte communities.

This is clearly reflected in our analysis of species composition. Species that are classified as epixylic specialists (according to Hill et al. 2007) and listed in the Czech Red List (Kučera et al. 2012) as threatened or near-threatened are all positively correlated with higher microclimatic scores. All these species (*Liochlaena lanceoloata, Calypogeia suecica, Harpanthus scutatus, Callicladium haldanianum, Syzygiella autumnalis* and *Cephalozia catenulata*) occur along the whole gradient, but their cover increases markedly with higher humidity and lower temperatures. Generally these species are strictly restricted to decaying wood in later decay stages, and in the Czech Republic mostly occur only in forests with old-growth structure and a long-term temporal continuity of dead wood. Therefore, their vulnerability has resulted from the decline in cultural landscapes and managed forests in Central Europe.

In addition to these red-listed species, mostly small liverworts (*Riccardia latifrons, Calypogeia muelleriana, Cephalozia bicuspidata, Riccardia palmata, Blepharostoma trichophyllum*) and two species of rather hygrophilic bryophytes (*Rhizomnium punctatum, Plagiothecium denticulatum*) responded positively to microclimatic scores. Most of these prefer a moist environment but are not as sensitive to desiccation as specialized species, and some can also occur on other substrates (such as shaded rocks) in the forest.

Those species that did not respond to the microclimatic gradient (eg. *Dicranodontium denudatum, Chiloscyphus polyanthos, Tetraphis pellucida, Herzogiella seligeri*) were the dominant species of decayed logs independently of their topographic positions. The last group of species, which were negatively related to microclimatic scores (eg. *Hypnum andoi, Hypnum pallescens, Dicranum montanum, Chiloscyphus profundus*), can often occur on the bark of living trees. Clearly, water availability is not a limiting factor for these species, and on dead wood they are just occupying niches that were not suitable for more demanding species. The response of *Nowellia curvifolia* was quite surprising, as this is generally considered an epixylic species growing almost exclusively on the wood of conifers, often accompanied by rare epixylic species. Its higher frequency and cover on logs of managed forests can likely be explained by its higher tolerance for desiccation.

## Conclusions

In this study we confirmed that epixylic bryophyte communities are significantly influenced by microclimatic conditions. Microclimatic conditions of large logs in an advanced decay stage are generally considered as very stable due to their high water-holding capacity. However, our research indicates that their ability to buffer changes in the water regime is limited. We found that the periods with more dynamic heterogeneous climatic pattern, namely spring and summer, had higher influence on bryophyte communities, whereas stable climatic conditions in the autumn were not reflected in the topographical microclimatic gradient. Comparing logs with similar physical properties but different microclimates of the immediate surroundings, we found out that the species richness of these communities as well as the total species cover increased with decreasing mean temperature and increasing mean air humidity. Focusing on single species responses, we distinguished three main groups of species responding differently to the microclimatic gradient. Epixylic specialists and small liverworts with smooth mat growth form occurred more frequently on the positive side of the gradient characterized by lower temperatures and higher humidity. On the other hand, more water stress tolerant species, which also often colonize the bark of living trees, dominated the negative side of the gradient, with a warmer and dryer microclimate. The most common and dominant species of the community had a neutral response to microclimate.

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Supplementary material, Paper III

## Appendix 1

List of species abbreviations used in Fig 4. Names of the species are based on (Kučera, Váňa, & Hradílek, 2012).

| | |
|---|---|
| HypnAndo | *Hypnum andoi* |
| HypnPall | *Hypnum pallescens* |
| NoweCurv | *Nowellia curvifolia* |
| DicrMont | *Dicranum montanum* |
| ChilProf | *Chiloscyphus profundus* |
| DicrScop | *Dicranum scoparium* |
| PlagCurv | *Plagiothecium curvifolium* |
| CalyAzur | *Calypogeia azurea* |
| HerzSeli | *Herzogiella seligeri* |
| TetrPell | *Tetraphis pellucida* |
| ChilPoly | *Chiloscyphus polyanthos* |
| DicrDenu | *Dicranodontium denudatum* |
| CephLunu | *Cephalozia lunulifolia* |
| PolyForm | *Polytrichum formosum* |
| LepiRept | *Lepidozia reptans* |
| BlepTric | *Blepharostoma trichophyllum* |
| CephCate | *Cephalozia catenulata* |
| RiccPalm | *Riccardia palmata* |
| PlagDent | *Plagiothecium denticulatum* |
| CephBicu | *Cephalozia bicuspidata* |
| SyzyAutu | *Syzygiella autumnalis* |
| CalyMuel | *Calypogeia muelleriana* |
| CallHald | *Callicladium haldanianum* |
| HarpScut | *Harpanthus scutatus* |
| CalySuec | *Calypogeia suecica* |
| RhizPunc | *Rhizomnium punctatum* |
| RiccLati | *Riccardia latifrons* |
| LiocLeia | *Liochlaena lanceolata* |

Reference:

Kučera, J., Váňa, J., & Hradílek, Z. (2012). Bryophyte flora of the Czech Republic: Updated checklist and red list and a brief analysis. Preslia, 84(3), 813–850.

## Curriculum Vitae

| | |
|---|---|
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| | |
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| 1993 – 2002 | Primary and Elementary school in Šumperk |
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| 2006 – 2009 | Masaryk University, Faculty of Science, Bachelor's degree in Systematic botany and ecology |
| 2009 – 2010 | Masaryk University, Faculty of Social studies, Master´s degree in Environmental studies, unfinished |
| 2009 – 2012 | Masaryk University, Faculty of Science, Master's degree in Systematic botany and ecology |
| 2012 – currently | Masaryk University, Faculty of Science, degree program Biology, field of study Botany, Ph. D. studies in Systematic botany and ecology, topic of thesis: “Diversity of epiphytic bryophytes on decaying wood in forest reserves.” |

Professional work experience:

| | |
|---|---|
| 2010 | Bryophyte monitoring on four permanent plots included in the NATURA biotope survey for Nature Conservation Agency of the Czech Republic. |
| 2008 – 2012 | Participation in the project GA 206/08/0389 – "Past and present changes in Sudeten mountain bogs". |
| 2012 | Monitoring of bryophytes on wet meadows in the Krkonoše National Park. (The study was conducted under the grant for Restoring Natural Landscape Functions, popfk-36-1318/2012, Bryological survey of selected meadow enclaves in Krkonoše.) |

| | |
|---|---|
| 2013, 2015 | Monitoring of selected species of bryophytes of European significance (*Scapania carinthiaca* var. *massalongoi*, *Leucobryum glaucum*). |
| 2013 – 2017 | Leader of bryological research in the project GA ČR P504/13-27454S – "Deadwood decomposition dynamics in natural temperate forests". |
| 2015 – 2016 | Participation in the project EHP-CZ02-OV-1-021-2014 "Monitoring of natural forests of the Czech Republic" supported by Norway grants. |
| 2015 – 2017 | Participation in the project EHP-CZ02-OV-1-013-2014 "Natural diversity of the Bohemian-Moravian Highlands" supported by Norway grants. |
| 2016 | Monitoring of bryophytes on wet meadows in the Krkonoše National Park. (The study was conducted under the grant for Restoring Natural Landscape Functions, popfk-36-1318/2012, Bryological survey of selected meadow enclaves in Krkonoše.) |
| 2016 – 2018 | Leader of bryological research in the project "Complex analysis of biological value of near-natural forest stands in the Protected Landscape Area Bohemian Forest and the proposal of it multifunctional silvicultural approach" granted by Forests of the Czech Republic state enterprise and Šumava National Park Administration. |
| 2017 | Participation in the project „Silva Gabreta Monitoring – Realisierung eines grenzüberschreitenden Monitorings von Biodiversität und Wasserhaushalt Silva Gabreta Monitoring – Implementation of cross-border monitoring of biodiversity and water regime (INTERREG 26)“, implemented in the years 2016 – 2019. Bryophyte monitoring on selected study plots in Šumava National Park. |
| 2018 – 2022 | Leader of bryological research in the project MŽP "Biological research and monitoring at landscape level of Czechia. Assuring expert support for environment department activities." Chapter F - Developmental dynamics and biodiversity changes of natural forests" granted by the Ministry of the Environment of the Czech Republic. |

Publications in international peer-reviewed journals (in English):

M. Táborská, T. Přívětivý, T. Vrška, P. Ódor (2015): **Bryophytes associated with two tree species and different stages of decay in a natural fir-beech mixed forest in the Czech Republic.** Preslia 87 (4): 387-401. ISSN 0032-7786.

M. Táborská, J. Procházková, A. Lengyel, T. Vrška, L. Hort, P. Ódor (2017): **Wood-inhabiting bryophyte communities are influenced by different management intensities in the past.** Biodiversity and Conservation, DOI 10.1007/s10531-017-1395-8.

Publications in Czech scientific journals (in Czech):

M. Táborská (2013): **Společenstva mechorostů na horských prameništích Hrubého Jeseníku a hlavní ekologické faktory, které je ovlivňují.** Zprávy Vlastivědného muzea v Olomouci 305:31-50

E. Mikulášková, M. Jiroušek, J. Procházková et M. Táborská (2013): **Mechorosty mokřadních biotopů na vybraných lučních enklávách Krkonoš.** Opera Corcontica 50: 107-118.

J. Kučera, V. Plášek, S. Kubešová, J. Bradáčová, E. Holá, J. Košnar, M. Kyselá, A. Manukjanová, E. Mikulášková, J. Procházková, M. Táborská, J. Tkáčiková, E. Vicherová (2014): **Mechorosty zaznamenané během podzimních 26. bryologicko - lichenologických dní (2013) v Beskydech.** Bryonora 54: 11-21.

Z. Rozbrojová et M. Táborská (2014): **Botanický průzkum Hrabětického lesa.** Zprávy Vlastivědného muzea v Olomouci 307: 49-64.

M. Kyselá et M. Táborská (2015): **Bryologický průzkum bývalého důlního díla Žebračka u Zlatých Hor.** Zprávy Vlastivědného muzea v Olomouci 309: 26-34. ISSN 1212-1134.

J. Kučera, P. Dřevojan, E. Ekrtová, E. Holá, Š. Koval, A. Manukjanová, T. Peterka, J. Procházková, T. Štechová, M. Táborská, J. Tkáčiková, E. Vicherová, M. Zmrhalová (2016): **Zajímavé bryofloristické nálezy XXV.** Bryonora 57 (1): 83-91. ISSN 0862-8904.

S. Kubešová, J. Kučera, J. Jandová, A. Manukjanová, I. Novotný, M. Táborská, J. Tkáčiková (2016): **Mechorosty zaznamenané během jarního bryologicko-lichenologického setkání na Mohelenském mlýně v dubnu 2016.** Bryonora 58: 28-37. ISSN 0862-8904.

M. Táborská et J. Procházková (2016): **Mechorosty doubrav národního parku Podyjí na příkladu lokality Lipina.** Bryonora 57 (1): 29-35. ISSN 0862-8904.

Conference presentations

*Oral presentations*

M. Táborská. **Bryophyte communities on dead wood in central European natural forests.** Presented at the Dead wood meeting & course, Lammi, Finaland, 7th August 2016.

*Poster presentations*

M. Táborská, R. Hédl, M. Jiroušek. **Are bryophyte communities on island biotopes determined by environmental factors or by dispersal limitation?** Presented at the poster session of the 56th IAVS Annual Symposium, Tartu, Estonia, 26–30 June 2013

M. Táborská, B. Kovács, T. Vrška, T. Přívětivý, P. Ódor. **Changes in bryophyte communities on decaying firs and the influence of microclimate.** Presented at the poster session of the 44th annual meeting of the GfÖ, Hildesheim, Germany, 8-12 September 2014

M. Táborská, T. Vrška, P. Ódor. **Dead wood inhabiting bryophytes and their relationship to tree species and decay stages in natural fir-beech mixed forest in Czech Republic.** Presented as a poster at the 58th IAVS Annual Symposium, Brno, Czech Republic, 19–24 July 2015

M. Táborská, J. Procházková, A. Lengyel, T. Vrška, L. Hort, P. Ódor. **Wood-inhabiting bryophyte communities are influenced by different management intensities in the past.** Presented at the poster session of the 2nd International Conference on Forests, Bavarian Forest National Park, Neuschönau, Germany. 26-29 April 2017.

*Invited oral presentations*

M. Táborská. **Mechorosty rostoucí na tlejícím dřevě a jejich ekologie.** University of Ostrava, Czech Republic, 2014.

M. Táborská and J. Procházková. **Diverzita přirozených lesů České republiky, aneb do pralesů nejen za mechorosty**. University of Ostrava, Czech Republic, 2017.

M. Táborská. **The project "Monitoring of natural forests of the Czech Republic".** Presented on the meeting of the foresters from the Nature Conservation Agency of the Czech Republic. Kladská, Czech Republic, June 2017

*Oral presentations given at Ph.D. student meetings*

M. Táborská, P. Ódor. **Changes in bryophyte communities on decaying wood and the influence of microclimate.** Presented at the 6th Meeting of Czech, Hungarian, Polish and Slovak Ph.D. students in Plant Ecology and Botany, Karpacz, Poland, 10–12 October 2014

M. Táborská. **Není les jako les aneb Studium společenstev epixylických mechorostů v NPR Salajka.** Presented at the Meeting of the Czech Ph.D. students in ecology and phytosociology (Setkání ekologicko-geobotanických doktorandů), Rožmberk, Czech Republic, 20-22 November 2015

Brno 20. 2. 2018

Signature: