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8 **Title: Factors influencing epiphytic bryophyte and lichen species richness at different**
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21

22 **Abstract**

23

24 The effect of management related factors on species richness of epiphytic bryophytes and
25 lichens was studied in managed deciduous-coniferous mixed forests in Western-Hungary. At

26 the stand level, the potential explanatory variables were tree species composition, stand
27 structure, microclimate and light conditions, landscape and historical variables; while at tree
28 level host tree species, tree size and light were studied.

29 Species richness of the two epiphyte groups was positively correlated. Both for lichen and
30 bryophyte plot level richness, the composition and diversity of tree species and the abundance
31 of shrub layer were the most influential positive factors. Besides, for bryophytes the presence
32 of large trees, while for lichens amount and heterogeneity of light were important. Tree level
33 richness was mainly determined by host tree species for both groups. For bryophytes oaks,
34 while for lichens oaks and hornbeam turned out the most favourable hosts. Tree size generally
35 increased tree level species richness, except on pine for bryophytes and on hornbeam for
36 lichens.

37 The key variables for epiphytic diversity of the region were directly influenced by recent
38 forest management; historical and landscape variables were not influential. Forest
39 management oriented to the conservation of epiphytes should focus on: (i) the maintenance of
40 tree species diversity in mixed stands; (ii) increment the proportion of deciduous trees (mainly
41 oaks); (iii) conserving large trees within the stands; (iv) providing the presence of shrub and
42 regeneration layer; (v) creating heterogeneous light conditions. For these purposes tree
43 selection and selective cutting management seem more appropriate than shelterwood system.

44

45

46 Keywords: stand structure, tree size, host preference, microclimate, light, diversity.

47 Abbreviations:

48 DBH Diameter at breast height

49 SD Standard deviation

50

51 **Introduction**

52

53 Forest management considerably influences the diversity and composition of forest dwelling
54 organisms (Bengtsson et al. 2000; Paillet et al. 2010; Peterken 1996) by a direct control on
55 many stand scale conditions such as tree species composition, size distribution of trees,
56 vertical structure, canopy closure, microclimate, dead wood availability and forest continuity.
57 Many studies across different management regimes proved that epiphytic bryophytes and
58 lichens are among the most sensitive components of the forest biota to management induced
59 effects (Aude and Poulsen 2000; Bardat and Aubert 2007; Berg et al. 2002; Nascimbene et al.
60 2007; Rose 1992; Vanderpoorten et al. 2004). Epiphytic species directly exploit trees as living
61 habitat and therefore tree species composition of stands considerably determines the epiphytic
62 assemblages (McGee and Kimmerer 2002). Many species have preferences to host trees,
63 characterized by different physical and chemical bark conditions (Barkman 1958; Jürriado et
64 al. 2009). More optimal bark conditions of broad-leaved trees (e.g. aspen) explain their
65 importance in the epiphytic diversity of boreal forests (Kuusinen and Penttinen 1999). Tree
66 size and age are also crucial stand level factors for epiphytic diversity (Fritz et al. 2008a; Lie
67 et al. 2009). Over-mature trees host more diverse epiphyte assemblages and many species are
68 significantly associated to them (McGee and Kimmerer 2002; Nascimbene et al. 2009a).
69 Beside the simple area effect, this pattern is also explained by higher habitat (bark) diversity
70 of old trees (Barkman 1958), and by the elongated colonization time, which is crucial for
71 dispersal limited species (Fritz et al. 2008a). During the ageing of trees a directional
72 compositional change (succession) is observed in epiphytic vegetation, which is influenced by
73 deterministic (e.g. changing bark conditions) and stochastic factors (Barkman 1958, Peck and
74 Frehlich 2008). The third important group of stand level variables influenced by management

75 are microclimate (air humidity and temperature) and light conditions, which can considerably
76 modify the host and size related effects (Hauck and Javkhlan 2008; Mazimpaka et al. 2010;
77 Ranius et al. 2008).

78 However, on coarser spatial and temporal scales, other drivers are crucial in the composition
79 of epiphytic communities, as macro-climatic conditions (Bates et al. 2004; Marini et al.
80 2011), elevation (Berryman and McCune 2006), landscape level forest continuity (Snäll et al.
81 2004) and historical factors (Berg et al. 2002; Rose 1992). Unfortunately, the separation of
82 the importance of different factors acting at different spatial levels is not obvious, because
83 most studies focused on one definite spatial scale (as tree, stand, landscape or continent
84 related factors).

85 Despite the fact that epiphytic bryophytes and lichens occupy the same physical space,
86 interact each other and are potentially limited by the same environmental conditions, only few
87 studies compared their environmental limitations and interactions. Beside the many
88 similarities (host preference, tree size and age effects, fragmentation effects), lichen
89 assemblages are supposed to be more limited by light and less sensitive to desiccation than
90 bryophytes (Gustafsson and Eriksson 1995; Ranius et al. 2008).

91 This study investigated the influence of potential environmental factors on epiphytic
92 bryophyte and lichen species richness at different spatial scales (stand and tree level) in
93 managed Central-European mixed forests. At stand level, tree species composition, stand
94 structure, light and microclimate conditions, landscape characteristics and management
95 history, while at tree level host species, tree size and light conditions were tested as potential
96 explanatory variables. At stand level, specialist epiphytic bryophytes and forest specialist
97 lichens were distinguished as functional groups. Beside the general exploration of the
98 relationships between environmental factors and epiphyte richness, this study aimed at
99 improving forest biodiversity conservation of the studied region.

100

101 **Material and methods**

102

103 Study area

104

105 The study area is in Órség National Park (N 46°51'-55' and W 16°07'-23') at the
106 westernmost part of Hungary (Fig. 1). The annual mean temperature is 9.0–9.5 °C, the
107 precipitation is 700-800 mm. The elevation is between 250-350 m, the landscape is divided
108 into hills and wide valleys (Dövényi 2010). The bedrock consists of alluviated gravel and
109 loess. On hills, the most common soil types are pseudogleyic and lessivage brown forest soils,
110 while in valleys mire and meadow soils with an acidic upper layer can be found. The soil of
111 forests is acidic and nutrient poor (0-30 cm, pH 4.3, carbon 3.09%, nitrogen 0.12%, A. Bidló
112 pers. comm.).

113 The vegetation is dominated by beech (*Fagus sylvatica* L.), sessile and pedunculate oak
114 (*Quercus petraea* L. and *Q. robur* L.), hornbeam (*Carpinus betulus* L.), Scots pine (*Pinus*
115 *sylvestris* L.) and Norway spruce (*Picea abies* (L.) Karst.), forming monodominant and mixed
116 stands as well. The proportion of different mixing tree species (*Betula pendula* Roth., *Populus*
117 *tremula* L., *Castanea sativa* Mill., *Prunus avium* L., etc.) is relatively high (Tímár et al.
118 2002).

119 Most of the original forests of the region were cut in the middle ages and in the secondary
120 stands the proportion of pioneer tree species (such as *Pinus sylvestris* and *Betula pendula*) and
121 the cover of acidofrequent herbs, bryophytes and lichens increased. Special cultivation forms
122 as ridging on arable lands and litter collection in forests contributed to the leaching and
123 acidification of the soil. The landscape is still determined by historical processes, however,
124 the traditional cultivation forms are given up, and this led to the increase of deciduous

125 trees and mesophytic herbs in forests. Nowadays, the largest part of the Órség National Park
126 (as all National Parks in Hungary) is managed harmonizing timber production and
127 conservation purposes. In private forests spontaneous stem selection system resulting in
128 uneven aged stands, while in state forests shelterwood silvicultural system with a rotation
129 period of 70–110 years are applied (Tímár et al. 2002).

130

131 Data collection

132

133 Thirty-five stands were selected by stratified random sampling from the database of the
134 Hungarian National Forest Service (Fig. 1). Preliminary inclusion criteria of site selection
135 were as follows: dominant trees older than 70 years, more or less level slope, absence of
136 ground-water influence and spatial independence of sites (the distance was minimum 500 m
137 between the stands). Because we wanted to represent the characteristic tree species
138 combinations of the region the compartments of the database were grouped according to tree
139 species combination types and the studied plots were randomly selected within the groups.

140 Within each stand, a 40 m x 40 m plot was pointed out for stand structural measurements.
141 Geographical position, circumference, species identity, height, height of crown base and
142 crown projection were measured of each tree with DBH (diameter at breast height) larger than
143 5 cm. Average diameter and length of logs thicker than 5 cm diameter and longer than 0.5 m
144 were recorded. Density of sapling species (tree or shrub individuals taller than 0.5 m and
145 thinner than 5 cm DBH) was recorded. Relative light conditions (percentage of above canopy
146 total light) was modelled in 36 systematically arranged points at 1.3 m height by tRAYcy
147 model (Brunner 1998) using tree position and size data (Tinya et al. 2009a). For tree level
148 analyses, the light conditions in the position of each tree individuals were modelled also by
149 the tRAYcy model predicting relative light values for the position of trees at 1.0 m height. Air

150 humidity and temperature were measured in the middle of the plots at 1.3 m height using
151 Voltcraft DL-120 TH data loggers in 24 hours measurements with 5 minutes recording
152 frequency. The measurements of all plots were carried out within a five days period. During
153 this period two reference plots were measured permanently. Eight temperature and air
154 humidity measurements were carried out during three vegetation periods (2009 June, October;
155 2010 June, August, September, October; 2011 March, May). Geographical position of the
156 plots was given in meters based on the Hungarian Geographical Projection (EOV). As
157 landscape variables, proportion of forests (stand age older than 20 yr), clearcuts (stand age
158 younger than 20 yr) and non-forested areas (settlements, meadows, arable lands) was
159 estimated around the plots within a circle with 300 m radius, using maps and data of the
160 Hungarian National Forest Service. Data on management history were generated based on the
161 map of the Second Military Survey of the Habsburg Empire from 1853 (Arcanum 2006). The
162 existence of forest in the plots was registered (as binary variable) and the proportion of
163 forested area in the historical landscape (in the circle of 300 m radius) was calculated.
164 Epiphytic bryophytes and lichens were recorded in 30 m x 30 m plots positioned in the middle
165 of the 40 m x 40 m plots. The occurrence of bryophyte and lichen species was recorded in
166 every living tree with minimum 20 cm DBH from the base to 1.5 m height. The nomenclature
167 followed Hill et al. (2006) for mosses, Grolle and Long (2000) for liverworts and Nimis and
168 Martellos (2003) for lichens.

169

170 Data analyses

171

172 At stand level, general linear regression models were built to explore relationships between
173 epiphyte richness and potential explanatory variables (Faraway 2005). As response variables
174 we considered the total number of species of both bryophytes and lichens and the species

175 richness of two functional groups: one including specialist epiphytic bryophytes (Orbán and
176 Vajda 1983; Smith 2004) and one including lichens mainly related to forest habitats (forest
177 specialists) according to their ecological requirements (Nimis and Martellos 2008).
178 Saxicolous bryophytes were ranked among specialist epiphytes, because rocks lack in the
179 region, and saxicolous species occur exclusively on trees (Online Resource Table 2).

180 The measured and derived explanatory variables are listed in Table 1. The proportion of tree
181 species was expressed based on their volumes. Volumes of trees were calculated by species
182 specific equations from DBH and height variables (Sopp and Kolozs 2000). *Quercus petraea*,
183 *Q. robur* and *Q. cerris* L. were merged as oaks, rare tree species were merged as mixing trees.
184 Tree species diversity was expressed by Shannon index with natural logarithm based on the
185 relative volume of species (Shannon and Weaver 1949). Diversity of landscape elements was
186 calculated in the same way. Plot level light conditions were expressed as the mean and
187 standard deviation of relative light using the 36 measurements. Because these two variables
188 were strongly correlated, a linear regression was used between standard deviation as
189 dependent and mean as explanatory variables. The residuals of standard deviation were used
190 during the modelling as descriptor of light heterogeneity independent from the mean. For air
191 humidity and temperature, differences were calculated from the two reference plots. Relative
192 daily mean and range values were expressed for both variables and averaged over the eight
193 measurements. Some explanatory variables (proportion of tree species, light variables) were
194 ln transformed before the analysis. All variables were standardized (zero mean, one standard
195 deviation).

196 Before modelling, preliminary selection and data exploration were performed. The dependent
197 variables satisfied the normality condition and were not transformed. Pairwise correlation
198 analyses and graphical explorations were carried out between the dependent variables and
199 potential explanatory variables. Inter-correlations among explanatory variables were also

200 checked. Only those explanatory variables were included to linear model selection that
201 significantly correlated with the dependent variables, had homogenous scatter plots with it,
202 and their inter-correlations with other explanatory variables were low (the absolute values of
203 the correlation coefficients were lower than 0.35). After the preliminary selection, 5-8
204 explanatory variables got into the selection procedure of regression models. The minimal
205 adequate model was built with backward elimination using deviance analysis with F-test
206 (ANOVA). Second order interactions were also considered. After modelling, the normality
207 and variance homogeneity of residuals were checked.

208 At tree level, species richness of bryophytes and lichens were analyzed by general linear
209 mixed models (Zuur et al. 2009). The dependent variables were ln transformed. The fixed
210 effects were tree species (beech, pine, hornbeam, oak, mixing species), DBH and tree level
211 relative light; plot was applied as random factor. Full models included all interaction terms.
212 Fixed effect selection was made by maximum likelihood method; random effect was tested by
213 restricted maximum likelihood method (Faraway 2006).

214 In all the models, trees without lichens or bryophytes were also included. Data analyses were
215 carried out by R 2.14.0 (The R Development Core Team 2011) and by the R package “nlme”
216 (Pinheiro et al. 2011).

217

218 **Results**

219

220 Stand level analyses

221

222 Sixty bryophyte and forty-four lichen species were recorded in 35 plots on 971 trees (Online
223 Resource). From the 971 studied tree individuals 225 were beech, 344 pine, 324 oak, 56
224 hornbeam and 22 mixing tree species. For bryophytes the mean stand level species richness

225 was 14.0 ± 5.0 (SD, standard deviation), the range was 5-27, while for lichens the mean was
226 9.8 ± 3.7 (SD), the range was 3-20. Bryophyte and lichen richness were significantly positively
227 correlated to each other ($r=0.39$, $p=0.019$, $df=34$). Twenty-five specialist epiphytic bryophytes
228 (the mean was 6.7 ± 2.5 (SD), the range was 1-11) and twenty forest specialist lichens (the
229 mean was 5.2 ± 2.2 (SD), the range was 2-11) were found. The correlation between the species
230 richness of specialist epiphytic bryophytes and forest specialist lichens was not significant
231 ($r=0.08$, $p=0.627$, $df=34$).

232 Considering the regression models (Table 2), for bryophyte species richness stand structure
233 was determinant: shrub density and tree species diversity were the most important positive
234 factors, while tree density with a negative effect and big trees with a positive one were far less
235 important; the model explained 54% of the total variance. These variables significantly
236 correlated with bryophyte species richness, the absolute values of correlation coefficients
237 were higher than 0.4 (Fig. 2). Air humidity was also significantly correlated with bryophyte
238 species richness (Fig. 2, $r=0.42$), however, it was excluded during the model selection. As an
239 alternative model air humidity could be used instead of shrub density, the two variables were
240 slightly inter-correlated ($r=0.36$, $p=0.034$). Because of higher R^2 and better model diagnostics,
241 shrub density was used in the final model. For lichens, the proportion of oaks and shrub
242 density were the most determinant factors accounting for 50% of the total variance (Table 2).
243 The interaction between these two factors had a negative influence in the model, so the
244 positive effect of shrub layer was less important in oak dominated stands than in other stand
245 types. High temperature range and the amount and heterogeneity of light also increased lichen
246 species richness. The model had high predictive power, R^2 was 0.68.

247 The visual interpretation of these relationships showed, that shrub density was a key variable
248 for the species richness of both organism groups (Fig. 2). However, for other variables their
249 responses were different: for epiphytic bryophytes big tree density, tree species diversity and

250 air humidity had higher importance, for lichens oak proportion and light were more
251 determinant (Fig. 2). In the model for specialist bryophytes, mean DBH was the most
252 determinant variable, pine proportion had a negative effect, but the positive effect of DBH
253 was more pronounced in pine dominated stands than in other stand types (positive interaction,
254 Table 2). The model explained 41% of the total variance. Forest specialist lichens were
255 positively determined by the amount and heterogeneity of light and tree species diversity (the
256 model explained 45% of the total variance). Generally, the R^2 of the models for specialist
257 groups were lower than for general species richness.

258

259 Tree level analyses

260

261 Mean tree level species richness was 2.9 ± 2.1 (SD) for bryophytes and 2.2 ± 1.5 (SD) for
262 lichens. For bryophytes oak, for lichens oak and hornbeam were the most species rich hosts
263 (Fig. 3). Correlation between tree level species richness of bryophytes and lichens was 0.34
264 ($p < 0.001$).

265 Tree species was the most determinant factor for both bryophytes and lichens (Table 3, Fig.
266 4). The effect of plot (random factor) was also considerable in both cases. The amount of light
267 and DBH had a quite strong effect for lichens, while in case of bryophytes they were far less
268 important (Table 3). The highest bryophyte species richness was predicted for oaks (between
269 3 and 5), the lowest (hardly more than 1) for pine (Fig. 4). Tree size effect was strong on
270 every broad-leaved species (the most important on hornbeam), while on conifers size effect
271 was not found. Light effect was strong on beech and mixing tree species, while bryophyte
272 species richness on oak, pine and hornbeam was independent from light conditions. For
273 lichens, hornbeam was the species-richest tree, however contrary to other tree species, its
274 richness was not influenced by tree size and light.

275 **Discussion**

276

277 In our managed forests epiphytic bryophyte and lichen richness are influenced by similar
278 environmental factors mainly related to tree species composition, stand structure and
279 microclimate. However, while tree species composition is strongly influential for both groups,
280 bryophytes proved to be more sensitive than lichens to forest structure and air humidity and
281 lichens were more to light conditions sensitive than bryophytes. Historical and landscape
282 factors were not influential.

283

284 Tree species composition and host tree species

285

286 The positive correspondence between the diversity of trees and epiphytes is a general
287 phenomenon in the forests of the temperate zone (McGee and Kimmerer 2002; Nascimbene et
288 al. 2009b). In our stands, tree species diversity greatly improved epiphyte richness. Deciduous
289 trees are generally species richer than coniferous and their presence in conifer dominated
290 stands is a key factor for epiphyte richness (Cleavitt et al. 2009; Gustafsson and Eriksson
291 1995; Kuusinen and Penttinen 1999).

292 This result is also corroborated by tree level analyses that emphasize the importance of tree
293 species reflecting the strong host preference of epiphytes (Berg et al. 2002; Király and Ódor
294 2010; Slack 1976; Szövényi et al. 2004). Host preference is driven by bark texture, chemistry,
295 water and nutrient supply of different tree species (Barkman 1958; Hauk and Javkhlan 2008).

296 The mesotrophic, wrinkle-rich bark of oaks provides wind-proof, moist microhabitats suitable
297 for both epiphyte groups. On this tree species, bryophytes may establish huge populations
298 with high cover values that are often overgrown by large lobed foliose lichens. Epiphytes on
299 the smoother bark of beech and hornbeam are more exposed to hardships of environment (e.g.

300 stemflows, sun exposure, desiccating winds). However, it is noteworthy that hornbeam is
301 relevant for lichen richness, mainly hosting crustose species that may be favoured because of
302 the lack of competition with bryophytes and foliose lichens (Ranius et al. 2008). Conifers
303 (especially pine) are colonized only by a few species. The bark of pine is very acidic, and its
304 loose flaked surface hinders the establishment and growth of epiphytes. Moreover, pine
305 minimizes the lead of rainwater to the trunk creating very dry conditions unsuitable for
306 bryophytes and lichens (Barkman 1958).

307

308 Stand structure and tree size

309

310 In general, both bryophytes and lichens are sensitive to stand structure and tree size (Fritz et
311 al. 2008a; McGee and Kimmerer 2002). However, in our study this group of environmental
312 factors was relevant especially for bryophytes, while it had a weaker effect on lichens. In
313 particular, the positive effect of the shrub layer for bryophytes can be explained in term of
314 local humidity (Gustafsson and Eriksson 1995; Ranius et al. 2008), providing shaded
315 conditions that protect bryophytes from wind and desiccation (Thomas et al. 2001). This
316 factor positively influences also lichen richness, although lichen diversity was not clearly
317 related to air humidity. The importance of the shrub layer for lichens is higher under less
318 favourable situations where it may mitigate the dryer condition of the bark. Where light is not
319 a limiting factor the positive effect of the shrub layer may override the potential negative
320 effect of shading (Aude and Poulsen 2000).

321 Density of big trees was also a significant explanatory variable for bryophyte species richness.
322 Large trees with cracked, decayed bark and deeper bark fissures have a variety of
323 microhabitats, and provide longer colonization and successional time for dispersal limited
324 species (Fritz et al. 2008a; Lie et al. 2009). Moreover, large over-mature trees can create a

325 temporal bridge between the tree generations before and after forest harvest providing the
326 stands with the survived, local source populations of epiphyte species (Moe and Botnen 1997;
327 Rose 1992). However, large, over-mature trees are very rare in the forests of the region (they
328 are practically missing from our dataset), which is probably a major limiting factor of the
329 regional epiphytic diversity. This can also be the explanation that on tree level the effect of
330 tree size was relatively low. However, the effect of tree size is specific to the studied
331 organism groups and hosts. For bryophytes the bark of pine is unfavourable independently
332 from the size of the trees. Hornbeam has a particular assemblage of preferential lichen
333 species, which can occur with similar probability on small as well as on large trees.

334

335 Microclimate and light

336

337 Microclimate conditions and the amount and heterogeneity of light had considerable
338 importance for lichens, while these factors did not directly influenced the diversity of
339 bryophytes, although shrub layer was correlated with air humidity. In the studied forests
340 terricolous bryophyte species show positive correlations with light, but epiphytes and epixylic
341 species are independent from it (Tinya et al. 2009b). For forest lichens, the heterogeneity of
342 light conditions has the same importance as tree species diversity. The stronger light demand
343 of lichens compared to bryophytes is supported by many studies (Gustafsson and Eriksson
344 1995; Humphrey et al. 2002). The higher light demand and better desiccation tolerance of
345 lichens is the reason that single, veteran trees as remnants of grazed forests or forested
346 meadows are more important for the conservation of lichens than for bryophytes (Löhmus and
347 Löhmus 2011; Moe and Botnen 1997; Rose 1992). In our study, a mosaic of sunny and shady
348 patches provides enough light for lichens and concurrently they avoid desiccation.

349

350 Historical and landscape-scaled factors

351

352 Many studies emphasized the importance of historical factors in the diversity of epiphytes.
353 The continuity of the forest stands (Fritz et al. 2008b; Rose 1992) and the permanent presence
354 of over-mature individuals (Hazell and Gustafsson 1999; Moe and Botnen 1997) are crucial
355 for the survival of sensitive and dispersal limited epiphytic species. Epiphytes, especially
356 lichens, are very sensitive to the landscape pattern (fragmentation and isolation) of their
357 potential habitat (Buckley 2011; Löbel et al. 2006a,b; Snäll et al. 2004). Neither historical nor
358 landscape level factors influenced the species richness of epiphytes in this study. The forest
359 cover in the near-by landscape of the plots (circle of 300 m radius) was high (89.8%, Table 1),
360 and it was also relatively high in the end of 19th century (76.6%, Table 1). These values were
361 much lower considering the whole studied region: 56% and 38%, respectively (Gyöngyösy
362 2008). The secondary stands of the region had been using by humans quite intensively for
363 centuries, over-mature, large trees are very rare in the region. The species pool of the recent
364 epiphyte assemblages mainly contains species adapted to these conditions, species sensitive to
365 fragmentation and forest continuity probably disappeared in the historical past.

366

367 **Conclusion**

368

369 Our study suggests that tree species diversity and composition are key factors for the diversity
370 of both epiphyte groups. Especially oaks hosts species rich assemblages, but for lichens
371 hornbeam is also important, while the species richness on pine is very low. However,
372 bryophytes are more influenced by stand structure of the managed forests (high shrub density,
373 presence of large trees), while lichens are more sensitive to light conditions. Bryophytes
374 prefer more humid, shaded forests, while for the current regional species pool of lichens more

375 open conditions are optimal. Most predictors that were included in the models can be directly
376 influenced by management. The main strategy of management focusing on epiphyte diversity
377 should be the maintenance of tree species diversity in mixed stands, increment the proportion
378 of deciduous trees (mainly oaks), conserving large trees within the stands, providing the
379 presence of shrub and regeneration layer, creating heterogeneous light conditions. Even-aged
380 forests with one-layered, closed canopy are adverse for epiphytes. Tree selection system and
381 selective cutting would be the best management to achieve these conditions. Some studies
382 support the usefulness of this management systems for epiphytes (Aude and Poulsen 2000;
383 McGee and Kimmerer 2002), while some others question it preferring shelterwood
384 management (Bardat and Aubert 2007). In forests maintained by shelterwood management
385 system the retention of relatively large patches of older trees is important for the diversity of
386 epiphytes (Hazell and Gustafsson 1999; Löhmus and Löhmus 2011). These patches will
387 provide safe-sites for the survival of epiphytes and mitigate microclimate stress after harvest.
388 In addition, extended rotation and regeneration periods may be applied in shelterwood
389 management to improve the conditions for epiphytic bryophytes and lichens.

390

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396

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540

541 **Table 1** Explanatory variables of stand level analyses and their minimum, maximum
 542 and mean values based on the 35 studied plots (DBH: diameter at breast height; ¹: the values
 543 are the percentage of forests)

Explanatory variable	Minimum	Maximum	Mean
Tree species composition			
Tree species richness	2.0	10.0	5.6
Tree species diversity (species-volume Shannon-diversity)	0.19	1.95	0.92
Relative volume of tree species (beech, hornbeam, oaks, Scotch pine, mixing species)	-	-	-
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) ¹	56.9	100.0	89.8
Diversity of landscape elements	0.11	1.86	1.11
Management history (in the 19th century)			
Proportion of forest in the landscape (%)	24.0	100.0	76.6
Plot was a forest (binary)	-	-	-

544

545 **Table 2** Significant explanatory variables in the stand level regression models for
 546 species richness. R^2 : adjusted coefficient of determination; estimate: the parameter of the
 547 variable in the regression equation; variance %: percentage of the explained variance by the
 548 explanatory variable within the model; F-statistics were used to estimate the significance of
 549 the variables and the models; df: degrees of freedom; significance levels are indicated by
 550 stars: *= $p < 0.05$; **= $p < 0.01$; *** = $p < 0.001$; DBH: diameter at breast height
 551

Explanatory variables	Estimate	Variance %	F-values
Bryophytes			
$R^2=0.54$, $F(4,30)=10.81$ ***			
Shrub density	2.2432	23.43	17.16***
Tree species diversity	1.7725	18.35	13.44***
Tree density	-1.7202	10.52	7.71**
Big tree density	1.0029	6.74	4.94*
Lichens			
$R^2=0.68$, $F(6,28)=13.06$ ***			
Oak proportion	1.2341	20.05	21.32***
Shrub density	1.0348	19.98	21.25***
Temperature range difference	1.1628	13.1	17.66***
Oak proportion: shrub density	-1.3548	10.99	11.69**
Standard deviation of relative light	0.8006	6.95	7.39*
Mean relative light	1.0029	4.76	5.06*
Specialist bryophytes			
$R^2=0.41$, $F(3,31)=9.02$ ***			
Mean DBH	1.3174	26.05	26.05***
Pine proportion	-0.0791	8.46	8.46*
DBH: pine proportion	1.0984	12.10	12.10*
Forest specialist lichens			
$R^2=0.45$, $F(3,31)=10.12$ ***			
Standard deviation of relative light	1.0786	22.67	13.91***
Tree species diversity	1.0307	18.57	11.39**
Mean relative light	0.9593	8.23	5.05*

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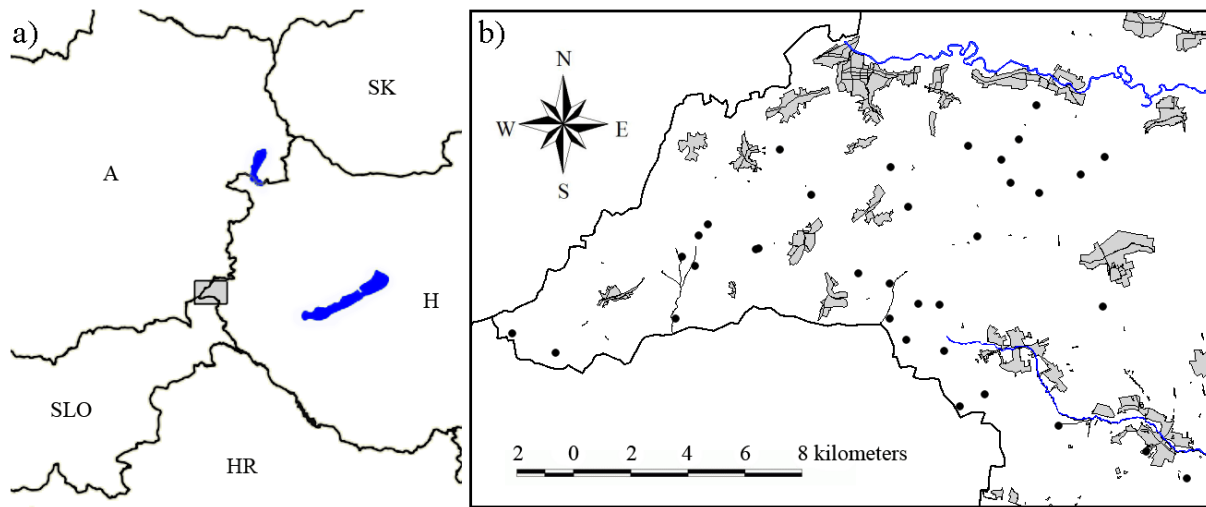
555 **Table 3** Mixed effect regression models for tree level bryophyte and lichen species
556 richness as dependent variables. Explanatory variables were tree species, DBH (diameter at
557 breast height), relative light and their interactions as fixed factors; and plot as random factor.
558 Fixed effect selection was made by maximum likelihood method (ML), random effect was
559 tested by restricted maximum likelihood method (REML) using the Chi² distribution for the
560 estimation of significance. For comparison the log.ratio (log-likelihood ratio) of the
561 explanatory variables within fixed effect was explained as percentage. Significance levels
562 were indicated by stars: *= p < 0.05; **= p < 0.01; ***= p < 0.001

	Log.ratio	
	Bryophytes	Lichens
Fixed effects	364.32*** (100%)	264.94*** (100%)
Tree species	295.94*** (81.2%)	169.18*** (63.9%)
DBH	22.86*** (6.3%)	47.37*** (17.9%)
Relative light	5.19* (1.4%)	60.96*** (23.0%)
Tree species: DBH	14.84** (4.1%)	12.39* (4.7%)
Tree: light	12.60* (3.5%)	9.15 ^{ns} (3.5%)
Random factor (plot)	347.46***	246.06***

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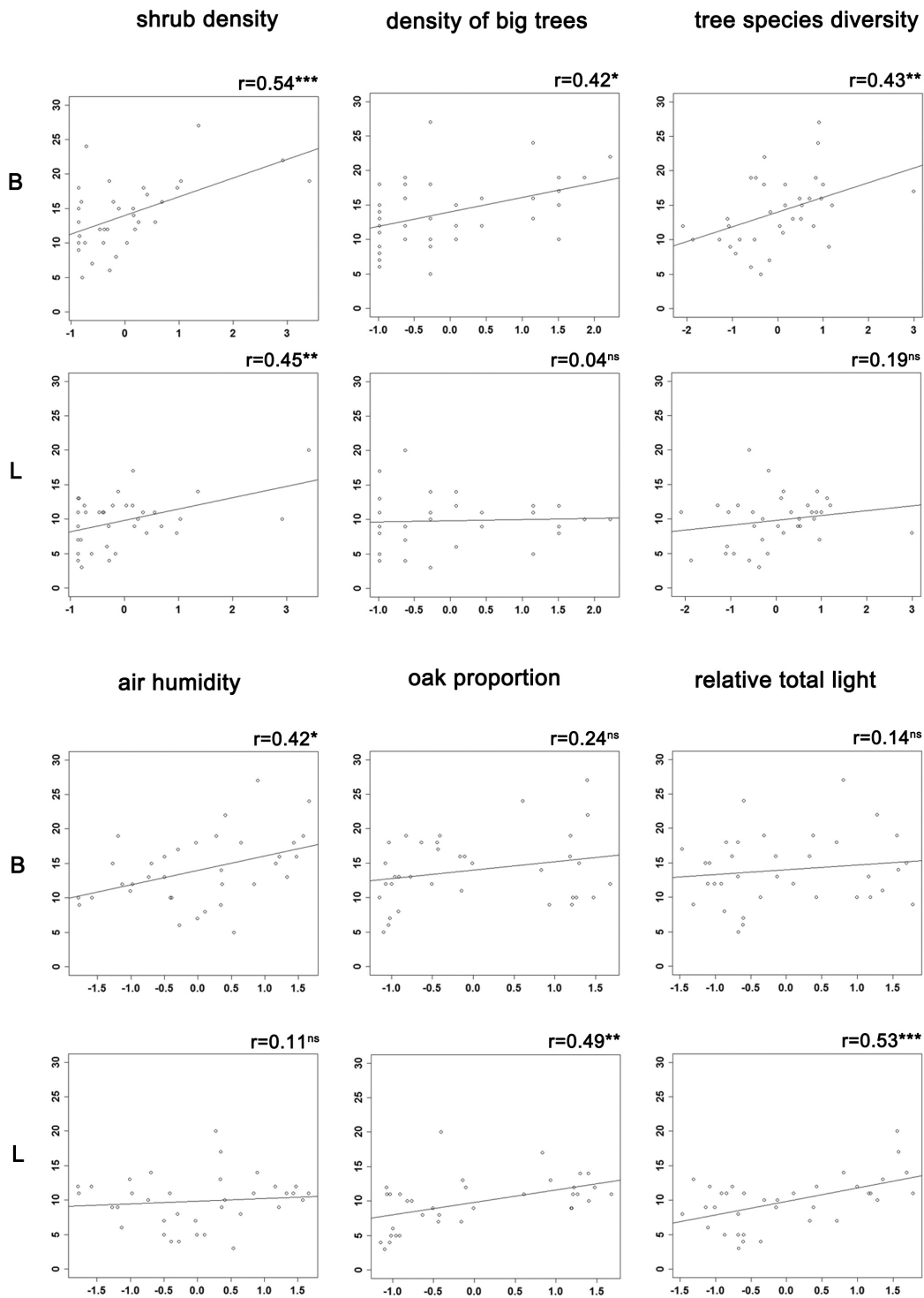
565 **Fig. 1** Geographical position of the studied area (a, grey rectangle) and the studied plots (b)
566 represented by black dots, built-up areas are grey.



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569 **Fig. 2** Correlations of bryophyte (B) and lichen (L) species richness between some selected
 570 explanatory variables, indicated as columns. Vertical axes: species richness values; horizontal
 571 axes: standardized values of the explanatory variables. 'r=' represents the correlation
 572 coefficients (n=35); their significance is indicated by stars: ns= non-significant; *= p<0.05;
 573 **= p<0.01; ***= p<0.001

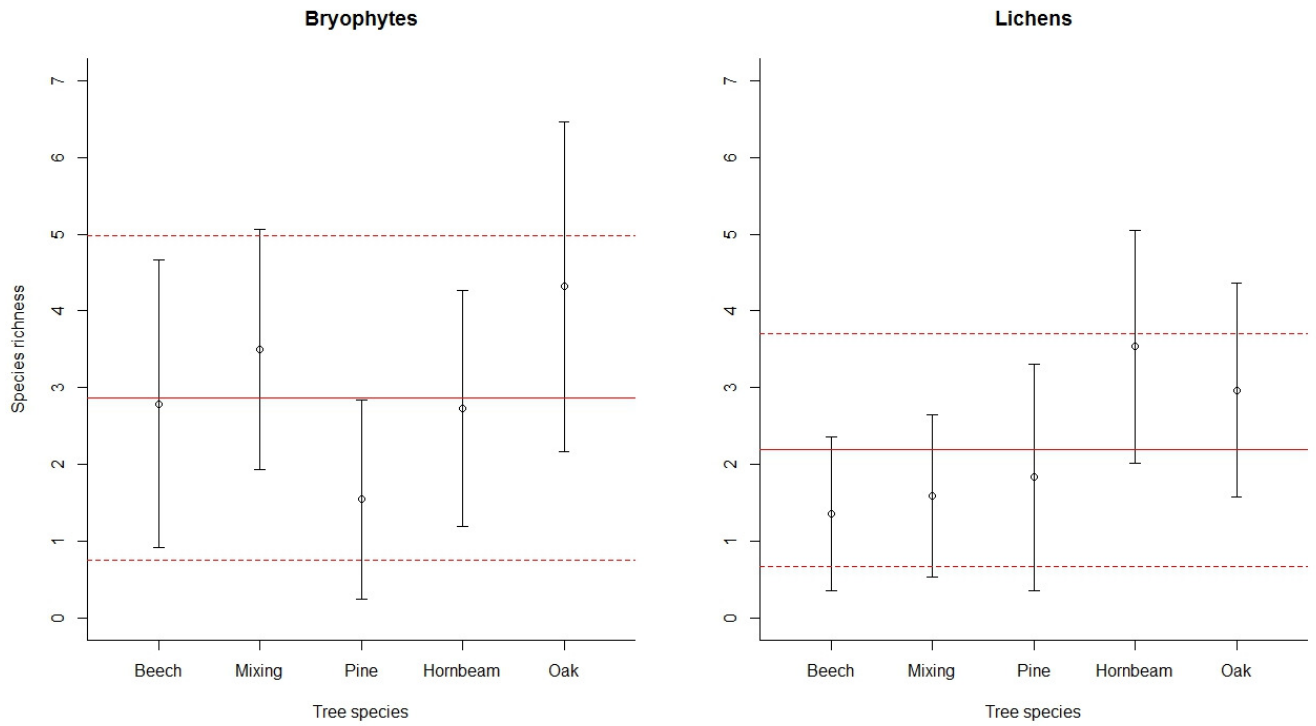


575 **Fig. 3** Tree level species richness of bryophytes and lichens on different tree species. Points

576 are the means, whiskers are the standard deviations. Solid lines are general means, dashed

577 lines are general standard deviations

578

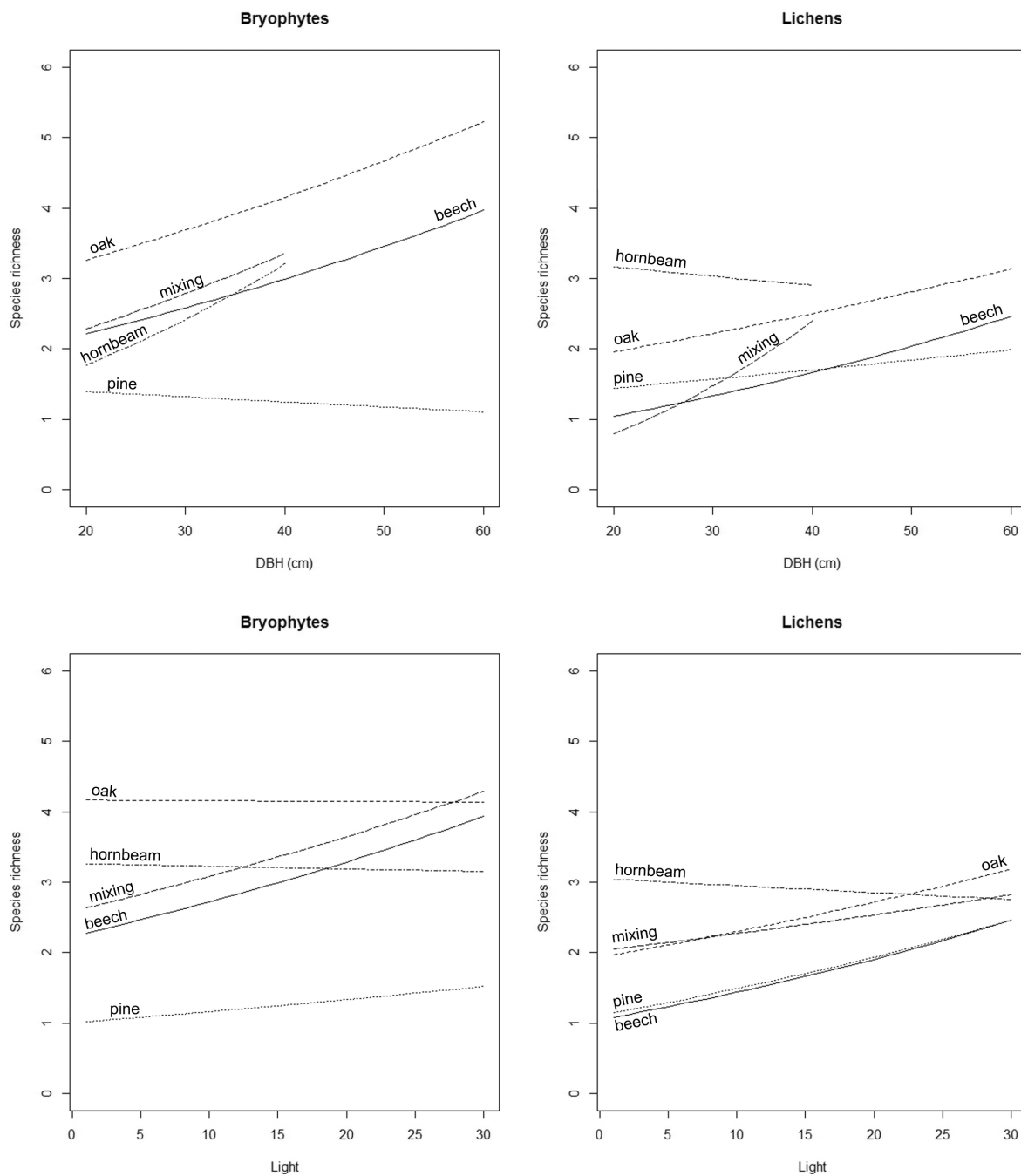


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582 **Fig. 4** Predicted tree level species richness values of bryophytes and lichens (in columns)
583 using tree species, DBH (top figures) and relative light (bottom figures) as explanatory
584 variables. For DBH effect light, for light effect DBH was fixed at their median values. Tree
585 species are indicated by different line types and text. For hornbeam and mixing trees the range
586 of diameter was lower than for other trees, because the abundance of larger individuals is low
587 in the studied region



588