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# Bryophytes associated with two tree species and different stages

## Mechorosty tlejícího dřeva a jejich vztah ke druhu stromu a stádiu rozkladu v přirozeném jedlobukovém lese v České Republice

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Species richness and composition of bryophyte communities on two species of trees at 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 favourable for epixylic species occurring on very acid and constantly moist substrates. Both at the stand- and log level, the highest species richness was recorded at intermediate stages of decay, which constitute a transitional phase in the 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 be focused on the preservation of mixed stands and the continuity of dead wood in the montane beech-fir zone of Europe.

Keywords: *Abies alba*, bryophytes, conservation, dead wood, decay stage, *Fagus sylvatica*, species diversity

## Introduction

It is well established that abundance of high-quality dead wood in all stages of decay is crucial for many groups of organisms, including arthropods, birds, small mammals, fungi, lichens and bryophytes (Maser & Trappe 1984, Harmon et al. 1986, Samuelsson et al. 1994, Jonsson et al. 2005). This habitat is a biodiversity hotspot in forests, which provides 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 abundance of dead wood in different stages of decay and different microclimatic conditions is much greater than in managed forests (Siitonen 2001, Jonsson et al. 2005). Therefore, 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 dead wood change and associated with these changes there is a succession of bryophyte communities. At the beginning of the process mainly epiphytic species are present, which survive as long as the bark remains. At this stage the bryophyte assemblages vary between species of trees because the structure of their bark differs (Schmitt & Slack 1990, Lewis & Ellis 2010, Mežaka et al. 2012, Király et al. 2013). In later stages of decay wood differs less than the bark, but nevertheless there are 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 epiphytes is better studied than their effect on epixylic bryophytes (McAlister 1997, Jansová & Soldán 2006).

Most species occur in the transition stage between early and late stages of decay when there are the most microhabitats, which can be colonized by species with various demands (Söderström 1988, Kruys et al. 1999, Heilmann-Clausen et al. 2005). At this stage the community is a mixture of epiphytic, opportunistic and strictly epixylic species. The strict epixylics are mostly small liverworts that are very sensitive to desiccation and occur mainly on particular substrates (Lesica et al. 1991, Ódor et al. 2006).

In later stages of decay epixylic specialists dominate, which are gradually replaced by species of the forest floor as the substrate is completely decomposed. On the floor of boreal zone forests there are mainly bryophytes (Söderström 1988) and in temperate deciduous forests mainly vascular plants (Ódor & van Hees 2004). This pattern in succession and changes in community composition are described in several studies (McCullough 1948, Söderström 1988, Ódor & van Hees 2004, Ódor et al. 2005, Jansová & Soldán 2006, Heilmann-Clausen et al. 2014), but there are few papers on the connection between decay stage and species richness (Ódor et al. 2006).

One of the important changes that occur during succession, which affects the germination, growth, survival and nutrient availability for propagules, is the pH of the substrate (Bates 2009, Goffinet & Shaw 2009). The pH of bark and that of decaying wood 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 decaying wood of the same species. As pH is a potentially important background variable influencing bryophytes we compared the pH of bark and wood of different species of trees at different stages of decay.

In this study we recorded the bryophyte species composition on *Fagus* and *Abies* at different stages of decay and the pH of substrate. We hypothesize that (i) the species richness recorded on these two trees is similar; (ii) the species richness is highest at intermediate stages of decay; (iii) the species composition on the two trees and at different stages of decay differ significantly; (iv) the effect of species of tree on species composition is stronger than that of stage of decay; (v) *Fagus* is characterized by epiphytic and opportunistic species, and *Abies* by epixylics (mainly liverworts); (vi) the pH of *Fagus* is higher than that of *Abies*; and (vii) pH decreases during decay.

## Materials and methods

### *Study area*

This study was carried out at the national nature forest reserve Salajka in the Moravskoslezské Beskydy Mts in the Czech Republic (49.401°N, 18.418°E). This forest occurs at an altitude of 715 to 815 m on two opposite-facing slopes, with a small creek between them. 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). 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 and 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 *Acer pseudoplatanus* L. (0.9% of standing volume) are also present (Král et al. 2014b). The site has been protected and unmanaged since 1937. It has an old-growth stand structure characterized by veteran trees, regeneration in gaps and a fine scale mosaic of forest developmental stages (Král et al. 2014a) and the timber volume is 556 $m^3$/ha (T. Vrška et al., unpublished data). The amount of dead wood is high, making up 40.3% of the timber volume. While deciduous trees (mainly *Fagus*) dominate the living volume, the opposite is the case for 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 herbaceous plants is low and dominated by *Dentaria enneaphyllos* L. and *D. bulbifera* L., and *Galeobdolon montanum* (Pers.) Rchb., *Carex sylvatica* Huds. and *Galium odoratum* (L.) Scop. are also frequent (Šamonil & Vrška 2007).

### *Data collection*

For the preselection of appropriate logs we used the stem geographic database of the Salajka reserve, which has been periodically updated since 1970s. This map contains information about the species of trees and their diameter at breast height (DBH) of both living and dead trees and also the stage of decay of the dead trees. For more details on deadwood 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 57 dead trees with DBH of 60 to 90 cm (Table 1) in one of three stages of decay (DS): (i) DS1 – earliest stage of decay: the species is still recognizable, the stem usually covered with bark and relatively healthy and the wood still hard, which is the distinctive feature, and branches are still present; (ii) 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); (iii) 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 follows the six levels of decay of Ódor & van Hees (2004) merging their 1–2, 3–4 and 5–6 categories. The sample included similar proportions of *Fagus* and *Abies* in all stages of decay (Table 1).

Bryophytes were recorded 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). We

Table 1. – The number of logs of the two species of trees at different stages of decay sampled: DS1 – early stage of decay, DS2 – intermediate stage of decay, DS3 – late stage of decay.

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

chose a relatively large sampling unit, because we wanted to determine the species pool and species richness on a similar sized area of each of the logs surveyed. The length of the sample was based on the authors' field experience and is considered to be sufficient for recording most of the species. It was set to standardize the size of the plots sampled. If the logs included an uprooted part it was not included in the survey. The species present along the 5 m surveyed 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. *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 epixylic, epiphytic, epilithic, terricolous and opportunistic (occurring on many substrates such as rock-bark, bark-dead wood, dead wood-soil etc.) following the classification of Heilmann-Clausen et al. (2014) and Jansová & Soldán (2006). The bryophyte species and substrate categories recorded are listed in Electronic Appendix 1. The sampling was done in 2013.

The pH of the surface of 38 logs was measured (subsample of the 57 logs studied for bryophytes). For each log three measurements were recorded along the section surveyed using a Vario pH meter. Depending on the log's condition we measured the pH of the bark or bare wood. If it was partly bare wood and partly covered by bark the three measurements were made in approximately the same ratio as that of bare wood to wood covered by bark. The pH measurements were carried out on all logs on the same day during which the weather conditions remained the same.

### *Data analysis*

The effect of species of tree (*Fagus* or *Abies*) and stage of decay (DS1–3) at the level of a stand or log on species richness were studied separately. The species richness recorded on logs and the effect of the explanatory factors were analysed using general linear models with Poisson error structure and log link function (Faraway 2006). During this analysis model selection was based on maximum likelihood methods, and tested using chi-square statistics, the explained variance was estimated using a pseudo R square. The differences between the different stages of decay were tested using Tukey's HSD tests (Zar 1999).

Species composition recorded on the logs was studied using multivariate methods (Podani 2000). For these analyses we used only species with 5 or more occurrences. The species data was square-root transformed. Detrended correspondence analysis was used as a preliminary indirect method for exploring the gradient length of the species variance (Lepš & 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 the direct ordination for the exploration of the associations between species and environmental factors (tree species and decay stages). The explained variance was tested using variation partitioning (Peres-Neto et al. 2006). During the CCA analysis the effect of explanatory variables was tested using F-statistics via Monte-Carlo simulation with 1000 permutations, the significance of the constrained axes and the whole CCA model was tested in a similar way (Borcard et al. 2011). Association of the different species of bryophytes with two species of trees and different stages of decay was tested using indicator species analysis (Dufrene & Legendre 1997, Legendre & Legendre 1998). The difference in the pH recorded for the two species of trees and different stages of decay was tested using a linear model (Faraway 2005) and a Tukey's HSD test was used for multiple comparisons.

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) and labdsv package for the indicator species analysis (Roberts 2012).

## Results

### *Species richness*

Altogether we sampled 57 logs on which we found 68 species (19 liverworts and 49 mosses; Table 2). The general stand-level species richness recorded for *Fagus* was higher than that for *Abies*. This was also true for only mosses, but in case of liverworts the stand-level species richness for both species of trees was similar. The highest stand-level species richness was recorded for intermediate stage of decay (DS2) and the values for DS1 and DS3 are similar. Again this pattern was the same for only mosses, but for liverworts the lowest stand-level species richness was recorded for DS1 and the highest for DS2.

The log-level species richness of both liverworts and mosses combined was only significantly associated with the stage of decay (P = 0.0002, quasi $R^2$=0.237). Neither species of tree (P = 0.67) nor the species of tree and stage of decay interaction (P = 0.39) had significant effects. The species richness associated with DS2 was significantly higher than with DS1 and DS3 (Table 2, Fig. 1). However, when the liverworts and mosses were analysed separately both species of tree and stage of decay had significant effects (see Electronic Appendix 2). For liverworts species richness on *Abies* was higher than for mosses, and the species richness associated with DS1 was lower than with DS2 and DS3. For mosses the species richness on *Fagus* was higher and that associated with DS2 higher than that with DS1 and DS3.

### *Species composition*

The two explanatory factors explained 20.4% of the total variance (F = 4.5, P = 0.005, Fig. 2). Species of tree explained 11.5% (P = 0.005) and stage of decay 5.4% (P = 0.005) of the species variance and the joint variance was zero. The first axis (15.6%, F = 10.4, P = 0.005) was related to species of tree with *Abies* dominant on the negative and *Fagus* on the positive side. The second axis (3.7%, F = 2.5, P = 0.005) represented an increasing effect of DS. Species with negative CCA1 values are associated with *Abies* (*Calypogeia suecica*, *Cephalozia bicuspidata*, *Cephalozia catenulata*, *Herzogiella seligeri*, *Nowellia*

Table 2. – Stand- and log-level species richness recorded for the two species of trees at different stages of decay and their combinations (DS1 – early, DS2 – intermediate, DS3 – late stage of decay). For log-level species richness the significant differences are marked by lower case letters (ns: non-significant).

| | | Stand-level species richness | Log-level species richness |
|---|---|---|---|
| Total | | 68 | 10.3±3.6 |
| Tree species | *Abies alba* | 42 | 10.1±3.5$^{ns}$ |
| | *Fagus sylvatica* | 59 | 10.5±3.7$^{ns}$ |
| Decay stage | DS1 | 38 | 8.2±2.7$^{a}$ |
| | DS2 | 56 | 12.4±3.5$^{b}$ |
| | DS3 | 41 | 9.8±3.2$^{a}$ |
| Combination | *Abies* DS1 | 21 | 7.4±1.3$^{ns}$ |
| | *Abies* DS2 | 40 | 11.9±3.7$^{ns}$ |
| | *Abies* DS3 | 26 | 10.5±3.1$^{ns}$ |
| | *Fagus* DS1 | 30 | 8.9±3.3$^{ns}$ |
| | *Fagus* DS2 | 43 | 12.9±3.2$^{ns}$ |
| | *Fagus* DS3 | 30 | 9.1±3.1$^{ns}$ |

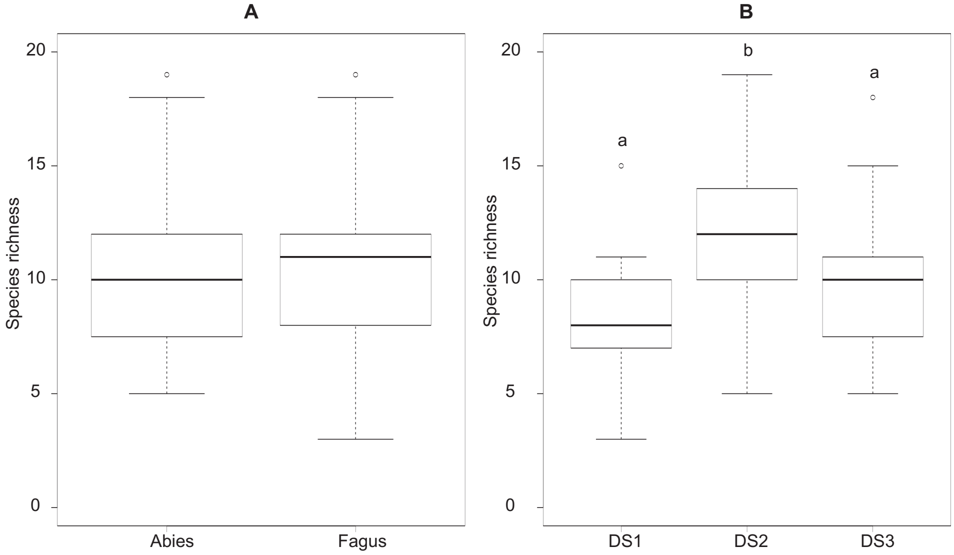

Fig 1. – Species richness recorded on logs of the two species of trees (A) at different stages of decay (B, see text for explanation). Significant differences based on Tukey's HSD tests are marked by different letters.

*curvifolia*, *Plagiothecium curvifolium*), while species on the positive side of CCA1 are associated with *Fagus* (*Brachytheciastrum velutinum*, *Bryum moravicum*, *Pterigynandrum filiforme*, *Radula complanata*, *Sciuro-hypnum reflexum*).

These results are supported by the indicator value analysis (Table 3, 4). Many epixylic liverwort species were associated with *Abies* (*Blepharostoma trichophyllum*, *Calypogeia suecica*, *C. lunulifolia*, *Nowellia curvifolia*). Most of the bryophytes associated with *Abies* were also epixylic species (*Herzogiella seligeri*, *Tetraphis pellucida*, *Dicranodontium denudatum*), with the exception of the epiphytic *Dicranum montanum* and opportunistic *Dicranum scoparium* and *Plagiothecium curvifolium*. On the other hand, most of the

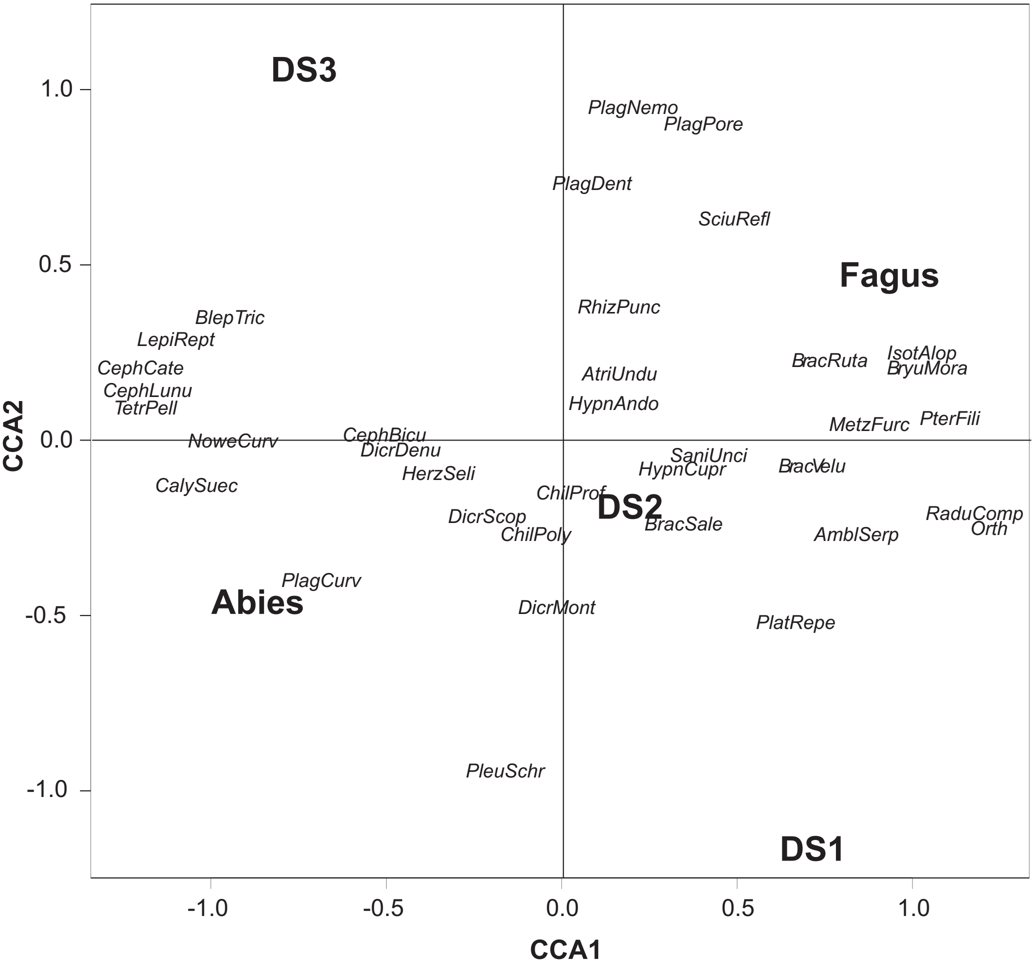

Fig 2. – Canonical correspondence analysis biplot of bryophyte species and environmental factors. The trees are *Abies alba* (Abies) and *Fagus sylvatica* (Fagus), the stages of decay are DS1, DS2 and DS3, respectively. Full names of the species are listed in Appendix 1.

species associated with *Fagus* are epiphytes (*Bryum moravicum*, *Metzgeria furcata*, *Pterigynandrum filiforme*, *Radula complanata*, *Orthotrichum* species) or opportunistic species (like *Brachythecium rutabulum*, *Brachytheciastrum velutinum*).

Only three species, *Sanionia uncinata*, *Dicranum montanum* and *Brachythecium salebrosum* were associated with DS2. The strict epixylic species *Blepharostoma trichophyllum*, *Cephalozia lunulifolia*, *C. catenulata*, *Herzogiella seligeri* and *Tetraphis pellucida* were associated with DS3. For DS3 there is also one indicator species classified as opportunistic, *Lepidozia reptans* (Table 4).

Table 3. – Species with significant indicator values recorded for the two species of trees (A – *Abies alba*, F – *Fagus sylvatica*). P = the significance that the indicator value is different from 0 (probability of first type error).

| Bryophyte species | Tree species | Indicator value | P | 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 | 0.2500 | 0.006 | 7 | 25–0 |
| *Cephalozia catenulata* | A | 0.2500 | 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 |

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

| Bryophyte species | DS | Indicator value | P | Frequency (DS2, DS3) | Occurrence (%) DS1–DS2–DS3 |
|---|---|---|---|---|---|
| *Sanionia uncinata* | 2 | 0.3817 | 0.010 | 15 | 41–71–21 |
| *Dicranum montanum* | 2 | 0.3472 | 0.041 | 16 | 65–76–26 |
| *Brachythecium salebrosum* | 2 | 0.2590 | 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 | 0.030 | 5 | 0–10–26 |

### *Tree surface pH*

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

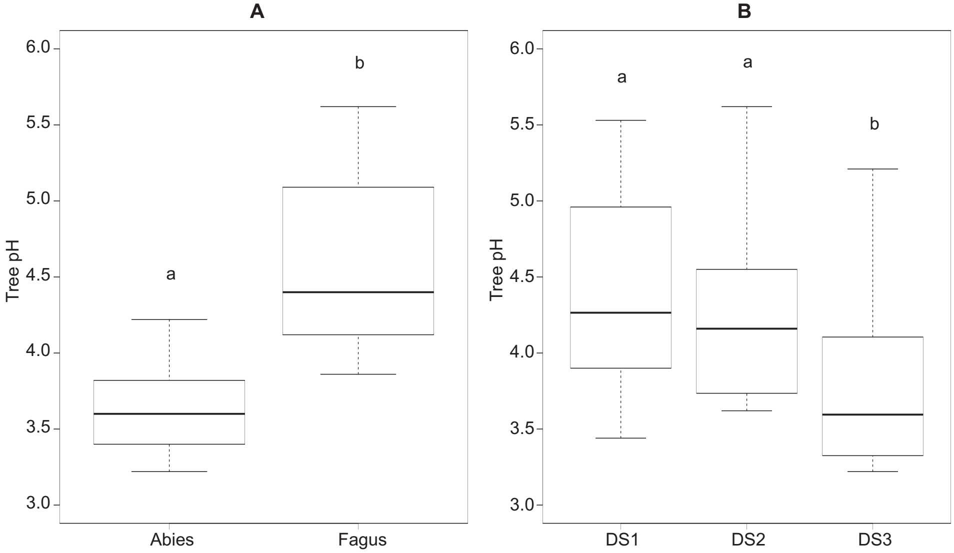

Fig 3. – The pH at the surfaces of logs of the two species of trees (A) at different stages of decay (B, see text for explanation). Significant differences are marked by different letters.

## Discussion

### *Bryophyte species richness associated with two species of trees and their stage of decay*

In terms of the questions addressed by hypotheses (i)–(ii), we found that species richness recorded on the two trees was similar and highest species richness was recorded on trees at the intermediate stage of decay. At the stand level the species richness associated with *Fagus* was higher than that associated with *Abies* (statistically not tested), but at the log level it was the same on the two trees. Both at the stand- and log levels, the highest species richness was associated with DS2. The higher species richness at the stand level recorded for *Fagus* could be due to the higher diversity of epiphytes recorded on *Fagus* during its early stages of decay, which increases the total number of species recorded on this species of tree. These species are mostly mosses, which is confirmed by the separate analyses of the two groups. Generally epiphytic species are much more common on deciduous trees. This is in part due to the more favourable structure and higher pH of their bark (Löbel et al. 2006, Mežaka et al. 2012) and more open canopy of *Fagus*, which results in there being more light for epiphytic species (Király & Ódor 2010, Király et al. 2013). At the log level there is no difference, with a similar general diversity recorded on *Abies* and *Fagus* logs. It means, that the heterogeneity in the surface structure of *Fagus* logs is greater than that of *Abies*. This is associated with a higher species diversity on *Fagus* during its early stages of decay, when the surface structure of the logs is heterogeneous and provides more microhabitats than that of *Abies*. Higher diversity of liverworts on *Abies* is due to the presence of epixylic specialists, which occur mostly on coniferous trees. At the transitional phase in the decay succession, DS2, when species associated with all stages of decay overlap in occurrence, the overall number of species is relatively high (Söderström 1988, Crites & Dale 1998, Kruys et al. 1999, Heilmann-Clausen et al. 2005). In the case of liverworts as many species were recorded at DS3 as DS2. Epixylic specialists are still present at these two stages of the decay process (Söderström 1988, Jansová & Soldán 2006, Ódor et al. 2006).

### *Species composition of the bryophytes associated with the two species of trees and the different stages in their decay*

Hypotheses (iii) to (v) were all supported. The species composition differed significantly on the two trees and different stages of decay, with the difference associated with the two trees greater than that associated with the different stages of decay, with epiphytic and opportunistic species characteristically associated with *Fagus* and epixylics, mainly liverworts, with *Abies*.

The results of many studies carried out in different parts of the temperate and boreal zone support the idea that stage of decay could be the main determinant of the succession in bryophyte species composition on decaying wood (McCullough 1948, Söderström 1988, Ódor & van Hees 2004, Kushnevskaya et al. 2007). However, on a continental scale the local effect of stage of decay is affected by regional factors (like climate and land-use history), which is not true for another well studied group, the saproxylic fungi (Heilmann-Clausen et al. 2014). While the effect of species of tree is widely accepted for epiphytes (Barkman 1958, Slack 1976, Smith 1982, Nascimbene et al. 2013), it is less well studied for epixylic bryophyte assemblages. Jansová & Soldán (2006) record a similar effect, the importance of the species of tree is greater for the epixylic bryophyte assemblage than the stage of decay in a beech-fir-spruce mixed forest. It is likely that the extremely high epixylic bryophyte diversity in the montane beech-fir forest zone is because these forests consist of a mixture of deciduous and coniferous trees unlike the temperate pure beech or boreal spruce forests in Europe. The occurrence of the different functional groups on the two species of trees studied is very different. On *Fagus* it is mostly epiphytes that colonize its bark during the decay process, or opportunistic species, which prefer moderately acid environments, of which dead wood is just one of the suitable substrates. In contrast, well-decayed logs of *Abies* usually provide a constantly humid substrate suitable for sensitive epixylic species (Lesica et al. 1991). Therefore species typically associated with *Abies* are mostly specialists, with a high representation of epixylic liverworts occurring on very acid and constantly moist substrates (based on their Ellenberg indicator values; Hill et al. 2007). *Fagus*, on the other hand, is very often decomposed by *Pyrenomycetes*, which 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 and therefore should be given special attention in future research (Ódor & van Hees 2004). The occurrence of the species is limited both by the acidity and the water holding capacity of the substrate, which mainly depends on the stage of decay of the log.

The species composition associated with DS1 and DS2 does not differ very much as it overlaps to a great extent. At the beginning and in the middle stages of decay the suitability of the substrate for bryophytes is similar as there are at least remnants of bark, the wood is still quite hard and therefore it is not wet enough for epixylic specialists. Mainly epiphytic and opportunistic species are associated with DS1 and DS2. In the later stages of decay the wood of at least *Abies* is softer, no longer covered with bark, usually always wet and provides a stable microclimate for sensitive epixylic liverworts.

### *Changes in pH and bryophyte communities recorded during the decay of dead wood*

Both hypotheses (vi) and (vii) were supported; the pH recorded for *Fagus* was higher than that for *Abies* and decreased during decay. It is well established that the pH of the bark of deciduous trees is higher than that of coniferous trees (Barkman 1958) and that this is associated with differences in the epiphytic communities recorded on these trees (Löbel et al. 2006, Hauck 2011). Other studies also support hypothesis (vii), that the pH of decaying wood decreases during decay, but in the last stages of decay can increase again due to nutrient and humus accumulation (Harmon et al. 1986). Higher variance in the values for *Fagus* is because there was a greater decrease in pH during decay and 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 records 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.

At the beginning there was a big difference between the two trees, therefore the variance in the pH values recorded at DS1 is very large. During decay the acidity of the surface of the logs decreased and at the end of the decay process (DS3) the pH of both types of substrate was relatively low and significantly different from that recorded at previous stages of decay. Generally, the chemical and physical changes in the wood and the long time it takes a log to decay provide suitable conditions for epixylic specialists (Crites & Dale 1998).

This observation supports our interpretation of the differences in species richness and composition associated with the two trees and their stage of decay. But it is likely, that pH is only one of the many potentially limiting factors determining the succession of bryophytes during decay. However, results of practically all of the studies on the composition of bryophyte communities on different trees at different stages of decay are similar. In addition, the spores of epixylic specialists germinate at a lower pH than those of epiphytic bryophytes and pH is more limiting for germination under dry than wet conditions (Wiklund & 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 with a single species of tree but there are definitely differences between the bryophyte communities on deciduous and coniferous trees. Many studies have emphasized the importance of tree species diversity in determining the diversity of epiphytic bryophytes (Király & Ódor 2010, Ellis 2012, Mežaka et al. 2012, Király et al. 2013), but it is also true for the assemblages of bryophytes growing on the surface of decaying logs. Not only the diversity, but also the continuity of the substrate is important (Söderström 1988, Löbel et al. 2006, Ellis 2012). Only permanently available abundance of well-decayed logs of large diameter provide suitable conditions for organism with a stepping-stone life strategy (Glime 2014).

Not just the conservation of natural forests is needed but also the improvement of the connectivity between them. One of the policies of forest management is to increase the amount of dead wood in managed forests and so provide sufficient suitable substrates for saproxylic and epixylic species. This can be achieved by nature-based forest management with a continuous forest cover, providing an uneven-aged forest structure, mixed stands and mainly natural regeneration, which results in an abundance of standing and lying dead wood and large old trees that are suitable habitats for sensitive species (Franklin et al. 2002, Gamborg & Larsen 2003, Larsen & Nielsen 2007, Burger 2009, Brunet et al. 2010).

See www.preslia.cz for Electronic Appendices 1–2

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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 jedlobukového 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, heterogenita mechorostů na kmenech buků je tudíž 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 jedlobučin je tedy důležité zachování smíšených porostů a stálá přítomnost mrtvého dřeva v různých stádiích rozkladu.

## References

Barkman J. J. (1958): Phytosociology and ecology of cryptogamic epiphytes. – Van Gorcum, Assen.

Bates J. W. (2009): Mineral nutrition and substratum ecology. – In: Goffinet B. & Shaw A. J. E. (eds), Bryophyte biology, p. 248–311, Cambridge University Press, Cambridge.

Bates J. W. & Brown D. H. (1981): Epiphyte differentiation between *Quercus patraea* and *Fraxinus excelsior* trees in a maritime area of southwest England. – Vegetatio 48: 61–70.

Borcard D., Gillet F. & Legendre P. (2011): Numerical ecology with R. – Springer-Verlag, New York.

Brunet J., Fritz Ö. & Richnau G. (2010): Biodiversity in European beech forests: a review with recommendations for sustainable forest management. – Ecol. Bull. 53: 77–94.

Burger J. A. (2009): Management effects on growth, production and sustainability of managed forest ecosystems: past trends and future directions. – For. Ecol. Manage. 258: 2335–2346.

Christensen M., Hahn K., Mountford E. P., Ódor P., Standovár T., Rozenbergar D., Diaci J., Wijdeven S., Meyer P., Winter S. & Vrška T. (2005): Dead wood in European beech (*Fagus sylvatica*) forest reserves. – For. Ecol. Manage. 210: 267–282.

Crites S. & Dale M. R. T. (1998): Diversity and abundance of bryophytes, lichens, and fungi in relation to woody substrate and successional stage in aspen mixedwood boreal forests. – Can. J. Bot. 76: 641–651.

Driessen P., Deckers J. & Nachtergaele F. (2001): Lecture notes on the major soils of the world. – World Soil Resour. Rep. 94: 1–334.

Dufrene M. & Legendre P. (1997): Species assemblages and indicator species: the need for a flexible asymmetrical approach. – Ecol. Monogr. 67: 345–366.

Ellis C. J. (2012): Lichen epiphyte diversity: a species, community and trait-based review. – Persp. Plant Ecol. Evol. Syst. 14: 131–152.

Faraway J. J. (2005): Linear models with R. – Chapmann & Hall, London.

Faraway J. J. (2006): Extending the linear model with R. – Chapmann & Hall, London.

Franklin J. F., Spies T. A, van Pelt R., Carey A. B., Thornburgh D. A, Berg D. R., Lindenmayer D. B., Harmon M. E., Keeton W. S., Shaw D. C., Bible K. & Chen J. (2002): Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. – For. Ecol. Manage. 155: 399–423.

Gamborg C. & Larsen J. B. (2003): "Back to nature" – a sustainable future for forestry? – For. Ecol. Manage. 179: 559–571.

Glime J. M. (2014): Adaptive strategies: travelling the distance to success. – In: Glime J. M. (ed.), Bryophyte ecology, Vol. 1. Physiological ecology, Chapter 4–8, Michigan Technological University and the International Association of Bryologists, URL: http://www.bryoecol.mtu.edu.

Goffinet B. & Shaw A. J. (2009): Bryophyte biology. – Cambridge University Press, Cambridge.

Grove S. J. (2002): Saproxylic insect ecology and the sustainable management of forests. – Annu. Rev. Ecol. Syst. 33: 1–23.

Harmon M. E., Franklin J. F., Swanson F. J., Sollins P., Gregory S. V., Lattin J. D., Anderson N. H., Cline S. P., Aumen N. G., Sedell J. R., Lienkaemper G. W., Cromack K. J. & Cummins K. W. (1986): Ecology of coarse woody debris in temperate ecosystems. – Adv. Ecol. Res. 15: 133–302.

Hauck M. (2011): Site factors controlling epiphytic lichen abundance in northern coniferous forests. – Flora 206: 81–90.

Heilmann-Clausen J., Aude E. & Christensen M. (2005): Cryptogam communities on decaying deciduous wood: does tree species diversity matter? – Biodiv. Cons. 14: 2061–2078.

Heilmann-Clausen J., Aude E., van Dort K., Christensen M., Piltaver A., Veerkamp M., Walleyn R., Siller I., Standovár T. & Odor P. (2014): Communities of wood-inhabiting bryophytes and fungi on dead beech logs in Europe: reflecting substrate quality or shaped by climate and forest conditions? – J. Biogeogr. 41: 2269–2282.

Hill M. O., Preston C. D., Bosanquet S. D. S. & Roy D. B. (2007): BRYOATT Atributes of British and Irish mosses, liverworts and hornworts. – Centre for Ecology and Hydrology, Huntingdon.

Jansová I. & Soldán Z. (2006): The habitat factors that affect the composition of bryophyte and lichen communities on fallen logs. – Preslia 78: 67–86.

Jonsson B. G., Kruys N. & Ranius T. (2005): Ecology of species living on dead wood: lessons for dead wood management. – Silva Fenn. 39: 289–309.

Király I., Nascimbene J., Tinya F. & Ódor P. (2013): Factors influencing epiphytic bryophyte and lichen species richness at different spatial scales in managed temperate forests. – Biodiv. Cons. 22: 209–223.

Király I. & Ódor P. (2010): The effect of stand structure and tree species composition on epiphytic bryophytes in mixed deciduous-coniferous forests of Western Hungary. – Biol. Cons. 143: 2063–2069.

Král K., McMahon S. M., Janík D., Adam D. & Vrška T. (2014a): Patch mosaic of developmental stages in central European natural forests along vegetation gradient. – For. Ecol. Manage. 330: 17–28.

Král K., Valtera M., Janík D., Šamonil P. & Vrška T. (2014b): Spatial variability of general stand characteristics in central European beech-dominated natural stands: effects of scale. – For. Ecol. Manage. 328: 353–364.

Kruys N., Fries C., Jonsson B. G., Lämas T. & Stahl G. (1999): Wood-inhabiting cryptogams on dead Norway spruce (*Picea abies*) trees in managed Swedish boreal forests. – Can. J. For. Res. 29: 178–186.

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.

Kushnevskaya H., Mirin D. & Shorohova E. (2007): Patterns of epixylic vegetation on spruce logs in late-successional boreal forests. – For. Ecol. Manage. 250: 25–33.

Larsen J. B. & Nielsen A. B. (2007): Nature-based forest management: where are we going? – For. Ecol. Manage. 238: 107–117.

Legendre P. & Legendre L. (1998): Numerical ecology. – Elsevier, Amsterdam.

Lepš J. & Šmilauer P. (2003): Multivariate analysis of ecological data using Canoco. – Cambridge University Press, Cambridge.

Lesica P., McCune B., Cooper S. V. & Hong W. S. (1991): Differences in lichen and bryophyte communities between old-growth and managed second-growth forests in the Swan Valley, Montana. – Can. J. Bot. 69: 1745–1755.

Lewis J. E. J. & Ellis C. J. (2010): Taxon compared with trait-based analysis of epiphytes, and the role of tree species and tree age in community composition. – Plant Ecol. Div. 3: 203–210.

Löbel S., Snäll T. & Rydin H. (2006): Species richness patterns and metapopulation processes: evidence from epiphyte communities in boreo-nemoral forests. – Ecography 29: 169–182.

Maser C. & Trappe J. (1984): Seen and unseen world of the fallen tree. – General Technical Report PNW-164, USDA Forest Service, Pacific Northwest Forest and Range Experiment Station.

McAlister S. (1997): Cryptogam communities on fallen logs in the Duke Forest, North Carolina. – J. Veg. Sci. 8: 115–124.

McCullough H. A. (1948): Plant succession on fallen logs in a virgin spruce-fir forest. – Ecology 29: 508–513.

Menčík E. (1979): Location of significant geological features, protected landscape areas and the scheme of regional-geological units. – Geologický a kartografický podnik, Praha.

Mežaka A., Brūmelis G. & Piterāns A. (2012): Tree and stand-scale factors affecting richness and composition of epiphytic bryophytes and lichens in deciduous woodland key habitats. – Biodiv. Cons. 21: 3221–3241.

Müller J., Hothorn T. & Pretzsch H. (2007): Long-term effects of logging intensity on structures, birds, saproxylic beetles and wood-inhabiting fungi in stands of European beech *Fagus sylvatica* L. – For. Ecol. Manage. 242: 297–305.

Nascimbene J., Thor G. & Nimis P. L. (2013): Effects of forest management on epiphytic lichens in temperate deciduous forests of Europe: a review. – For. Ecol. Manage. 298: 27– 38.

Ódor P., Heilmann-Clausen J., Christensen M., Aude E., van Dort K. W., Piltaver A., Siller I., Veerkamp M. T., Walleyn R., Standovár T., van Hees A. F. M., Kosec J., Matočec N., Kraigher H. & Grebenc T. (2006): Diversity of dead wood inhabiting fungi and bryophytes in semi-natural beech forests in Europe. – Biol. Cons. 131: 58–71.

Ódor P., van Dort K., Aude E., Heilmann-Clausen J. & Christensen M. (2005): Diversity and composition of dead wood inhabiting bryophyte communities in European beech forests. – Bol. Soc. Esp. Briol. 26–27: 85–102.

Ódor P. & van Hees A. F. M. (2004): Preferences of dead wood inhabiting bryophytes for decay stage, log size and habitat types in Hungarian beech forests. – J. Bryol. 26: 79–95.

Oksanen J., Blanchet F. G., Kindt R., Legendre P., Minchin P. R., O'Hara R. B., Simpson G. L., Solymos P., Stevens M. H. H. & Wagner H. (2013): vegan: community ecology package. R package version 2.0-10. – URL: http://CRAN.R-project.org/package=vegan.

Paillet Y., Berges L., Hjältén J., Ódor P., Avon C., Bernhardt-Römermann M., Bijlsma R.-J., de Bruyn L., Fuhr M., Grandin U., Kanka R., Lundin L., Luque S., Magura T., Matesanz S., Mészáros I., Sebastia M.-T., Schmidt W., Standovár T., Tóthmérész B., Uotila A., Valladares F., Vellak K. & Virtanen R. (2010): Biodiversity differences between managed and unmanaged forests: meta-analysis of species richness in Europe. – Cons. Biol. 24: 101–112.

Peres-Neto P. R., Legendre P., Dray S. & Borcard D. (2006): Variation partitioning of species data matrices: estimation and comparison of fractions. – Ecology 87: 2614–2625.

Podani J. (2000): Introduction to the exploration of multivariate biological data. – Backhuys Publishers, Leiden.

R Core Team (2013): R: A language and environment for statistical computing. – R Foundation for Statistical Computing, Vienna, Austria. URL: http://www.R-project.org.

Roberts D. W. (2012): labdsv: Ordination and multivariate analysis for ecology. R package version 1.5–0. – URL: http://CRAN.R–project.org/package=labdsv.

Šamonil P. & Vrška T. (2007): Trends and cyclical changes in natural fir-beech forests at the north-western edge of the Carpathians. – Folia Geobot. 42: 337–361.

Samuelsson J., Gustafsson L. & Ingelog T. (1994): Dying and dead trees: a review of their importance for biodiversity. – Swedish Threatened Species Unit, Uppsala.

Schmitt C. K. & Slack N. G. (1990): Host specificity of epiphytic lichens and bryophytes: a comparison of the Adirondack Mountains (New York) and the Southern Blue Ridge Mountains (North Carolina). – Bryologist 93: 257–274.

Siitonen J. (2001): Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. – Ecol. Bull. 49: 11–41.

Slack N. G. (1976): Host specificity of bryophytic epiphytes in eastern north America. – J. Hattori Bot. Lab. 41: 107–132.

Smith A. J. E. (1982): Epiphytes and epiliths. – In: Smith A. J. E. (ed.), Bryophyte ecology, p. 191–227, Champman & Hall, London.

Söderström L. (1988): Sequence of bryophytes and lichens in relation to substrate variables of decaying coniferous wood in Northern Sweden. – Nord. J. Bot. 8: 89–97.

Stokland J. N., Siitonen J. & Jonsson B. G. (2012): Biodiversity in dead wood. – Cambridge University Press, Cambridge.

Tolasz R., Míková T., Valeriánová A. & Voženílek V. (eds) (2007): Atlas podnebí Česka [Climate atlas of Czechia]. – Český hydrometeorologický ústav Praha a Univerzita Palackého v Olomouci, Olomouc.

Wiklund K. & Rydin H. (2004): Ecophysiological constraints on spore establishment in bryophytes. – Funct. Ecol. 18: 907–913.

Zar J. H. (1999): Biostatistical analysis, Ed. 4. – Prentice Hall, New Jersey.

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