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8 **Title: Patterns and drivers of species composition of epiphytic bryophytes and lichens in
9 managed temperate forests**

10
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22
23 **Abstract:**

24 Epiphytic bryophytes and lichens are an important component of the endangered forest biota
25 in temperate forests, their diversity and composition patterns being regulated by tree, stand
26 and landscape scale factors. The aim of this study is to improve ecological understanding of
27 such factors in managed coniferous-deciduous mixed forests of Hungary in the context of
28 forest management. In particular, this study investigate the effect of tree species composition,
29 stand structure (tree size distribution, shrub layer, dead wood), microclimate (light,
30 temperature, air humidity), landscape and historical factors on the stand level and tree level
31 composition of epiphytic bryophytes and lichens. The relationships were explored by
32 multivariate methods (redundancy analysis, canonical correspondence analysis, variation
33 partitioning) and indicator species analysis. Tree species is among the most important driver
34 of species composition in both organism groups. For bryophytes, the continuity of forest

35 microclimate and the presence of shrub layer are also important, while lichen assemblages are
36 influenced by light availability. Landscape and historical variables were less influential than
37 stand scale factors. On the basis of our results, the main strategy of management focusing on
38 epiphyte diversity conservation should include: 1) the maintenance of tree species diversity in
39 mixed stands; 2) increasing the proportion of deciduous trees (mainly oaks and hornbeam); 3)
40 the maintenance of large trees within the stands; 4) the presence of shrub and regeneration
41 layer; 5) the creation of heterogeneous light conditions.

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45 Keywords: mosses, lichenized fungi, tree species composition, microclimate, light conditions

46

47 Abbreviations: CCA – canonical correspondence analysis; DBH – diameter at breast height;

48 DCA – detrended correspondence analysis; ISA – indicator species analysis; RDA –

49 redundancy analysis; SD – standard deviation.

50

51 **1. Introduction**

52

53 Epiphytic bryophytes and lichens comprise a considerable part of the forest biota in the
54 temperate and boreal zone (Barkman, 1958; Ellis, 2012; Smith, 1982). In moist boreal
55 coniferous forests they play an important role in ecosystem processes, influencing water
56 balance and nutrient accumulation (McCune, 1993; Pike, 1978; Pypker, et al. 2006a, 2006b).
57 In deciduous and mixed forests their biomass is smaller, but they largely contribute to forest
58 biodiversity (Coppins and Coppins, 2005; Slack, 1977).

59 Their diversity and composition patterns are regulated by tree, stand and landscape scale
60 factors (Barkman, 1958; Bartels and Chen, 2012; Ellis, 2012; Hauck, 2011; Marini et al.,
61 2011; Nascimbene et al., 2012). Many studies focused on tree level patterns have emphasized
62 that different tree species in the same locality maintain diverse epiphytic assemblages
63 (Mezaka et al., 2012; Slack, 1976; Szövényi et al., 2004) as an effect of different chemical-
64 physical features of the bark (Bates and Brown, 1981; Fritz and Heilmann-Clausen 2010;
65 Gustafsson and Eriksson, 1995). Tree size and age are also relevant determinants of epiphyte
66 diversity; larger and older trees maintain more diverse assemblages than younger ones, with
67 many associated species (Fritz et al., 2008a; Lie et al., 2009; Nascimbene et al., 2009a). This
68 phenomenon has a complex explanation: big trees provide larger colonization surface (area
69 effect), and old trees ensure longer time for the establishment and growth of local populations,
70 also providing higher microhabitat diversity. On a tree, a clear vertical zonation of epiphytes
71 is observed, which appears in the vertical distribution of different growth forms, and
72 functional traits (Fritz, 2009; McCune, 1993). This is influenced mainly by microclimatic
73 factors as light availability and air humidity (Hosokawa and Odani, 1957; Peck et al., 1995).
74 At the stand scale, the importance of tree species diversity in driving epiphytic assemblages
75 reflects the host preferences of many epiphytes (Mezaka et al., 2012; Palmer, 1986).

76 However, at this spatial scale also microclimatic factors (light, air humidity, temperature), and
77 structural elements modifying microclimate (canopy openness, shrub layer, vertical structure
78 of the canopy) are very influential for epiphytes (Király et al., 2013; Song et al., 2012).

79 Moreover, old-growth unmanaged stands maintain more diverse epiphytic communities than
80 managed forests (Lesica et al., 1991), providing higher microhabitat and substrate diversity
81 (e.g. higher tree species richness, tree size heterogeneity and presence of veteran trees,
82 quantity and quality of dead wood). The continuity of the forest stands and the available
83 substrates is determinant for many dispersal limited species (Fritz et al., 2008b; Rose, 1992).

84 At the landscape scale, many epiphytic species are regulated by metapopulation dynamics
85 (Johansson et al., 2012; Löbel et al. 2006; Snäll et al. 2003). The mortality of the local
86 populations is regulated mainly by deterministic factors, as the cessation of the host trees,
87 while the colonization of new areas is influenced by stochastic factors (Löbel et al., 2006;
88 Roberge et al., 2011). The landscape scale distribution of many epiphyte species is limited by
89 their dispersal ability, especially for asexual species with high substrate specificity (Johansson
90 et al., 2012; Löbel and Rydin, 2009), particularly where potential microhabitats have very
91 isolated distributions across the landscape. These species are very sensitive to past and recent
92 habitat fragmentation, and the longevity of the available substrates (Snäll et al., 2004).
93 Tree, stand and landscape scale factors are considerably modified by human activities which
94 have made cryptogamic epiphytes a threatened group in temperate forests (Paillet et al. 2010).
95 Supported by historical and archeobotanical evidences, 30-80% of these species disappeared
96 from the Atlantic region of Europe before the 18th century (Rose, 1992; Ellis et al., 2011).
97 Recent land use, especially forest management (including timber production and conservation
98 purposes), has considerable influence on survival and local population size of these organisms
99 (Nascimbene et al., 2013a). For this reason, it is necessary to explore the most important
100 regulating factors acting at different spatial scales across regions. While the effect of host
101 species is relatively widely studied for epiphytes there is a lack of information concerning the
102 effect microclimate and stand structure that in our study are accounted for with a set of
103 directly measured variables. The separation of stand level and tree level composition and the
104 comparison of the effects of environmental constraints between epiphytic bryophytes and
105 lichens are also novel to this study.

106 This study aimed to investigate the effect of potentially relevant factors in determining the
107 bryophyte and lichen diversity of coniferous-deciduous mixed forests in Hungary. In
108 particular, it will explore the effect of tree species composition, stand structure (tree size
109 distribution, shrub layer, dead wood), microclimate (light, temperature, air humidity), and
110 landscape and historical factors on the stand level composition of epiphytic bryophytes and
111 lichens. A similar analysis was also conducted at the tree level, assessing the effect of tree
112 species, tree size and light conditions on epiphytic assemblages on individual trees.
113 Preferences of individual epiphyte species to different tree species were also tested. This
114 study is closely related to Király et al. (2013), which investigated species richness patterns of
115 epiphytes utilising the same dataset.

116

117 **2. Material and methods**

118

119 2.1. Study area

120

121 The study area is located in Őrség National Park (N 46°51'-55' and W 16°07'-23'), West
122 Hungary (Fig. 1). The elevation is 250-350 m, the mean annual temperature is 9.0–9.5 °C and
123 the precipitation is 700-800 mm (Dövényi, 2010). The bedrock consists of alluviated gravel
124 and loess, the most common soil types are pseudogleyic and lessivage brown forest soils,
125 which are nutrient poor and slightly acidic (pH of the 0-30 cm layer is 4.0-4.8, Bidló pers.
126 comm.).

127 The study area is dominated by beech (*Fagus sylvatica* L.), sessile and pedunculate oak
128 (*Quercus petraea* L. and *Q. robur* L.), hornbeam (*Carpinus betulus* L.), Scots pine (*Pinus*
129 *sylvestris* L.) and Norway spruce (*Picea abies* (L.) Karst.), forming monodominant and mixed
130 stands as well. The proportion of different subordinate tree species (*Betula pendula* Roth.,
131 *Populus tremula* L., *Castanea sativa* Mill., *Prunus avium* L., etc.) is relatively high (Tímár et
132 al., 2002). The main forest habitat types of the region are sessile oak-hornbeam woodlands
133 (Hungarian habitat code: K2), acidofrequent beech woodlands (Hungarian habitat code: K7a),
134 and acidofrequent mixed coniferous forests (Hungarian habitat code: N13) (Bölöni et al.,
135 2008).

136 Most of the original forests of the region were cut in the middle ages and in the regrown
137 secondary forest the proportion of pioneer tree species (such as *Pinus sylvestris* and *Betula*
138 *pendula*) and the cover of acidofrequent herbs, bryophytes and lichens increased (Gyöngyössi
139 2008, Tímár et al. 2002). Today, the mixed forests with natural tree species composition are
140 increasingly managed harmonizing timber production and conservation purposes. In private
141 forests, stem selection is applied by local farmers without real management planning, while
142 state forests are managed by shelterwood silvicultural systems with a rotation period of 70–
143 110 years (Tímár et al., 2002).

144

145 2.2. Data collection

146

147 Thirty-five 2-10 ha sized stands were selected by stratified random sampling from the
148 database of the Hungarian National Forest Service (Fig. 1). In all studied stands the age of the
149 dominant trees was between 70 and 110 years. The topography was more or less flat and the
150 top-soil was not influenced by ground-water. The forest stand compartments of the database
151 were grouped according to tree species combination types and the studied plots (5-10 per

152 type) were randomly selected within the groups. In this way the sample represented the main
153 tree species combinations of the region, including a continuous gradient in the proportion of
154 the main tree species. The distance between selected stands was a minimum of 500 m.
155 Within each stand, a 40 m x 40 m plot was established for stand structure measurements. For
156 each tree with DBH larger than 5 cm geographical position, circumference, species identity,
157 height, height of crown base, and crown projection were recorded. Average diameter and
158 length of logs thicker than 5 cm diameter and longer than 0.5 m were also recorded as well as
159 density of sapling species (tree or shrub individuals taller than 0.5 m and thinner than 5 cm
160 DBH). Relative light conditions (percentage of above canopy total light) were modelled by
161 the tRAYci model (Brunner, 1998) using the position, size and canopy data of the trees (see
162 details in Tinya et al., 2009). For stand level conditions, light values were predicted in 36
163 systematically arranged points at 1.3 m height using a grid of 5 m intervals. For tree level
164 analyses, relative light values were predicted in the position of each individual tree. Air
165 humidity and temperature were measured in the middle of the plots at 1.3 m height using
166 Voltcraft DL-120 TH data loggers in 24 hours measurements with 5 minutes recording
167 frequency. The measurements of all plots were carried out within a five days period. During
168 this period two reference plots were measured permanently. Eight temperature and air
169 humidity measurements were carried out during three vegetation periods (2009 June, October;
170 2010 June, August, September, October; 2011 March, May). Geographical position of the
171 plots was given in meters based on the Hungarian Geographical Projection (EOV).
172 Landscape variables including proportion of forests (stand age older than 20 yr), clearcuts
173 (stand age younger than 20 yr) and non-forested areas (settlements, meadows, arable lands)
174 were estimated around the plots within a circle of 300 m radius, using maps and data of the
175 Hungarian National Forest Service. Data on management history were generated based on the
176 map of the Second Military Survey of the Habsburg Empire from 1853 (Arcanum, 2006). The
177 existence of forest in the plots (as a presence/absence variable) was recorded and the
178 proportion of forested area in the historical landscape (in the circle of 300 m radius) was
179 calculated.

180 Epiphytic bryophytes and lichens were recorded in 30 m x 30 m plots positioned in the middle
181 of the 40 m x 40 m plots. The absolute cover of bryophyte and lichen species (in dm²) was
182 estimated on every living tree with minimum 20 cm DBH, surveying the whole trunk from the
183 base to 1.5 m height. Nomenclature of bryophytes followed Hill et al. (2006) and Grolle and
184 Long (2000), while ecological requirements follow Király et al.(2013). For bryophytes,
185 specialist and facultative epiphytes were separated, species belonging to the first group occur

186 exclusively on bark in the region, while facultative epiphytes can also live on soil or decayed
187 wood; the categorisation of each species is included in Király et al. (2013). Nomenclature and
188 ecological information on lichens are based on Nimis and Martellos (2008).

189

190 2.3. Data analysis

191

192 The relationships between species composition of the two epiphyte groups and environmental
193 variables were explored by ordination techniques both at stand and tree level. For both taxon
194 groups, principal component analysis and Detrended Correspondence Analysis (DCA) were
195 used as indirect preliminary analysis. At stand level, the DCA revealed relatively short
196 gradient lengths along the ordination axes for both organism groups (1.7-2.4 SD units), which
197 presume a linear response between species and explanatory variables (ter Braak and Smilauer,
198 2002). Therefore, the relationships between species composition and environmental variables
199 were further explored by variation partitioning (Peres-Neto et al. 2006) and Redundancy
200 Analysis (RDA, Leps and Smilauer, 2003; Podani, 2000). At tree level, the gradient length of
201 the DCA axes were longer (5.2-7.4 SD units) presuming a unimodal species-environmental
202 gradient response (ter Braak and Smilauer, 2002). For this reason, Canonical Correspondence
203 Analysis (CCA) was used as direct ordination techniques. At tree level, the association of
204 epiphytic species to tree species were evaluated by Indicator Species Analysis (ISA, Dufrene
205 and Legendre, 1997; Legendre and Legendre, 1998). In all cases, bryophytes and lichens were
206 analysed separately. In stand level ordinations, the performance of each epiphyte species was
207 expressed as total cover (in dm^2) within each plot. Cover values were ln transformed before
208 the analysis and species occurring in less than four plots were excluded.

209 The measured and derived explanatory variables used for RDA are listed in Table 1. The
210 proportion of tree species (beech, hornbeam, oak, Scots pine, Norway spruce, subordinate
211 trees) was expressed based on their volumes. Volume of trees was calculated by species
212 specific equations from DBH and tree height (Sopp and Kolozs, 2000). *Quercus petraea*, *Q.*
213 *robur* and *Q. cerris* L. were merged as oaks, rare tree species were merged as subordinate
214 trees. Tree species diversity was expressed by Shannon index with natural logarithm based on
215 the relative volume of species (Shannon and Weaver, 1949). The Shannon index with natural
216 logarithm was also used for the expression of landscape diversity using the relative cover of
217 the landscape elements. Stand level light conditions were expressed as the mean and standard
218 deviation of relative light using 36 measurements. Since these two variables were strongly
219 correlated, a linear regression was performed between standard deviation as dependent and

220 mean values as explanatory variable. The residuals of standard deviation were then used as
221 independent descriptor of light heterogeneity. For air humidity and temperature, differences
222 were calculated from the two reference plots. Relative daily mean and range values were
223 expressed for both variables and averaged over the eight measurements.

224 For fulfilling normality conditions, some explanatory variables (proportion of tree species,
225 light variables) were ln transformed before the analyses. All variables were standardized (zero
226 mean, one standard deviation). Variation partitioning was carried out to explore the amount of
227 variance in the species assemblages accounted for by the main groups of explanatory
228 variables (Leps and Smilauer 2003, Peres-Neto et al. 2006). The studied groups of
229 explanatory variables were tree species composition, stand structure, microclimate (including
230 light conditions) and landscape-historical variables (Table 1). For the final RDA model
231 individual explanatory variables were used (Table 1). The significant explanatory variables
232 were selected by manual forward selection. Before the statistical selection, collinearity
233 between the explanatory variables was checked by pairwise correlations. Strongly correlated
234 variables ($r > 0.6$) were excluded from the selection. The effect of explanatory variables was
235 tested by F-statistics via Monte-Carlo simulation with 499 permutations. The accepted
236 significance level was 0.05 (Leps and Smilauer, 2003; ter Braak and Smilauer, 2002). The
237 significance of the first and all canonical axes was tested in a similar way. Because the
238 longitude geographical position had a significant effect in the RDA of lichens it was used in
239 the final model as covariable.

240 For tree level ordinations, species occurring on less than 5 trees and trees bearing less than 3
241 epiphytic species were eliminated from the analysis. Tree level cover values of the epiphytic
242 species were ln transformed before the analysis. In CCA, the explanatory variables included
243 were tree species identity, DBH and light conditions. Tree species identity was used as a
244 factor (beech, hornbeam, oak, pine and subordinate species) and plot identity was treated as
245 covariable. The effects of the explanatory variables, as well as the effect of the canonical axes
246 (first and all axes) were tested with the same method used for stand level analysis. The
247 permutations were restricted to the blocks of the covariable (plots). In all direct ordinations,
248 the scaling of biplots was focused on species correlations (Leps and Smilauer, 2003; ter Braak
249 and Smilauer, 2003).

250 For ISA, the preference of each epiphytic species to tree species was analysed separately
251 considering only species occurring on minimum 10 trees. Trees without epiphytes were
252 included in this analysis, considering beech, hornbeam, oak, and pine. The indicator values of

253 the epiphytic species were tested via Monte-Carlo simulation using 1000 permutations. The
254 accepted significance level was lower than 0.01.
255 Multivariate analyses were carried out with Canoco for Windows 4.5 (ter Braak and Smilauer,
256 2002), the ISA was performed in R 2.14.0 environment (The R Development Core Team,
257 2011) using the labdsv package (Roberts, 2012), for variation partitioning the vegan package
258 were used (Oksanen et al., 2011).

259

260 **3. Results**

261

262 *3.1. Descriptive statistics*

263

264 60 bryophyte and 44 lichen species were recorded in 35 plots on 971 trees (225 beeches, 344
265 pines, 324 oaks, 56 hornbeams, and 22 subordinate trees). For bryophytes the mean stand
266 level species richness was 14.0 ± 5.0 (SD, standard deviation), the range was 5-27, while for
267 lichens the mean was 9.8 ± 3.7 (SD), the range was 3-20. Mean tree level species richness was
268 2.9 ± 2.1 (SD) for bryophytes and 2.2 ± 1.5 (SD) for lichens. Details of species richness patterns
269 can be found in Király et al. (2013). In the stand level ordinations, 27 bryophytes and 26
270 lichens were included. In the tree level ordinations, 27 species and 492 trees were included for
271 bryophytes and 30 species and 349 trees for lichens. For ISA, 22 bryophytes and 22 lichens
272 occurring on 949 trees were considered. The species and their authorities, their stand level
273 frequencies, abbreviations and inclusions in different analyses are listed in the Appendix.

274

275 *3.2. Stand level species composition*

276 For bryophytes, variables related to tree species composition and stand structure explained the
277 largest part of the species variance, while for lichens tree species composition and
278 microclimate were the most important (Fig. 2). The effect of landscape-historical variables
279 was less influential for both organism groups than stand level explanatory variables.

280 After forward selection, six explanatory variables were significant in the RDA model of
281 bryophytes, oak proportion being the most important and only one variable was related to
282 landscape (Table 2). The first two canonical axes of the RDA explained 30.3% of the species
283 variance, both the first and all canonical axes were significant ($F=7.12$, $P<0.002$ and $F=3.65$,
284 $P<0.002$, respectively). The first RDA axis (explained variance 20.3%) expressed a tree
285 species composition gradient (pine-oak), but tree size and forest cover also influence it (Fig.
286 3). The second RDA axis (explained variance 10.1%) was mainly a shrub layer – forest

287 microclimate gradient. The most common epiphytic species (*Hypnum cupressiforme*,
288 *Platygyrium repens*, *Isothecium alopecuroides*, *Radula complanata*, *Frullania dilatata*) were
289 related to oak. Beside their oak preference, some specialist epiphytic species (*Metzgeria*
290 *furcata*, *Ulota crispa*, *Homalia trichomanoides*) were also related to larger trees. Species
291 enhanced by shrub layer, and cooler microclimate were facultative epiphytes (*Polytrichastrum*
292 *formosum*, *Dicranum scoparium*, *Pleurozium schreberi*, *Plagiothecium laetum*,
293 *Brachytheciastrum velutinum*, *Plagiomnium affine*), mainly occurring on the bottom of the
294 trunks. These species can establish also on soil and dead wood. Most epiphytic bryophytes
295 avoided pine dominated stands, exceptions were the epixylic *Lophocolea heterophylla* and
296 *Dicranella heteromalla* living mainly on bare soil.

297 For lichens, five significant explanatory variables were included in the RDA model, from
298 which light was the most important, and three variables represented tree species composition
299 (Table 2). Landscape-historical variables were not selected for the model. The first two
300 canonical axes of the RDA explained 51.9% of the species variance, both the first and all
301 canonical axes were significant ($F=12.71$, $P<0.002$ and $F=8.00$, $P<0.002$, respectively). The
302 first RDA axis was positively correlated with mean relative light and oak proportion and
303 negatively correlated with basal area and hornbeam proportion (Fig. 4). The second RDA axis
304 represented a pine proportion gradient. Species associated with pine (e.g. *Dimerella pineti*,
305 *Chaenotheca ferruginea*, *Hypocenomyce scalaris*) were acidophytic lichens which typically
306 establish on the bark of conifers. Species associated with hornbeam and positively correlated
307 with basal area (e.g. *Graphis scripta*, *Lecanora expallens*) are typical of sub-acidic smooth
308 barked trees, mostly in deciduous forests. *Pertusaria amara* has a wide ecological range and it
309 often behaves as an aggressive competitor, being able to overgrow other crustose lichens and
310 even bryophytes. *Phlyctis argena*, which was abundant on hornbeam, beech and oak is an
311 aggressive colonizer with optimum in deciduous forests.

312 The other species associated to oak were mainly large-lobed foliose lichens (e.g. *Parmelia*
313 *sulcata*, *Flavoparmelia caperata*) with a relatively wide ecological range, preferring open
314 forest sites.

315

316 3.3. Tree level species composition

317

318 The canonical axes of bryophyte CCA explained 8.15% of the species variance (6.2% for the
319 first two axes) and both the first and all canonical axes were significant ($F=18.97$, $P<0.002$
320 and $F=6.69$, $P<0.002$, respectively). All the explanatory variables were significant, but host

321 tree species was the most important, while the effects of DBH and light were less influential
322 (Table 3). The first CCA axis represented an oak-pine gradient (Fig. 5), similarly to stand
323 level results. Very few species preferred pine (positive side of the first axis), most of them
324 were terricolous bryophytes. Only the epiphytic-epixylic species *Lophocolea heterophylla*
325 occurred often on pine. The weft and mat forming pleurocarpic species preferred oak. Some
326 of them were specialists (e.g. *Homalia trichomanoides*, *Isothecium alopecuroides*), but most
327 of them were facultative epiphytes, like *Brachythecium* and *Plagiothecium* species. The
328 second CCA axis was associated with beech and hornbeam. Some small cushion-forming
329 specialists (*Orthotrichum* species, *Ulota crispa*) preferred the smooth bark of these trees.
330 These bryophytes were less related to large trees than pleurocarpic mosses preferring oak. The
331 ISA corroborated the associations found by CCA (Table 4). Many species were significantly
332 associated with oak, most of them were pleurocarpic, weft-forming bryophyte, but some
333 liverworts (*Metzgeria furcata*, *Radula complanata*) also occurred among them. Cushion-
334 forming *Orthotrichum* species and *Plagiothecium denticulatum* var. *undulatum* were
335 associated with beech. The only species related to pine was *Lophocolea heterophylla*.
336 For lichens, the canonical CCA axes explained 13.6% of the species variance (10.8% the first
337 two axes). Similarly to bryophytes, the most important factors for lichens were related to host
338 tree species (Table 3). The first CCA axis mainly represented a pine-oak gradient (Fig. 6).
339 Species associated with pine were typical and common acidofrequent lichens mainly
340 occurring on conifers (*Hypocenomyce scalaris*, *Hypogymnia physodes*). The most typical
341 species on oak were parmelioid sub-acidofrequent lichens such as *Flavoparmelia caperata*
342 and *Parmelia sulcata*, but also *Cladonia coniocraea* was frequent, mainly at the base of the
343 trunks. This oak-related assemblage was potentially noteworthy for conservation since it is
344 locally enriched by sensitive and rare species as *Cetrelia olivetorum* or *Parmotrema perlatum*.
345 The second CCA axis was positively related to hornbeam and negatively to DBH and light
346 conditions. Hornbeam mainly hosted crustose species that usually establish on smooth bark in
347 relatively shaded conditions such in the case of *Graphis scripta*, *Plyctis argena*, and *Pyrenula*
348 *nitida*. The results of ISA confirmed those of CCA (Table 5). Hornbeam had the highest
349 number of associated species. Although hornbeam had a similar smooth bark as beech, beech
350 had much less associated species (only *Lecanora expallens*). Species related to oak and pine
351 are the same of those highlighted in the CCA section above.

352

353 **4. Discussion**

354

355 In our managed forests, tree species composition, stand structure, and microclimate
356 influenced species composition of both epiphytic bryophytes and lichens. Their patterns are
357 mainly driven by similar factors. However, some differences were found that should be
358 accounted for in management practices to enhance the conservation of these important groups.

359

360 4.1. Tree species

361

362 Tree species was the most important factor driving the composition of both epiphyte groups.
363 In general, this study supports results of other stand scale studies indicating that epiphytic
364 diversity is closely related to tree species richness, especially in mixed coniferous-deciduous
365 forests, because of the different epiphytic assemblages hosted by different tree species (Berg
366 et al., 2002; McGee and Kimmerer, 2002; Mezaka et al., 2012; Nascimbene et al., 2009b;
367 Schmitt and Slack, 1990). Only at higher spatial scales this effect is likely to be overridden by
368 factors operating at regional scale such in the case of climate, air condition, and landscape
369 types (Bates et al., 1997, 2004; Frisvoll and Presto, 1997; Marini et al., 2011).

370 Many epiphytic bryophytes, mainly weft-forming mosses and mat-forming liverworts, are
371 related to oaks as well as lichen assemblages dominated by large foliose species that are
372 enhanced by the wrinkle rich bark of this tree providing a humid microhabitat. In these
373 favourable conditions large epiphytes outcompete smaller species, occupying the available
374 surface. On smooth barked trees, epiphytes are likely to experience more stressful conditions
375 (e.g. more exposed to desiccation). Species associated with these trees have more stress-
376 tolerant and pioneer traits. However, these species can be also replaced by weft-forming large
377 species along with tree aging (Boudreault et al., 2000, Cobb et al. 2001, Sillett et al. 2000).
378 Bryophytes and lichens have contrasting species richness pattern on these trees. Bryophyte
379 assemblages are species poor both on beech and hornbeam, including only a few cushion-
380 forming specialists (e.g. *Orthotrichum spp.*). On hornbeam, lichens form species rich
381 assemblages, dominated by crustose species that otherwise are outcompeted by bryophytes
382 and foliose lichens on oak (Aptroot, 2012; John and Dale, 1995; Ranius et al., 2008). The
383 relevance of hornbeam as lichen substrate in European temperate forests was recently
384 highlighted also by Hauck et al. (2013). Interestingly, that study provided evidence for a
385 dramatic impoverishment of lichen assemblages on beech as a consequence of centuries of
386 forest management for timber production. Our results corroborate this view since on beech we
387 found species poor lichen communities composed by common species (see also Nascimbene
388 et al., 2012).

389 Pine hosts species poor bryophyte assemblages, which is explained by its loose flaked
390 unstable acidic bark (Barkman, 1958; Hauck and Javkhlan, 2008). However, some
391 acidofrequent lichens are strongly related to this tree species, mainly establishing at the base
392 of the trunks where the bark is more stable.

393 Tree species richness is a key element for forest biodiversity in this region. It was the most
394 important variable for the diversity and composition of many other organism groups (herbs,
395 seedlings, spiders, terricolous bryophytes, Ódor unpubl.). Compared to other regions of
396 Hungary, fine scale tree species diversity of this region is extremely high. Conservation
397 oriented forest management should maintain this high tree species richness in mixed stands.
398 Silvicultural systems based on natural regeneration process could easily sustain this diversity.
399 Some tree species not favoured for timber production could be relevant for biodiversity, as
400 hornbeam for lichens.

401

402 *4.2. Tree size*

403

404 Large and old trees considerably influence the composition of epiphytes with many threatened
405 species and high epiphyte diversity in old-growth forests (Lie et al., 2009; Mazdule et al.
406 2012; McGee and Kimmerer, 2002; Nascimbene et al., 2009a). However, in our study tree
407 size has a small effect on the composition of bryophyte and no effect on lichen assemblages.
408 This result is probably related to the fact that our forests are managed with relatively short
409 rotation cycles and old, large trees are virtually absent. The age range of our trees was
410 accordingly small even if the range of DBH was probably enough (20-50 cm) to determine an
411 area effect that is however more influential for bryophytes than for lichens (Fritz et al.,
412 2008a). Since forests have a long history of management for timber production it is supposed
413 that dispersal limited species, sensitive to the longevity of the substrate, already disappeared
414 from this region (Hauck et al., 2013).

415 However, creating set aside areas (like core zones of forest reserves), leaving high density of
416 retention trees after clearcuts, and sparing veteran trees in tree selection silvicultural system
417 could contribute to increase the density of old, large trees of the region. Higher density of
418 these trees could enable the recolonization of the sensitive epiphytic species in the area.

419

420 *4.3. Microclimate and shrub layer*

421

422 Light was among the main drivers of lichen composition, while it had scarce effect on
423 bryophytes. It is a general phenomenon that the composition of epiphytic lichens is related to
424 light conditions, determining high diversity of lichens in open forests and on solitary trees
425 (Aptroot, 2012; Coote et al., 2007; Moe and Botnen, 1997; Nascimbene et al., 2013b; Norden
426 et al., 2012). Bryophytes generally prefer more shaded conditions and higher air humidity
427 (Hosokawa and Odani, 1957; Humphrey et al., 2002; Lesica et al., 1991; Ranius et al., 2008).
428 However, some studies emphasize that many specialist epiphytic bryophytes prefer more open
429 conditions as forest edges and solitary trees (Moe and Botnen, 2000, Vanderporten et al.,
430 2004). Studies supporting the positive effect of shaded conditions were carried out in forested
431 regions, as in our case, while studies supporting the positive effect of open conditions were
432 focused on areas where forest cover was low in the landscape. In our forests, only terricolous
433 bryophytes are enhanced by increasing light availability, while epixylic and epiphytic species
434 are related to shaded conditions (Tinya et al., 2009). Many facultative epiphytes are sensitive
435 to microclimatic conditions, preferring relative cool and humid stands (Király et al. 2013). In
436 this perspective, the relevance of the shrub layer in driving bryophytes assemblages could be
437 related to the fact that it enhances local air humidity (Aude and Poulsen, 2000; Brunialti et al.,
438 2010). In our study region, this structural factor was influential also for the species richness of
439 epiphytic (Király et al., 2013) and ground-floor bryophyte assemblages (Márialigeti et al.,
440 2009). The continuity of forest microclimate, heterogeneous light conditions, and permanent
441 presence of shrub layer could be more easily maintained using tree selection silvicultural
442 system and continuous forest cover forestry methods than in the framework of shelterwood
443 system.

444

445 *4.4. Landscape and historical factors*

446

447 Many dispersal limited epiphytic species are sensitive to the fragmentation of their habitat.
448 Both recent (Kuusinen and Penttinen, 1999; Snäll et al., 2003) and historical (Berglund and
449 Jonsson, 2005; Snäll et al., 2004) landscape patterns can determine the spatial distribution of
450 these organisms. However, in our study the effect of these factors was far less important than
451 that of stand level drivers. Landscape and historical factors had no effect on lichen
452 composition, while recent forest cover had a marginal effect on bryophytes. These forests had
453 been managed for centuries, and the forest cover was lower in the past than today
454 (Gyöngyössy, 2008). It is supposed that dispersal limited, specialist species disappeared from
455 the region in the past (Ellis et al., 2011), and the current species pools are adapted to more

456 closed and disturbed conditions. This interpretation is also corroborated by Hauck et al.
457 (2013) that relate the pauperization of the epiphytic lichen flora in temperate forests of north-
458 western Germany with the long lasting human disturbance that caused the replacement of
459 native stands, mainly composed of beech, with oak-hornbeam dominated secondary stands.

460

461 **5. Conclusions, implications for management**

462

463 In our study region, forest management aims to harmonize timber production with
464 biodiversity conservation to accomplish the policies of nature protection of the National Park,
465 fitting to the general concept of sustainable forest management. In this perspective, this study
466 proved that the most determinant factors influencing the composition of epiphytes primarily
467 reflect on trends in recent forest management (tree species richness and composition, light and
468 microclimate conditions, shrub layer, presence of large trees) giving a real opportunity to
469 improve forest biodiversity conservation.

470 The maintenance of mixed stands including oaks, beech and pine as dominant trees
471 considerably increases the diversity of epiphytic assemblages because of the host preferences
472 of the species. The presence of subordinate trees (thus stands with higher overall tree species
473 richness) is also very important. In particular, hornbeam is a highly suitable host for several
474 lichen species. This tree species is usually not favoured by management practices focused on
475 timber production, but its enhancement should be included in more conservation-oriented
476 practices.

477 For bryophytes, the continuity of forest microclimate (high and balanced air humidity) is very
478 important. This habitat condition could be provided by enhancing continuous forest cover
479 forestry, presence of shrub layer and heterogeneous vertical structure (Aude and Poulsen,
480 2000; Király and Ódor, 2010). Lichen assemblages are limited by light availability and the
481 optimal light conditions could be provided by small scale thinning and gap creation (Nordén
482 et al., 2012).

483 On the basis of our results, the main strategy of management focusing on epiphyte diversity
484 conservation should include: 1) the maintenance of tree species diversity in mixed stands; 2)
485 the increase of the proportion of deciduous trees (mainly oaks and hornbeam); 3) the
486 maintenance of large trees within the stands; 4) the presence of shrub and regeneration layer;
487 5) the creation of heterogeneous light conditions. In this perspective, tree selection
488 silvicultural systems and the approaches of continuous forest cover forestry are likely to be
489 more appropriate for the conservation of epiphytes than shelterwood systems (Aude and

490 Poulsen, 2000; McGee and Kimmerer, 2002; Nascimbene et al., 2013a), even if Bardat and
491 Aubert (2007) emphasized that shelterwood system could provide better conditions for
492 epiphytes at higher spatial scales. In the framework of shelterwood system, the extension of
493 rotation and regeneration periods and the maintenance of a large proportion of retention trees
494 after harvest are widely supported measures to enhance forest epiphytes (Caners et al. 2013;
495 Hannerz and Hanell, 1997; Hazzell and Gustafsson, 1999; Löhmus and Löhmus, 2011).

496

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504

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747

748 **Table 1** Explanatory variables used in stand level analyses. Their minimum, maximum and
 749 mean values are given where appropriate from the 35 studied plots

Explanatory variable	Minimum	Maximum	Mean
Tree species composition			
Tree species richness	2.0	10.0	5.6
Tree species diversity ¹	0.19	1.95	0.92
Proportion of tree species (beech, hornbeam, oaks, Scots pine, subordinate trees)	-	-	-
Stand structure			
Mean DBH (cm)	13.6	40.6	26.3
Coefficient of variation of DBH	0.2	1.0	0.5
Tree density (stems/ha)	218.7	1318.7	591.2
Shrub density (stems/ha)	0.00	4706.2	952.2
Big tree density (DBH>50 cm, stems/ha)	0.0	56.2	17.3
Basal area (m ² /ha)	24.1	49.7	34.2
Snag volume (m ³ /ha)	0.0	64.6	12.1
Log volume (m ³ /ha)	1.2	35.6	10.8
Light conditions			
Mean relative light (%)	4.8	40.3	16.0
Standard deviation of relative light	0.7	15.2	3.9
Microclimate			
Temperature difference (K)	-0.9	0.7	-0.1
Temperature range difference (K)	-0.4	2.5	0.9
Air humidity difference (%)	-1.8	3.3	0.8
Air humidity range difference (%)	-2.3	6.6	1.9
Geographical position			
EOV (Hungarian Geographical Projection) coordinates of longitude and latitude (m)	-	-	-
Landscape variables			
Proportion of landscape elements (% , forests, clearcuts, non-forested areas) ²	56.9	100.0	89.8
Diversity of landscape elements ¹	0.11	1.86	1.11
Management history (in the 19 th century)			
Proportion of forest in the landscape (%)	24.0	100.0	76.6
Plot was a forest (binary)	-	-	-

750

751 *DBH* diameter at breast height

752 ¹ Shannon diversity

753 ² the values are the percentage of forests

754

755 **Table 2** Explained variance of the significant explanatory variables used in the stand level

756 Redundancy Analysis (RDA)

Variables	Variance (%)	F-value	P
Bryophytes			
Oak proportion	14	5.5	0.002
Temperature difference	8	3.2	0.002
Mean DBH	8	3.4	0.002
Pine proportion	5	2.5	0.002
Recent forest cover	5	2.4	0.014
Shrub density	4	1.9	0.042
Lichens			
Mean relative light	22	9.5	0.002
Pine proportion	20	11.2	0.002
Oak proportion	7	4.7	0.002
Hornbeam proportion	4	2.8	0.004
Basal area	4	2.3	0.008

757

758

759 **Table 3** Explained variance (conditional effect) of the significant explanatory variables in tree
760 level Canonical Correspondence Analysis (CCA)

761

Variables	Variance (%)	F-value	P
Bryophytes			
Tree species	7.2	16.7	0.002
DBH	0.6	2.8	0.026
Relative light	0.4	2.0	0.006
Lichens			
Tree species	12.6	18.2	0.002
Relative light	0.5	1.9	0.034
DBH	0.5	1.7	0.012

762

763

764 **Table 4** Indicator Species Analysis of bryophytes related to tree species. Only bryophyte
 765 species which were significantly ($P < 0.01$) related to a tree species are listed,. Values represent
 766 the number of occurrences (frequency) on different tree species

Species	Beech	Hornbeam	Oak	Pine	Total	Indtree	Indval	P
Number of trees	225	56	324	344	949			
<i>Orthotrichum pallens</i>	24	4	1	0	29	Beech	0.0917	0.001
<i>Orthotrichum stramineum</i>	41	0	6	0	47	Beech	0.1751	0.001
<i>Plagiothecium denticulatum var. undulatum</i>	1	3	6	1	11	Hornbeam	0.0405	0.006
<i>Brachytheciastrum velutinum</i>	20	5	85	5	115	Oak	0.1791	0.001
<i>Dicranum montanum</i>	68	6	121	136	331	Oak	0.1973	0.001
<i>Homalia trichomanoides</i>	0	1	20	0	21	Oak	0.0542	0.005
<i>Hypnum cupressiforme</i>	203	56	324	108	691	Oak	0.428	0.001
<i>Isothecium alopecuroides</i>	6	6	46	0	58	Oak	0.0775	0.004
<i>Metzgeria furcata</i>	22	6	65	0	93	Oak	0.1395	0.001
<i>Plagiomnium affine</i>	0	1	20	1	22	Oak	0.0571	0.004
<i>Plagiomnium cuspidatum</i>	0	0	13	0	13	Oak	0.0401	0.009
<i>Platygyrium repens</i>	8	3	162	2	175	Oak	0.4533	0.001
<i>Radula complanata</i>	77	21	160	0	258	Oak	0.2248	0.001
<i>Chiloscyphus profundus</i>	22	8	40	186	256	Pine	0.4059	0.001

767 *Total* Summed number of occurrences (frequencies)

768 *Indtree* Tree species with the highest indicator values

769 *Indval* Indicator value related to the tree species

770 *P* significance of the indicator value

771

772 **Table 5** Indicator species analysis of lichens related to tree species. Only lichen species which
 773 were significantly ($P < 0.001$) related to a tree species are listed. Values represent the number
 774 of occurrences (frequency) on different tree species.

775

Species	Beech	Hornbeam	Oak	Pine	Total	Indtree	Indval	P
Number of trees	225	56	324	344	949			
<i>Lecanora expallens</i>	32	1	2	0	35	Beech	0.1164	0.001
<i>Arthonia radiata</i>	1	16	0	0	17	Hornbeam	0.2849	0.001
<i>Graphis scripta</i>	92	49	3	0	144	Hornbeam	0.698	0.001
<i>Lecanora carpinea</i>	1	8	2	0	11	Hornbeam	0.1372	0.001
<i>Lecanora chlarotera</i>	2	18	0	0	20	Hornbeam	0.313	0.001
<i>Pertusaria amara</i>	0	7	8	0	15	Hornbeam	0.1201	0.001
<i>Phlyctis argena</i>	104	47	216	1	368	Hornbeam	0.4552	0.001
<i>Pyrenula nitida</i>	0	12	0	0	12	Hornbeam	0.2143	0.001
<i>Cladonia coniocraea</i>	2	0	145	66	213	Oak	0.3132	0.001
<i>Flavoparmelia caperata</i>	2	0	166	1	169	Oak	0.5114	0.001
<i>Lepraria sp.</i>	46	16	257	65	384	Oak	0.5885	0.001
<i>Parmelia sulcata</i>	2	1	41	1	45	Oak	0.1148	0.001
<i>Chaenotheca ferruginea</i>	0	0	2	32	34	Pine	0.0814	0.002
<i>Dimerella pineti</i>	1	1	7	246	255	Pine	0.6918	0.001
<i>Hypogymnia physodes</i>	0	0	13	81	94	Pine	0.2201	0.001
<i>Hypocenomyce scalaris</i>	0	0	1	86	87	Pine	0.2477	0.001

776 *Total* Summed number of occurrences (frequencies)

777 *Indtree* Tree species with the highest indicator values

778 *Indval* Indicator value related to the tree species

779 *P* significance of the indicator value

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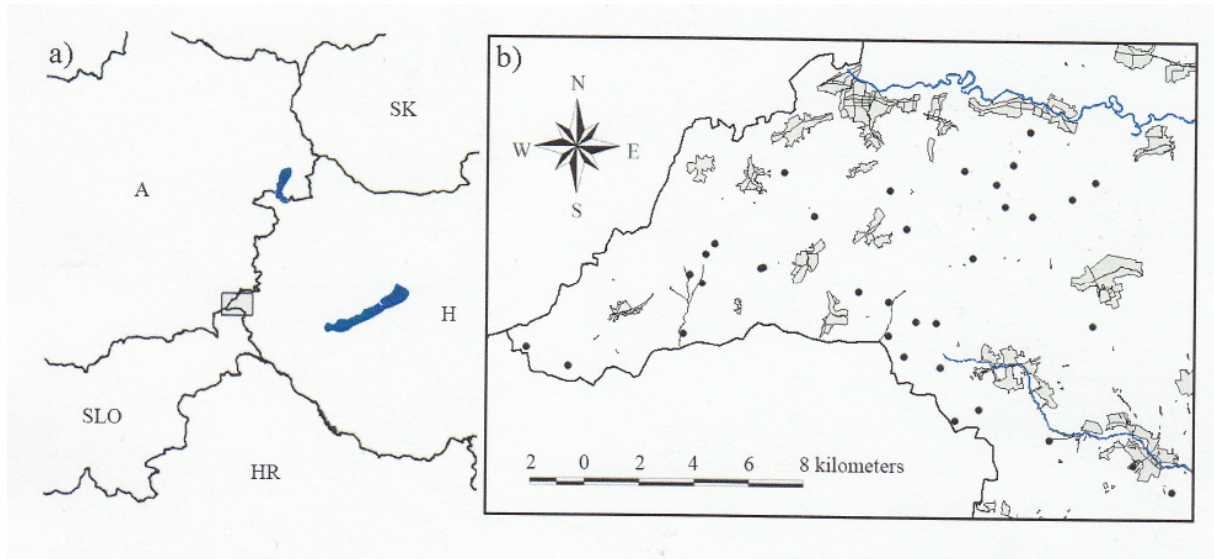
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782 **Fig. 1.** Location of the study area (a, grey rectangle) and the geographical positions of the 35

783 plots (b, black dots), built-up areas are shown by grey. A = Austria; SLO = Slovenia; HR =

784 Croatia; H = Hungary; SK = Slovakia.

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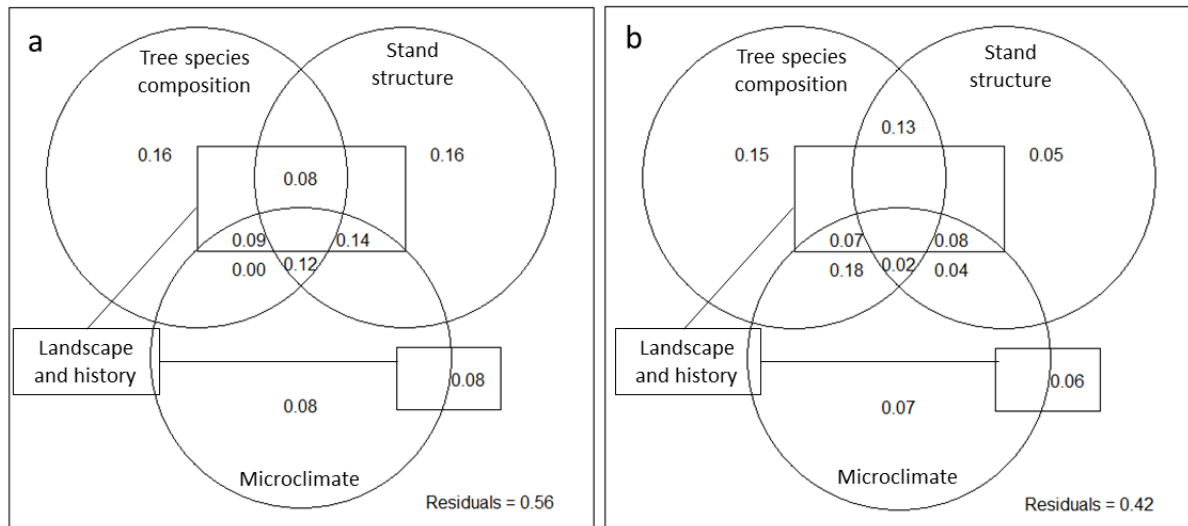
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789 **Fig. 2.** Variation partitioning of bryophyte (a) and lichen (b) assemblages among the
 790 following groups of explanatory variables: tree species composition, stand structure,
 791 microclimate (including light) and landscape-historical variables (boxes).

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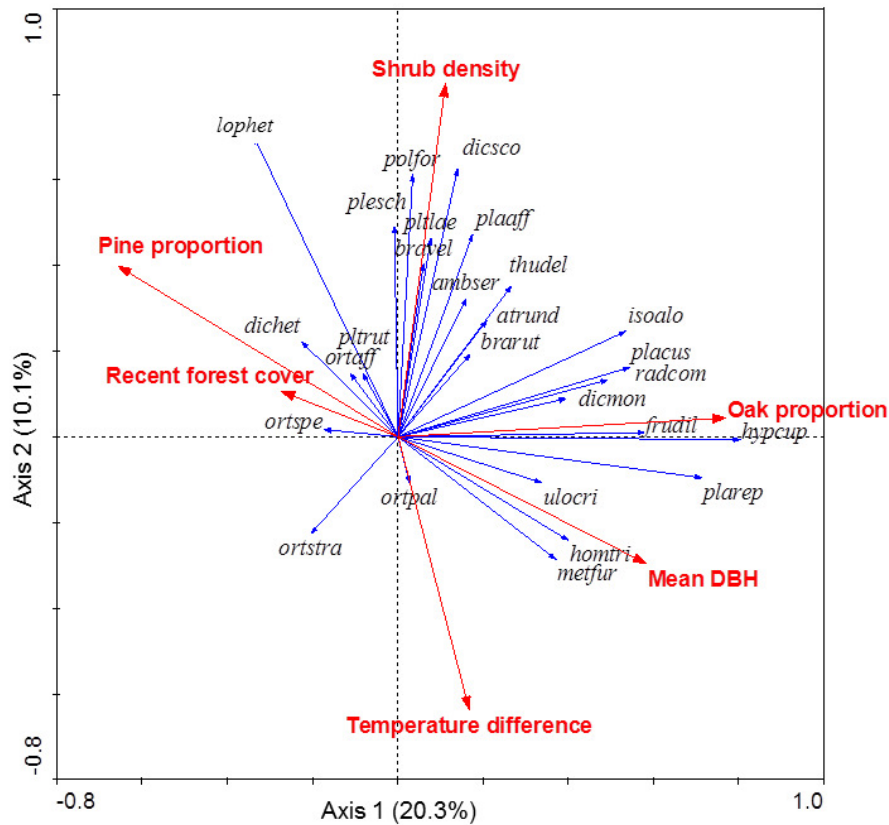


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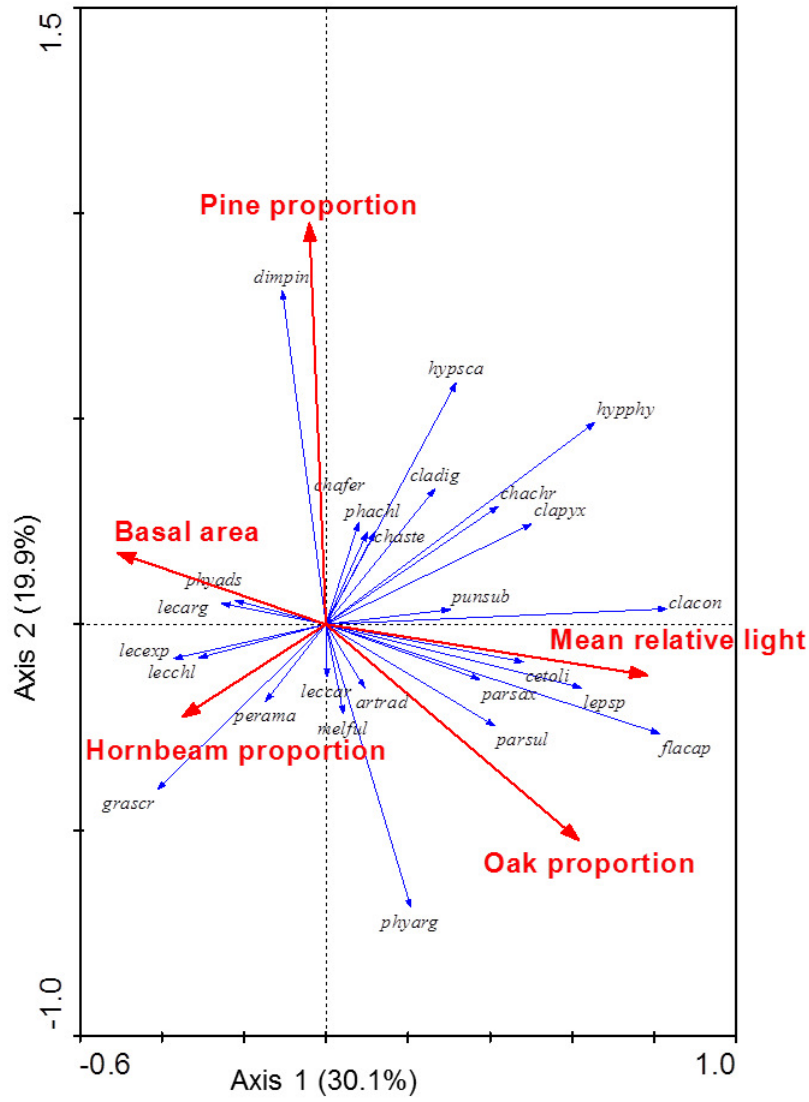
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796 **Fig. 3.** Ordination biplot of the stand level Redundancy Analysis of bryophytes. Species are
 797 indicated by blue arrows, labelled by the six letter codes (three letters from genus and three
 798 from species names, see Table A.1). Explanatory variables are represented by red arrows.
 799 Explained variances (%) of the axes are indicated. DBH: diameter at breast height
 800



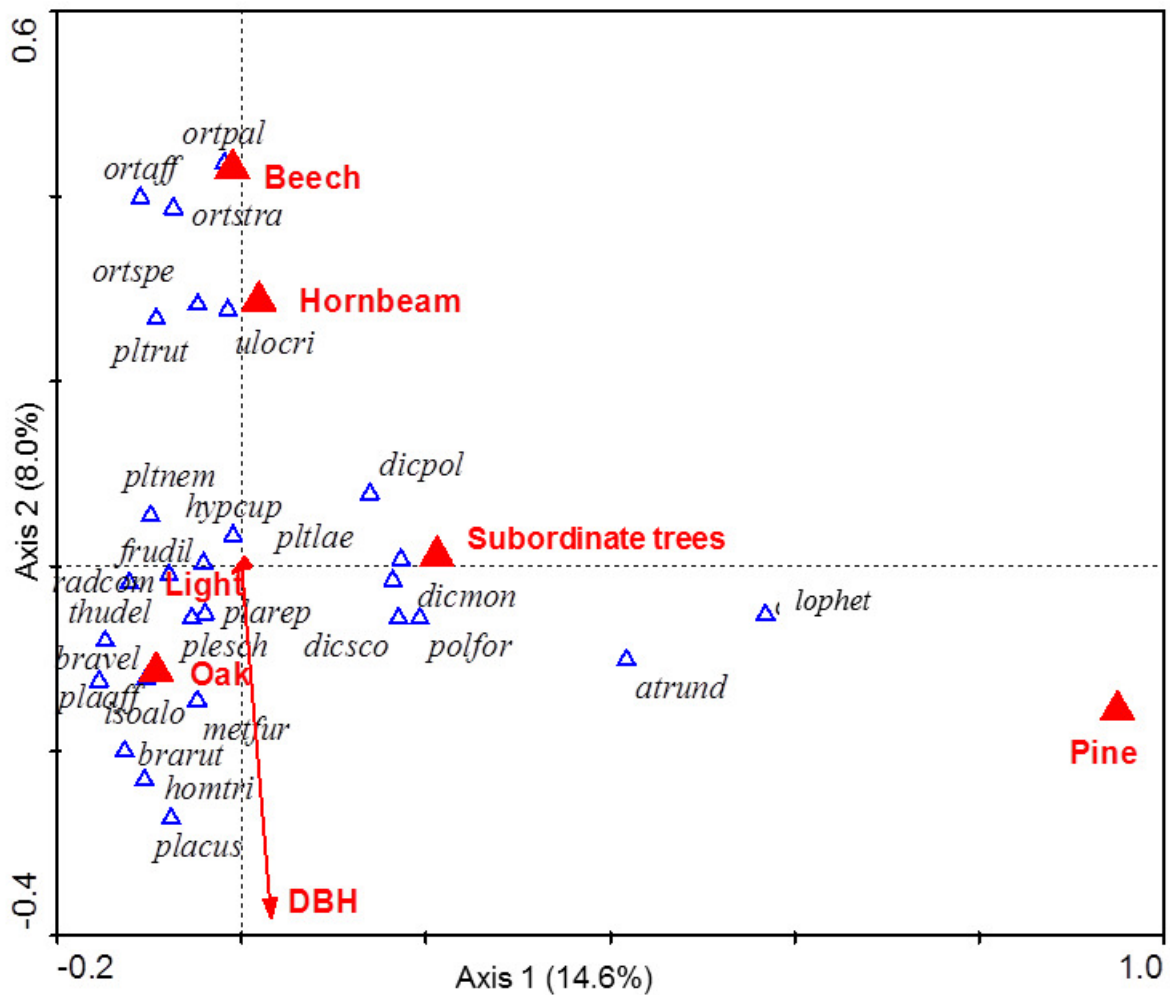
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804 **Fig. 4.** Ordination biplot of the stand level Redundancy Analysis of lichens. Species are
 805 indicated by blue arrows, labelled by the six letter codes (three letters from genus and three
 806 from species names, see Table A.2). Explanatory variables are represented by red arrows.
 807 Explained variances (%) of the axes are indicated.
 808



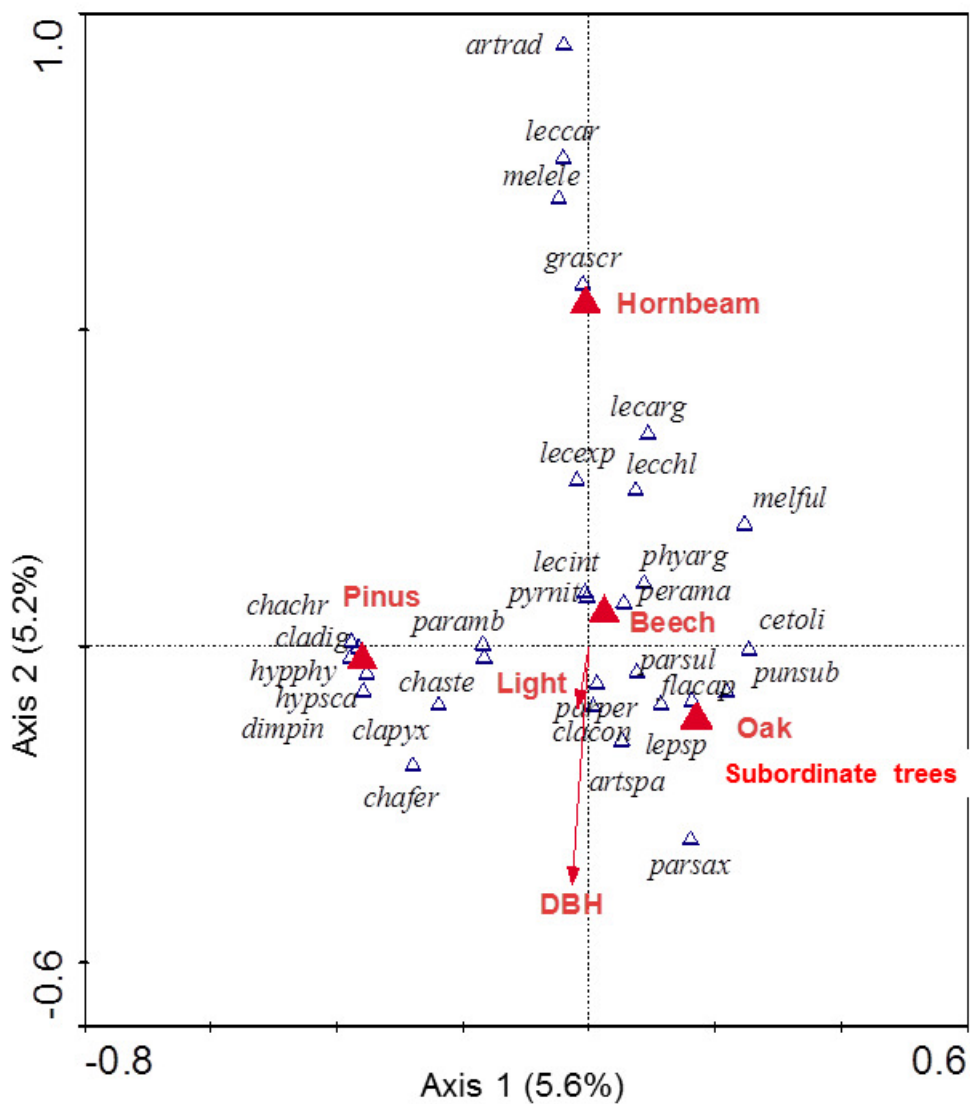
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812 **Fig. 5.** Ordination biplot of tree level canonical correspondence analysis of bryophytes.
 813 Species are indicated by blue triangles, labelled by the six letter codes (three letters from
 814 genus and three from species names, see Table A.1). Explanatory variables are represented by
 815 red triangles (factors) or red arrows (numeric variables). Explained variances (%) of the axes
 816 are indicated. DBH: diameter at breast height
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819
 820

821 **Fig. 6.** Ordination biplot of tree level canonical correspondence analysis of lichens. Species
 822 are indicated by blue triangles, labelled by the six letter codes (three letters from genus and
 823 three from species names, see Table A.2). Explanatory variables are represented by red
 824 triangles (factors) or red arrows (numeric variables). Explained variances (%) of the axes are
 825 indicated. DBH: diameter at breast height
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