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31

32 **Abstract**

33 Aim: Dead wood inhabiting bryophyte communities are formed by several important factors. Besides  
34 the amount, quality and continuity of the substrate, there are also external factors indirectly  
35 influencing their structure. One of the most important is local microclimate. This fact has been  
36 recognized by many previous authors, yet studies exploring the direct effect of the microclimate on  
37 epixylic bryophytes are still sparse. Based on directly measured values of local temperature, air  
38 humidity and canopy openness, we explored the associations between microclimate and epixylic  
39 bryophyte communities.

40 Location: Old-growth mixed *Fagus sylvatica-Abies alba* montane forest in the Czech Republic (West  
41 Carpathians).

42 Methods: The associations between microclimate and bryophyte communities were studied on 61  
43 large logs of *Abies alba* in advanced decay stage. Air temperature and humidity was measured in three  
44 periods of the year 2017, canopy openness was measured in leafless and leaf-on periods. Water  
45 potential ( $\Psi$ ) values were calculated from the data. The importance of the seasons was compared, the  
46 effect of microclimate variables on the species composition of logs was explored by canonical  
47 correspondence analysis. The effect on total cover and species richness was analyzed by linear models.

48 Results: Our analysis revealed a clear relationship between the communities and the microclimatic  
49 gradient. The most important factors for bryophyte composition were the spring and summer water  
50 potential and canopy openness in the leaf-on period. Total species richness and cover increased with  
51 increasing water potential (relatively cool and humid conditions). Also, the appearance of sensitive  
52 epixylic specialists (mainly liverworts) was positively correlated with these microclimatic conditions.  
53 On the other hand, species more tolerant to desiccation preferred logs with a drier and warmer  
54 microclimate.

55 Conclusions: Comparing logs with similar physical properties but different microclimates, we  
56 confirmed that epixylic bryophyte communities are significantly associated to microclimatic conditions  
57 in natural temperate forest.

58 **Keywords:** Bryophytes, Canopy openness, Central Europe, Dead wood, Microclimate, Natural forest,  
59 Temperature

60

## 61 **Introduction**

62 Dead wood is an essential element for the maintenance of forest biodiversity, 30-40% of the forest  
63 dwelling species are related to this special substrate in temperate and boreal zone, which has also a  
64 crucial role in nutrient and carbon cycling and forest site conditions (Stokland et al. 2012). While the  
65 most important agents of decomposition are the fungi and insects, many other organism groups use  
66 dead wood as a substrate, nesting or breeding site (plants, lichens, birds, bats) (Harmon et al. 1986).  
67 Many studies have demonstrated the importance of decaying wood as a key substrate for bryophyte  
68 diversity in forests (e.g. Berg et al. 2002; Hofmeister et al., 2015a; Söderström, 1993). Some properties  
69 of decaying wood have a major influence on the structure and quality of the bryophyte communities.  
70 In particular, the total amount, continuity, structural diversity (logs, branches, snags, stumps) of dead  
71 wood, as well as the presence of all decay stages are crucial for the continuous occurrence of  
72 bryophytes with specific habitat requirements (Kruys et al. 1999; Mills and Macdonald 2004; Ódor and  
73 van Hees 2004). Different combinations of these factors create a wide spectrum of microhabitats that  
74 can be colonized.

75 The size of the dead woody material is also a determining factor of epixylic bryophyte diversity (Ódor  
76 et al. 2006). Larger pieces tend to decay longer and give species with dispersal limitations a better  
77 chance to colonize them. They usually consist of a mosaic of different decay stages, and their  
78 heterogeneous surface can host many species with different ecological demands. Because of their size,  
79 they are also prevented from being overgrown by forest floor generalists and vascular plants (Ódor  
80 and van Hees 2004; Jansová and Soldán, 2006) or buried by litter from forest canopy (Muhle and  
81 LeBlanc 1975).

82 Another factor directly determining bryophyte community structure is tree species composition. In the  
83 temperate forest zone, there is a major difference between bryophyte species colonizing deciduous  
84 and coniferous trees. Tree species vary in physical, chemical and structural properties of their wood  
85 and bark and consequently in the decomposability of the substrate (Weedon et al. 2009; Shorohova et

86 al. 2016). Epixylic communities respond to differences in the pH of the substrates, water content and  
87 decay type of the wood, which are strongly modified by the tree species-specific decomposers  
88 represented mostly by saproxylic fungi (Heilmann-Clausen et al. 2005; Freschet et al. 2012; Fukasawa  
89 et al. 2015). Therefore, the mutual presence of both deciduous and coniferous species increases the  
90 total bryophyte species richness (Táborská et al. 2015).

91 In addition to the direct influence of dead wood and its quality, there are also external factors shaping  
92 bryophyte communities. Continuity, land-use history and naturalness of the forest stands considerably  
93 determine the local species pool of bryophyte assemblages (Ódor et al. 2006). Many recent studies  
94 have focused on comparisons of natural and managed forest stands, and have found that species  
95 richness and the quality of the community both increase with decreasing human influence, not only in  
96 the present but also in the past (Söderström 1988; Ódor and Standovár 2001; Brunet et al. 2010;  
97 Hofmeister et al. 2015b; Táborská et al. 2017). In particular, rare and endangered species are  
98 dependent on the continuous presence of sufficient amounts and quality of dead wood, which is very  
99 often completely missing in managed forests. There is also a known relationship between bryophyte  
100 species richness and regional climatic factors on a larger geographical scale. Heilmann-Clausen et al.  
101 (2014) showed that site and landscape filters such as forest naturalness and climate are more  
102 important drivers than local filters, represented mostly by available decay stages, on a gradient from  
103 Central to Western Europe.

104 Furthermore, microclimate has repeatedly been pronounced as an important factor driving growth,  
105 survival and reproductive success and consequently the total species richness of a site and the local  
106 distribution of species in a forest (e.g. Ódor et al. 2013; Zellweger et al. 2019). It is usually described as  
107 a combination of temperature and air humidity (Haughian and Frego 2017a). In the forest, these two  
108 aspects are influenced by different factors on many levels. Generally, microclimate is largely defined  
109 by the regional climate of the area (Geiger et al. 1995; Chen et al. 1999). However, forest site and stand  
110 structural characteristics considerably modify the regional climate creating specific below canopy

111 microclimates (Kovács et al. 2017). The main drivers significantly influencing bryophyte communities  
112 in the forest are the topography as elevation, slope and aspect (Holland and Steyn 1975; Åström et al.  
113 2007; Oldén et al. 2019), the microtopography of the site (Beatty 1984; Ulanova 2000), local water  
114 regime (Hylander et al. 2002; Stewart and Mallik 2006; Staniaszek-Kik et al. 2016) and canopy openness  
115 (Tinya et al. 2009; Haughian and Frego 2017b)

116 From the site characteristics, forest canopy is a key driver determining ground microclimate.  
117 Bryophytes, as poikilohydric organisms, are especially sensitive to moisture and air humidity (Proctor  
118 2009). Different species have different water management strategies, with some being desiccation  
119 tolerant, and others rather dependent on a stable water supply. Many epixylic specialists belong to the  
120 latter category, creating humidity-sensitive, tiny, single-layer mats on the wood surface. Their  
121 occurrence is therefore bound to stable moisture conditions (Söderström 1988; Jansová and Soldán  
122 2006). A closed canopy buffers extremes of maximum temperature and vapor pressure deficit on the  
123 forest floor (Kovács et al. 2017; Davis et al. 2019), creating optimal environment for this sensitive  
124 species. On the contrary, some species favors spots under sparser canopy with easier access of rainfall  
125 and light (Haughian and Frego 2017b; Górski et al. 2019).

126 In the temperate forest zone, microclimate changes significantly during the season and so do the  
127 dynamics of the bryophyte growth. Generally, authors agree that the most important period for annual  
128 growth is autumn (Tamm 1953; Pitkin 1975), though others report the highest growth rates in late  
129 winter and early spring (Jansová 2006; Rincon and Grime 2009). In the temperate zone – and especially  
130 in mountainous regions – both these periods are characterized by very stable low temperatures and  
131 high atmospheric humidity associated with frequent precipitation, which is crucial for poikilohydric  
132 bryophytes.

133 In the past, many authors presumed that due to their high water holding capacity, the logs themselves  
134 strongly modify their surface microclimate by providing more water to the epixylic flora living on its  
135 surface (Rambo and Muir 1998; Botting and DeLong 2009; Stokland et al. 2012). However recent

136 studies from Haughian and Frego (2017a; 2017b) showed that in logs, water is not likely to be supplied  
137 to the surface from their internal parts and there might be other physical and biological factors shaping  
138 bryophyte assemblages which have not been described yet.

139 With developing technical possibilities, studies of the forest microclimate and its dynamics begin to  
140 emerge (Wild et al. 2019). Besides general studies mostly related to stand structure (Frey et al. 2016;  
141 Kovács et al. 2017; Ehbrecht et al. 2017) and forest management (Chen and Franklin 1997; Ma et al.  
142 2010; Kovács et al. 2020), there also several studies focusing on the effect of microclimate on forest-  
143 dwelling organisms in their natural habitats, such as decaying wood. In the past, substitute variables  
144 have usually been used, such as macroclimatic variables (Raabe et al. 2010), elevation (Spitale 2016),  
145 aspect (Dahlberg et al. 2014), and estimates of moisture (Chmura et al. 2018). Currently more and  
146 more studies present the directly measured microclimatic data. The authors mostly define  
147 microclimatic conditions based on temperature and air humidity measured on the surface or in the  
148 sub-surface of the logs. These methods have been used to answer various questions involving a  
149 diversity of colonizing species of bryophytes and fungi (Király et al. 2013; Dahlberg et al. 2014; Pouska  
150 et al. 2016), bryophyte growth (Haughian and Frego 2017b) or factors determining the occurrence of  
151 rare species (Górski et al. 2019).

152 With this study we would like to contribute to the topic and explore the epixylic bryophyte  
153 assemblages association with a microclimatic gradient on a local scale in a mixed *Fagus sylvatica-Abies*  
154 *alba* natural forest in the Czech Republic. We address the following questions:

155 (i) What are the seasonal differences in microclimate, and which periods are most important  
156 in terms of the regulation of bryophyte communities?

157 (ii) What are the shape and direction of the relationships between microclimate and the  
158 assemblage or single species? Do epixylic specialists more strongly associate with more  
159 humid microclimates?

160 (iii) What is the relationship between total species richness, cover and microclimate?



## 161 **Material and methods**

### 162 *Study area*

163 The study was conducted in the national nature forest reserve Salajka in the Moravskoslezské Beskydy  
164 Mts. in the Czech Republic (49.401°N, 18.418°E). The total area of the forest reserve is 21.86 ha, where  
165 elevation ranges from 715 to 820 m above sea level. The forest is dominated by European beech (*Fagus*  
166 *sylvatica* L., 67.6% of standing volume) and silver fir (*Abies alba* Mill., 22.8% of standing volume); the  
167 two most common admixing tree species are Norway spruce (*Picea abies* (L.) Karst., 8.6% of standing  
168 volume) and sycamore maple (*Acer pseudoplatanus* L., 1% of standing volume) (Král et al. 2014a). The  
169 forest has an old-growth structure characterized by veteran trees, regeneration in gaps and a fine-  
170 scale mosaic of patches of various forest developmental stages (Král et al. 2014b). The amount of the  
171 dead wood is high (110 m<sup>3</sup>/ha), representing 21% of the living standing volume. In contrast to the  
172 standing trees, the dead wood is dominated by silver fir (63.3% of the total dead wood volume),  
173 followed by European beech (29.5% of the total dead wood volume) and Norway spruce (6.5% of the  
174 total dead wood volume) (Král et al. 2014a). The site is under protection and has been unmanaged  
175 since 1937.

176 This site was chosen for a microclimatic study because of its topography: the forest stand occurs on  
177 two opposite-facing slopes, one facing south-east and the other facing north-east (Fig. 1). We  
178 supposed that the heterogeneous topography of the area provides that the studied logs are  
179 characterized by different microclimate. The bedrock in the area is flysch rock of the Solan system  
180 made up of sandstone, clay stone and argillaceous shale layers (Menčík 1979), the soil is silt-loam,  
181 loam and clay-loam Haplic Cambisols (Driessen et al. 2001). The area has a temperate montane  
182 climate, with a mean annual temperature of 6.2 °C and annual precipitation of 1142 mm (CHMI 2016).

### 183 *Study design and data collection*

184 This study focused on the direct effects of microclimate on bryophyte communities on dead wood. To  
185 eliminate the effects of log-related variables like tree species, decay stage and dead wood volume, logs

186 with similar characteristics were selected. For the pre-selection of appropriate logs, a stem database  
187 of the Salajka reserve was used. This database has been periodically updated since 1974, with repeated  
188 mapping and measurements taking place over the years 1974, 1994, 2007 and 2014 (Přívětivý et al.  
189 2016). The database contains, among others, information about the tree species, live status, diameter  
190 at breast height (DBH) and also the decay stage of the dead trees (Král et al. 2014a). All information is  
191 also processed in the form of a stem position map. Only logs of silver fir with diameter 60–90 cm in an  
192 advanced decay stage were selected. This was defined as being in an advanced stage of wood rot, with  
193 bark missing, soft wood, the log often broken, the outline deformed and the log partly sunk in the soil  
194 (decay stage 4 and 5 according to Ódor and van Hees 2004). The reason for this selection of logs was  
195 their high availability at the site, and the presence of epixylic specialists that were the subject of  
196 interest and that are significantly less frequently present on the dead wood of deciduous species  
197 (Táborská et al. 2015). On each log, a 5 m long segment measured from the stem base was examined  
198 for bryophytes during one survey in the vegetation period of 2017. The presence of species and their  
199 percentage cover were recorded, but the uprooted parts of the logs were not included in the sampling.  
200 Species were identified in the field or transported to the laboratory for microscopic identification.  
201 Voucher specimens of all the species are deposited in the herbarium of the first author. The  
202 nomenclature follows Kučera et al. (2012). Microclimate was measured in three periods through the  
203 year of 2017, each lasting minimum 8 days. The first period was in spring from 29 March to 7 April,  
204 then in summer from 8 August to 15 August, and in autumn, from 11 November to 22 November  
205 (hereafter seasons). 62 MCC USB-502 combined air temperature and humidity loggers (Measurement  
206 Computing Corp., Norton, MA, Appendix S1, Fig. 1a) were used for temporally synchronized  
207 microclimate measurements, recording air temperature and relative humidity at every five minutes.  
208 All loggers were covered by passively ventilated plastic shields to prevent the sensors from direct solar  
209 radiation (Appendix S1, Fig. 1b, c). They were temporarily installed on the sides of the logs (average  
210 distance of the sensors from log surface was 8 cm), in the middle of the sampled segment and at the  
211 height of the half of the log's diameter (Appendix S1, Fig. 1d.). A reference logger in each sampling

212 period was installed nearby in the forest reserve but independently from the surveyed logs (Fig. 1.).  
213 Using the measurements of this unit, relative values were calculated: reference values were subtracted  
214 from every logged record. These relative values were positive if the logged records were higher than  
215 the reference and negative if they were lower. These derived differences were used for the further  
216 analyses to minimize the effects of larger-scale weather patterns and diurnal fluctuations. Besides  
217 temperature and relative humidity, indirect light measurements estimating the canopy openness (CO;  
218 proportion) were performed using type-A spherical densiometer two times in 2017, next to the loggers  
219 (Lemmon 1957). We characterized the light regime of the leafless and leaf-on periods by this method  
220 on the last days of microclimate campaigns in spring (before bud break) and in summer. For the light  
221 estimations, a third measurement in autumn was not necessary since hypothetically the results are  
222 the same as in spring.

### 223 *Data analysis*

224 The 474 912 temperature and relative humidity data pairs were first screened for obvious inaccuracies  
225 and missing values. Due to measurement errors of the microclimate loggers, three logs were excluded  
226 from further analyses. In autumn 10 logs were excluded from the analysis because of technical failures  
227 of the microclimate loggers. Therefore, 58 logs were analyzed in spring and summer, whereas 48 logs  
228 were analyzed in fall. Water potential ( $\Psi$ ; Pa; Eq.1) was also computed based on the measured air  
229 temperature (T; °C) and relative humidity (RH; %) data since it is a useful variable for the  
230 characterization of the desiccation power of air on cryptogams (Jonsson et al. 2008; Proctor 2009;  
231 Haughian and Frego 2017a). Water potential varies between  $-\infty$  and 0, with 0 indicating complete  
232 saturation, lower (more negative) values mean higher desiccation power of the air.

$$233 \quad \Psi = \frac{8.3144 \times (T + 273.15)}{18.021 \times 10^{-6}} \times \ln(RH) \quad (\text{Eq.1}),$$

234 in that  $\Psi$  is the water potential, T is air temperature in °C and RH is relative air humidity in %.

235 For water potential the relative values ( $\Delta\Psi$ , compared to reference logger) were also computed.

236 Descriptive statistics were calculated for the original values of the measured microclimate variables (T,

237 RH,  $\Psi$  and CO). For each log the mean values of the studied variables were calculated for the three  
238 seasons separately. Because of the obvious differences between the seasonal means of the original  
239 values, differences between the seasonal means were not tested statistically. However, we compared  
240 the spatial (i.e. among log) variances of the microclimate variables of the different seasons by pairwise  
241 F variance tests with Bonferroni-Holm corrections (Holm 1979).

242 The relationship between microclimate variables and bryophyte species composition was explored by  
243 canonical correspondence analysis (CCA, Borcard et al. 2011). Only species with 3 and more  
244 occurrences were included into analysis. Log-level means of relative water potential ( $\Delta\Psi$ ) values in  
245 spring, summer and autumn, as well as canopy openness values of leafless and leaf-on periods were  
246 used as explanatory variables. The cover values of the species were *ln*-transformed before the analysis.  
247 Separate CCA's were performed for every potential microclimate variable, and their explained variance  
248 was tested by Monte-Carlo simulations (Borcard et al. 2011). A final CCA model was created from the  
249 explanatory variables using a forward selection approach, the explained variance of the axes was  
250 tested by Monte-Carlo simulations, and the first axis (CCA1) of this final model was used as a  
251 generalized microclimate variable (Borcard et al. 2011). The distribution of species along CCA1 was  
252 described by descriptive statistics. The individual cover response of the species (with frequency higher  
253 than 4, 6.9%) on CCA1 was evaluated by non-parametric LOESS smoothing on the observed data (Zuur  
254 et al. 2009). The effect of CCA1 on total cover and species richness was analyzed by linear models. For  
255 cover, square root transformation was used before the analysis.

256 All analyses were performed in the R.3.6.1 statistical environment (R Core Team 2019); for CCA the  
257 package "vegan" (Oksanen et al. 2017) was used.

## 258 **Results**

### 259 *Effect of microclimate on bryophytes*

260 Altogether we sampled 61 logs and found 42 species of bryophytes, of which 20 were liverworts and  
261 22 mosses (Appendix 1, Table 1). The most common species were *Dicranodontium denudatum*,

262 *Tetraphis pellucida*, *Herzogiella seligeri*, *Lepidozia reptans* and *Dicranum scoparium*. Three Red-Listed  
263 species for the Czech Republic (Kučera et al. 2012) have been recorded (*Harpanthus scutatus*,  
264 *Callicladium haldanianum* and *Syzygiella autumnalis*) and three species are classified as Lower Risk-  
265 Near Threatened (*Calypogeia suecica*, *Cephalozia catenulata* and *Liochlaena lanceolata*) (Kučera et al.  
266 2012). The maximum number of the species recorded on one log was 18, the minimum 5 and the  
267 average was 12.6 species per log. The mean air temperature values were 8.6 °C in spring, 18.2 °C in  
268 summer and 0.1 °C in autumn (Fig. 2a), the relative humidity was 77% in spring, 79% in summer and  
269 99% in autumn (Fig. 2b). Following these differences, the water potential of the air was lower in spring  
270 and summer (-37.9 and -34.1 MPa, respectively) than in autumn (-2.3 MPa, Fig2c). The mean canopy  
271 openness was 46.5% in leafless and 14.9% in leaf-on period. Because of the obvious climate differences  
272 among the seasons these mean values were not tested statistically. The variance of the air temperature  
273 among the logs was the highest in spring, intermediate in summer and lowest in autumn (Fig. 2a,  
274 Appendix S1, Table 2). The variance of air-humidity was higher in spring and summer than in autumn  
275 (Fig. 2b, Appendix S1, Table 2). Similarly to the temperature, the variance of water potential was the  
276 highest in spring, intermediate in summer and the lowest in autumn (Fig. 2c, Appendix S1, Table 2).  
277 The variance of canopy openness was similar in the leafless and leaf-on periods (Fig. 2d, Appendix S1,  
278 Table 2).

279 Based on the partial CCA's of bryophyte assemblages, both the water potential in spring and summer  
280 and canopy openness in the leaf-on period were significant drivers (8.14%, 6.54% and 3.69% of  
281 explained total variance, respectively, Table 1). The effect of water potential in autumn and canopy  
282 openness in the leafless period were not significant (Table 1). The final CCA model containing the  
283 significant variables explained 13.34% of the total variance ( $F_{(3,54)} = 2.7705$ ;  $P < 0.001$ ; Fig. 3).

284 The first canonical axis (CCA1; 8.76% of the total variance) displayed a water potential gradient with  
285 drier conditions on the negative side of the gradient and more cool and humid environment on the  
286 positive end. Canopy openness correlated more with the second axis (3.24% of variance explained)

287 and indicated a light gradient. Based on the CCA, species showed a clear separation along the water  
288 potential gradient (Fig. 3), which was strongly related to the individual response of the species (Fig. 4).  
289 On the positive side of the gradient, the cover of epixylic and humidity sensitive species exponentially  
290 (e.g. *Liochlaena lanceolata*, *Riccardia latifrons*, *Calypogeia suecica*, *Rhizomnium punctatum* and  
291 *Harpanthus scutatus*), or more or less linearly increased (*Cephalozia bicuspidata*, *Lepidozia reptans*).  
292 Most of these species are tiny liverworts creating smooth mats on the log surface. In the middle part  
293 of the gradient there were opportunistic species with unimodal response (*Dicranodontium*  
294 *denudatum*, *Tetraphis pellucida*) and species that did not respond to the microclimate gradient (e.g.  
295 *Cephalozia lunulifolia*, *Herzogiella seligeri*, *Dicranum scoparium*, *Chiloscyphus profundus*). This was a  
296 structurally heterogeneous groups including liverworts, acrocarpic and pleurocarpic mosses. The  
297 negative side of the gradient represented by drier and warmer microclimate was correlated with  
298 species with an exponentially decreasing response (*Hypnum andoi*, *Dicranum montanum*). These were  
299 pleurocarpic and acrocarpic mosses, which can occur not only on dead wood but often on the bark of  
300 standing trees as epiphytic species.

301 The effect of microclimate (CCA1 axis) on bryophyte cover and richness was also tested. Both variables  
302 correlated positively with the microclimate scores (Fig. 5., cover:  $R^2_{\text{adj}} = 0.16$ ,  $F_{(1,56)} = 12.123$ ,  $p = 0.0009$ ;  
303 species richness:  $R^2_{\text{adj}} = 0.25$ ,  $F_{(1,56)} = 19.97$ ,  $p < 0.0001$ ).

## 304 **Discussion**

### 305 *Seasonal changes in microclimatic gradient*

306 Seasonality in bryophyte growth rates has already been demonstrated by several studies (Stark 2002;  
307 Jansová and Soldán 2006). Although autumn, late winter and early spring are favorable for the  
308 bryophyte growth, spring and summer are the periods that may be more important in actually shaping  
309 the bryophyte assemblages. Our results show that the variance in measured microclimatic components  
310 during these two periods is much higher than in autumn. Mean water potential values are much lower  
311 in spring and summer, and this could be limiting for species growth or even survival. We can suppose,

312 that although autumn and early spring are the most active period for bryophyte growth, the species  
313 composition of the logs (the survival of species) is determined mainly by the humidity and temperature  
314 limited spring and summer periods.

#### 315 *Epixylic bryophyte response to microclimatic gradient*

316 Epixylic bryophyte communities significantly responded to the microclimatic gradient. The CCA  
317 explained 13.34% of the variance, which is a significant share. Although we selected only similar logs  
318 with well-defined features, in the reality the logs are a mosaic of different decay stages and their  
319 proportion could be heterogeneous. The bryophyte species are often related to special microsites as  
320 fissures, bark patches and wounds that can occur accidentally on the logs and could not be controlled  
321 by the study design.

322 As expected, total species richness and cover increased with positive CCA scores, which means that  
323 the higher diversity and cover of this community is related to more humid and cool microclimate within  
324 a stand (higher water potential of the air). In these conditions, bryophyte communities are enriched  
325 with desiccation-intolerant epixylic species, mainly with liverworts. This pattern confirms the findings  
326 of Haughian and Frego (2017a; 2017b), who stated that the water-holding capacity and microclimate  
327 buffering ability of the logs is limited and the occurrence of the sensitive species is mainly determined  
328 by microclimate *per se*. The similar fact has been demonstrated for fungi (Pouska et al. 2016) and  
329 lichens (Marini et al. 2011), where microclimate also can modify successional pathways in otherwise  
330 similar logs. We can suppose that this microclimatic effect is related to the topography (aspect, slope  
331 position etc.) of the site. Other studies using topography as explanatory variables found, that within a  
332 stand the cooler and more humid topographic conditions (northern slopes, ravines etc.) maintain more  
333 diverse epixylic bryophyte communities than more sun exposed or flat topographies (Ódor and van  
334 Hees 2004; Raabe et al. 2010). However, these conditions are not necessarily true for other saproxylic  
335 organisms, for example lichens and beetles are more related to more open and warm conditions  
336 (Hauck 2011; Király et al. 2013; Seibold et al. 2016).

337 The microclimate preference of bryophytes is clearly reflected in our analysis of the species  
338 composition. Species that are classified as epixylic specialists (according to Hill et al. 2007) and listed  
339 in the Czech Red List (Kučera et al. 2012) as threatened or near-threatened are all positively associated  
340 with relatively cool and humid microclimate. All these species (*Liochlaena lanceolata*, *Calypogeia*  
341 *suecica*, *Harpanthus scutatus*, *Syzygiella autumnalis* and *Cephalozia catenulata*) occur along the whole  
342 gradient, but their cover increases markedly with higher water potential values. Generally, these  
343 species are restricted to decaying wood in later decay stages, and in the Czech Republic mostly occur  
344 only in forests with old-growth structure and a long-term temporal continuity of dead wood.  
345 Therefore, the vulnerability of these species is connected to the decline of primary, old-growth forests  
346 in Europe (Berg et al. 2002; Ódor et al. 2006; Sabatini et al. 2018).

347 In addition to these red-listed species, mostly small liverworts (*Riccardia latifrons*, *Cephalozia*  
348 *bicuspidata*, *Lepidozia reptans*) and one rather hygrophilic moss (eg. *Rhizomnium punctatum*)  
349 responded positively to more humid and cool microclimate. Most of these prefer a moist environment  
350 but are not as sensitive to desiccation as specialized species, and some can also occur on other  
351 substrates (such as shaded rocks) in the forest.

352 Those species that did not respond to the microclimatic gradient (eg. *Dicranum scoparium*,  
353 *Chiloscyphus polyanthos*, *Tetraphis pellucida*, *Herzogiella seligeri*) were the dominant species of  
354 decayed logs independently of their topographic positions. The species negatively related to relatively  
355 humid and cool microclimatic conditions (*Hypnum andoi*, *Dicranum montanum*) can often occur on the  
356 bark of living trees. We can suppose that air humidity is not a limiting factor for these species in this  
357 forest site, and on dead wood they are just occupying niches that were not suitable for more  
358 demanding species. The response of *Nowellia curvifolia* was quite surprising, as this is generally  
359 considered as specialized epixylic species growing almost exclusively on the wood of conifers, often  
360 accompanied by rare epixylic species. Based on these results its higher frequency and cover on logs of  
361 managed forests can likely be explained by its higher tolerance for desiccation.



362 **Conclusions**

363 In this study, we confirmed the significant relationship between epixylic bryophyte communities and  
364 microclimatic conditions. We found that the periods with more dynamic heterogeneous climatic  
365 pattern, namely spring and summer, had stronger association with bryophyte communities, whereas  
366 stable climatic conditions in the autumn were not reflected in the microclimatic gradient. Comparing  
367 logs with similar physical properties but different microclimates of the immediate surroundings, we  
368 found out that the species richness of these communities as well as the total species cover increased  
369 with increasing water potential. The species had very different individual responses to the  
370 microclimatic gradient. Epixylic specialists and small liverworts with a smooth mat growth form  
371 occurred more frequently on the positive side of the gradient characterized by lower temperatures  
372 and higher humidity (higher water potential). On the other hand, more desiccation-tolerant species,  
373 which also often colonize the bark of living trees, dominated the negative side of the gradient, with a  
374 warmer and drier microclimate (lower water potential). The most common and dominant species of  
375 the community had a neutral response to microclimate. Our study emphasizes that the accumulation  
376 of dead wood in humid forest sites could be more effective for the maintenance of epixylic bryophyte  
377 communities than logs occurring in drier and warmer conditions in temperate and boreal forests.  
378 However, dead wood management should consider that other saproxylic organism groups (e.g.  
379 beetles, lichens) could have different microclimate requirements.

380

381

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387 **Authors' contributions**

388 MT and PÓ developed the research idea and methodology, all authors were involved in data collection  
389 and manuscript writing, which was led by MT; BK, MT and PÓ did the data analysis. MT and PÓ were  
390 responsible for bryophyte inventory, while BK and CN were responsible for microclimate  
391 measurements. All authors approved the final version of the manuscript and agreed to be accountable  
392 for the aspects of the work that they conducted.

393 **Data accessibility**

394 The data are accessible online on GitHub <https://doi.org/10.5281/zenodo.3899953>

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396 **Reference**

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629 **List of Appendices:**

630  
631 Appendix S1: Supplementary information about recorded species, seasonal variances of microclimatic  
632 variables and microclimate measurements.

633

634

635 **Tables**

636 Table 1. Results of the partial CCA analyses using the log-level means of relative water potential ( $\Delta\Psi$ ) and canopy  
637 openness (CO) values of the different seasons as explanatory variables.

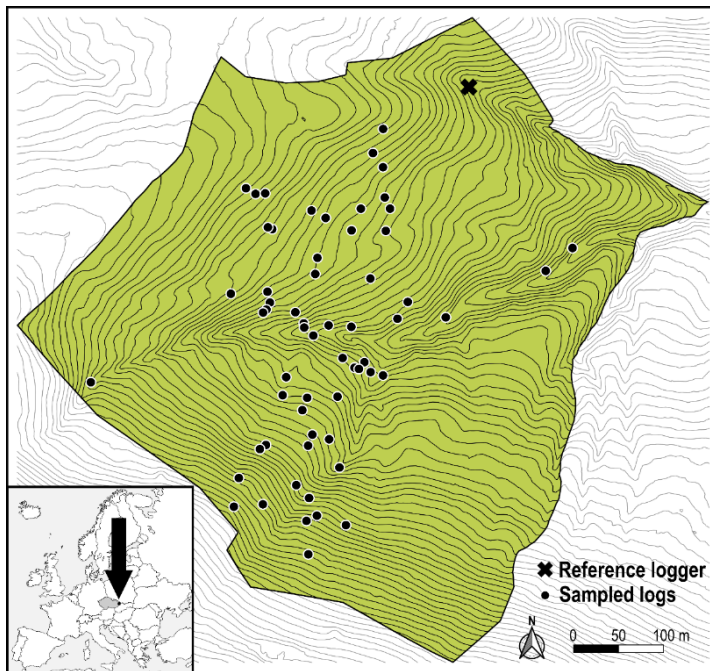
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Variable	F <sub>(1,56)</sub>	P	R <sup>2</sup> <sub>adj</sub>
$\Delta\Psi_{\text{mean spring}}$	4.965	< 0.001	0.0650
$\Delta\Psi_{\text{mean summer}}$	3.919	< 0.001	0.0486
$\Delta\Psi_{\text{mean autumn}}$	0.961	0.477	-0.0006
CO <sub>leafless</sub>	1.386	0.118	0.0069
CO <sub>leaf-on</sub>	2.146	0.017	0.0195

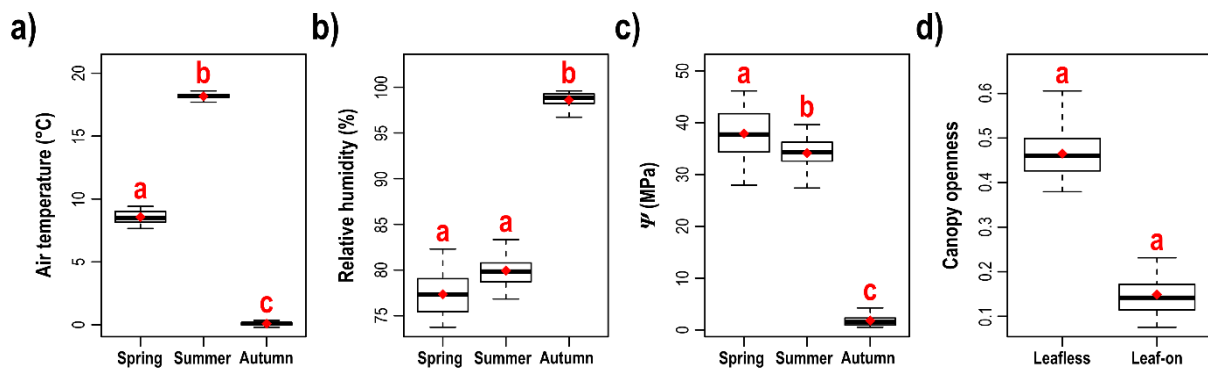
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641 **Figures**  
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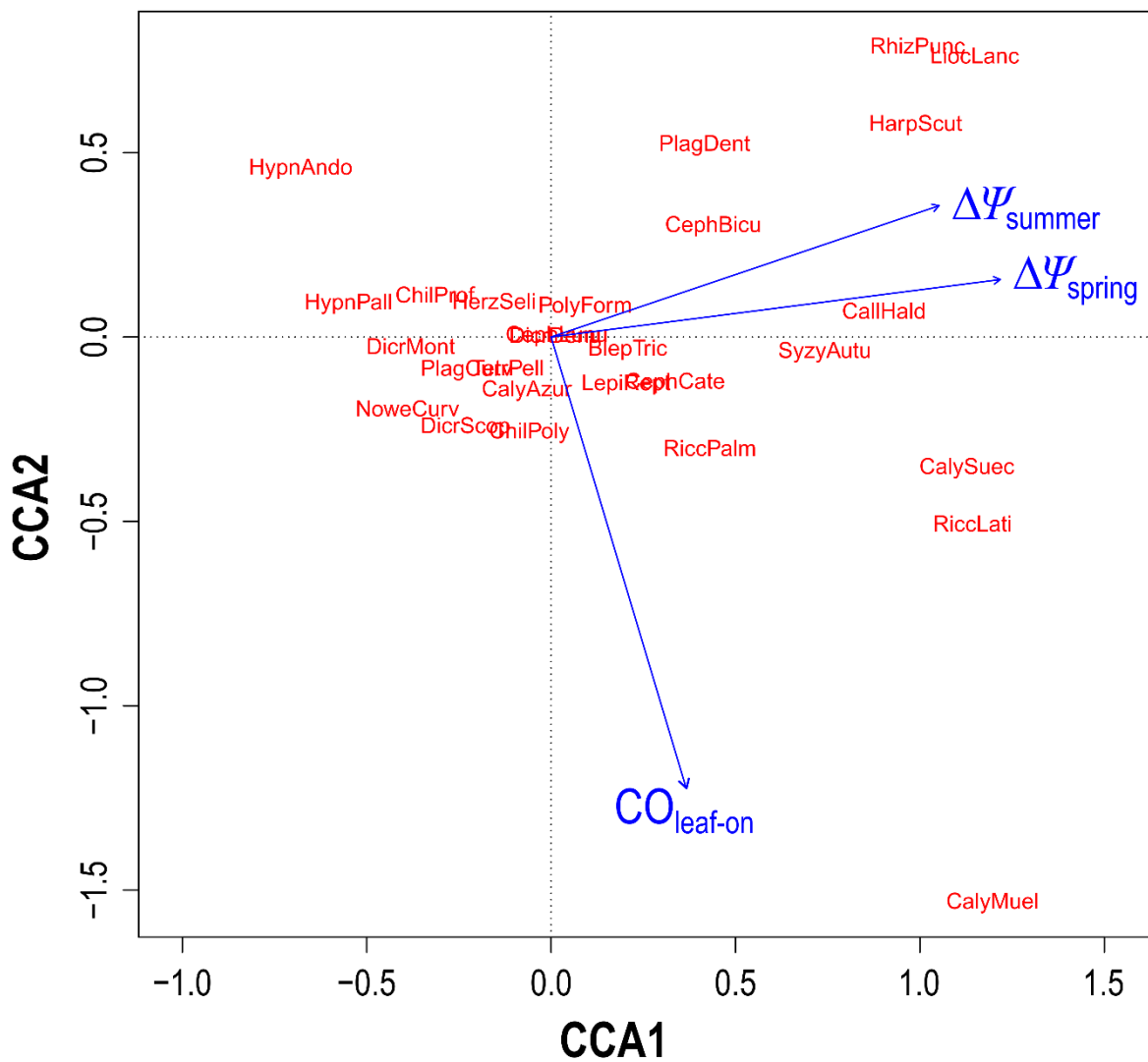


643  
 644  
 645 Fig. 1 Overview of the study site, Salajka forest reserve, Czech Republic (49.401°N, 18.418°E). The sampled logs  
 646 (dots) were distributed along a presumed, topography-driven microclimatic gradient. Reference logger (x-mark)  
 647 with synchronized sampling was applied for data consistency.



648  
 649  
 650 Fig. 2 Boxplots (median, interquartile range and range without outliers) of air temperature (a), relative humidity  
 651 (b), water potential (c) and canopy openness (d) values of the studied periods. The means are represented by  
 652 red dots. The letters indicate homogeneous subsets for the variables of the seasons, based on F-tests. For water  
 653 potential, the negative values were multiplied by -1, higher values mean higher desiccation power of the air.

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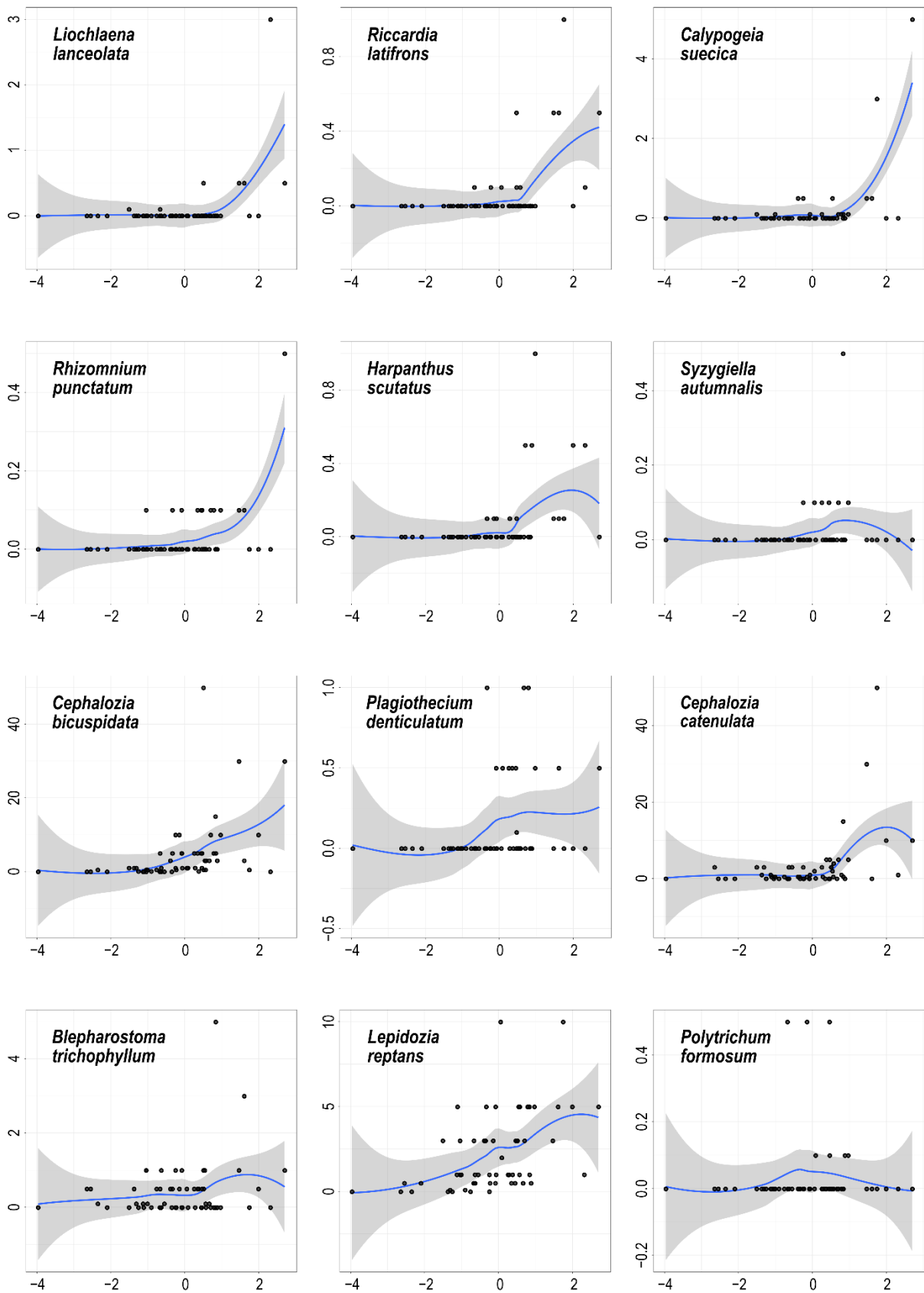
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658 Fig. 3 Species – environmental variables biplot of the canonical correspondence analysis using spring and summer

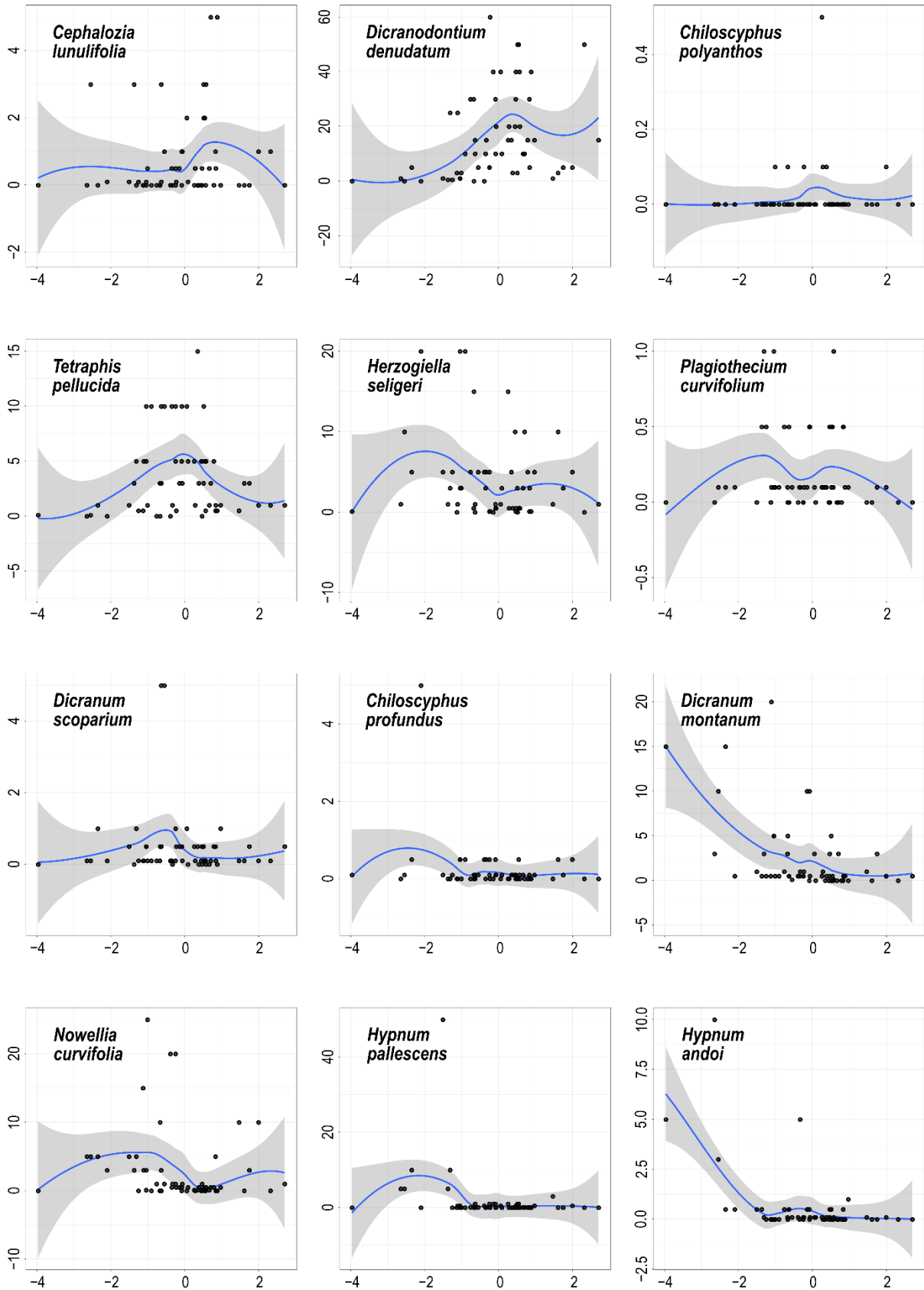
659 log-level means of relative water potential ( $\Delta\Psi$ ) and canopy openness of the fully-leaved period ( $CO_{\text{leaf-on}}$ ) as

660 explanatory variables. Species codes are explained in Appendix S1, Table 1.

661



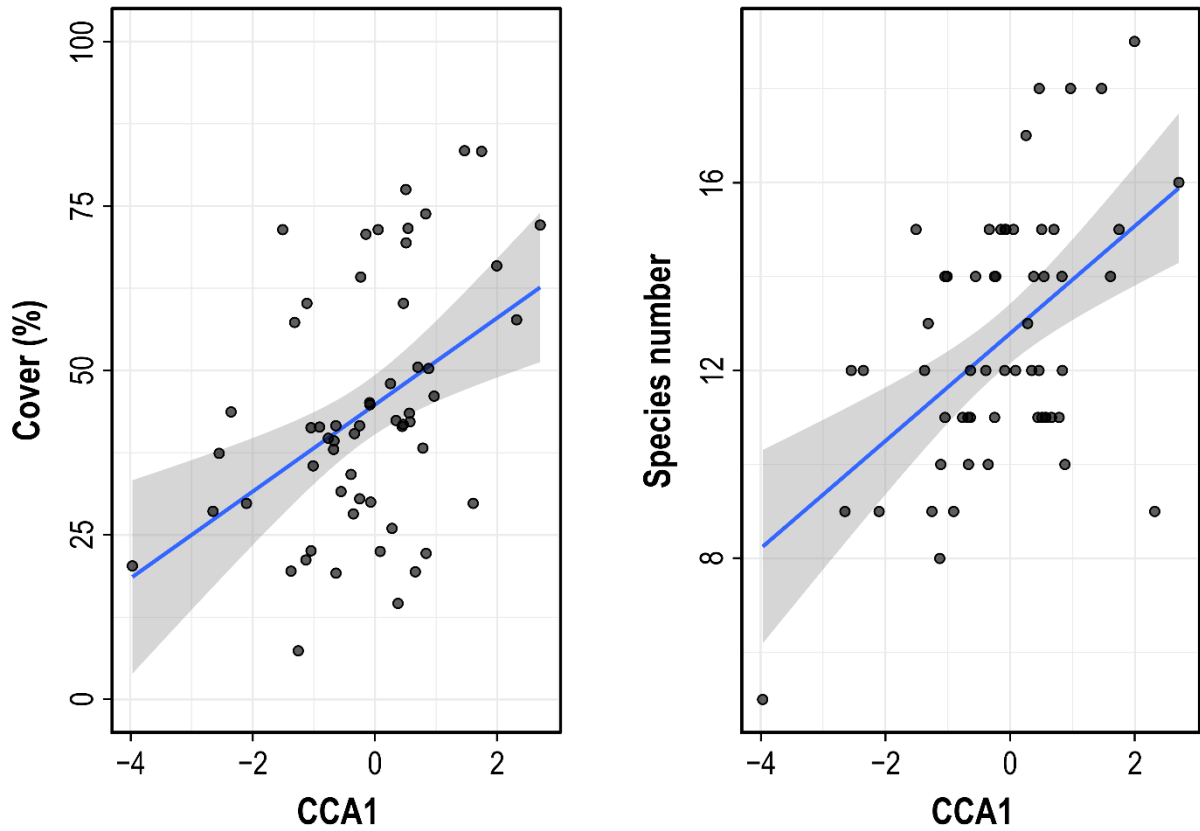




666 Fig. 4 LOESS-smoothed cover response of individual species along the microclimatic gradient represented by the  
667 first CCA axis scores for the studied logs. The order of the species is determined by their decreasing score along  
668 the first CCA axis. Only species with 5 and more occurrences are presented.

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673 Fig. 5 Relationship between the generalized microclimate variable (CCA1) and the total bryophyte cover and

674 species number. The positive side of CCA1 has higher humidity, lower temperature and higher water potential.

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