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1 **Patterns and drivers of β -diversity and similarity of *Lobaria pulmonaria***
2 **communities in Italian forests**

3
4 Juri Nascimbene^{1*}, Renato Benesperi², Giorgio Brunialti³, Immacolata Catalano⁴, Marilena Dalle
5 Vedove⁵, Maria Grillo⁶, Deborah Isocrono⁷, Enrica Matteucci⁷, Giovanna Potenza⁸, Domenico
6 Puntillo⁹, Michele Puntillo⁹, Sonia Ravera¹⁰, Guido Rizzi¹¹, Paolo Giordani¹¹

7
8 ¹Dipartimento di Scienze della Vita, Università di Trieste, Italy; ²Dipartimento di Biologia
9 Evoluzionistica, Università di Firenze, Italy; ³TerraData environmetrics, Spin off accademico
10 dell'Università di Siena, Monterotondo Marittimo (GR) , Italy; ⁴Dipartimento ARBOPAVE,
11 Università di Napoli Federico II, Italy; ⁵Via Col Maoro, Pedavena, Belluno, Italy; ⁶Dipartimento di
12 Scienze Biologiche, Ecologiche ed Ambientali, Università di Catania, Italy; ⁷Dipartimento di
13 Scienze Agrarie, Forestali e Alimentari, Università di Torino, Italy; ⁸Dipartimento di Biologia,
14 Difesa e Biotecnologie Agro-Forestali Università della Basilicata, Italy; ⁹Museo di Scienze Naturali
15 della Calabria ed Orto Botanico, Università della Calabria, Italy; ¹⁰DiBT, Università del Molise,
16 Italy; ¹¹Polo Botanico Hanbury, DISTAV, Università di Genova, Italy

17
18 *Correspondence author.

19 E-mail: junasc@libero.it

20
21 **Running title:** Lichen communities in Italian forests

24 **Summary**

25 **1.** We attempted to elucidate the roles of β -diversity components and similarity in shaping *Lobaria*
26 *pulmonaria* lichen communities in Italian forests to provide scientific tools for improving their
27 long-term conservation.

28 **2.** A total of 20 sites were selected by stratified random sampling, including 5 chestnut forests, 7
29 beech-silver fir forests, and 8 oak forests distributed across 10 administrative regions of Italy. Site
30 selection was based on a national database including all the available records of *L. pulmonaria* in
31 Italy. In each forest, 4 plots were randomly placed, and in each plot 5-6 trees were randomly
32 selected for lichen sampling. For each forest and plot, meaningful predictors of lichen patterns were
33 quantified. In particular, factors indicative of both geographic conditions and forests structure were
34 considered. The SDR simplex approach was used to estimate the relative importance of similarity
35 (S), relative species replacement (R), and relative richness difference (D) to β -diversity and
36 similarity, while a hierarchical partitioning method was used to evaluate the relative importance of
37 environmental predictors in explaining their patterns.

38 **3.** A total of 201 lichens and 3 non-lichenized fungi were found, including 51 species of
39 conservation concern. The components of β -diversity and similarity contributed to shaping *L.*
40 *pulmonaria* communities at both forest and plot scales across Italy, resulting in nearly-random
41 compositions, i.e. the species set on each tree was a random sample from the available species pool.
42 Species replacement and similarity were generally associated with forest structure predictors, while
43 richness difference was mainly associated with geographic predictors. The implication of this is that
44 the long-term conservation of *L. pulmonaria* communities could be promoted by maintaining
45 scattered nodes and appropriate habitat traits, especially in large forested landscapes where species
46 turnover is higher.

47 **4. Synthesis.** In this work, we used a new approach for analysing a country-wide dataset improving
48 the ecological understanding of the dynamics regulating epiphytic communities. In particular, this
49 study improves the understanding of the contribution of different components of diversity across

50 two spatial scales and evaluates the relative importance of environmental predictors in explaining
51 variation of each diversity component.

52

53 **Key-words:** conservation, determinants of plant community diversity and structure, epiphytes,
54 forest structure, hierarchical partitioning, lichen, Natura 2000, richness difference, SDR simplex,
55 species replacement

56

57 **Introduction**

58 Most research on epiphytic lichens in forests has focused on analysing species richness and
59 composition patterns along ecological gradients, including climate and forest structure (Ellis 2012).
60 These studies have indicated that diversity patterns may depend on forest management, and provide
61 recommendations for improving lichen conservation (Ellis 2012). However, studies on community
62 patterns and background processes may contribute further information for refining conservation
63 measures. Analyses of β -diversity may provide insights into mechanisms and drivers influencing
64 lichen communities.

65 The way in which to properly define and quantify β -diversity remains controversial (e.g.
66 Whittaker 1960, 1972; Legendre *et al.* 2005; Baselga 2010; Podani & Schmera 2011). Podani &
67 Schmera (2011) considered three complementary indices that measure similarity (S), relative
68 species replacement (R), and relative richness difference (D) for given pairs of observations. These
69 authors evaluated the relative importance of β -diversity, defined as the additive result of R and D,
70 versus other possible ecological phenomena, namely nestedness and richness agreement, which
71 result from the additive effects of similarity with the other two complementary components (S+D
72 and S+R). In particular, similarity is considered to be the total number of species shared (*sensu*
73 Jaccard) between two observations.

74 The relative importance of these components on the target community may have different
75 implications for conservation ecology (Legendre *et al.* 2005). For instance, epiphytic lichen
76 communities characterized by high rates of species replacement (i.e. trees strongly differ in lichen
77 species composition) would require a number of protected sites to preserve the gene pools of the
78 species. A high plot-level replacement rate may correspond to a low level of nestedness at a higher
79 spatial scale, suggesting that effective conservation could be achieved by preserving a few scattered
80 groups of trees hosting the target community. This approach has rarely been adopted in lichen
81 ecology (e.g. Will-Wolf *et al.* 2006), and to our knowledge, no study has evaluated the effects of

82 different drivers on the components of β -diversity and species similarity along both geographical
83 and forest structure gradients at different spatial scales.

84 In this study, we targeted an epiphytic lichen community characterized by the occurrence of the
85 large foliose species *Lobaria pulmonaria* L. (Hoffm.). This assemblage is widespread across Italy in
86 different forest types, but is relatively rare. It is composed of several species restricted to humid,
87 scarcely-disturbed forests that are of conservation concern. The general aim of this work was to
88 elucidate the role of β -diversity components and similarity in shaping *L. pulmonaria* communities
89 in Italian forests to provide scientific tools to improve their long-term conservation.

90 First, we analysed patterns of β -diversity components (species replacement, R and richness
91 difference, D) and similarity (S) using the conceptual and methodological framework provided by
92 Podani & Schmera (2011). We tested for the consistency of R and D and S across two spatial scales
93 (within individual plots, and within the whole forest) that are usually addressed by conservation
94 studies. The contributions of β -diversity components and similarity may vary from plot to forest
95 scale, reflecting dispersal dynamics (e.g. Sillett *et al.* 2000), substrate features and forest conditions.
96 In general, we expected a mixed contribution of the three factors, but we hypothesized that species
97 replacement would prevail in pair-wise comparisons among trees of different plots (due to dispersal
98 limitations), while similarity would be most important in pair-wise comparisons among trees in the
99 same plot, where distances between pairs were low. Because we operated within the same
100 community, richness differences were expected to have a minor contribution, but may gain
101 importance under more favorable conditions where the local species pool is richer.

102 Second, we evaluated the roles and scale-consistencies of environmental factors indicative of
103 geographic conditions and forest structure in driving the patterns of β -diversity components. This
104 analysis was expected to elucidate the background mechanisms of community organization and to
105 result in practical suggestions for improving lichen conservation.

106 Finally, we contrasted common species with species of conservation concern, testing whether
107 patterns and drivers differed between these two groups. For each scale of observation (plot and

108 forest), our analyses were based on three datasets, one including all tree pairs, one including only
109 pairs of trees hosting species of conservation concern, and one including only pairs of trees without
110 species of conservation concern.

111

112 **Materials and methods**

113 *Sampling design and data collection*

114 A total of 20 macrosites were located within forest areas far from air pollution sources and with
115 negligible predicted modeled depositions of the main atmospheric pollutants (ISPRA 2008), where
116 the presence of *Lobaria pulmonaria* was known from previous observations and is indicative of
117 unpolluted conditions. Site selection was based on a national database including all the available
118 records of *L. pulmonaria* in Italy (unpublished data). Sites for which only historical information
119 (i.e. older than 50 years) was available and those for which habitat type was not clearly coded were
120 not considered. A further restriction was the inclusion of selected habitat types: we only considered
121 the three main habitat types that were suitable for *L. pulmonaria* and were widespread across Italy:
122 1) oak-dominated forests (including both deciduous species and *Quercus ilex* L.), 2) montane beech
123 forests (including mixed beech-silver fir formations), and 3) chestnut forests. The macrosites
124 included 5 chestnut forests, 7 beech-silver fir forests, and 8 oak forests distributed across 10
125 administrative regions (Figure 1). A total of 68 plots were selected by stratified random sampling.
126 In particular, in each forest macrosite, 4 plots (30×30 m) were randomly placed; the minimum
127 distance between plots was more than 500 m and the borders of the plots were at least 30 m from
128 the forest edge. Because of the small dimensions of the forests in Sardinia, only one plot per
129 macrosite was selected. Although the Sardinia sites biased the symmetry of the sampling design, we
130 retained these data in our analyses to obtain important information from a complete set of
131 biogeographic regions throughout the country.

132 For each forest and plot, some meaningful predictors of lichen patterns were quantified. In
133 particular, we considered factors indicative of both geographic conditions (including climate and

134 topography), responsible for large scale patterns (Giordani & Incerti, 2008; Marini *et al.* 2011), and
135 forests structure, such as tree species diversity, tree density, and size, responsible for local patterns
136 (Ellis, 2012; Table 1). Our variables did not show any significant deviation from normal
137 distribution as a result of a Shapiro-Wilk W test that was run preliminarily to further analysis. We
138 did not include factors indicative of air pollution since they are assumed to be of minor relevance in
139 our clean-aired forest sites. Moreover, we did not take into account other substrate-related
140 predictors (e.g. bark water retention and morphology), since we assumed that they play a relatively
141 minor role with respect to other variables, although that they were shown to drive to a certain extent
142 the distribution of lichen communities (e.g. Giordani 2006). In each plot, 5–6 trees (circumference
143 ≥ 40 cm) were randomly selected for lichen sampling. For each forest type, only trees of the same
144 species were selected. Lichen sampling followed the European guidelines for lichen monitoring
145 (Asta *et al.* 2002). A total of 368 trees were complexively sampled. Lichens were sampled using
146 four standard frames (10×50 cm, subdivided into 5 10×10 cm quadrats) that were attached to the
147 tree trunk facing the cardinal points with the bottoms 100 cm from the ground. All lichen species
148 inside the frames were tallied, and their frequencies were computed as the number of 10×10 cm
149 quadrats in which the species occurred. Nomenclature and general information on species biological
150 traits and ecology were retrieved from Nimis & Martellos (2008). In a few cases, *taxa* have been
151 only determined at genus level. However, at those trees where this situation occurred we have not
152 registered any possible overlapping with other possible confounding species already occurring in
153 the sample, which could have affected the calculation of S, D and R indices. Moreover, we
154 considered as species of conservation concern (see Appendix S1 in Supporting Information) those
155 classified as 'very rare' and 'extremely rare' in ITALIC, the reference Information System on Italian
156 Lichens (Nimis & Martellos 2008).

157

158 (B) *Multi Response Permutation Procedures*

159 Compositional differences among forest types were tested by multi response permutation
160 procedures (MRPP) as implemented in PC-ORD (McCune & Mefford, 1999). MRPP was used to
161 test differences between stand types as well as for the total, i.e. all the stand types pooled together.
162 Jaccard dissimilarity was used to calculate the distance matrix between plots. The mean within-
163 group distance was weighted as $C_i = n_i/N$, where n_i is the number of plots in forest type i and N is
164 the total number of plots. Finally, the effect size was calculated as the chance-corrected within-
165 group agreement (A) and the P value was used for evaluating how likely an observed difference
166 was due to chance ($A = 1$ indicates perfectly homogenous groups, while $A = 0$ indicates within-
167 group heterogeneity equal to chance expectation).

168

169 (B) *SDR simplex*

170 We used the SDR simplex approach (Podani & Schmera 2011) to estimate the relative
171 importance of β -diversity and similarity in our presence/absence data matrices. The SDR partitions
172 pairwise gamma diversity into additive components, which are calculated as three complementary
173 indices measuring similarity, relative species replacement, and relative richness difference for all
174 pairs of trees. Calculations were computed using the computer program SDR Simplex (Podani
175 2011). In particular, the three indices were calculated as follows (see Podani & Schmera 2011 for
176 more details).

177 Similarity (S) was calculated according to the Jaccard coefficient of similarity:

$$178 \quad S_{\text{Jac}} = a/n \quad \text{Eqn 1}$$

179 where a is the number of species shared by two sites (trees, in our context) and n is total number of
180 species.

181 Richness difference (D) was calculated as the ratio of the absolute difference between the species
182 numbers of each site (b, c) and the total number of species, n :

$$183 \quad D = |b - c|/n \quad \text{Eqn 2}$$

184 Finally, species replacement (R) was given by

185
$$R = 2 * \min\{b, c\} / n$$
 Eqn 3

186 The SDR results can be graphed with a ternary plot using the Ternary Plot option in the NonHier
187 routine of the SYN-TAX 2000 package (Podani 2001). In the ternary plot, each vertex corresponds
188 to one index (S, D, or R). Each pair of data in the presence/absence data matrix is plotted according
189 to its similarity, richness difference and species replacement values, so that the proximity of a point
190 to a vertex is proportional to the respective coefficient value.

191 The analyses were conducted on three distinct datasets at both forest- and at plot-levels. Datasets
192 were compiled based on the conservation status of the species (Figure 2):

- 193 - The c dataset included only between-plot or between-forest pairs involving trees hosting species of
194 conservation concern.
- 195 - The o dataset included only between-plot or between-forest pairs involving trees hosting species
196 not of conservation concern.
- 197 - The t dataset included all the possible between-plot or between-forest pairs.

198

199 *(B) Beta diversity sensu Baselga (2012)*

200 The debate on the most appropriate way to decompose β -diversity is a current issue in ecology (see
201 Podani & Schmera 2011; Almeida-Neto *et al.* 2012). Although most of our analyses were based on
202 the SDR approach by Podani & Schmera (2011), we also performed calculations of species
203 replacement (turnover, β_{jtu}) and nestedness (β_{jne}) sensu Baselga (2012) for the t dataset, as a further
204 validation of the models describing the drivers of community composition in our dataset. In
205 particular, the species turnover is defined as

206

207
$$\beta_{jtu} = 2 \min(b, c) / a + 2 \min(b, c)$$
 Eqn 4

208

209 where $\min(b, c)$ is the minimum number of exclusive species.

210 We measured nestedness as:

211

$$\beta_{jne} = [\max(b - c) - \min(b, c)] / (a + b + c) * [a / a + 2 \min(b, c)] \quad \text{Eqn 5}$$

213

214 Computations on β -diversity *sensu* Baselga were performed using the betapart package (Baselga &
215 Orme, 2012) for R (R Development Team, 2012).

216

217 (B) *Friedman ANOVA and Kruskal-Wallis ANOVA*

218 We performed a Friedman ANOVA for multiple dependent variables on species replacement,
219 richness difference, and similarity components, by comparing the t, c and o datasets at those forests
220 and plots for which no missing cases occurred.

221 Data were also analysed by Friedman's ANOVA by ranks. This test is an alternative to one-way
222 within-subjects analysis of variance. This test compares variables measured in dependent samples.
223 The Friedman ANOVA by ranks test assumes that the variables (levels) under consideration were
224 measured on at least an ordinal (rank order) scale. The null hypothesis for the procedure is that the
225 different columns of data contain samples drawn from the same population, or specifically,
226 populations with identical medians.

227 Finally, the non-parametric Kruskal–Wallis ANOVA was used to check the significance of the
228 differences in species replacement, richness difference, and similarity components among plot and
229 forest level.

230

231 (B) *Hierarchical Partitioning*

232 We used hierarchical partitioning (HP) (Chevan & Sutherland 1991) to evaluate the relative
233 importance of environmental predictors in explaining variation in β -diversity components (D and R)
234 and similarity (S). Hierarchical partitioning jointly considers all possible models in a multiple
235 regression and identifies the most likely causal factors. The analysis splits the variation explained
236 by each variable into a joint effect together with the other explanatory variables and into an

237 independent effect not shared with any other variable. The HP was conducted using the Hier.Part
238 package (version 1.0–3; Walsh & Mac Nally 2008) implemented in R version 2.14.1 (R
239 Development Core Team 2012). The estimated relative importance of each variable was represented
240 by the size of its pure effect.

241

242 **Results**

243 *Lichen species in Lobaria pulmonaria-dominated communities of Italian forests*

244 A total of 201 lichens and 3 non-lichenized fungi were found, including 51 species of
245 conservation concern (see Appendix S1 in Supporting Information). Crustose lichens comprised
246 107 of the species; the remaining were macrolichens, including squamulose species. Most of the
247 species (148) had chlorococcoid green algae as main photobiont, while 27 had trentepohlioid green
248 algae and 26 cyanobacteria. *Lobaria pulmonaria* was found on 43% (206 out of 480) of the trees.
249 The mean numbers of species were 39.6 (9–68) per forest, 25.2 (5–53) per plot, and 11.2 (1–30) per
250 tree.

251

252 *MRPP*

253 We used MRPP to evaluate the most significant differences of lichen species composition between
254 forest types at plot level (Table 2). The higher the A value (chance-corrected within-group
255 agreement), the stronger the between-group difference ($P < 0.05$). The overall forest type
256 categorization did not show significant compositional dissimilarities. The pairwise comparisons
257 among forest types also showed weak and insignificant A-statistics.

258

259 *Patterns of β -diversity components and similarity*

260 The SDR simplex analysis revealed that the structures of *L. pulmonaria*-dominated communities
261 were nearly random, with a substantial equilibrium between β -diversity, nestedness, and richness
262 agreement (Figure 3). Even when considering both spatial scales (plot and forest) and the

263 disaggregated c and o datasets, the relative contributions of species replacement, richness
264 difference, and similarity were comparable. For most cases, the distributions of the components of
265 diversity were consistent among spatial scales when analysed using KW-ANOVA (Table 3).
266 Significant differences were only observed for β_{jtu} , β_{jne} and St, the former being higher at forest
267 level, whereas the two latter showed a higher contribution at plot level.

268 However, when considering the same dataset and spatial level, R was always the main
269 component (Table 4); its contribution ranged from 40–50%, while S ranged from 27–39%,
270 whereas D was the least important component in all cases, never exceeding 26% (Table 1).

271 At the plot level, the S of trees both with and without species of conservation concern was
272 significantly lower than that observed for the whole dataset ($P=0.031$; Table 4). Significant
273 differences were not found for the remaining comparisons, meaning that species replacement,
274 species similarity, and richness difference were essentially the same, irrespective of whether species
275 of conservation concern occurred on the trees. These latter results were mostly consistent across the
276 two spatial scales of this study (plot and forest level; Table 3 and Table 4).

277

278 *Hierarchical partitioning of independent effects of environmental predictors of β -diversity and*
279 *similarity components*

280 *Species replacement (R)*

281 Both at both plot and forest levels, R was generally associated with forest structure predictors
282 (Table 5 and Table 6), with minor differences among the c, o and t datasets concerning the total
283 amount of variation explained, the best predicting variables, and the percentage of variation for
284 which they accounted. In particular, the average distance between trees was positively correlated
285 with species replacement, especially at the forest level, where this factor was the best predictor both
286 for the T and C datasets. Increasing the distance between trees from 2 to 8 m increased species
287 replacement up to 55% (Figure 4). For Ro (R for the o dataset), the best variables at the forest level
288 were the number of large trees with a modeled replacement increasing from 40% to 60%, along

289 with an increase in the number of large trees from 0 to 60, although the distance between trees was
290 also relevant. Moreover, species replacement for lichens of conservation concern (R_c) was higher in
291 larger than in smaller forests. Species replacement between trees hosting species of conservation
292 concern (R_c) was higher in disetaneous plots (i.e. with higher standard deviation of circumference),
293 whereas only R_o was positively associated with a geographic predictor, being higher in northern
294 than in southern plots.

295

296 *Similarity (S)*

297 At the forest level, forest structure variables were the best predictors of species similarity (Table
298 5 and Table 6). In particular, the estimated St and Sc in forests with only one tree species was twice
299 as high as those with eight species. At the plot level, St was negatively related to longitude, and
300 both Sc and So were mainly associated with habitat type, with habitat explaining 46.1% and 44.6%
301 of the total variation, respectively. Tree pairs including species of conservation concern showed a
302 lower similarity (Sc) in *Quercus* forests than in other habitats, whereas So was higher in beech-
303 silver fir forests (Figure 6).

304

305 *Richness difference (D)*

306 Richness difference between trees was largely associated with geographic predictors, even
307 though a contribution of forest structure variables (especially $StDevCirc$ and $NLargeTree$) was also
308 detectable (Table 5 and Table 6). The D_c and D_o at the forest level and D_t at the plot level
309 decreased from $\approx 30\%$ to $\approx 10\%$ from western to eastern forests; the latter showed considerable
310 uniformity of richness between trees (Figure 5). A similar decrease also occurred with an increase
311 in elevation, which was the best predictor for D_t at the forest level and D_c at the plot level. An
312 independent effect of rainfall, up to 43% of the total variation, drove R_o at the plot level.

313

314 *Species turnover and nestedness sensu Baselga (2012)*

315 At the plot level β_{jtu} and β_{jne} showed opposite and comparable patterns in relation with the average
316 distance between trees (AvDistTree). This variable accounted for most variation (37.6%) of β_{jne} also
317 at forest level, whereas main differences of β_{jtu} at this scale were related to the habitat, being the
318 species turnover higher in *Castanea* and *Fagus* than in *Quercus* forests (Figure 7).

319

320 **Discussion**

321 The components of β -diversity and similarity contributed to shaping *L. pulmonaria* communities
322 at both forest and plot scales across Italy, resulting in nearly-random compositions, i.e. the species
323 set on each tree was a random sample from the available species pool. Consequently, the working
324 hypothesis of a prevailing effect of replacement at the forest level due to dispersal limitations,
325 versus a higher importance of similarity at the plot level, should be rejected. This pattern was
326 consistent across the three datasets, indicating that species of conservation concern are subjected to
327 the same processes ruling the whole community, although in some cases the driving factors may
328 differ. In the study conducted by Will-Wolf *et al.* (2006), who investigated the species turnover
329 across spatial scales in the USA, the datasets coming from two different forest biomes with different
330 lichen floras, had several similarities in lichen community structure and relationships with
331 environmental variables, corroborating the hypothesis that comparisons in term of community
332 structure may give valuable insights into the generality of relations between community patterns
333 and environmental variables across spatial scales and regions.

334 Despite the mixed contribution of the two β -diversity components and of similarity, at both
335 spatial scales species replacement was in general the main component. Species replacement is likely
336 to gain importance in larger forests where, according to an area effect (Berglund & Jonsson 2001;
337 Jönsson *et al.* 2011), the available species pool is expected to be richer than in smaller ones, as
338 indicated by our results. This β -diversity component was mainly influenced by factors indicative of
339 forest structure, being positively related with the distance between trees, which is likely to reflect
340 dispersal dynamics and habitat conditions. This outline is also corroborated by the results on species

341 turnover and nestedness *sensu* Baselga (2012), indicating that these components of β -diversity are
342 basically driven by the same forest structure factors. The increase of species replacement is likely to
343 increase the species pool of the community which in turn could benefit from the maintenance or the
344 creation of relatively open-canopied forests (Jönsson *et al.* 2011). This interpretation is supported
345 by the tendency to have higher species replacement in chestnut forests, which are usually less dense
346 than beech and oak forests. Two further factors related to forest structure influence patterns of
347 species replacement: tree size heterogeneity, indicative of forest habitat heterogeneity, and the
348 presence of large old trees. In both cases, the increase in species replacement may reflect the
349 positive effect of these factors on the available species pool (e.g. Brunialti *et al.* 2010; Jüriado *et al.*
350 2009). In particular, large old trees are known to be more lichen rich and to host more
351 heterogeneous species assemblages than young trees (Nascimbene *et al.* 2009a). The consistent
352 patterns of species replacement across both plot and forest scales may be due to the fact that we
353 operated in homogeneously-forested landscapes and within the same community. In this situation,
354 unlike in fragmented landscapes, species dispersal is likely to be ruled by short-distance dynamics,
355 and the available species pool is limited by the ecological requirements of species. However, the
356 consistency of this pattern across scales may also reflect the importance of autogenic processes in
357 shaping lichen communities. These processes are rarely addressed (e.g. Rogers 1990), and further
358 research in this field could better elucidate the background processes determining species
359 replacement.

360 The contribution of pairwise similarity in shaping *L. pulmonaria* communities was higher at plot
361 level when considering the t dataset, but it was consistent across the two spatial scales when c and o
362 disaggregated datasets were concerned. The drivers of similarity at the two spatial scales were
363 different. At the forest scale, tree species diversity was far more important, while at the plot scale
364 habitat type prevailed, with some differences between pairs with or without species of conservation
365 concern. The importance of tree species for epiphytic lichens is well documented (e.g. Lewis &
366 Ellis 2010; Nascimbene *et al.* 2009b; Thor *et al.* 2010; Uliczka & Angelstam 1999), and is mainly

367 because of chemical and physical features of the bark (for a synthesis see Ellis 2012). Our results
368 suggest that increasing forest composition diversity should trigger an increase in the species pool of
369 *L. pulmonaria* communities, including species of conservation concern. At the plot level, our results
370 highlight the importance of habitat type. In particular, in oak-dominated plots, lichen assemblages
371 between trees hosting species of conservation concern were less similar than in other habitats, while
372 similarity between trees was higher in beech-silver fir plots. This is the only forest type in which
373 this component, calculated for the whole dataset (t), has even higher values than species
374 replacement, indicating higher compositional homogeneity between trees than in the other forest
375 types. These findings suggest that management practices to ensure lichen conservation should be
376 tailored to habitat type. For example, in Italy, retention groups in oak forests should be larger than
377 in other habitats, while in beech-silver fir forests they could consist of a few trees which are likely
378 to host similar assemblages of lichens. Furthermore, these results support the background idea of
379 this study highlighting that the analysis of underlying processes structuring lichen communities may
380 contribute relevant information for refining conservation measures. The analysis of species
381 composition did not reveal differences among forest types suggesting that similar management
382 could be applied to conserve *L. pulmonaria* communities across forest habitats. However, the
383 analyses on β -diversity components and similarity revealed that some processes structuring *L.*
384 *pulmonaria* communities may differ among habitats, such in the case of species similarity,
385 supporting the need for habitat-specific management.

386 As expected, differences in species richness played a minor role in lichen β -diversity and
387 similarity, because they were mainly influenced by bioclimatic conditions. Pairwise differences in
388 species richness increased along a longitudinal gradient, from eastern to western forests, which may
389 be due to the fact that many suboceanic lichens of the *L. pulmonaria* community occupied more
390 favorable conditions along the western side of the peninsula that were influenced by humid
391 Tyrrhenian winds (Nimis & Tretiach 1995; Giordani & Incerti 2008; Marini *et al.* 2011). These
392 findings were also corroborated by the importance of elevation and rainfall. In both cases, under

393 less favorable conditions (i.e. higher elevation and lower rainfall) the differences between tree pairs
394 decreased. However, these differences were also caused by the same forest structure-related factors
395 that drive species replacement, such as the distance among trees, tree size heterogeneity, and the
396 number of large trees. According to the framework proposed by Podani & Schmera (2011), species
397 replacement and richness differences define species turnover between pairs. Our results suggest that
398 these parameters are in part determined by similar background mechanisms.

399 Our research indicated that in Italy the long-term conservation of *L. pulmonaria* communities
400 could be promoted by maintaining scattered nodes and appropriate habitat traits (e.g. large trees,
401 open canopy, high tree diversity), especially in large forested landscapes where species turnover is
402 higher. This finding highlights the usefulness of the ecological networking approach, based on
403 rigorous habitat mapping, promoted by Natura 2000 (e.g. see Council Directive 92/43/EEC), the
404 application of which may benefit from the use of rapid methods for detecting priority forests
405 (Nascimbene *et al.* 2010). As already determined for some vascular plants of conservation concern
406 (e.g. orchids) whose presence indicates habitat priority, the presence of an *L. pulmonaria*
407 community could be a criterion for attributing a priority status to chestnut, oak, and beech-silver fir
408 forests. This community, that in our survey is mainly composed of species preferring trees with
409 subacid- to subneutral bark and avoids eutrophication (Nimis and Martellos 2008), may also be a
410 suitable indicator of environmental conditions related to air pollution. In particular, the
411 sensitiveness of *L. pulmonaria* and associated species to eutrophication would allow to use it
412 countrywide for monitoring the effects of nitrogen deposition which are increasingly threatening
413 natural ecosystems (Sutton *et al.* 2009; Gillian *et al.* 2011) and are detectable in term of shifts in
414 species composition of lichen communities (Geiser *et al.* 2010; Pinho *et al.*, 2012).

415

416

417

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421 his constructive remarks on the structure of the work. We are also grateful to two anonymous
422 referees and to the associate Editor Frank Gilliam for their constructive suggestions that helped us
423 in improving the effectiveness of our work.

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519

520 SUPPORTING INFORMATION

521 Additional supporting information may be found in the online version of this article:

522 Appendix S1- **Lichenized and non-lichenized fungi considered in this study**

523

524 Table 1. Descriptive statistics of *Lobaria pulmonaria* communities: response variables and
525 environmental predictors (forest type mean \pm SD). The variable “number of tree species (NspTree)”
526 indicates the number of different tree species that occurred within plots and forest types. * *sensu*
527 Baselga (2012)

Subset	Code	Description	Forest level			Plot level		
			Beech forests (Fag)	Chestnut forests (Cast)	Oak-dominated forests (Querc)	Beech forests (Fag)	Chestnut forests (Cast)	Oak-dominated forests (Querc)
Response variables	β_{jtu}	Species turnover* (Tdataset)	0.60 \pm 0.13	0.71 \pm 0.08	0.61 \pm 0.18	0.59 \pm 0.12	0.72 \pm 0.09	0.63 \pm 0.17
	β_{jne}	Species nestedness* (T dataset)	0.10 \pm 0.06	0.07 \pm 0.03	0.12 \pm 0.10	0.02 \pm 0.07	0.06 \pm 0.03	0.13 \pm 0.13
	R _T	Species replacement (T dataset)	42.5 \pm 4.4	53.0 \pm 7.5	41.1 \pm 14.7	35.7 \pm 10.3	46.1 \pm 9.7	38.6 \pm 14.4
	R _C	Species replacement (C dataset)	45.0 \pm 4.7	52.7 \pm 9.6	45.2 \pm 11.1	43.4 \pm 8.7	47.3 \pm 12.8	49.1 \pm 14.8
	R _O	Species replacement (O dataset)	49.8 \pm 16.2	56.1 \pm 10.9	43.7 \pm 15.8	41.9 \pm 10.9	51.9 \pm 10.2	46.1 \pm 15.9
	D _T	Richness difference (T dataset)	20.3 \pm 6.3	19.9 \pm 6.1	27.7 \pm 13.2	19.5 \pm 8.1	19.4 \pm 7.5	25.1 \pm 12.3
	D _C	Richness difference (C dataset)	19.8 \pm 5.3	19.8 \pm 5.5	24.7 \pm 9.1	22.5 \pm 8.5	20.9 \pm 16.3	29.0 \pm 16.1
	D _O	Richness difference (O dataset)	13.9 \pm 10.6	19.8 \pm 6.0	23.9 \pm 13.3	25.0 \pm 10.3	21.8 \pm 11.6	31.9 \pm 10.9
	S _T	Similarity (T dataset)	37.2 \pm 5.7	27.1 \pm 9.5	31.2 \pm 9.3	44.8 \pm 9.5	34.5 \pm 11.0	36.3 \pm 13.4
	S _C	Similarity (C dataset)	35.3 \pm 8.6	27.6 \pm 10.6	30.1 \pm 8.8	34.1 \pm 11.7	31.8 \pm 13.1	21.9 \pm 10.1
	S _O	Similarity (O dataset)	37.3 \pm 7.4	24.1 \pm 11.8	32.4 \pm 13.7	33.1 \pm 9.4	26.3 \pm 9.4	22.0 \pm 11.8
Location, climate	Lat	UTM WGS84 Latitude (m)	4653261 \pm 379818	4718576 \pm 261489	4407293 \pm 138686	4666609 \pm 364684	4718576 \pm 239965	4348239 \pm 156365
	Long	UTM WGS84 Longitude (m)	565104 \pm 130514	514983 \pm 100811	470612 \pm 51042	567344 \pm 127593	514983 \pm 92520	460048 \pm 62706
	Elev	Elevation (m)	1223 \pm 229	876 \pm 167	850 \pm 202	1237 \pm 126	619 \pm 32	988 \pm 36
	LogArea	Logarithm of the forest site area	-0.2 \pm 0.6	0.4 \pm 0.9	-0.3 \pm 1.3	NA	NA	NA
	Rain	Yearly average rainfall (mm/m ² year)	1641 \pm 466	1828 \pm 758	1018 \pm 249	1644 \pm 592	1828 \pm 696	1002 \pm
Forest structure	NspTree	Number of tree species (#)	1.3 \pm 0.8	2.2 \pm 2.7	2.8 \pm 1.8	2.1 \pm 0.8	1.8 \pm 1.4	3.1 \pm 1.7
	AvDistTree	Average distance between trees (m)	4.7 \pm 1.1	7.0 \pm 1.4	5.4 \pm 1.3	4.5 \pm 1.4	6.7 \pm 2.0	4.9 \pm 1.2
	NLargeTree	Number of large trees (trunk circumference > 120 cm)	36.6 \pm 22.1	36.4 \pm 13.3	8.1 \pm 6.9	9.8 \pm 6.5	9.1 \pm 3.4	4.1 \pm 3.7
	StDevCirc	Standard deviation of the trunk circumference	36.4 \pm 15.7	47.1 \pm 9.4	34.9 \pm 17.5	32.8 \pm 13.6	56.5 \pm 9.9	20.1 \pm 8.6

528

529 Table 2. A-statistics (chance-corrected within-group agreement) after MRPP analysis on forest types at forest
530 level. The *P* value is the significance of the pairwise delta value for differences between groups (ns = non
531 significant differences)

	A-statistics	P level
All forest types	0.050	0.099 ^{ns}
Cast vs. Fag	0.052	0.133 ^{ns}
Querc vs. Fag	0.013	0.312 ^{ns}
Querc vs. Cast	0.046	0.148 ^{ns}

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540 Table 3. Kruskal-Wallis ANOVA for comparing the consistency of the distribution of β -diversity
541 and similarity components among spatial levels

542

	ANOVA K-W	<i>P</i>
β_{tu}	27.204	0.0001***
β_{jne}	10.219	0.0014**
Rt	3.117	0.077
Rc	0.013	0.909
Ro	0.330	0.565
Dt	0.691	0.406
Dc	0.036	0.849
Do	2.444	0.118
St	6.035	0.014*
Sc	0.004	0.951
So	1.017	0.313

543

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545

546 Table 4. Friedman ANOVA on similarity (S), relative species replacement (R), and relative richness
 547 difference (D) components of *Lobaria pulmonaria* communities. Comparisons were made between
 548 of pairs of trees including all lichen species (t), only pairs with species of conservation concern (c),
 549 and only pairs with other species not of conservation concern (o) in the same plots and forests. *
 550 $P < 0.05$. Degree of freedom = 2 for all the comparisons.

551

	Plot Level			Forest level		
	Average ± st. dev.	Chi square	<i>P</i>	Average ± st. dev.	Chi square	<i>P</i>
Rt	44.4±11.8	0.636 (n=22)	0.727	49.0±7.5	2.426 (n=12)	0.297
Rc	47.4±15.0			48.6±9.5		
Ro	48.7±12.4			53.4±11.4		
Dt	19.8±9.2	0.636 (n=22)	0.727	19.7±6.8	2.783 (n=12)	0.249
Dc	25.2±17.8			21.1±6.7		
Do	23.7±12.0			17.2±8.5		
St	35.7±11.3	6.909 (n=22)	0.031*	31.3±10.3	1.167 (n=12)	0.558
Sc	27.4±14.6			30.3±10.4		
So	27.6±11.5			29.7±12.7		
Rt	44.6±11.0	15.700 (n=20)	0.0004*	39.8±12.0	45.129 (n=68)	0.000001*
Dt	23.2±9.9			20.9±9.4		
St	32.3±8.8			39.3±11.9		
Rc	47.2±9.2	18.778 (n=18)	0.00008*	46.3±11.9	31.600 (n=45)	0.000001*
Dc	21.7±7.1			23.5±13.9		
Sc	31.1±9.3			30.2±12.7		
Ro	49.8±14.3	9.143 (n=14)	0.010*	47.3±12.8	17.077 (n=39)	0.0002*
Do	19.6±10.4			25.8±11.6		
So	30.8±12.0			26.9±10.8		

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554

555 Table 5. R² and hierarchical partitioning of independent effects (%) of statistically significant
556 (p<0.05) predictors on β -diversity variables for pairs of trees of the complete dataset (t). Best
557 predictors for each response variable are in bold; the signs (+, -) represent the direction of the
558 correlations

	Rt	Dt	St	β_{ju}	β_{ne}	Rt	Dt	St	β_{ju}	β_{ne}
R ² Independent	0.442	0.536	0.452	0.613	0.477	0.325	0.222	0.522	0.191	0.197
R ² Total	0.749	0.927	0.966	0.813	0.515	0.488	0.299	0.763	0.256	0.287
Level	Forest				Plot					
Predictor										
Lat										
Long					24.9	36.5 (-)		48.3 (+)		
Elev	42.3 (-)		24.8		12.3	27.6		18.4		
LogArea	30.6				24.1					
Rain			8.6							
AbiFag			15.3		9.6		11.9			
Cast	23.9				28.2				27.9	20.6
Querc			16.8		46.2					
NspTree	13.1		37.1 (-)		30.2		21.3		16.2	
AvDistTree	32.5 (+)		22.8		37.6 (-)		32.1 (+)		55.9 (+)	
NLargeTree							35.8		23.5	
StDevCirc			32.3		29.6		25.2			

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564 Table 6. R² and hierarchical partitioning of independent effects (%) of statistically significant
 565 (P<0.05) predictors on β-diversity variables for pairs of trees with lichen species of Conservation
 566 Concern (c) and other species (o). Best predictors for each response variable are in bold; the signs
 567 (+, -) represent the direction of the correlations

568

	Rc	Ro	Rc	Ro	Dc	Do	Dc	Do	Sc	So	Sc	So
R ² Independent	0.337	0.606	0.400	0.558	0.310	0.572	0.415	0.374	0.451	0.414	0.352	0.434
R ² Total	0.484	0.858	0.882	0.922	0.441	0.349	0.619	0.916	0.498	0.605	0.953	0.946
Level	Forest		Plot		Forest		Plot		Forest		Plot	
Predictor												
Lat		37.6		42.3 (+)				28.1			34.9	
Long				16.2	23.2 (-)	57.5 (-)						
Elev						21.3	43.0 (-)		26.7		44.3	
LogArea												
Rain			22.2		15.7		40.1	43.2 (-)				26.1
AbiFag			12.8	16.9							9.6	44.6
Cast	25.8			12.2						18.4		
Querc					23.0						46.1	16.5
NspTree	33.3								73.3 (-)			
AvDistTree	40.8 (+)	24.1		12.2	18.4			28.7		37.7 (-)		
NLargeTree		38.6 (+)	7.8			21.2				9.0		12.8
StDevCirc			57.2 (+)		19.7		16.1					

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570

571 **Figure captions:**

572 Fig 1. Geographic locations of survey sites of *Lobaria pulmonaria* communities. Circles: chestnut
573 forests; squares: oak-dominated forests; triangles: beech forests.

574

575 Fig 2. Schematic representation of tree-pair datasets used in this work. Two plots (1 and 2) are
576 located within Forest 1. Black dots represent trees colonized by species of conservation concern,
577 whereas white dots represent trees with other species. Six datasets were built using the similarity,
578 relative species replacement, and relative richness difference components of tree pairs. The plot-
579 level o dataset included only within-plot pairs of trees without lichens of conservation concern
580 ('other species') (pair #1 for Plot 1 and Pair #2 for Plot 2). The plot-level c dataset included only
581 within-plot pairs of trees hosting species of conservation concern (pair #3 for Plot 1 and Pair #4 for
582 Plot 2). The forest-level o dataset included only between-plots pairs of trees without species of
583 conservation concern (pairs #5 to #8). The forest-level c dataset included only between-plots pairs
584 of trees hosting species of conservation concern (pairs #9 to #12). The forest-level and plot-level t
585 datasets included all possible between-plot pairs and all possible within-plots pair, respectively
586 (some links not shown).

587

588 Fig 3. SDR simplex ternary plots for the *Lobaria pulmonaria* community datasets. The
589 abbreviations S, D and R refer to relative similarity, richness difference, and species replacement,
590 respectively. Dots represent pairs included in the datasets of each plot (left column) and forest (right
591 column).

592

593 Fig 4. Scatterplots of best predictors for lichen species replacement at forest and plot levels.

594

595 Fig 5. Scatterplots of best predictors for lichen richness differences at forest and plot levels.

596

597 Fig 6. Scatterplots of best predictors for lichen similarity at forest and plot levels.

598

599 Fig 7. Scatterplots of best predictors for species replacement (turnover, β_{tu}) and nestedness (β_{jne})

600 *sensu Baselga* (2012) for the t dataset at forest and plot levels.

601

602

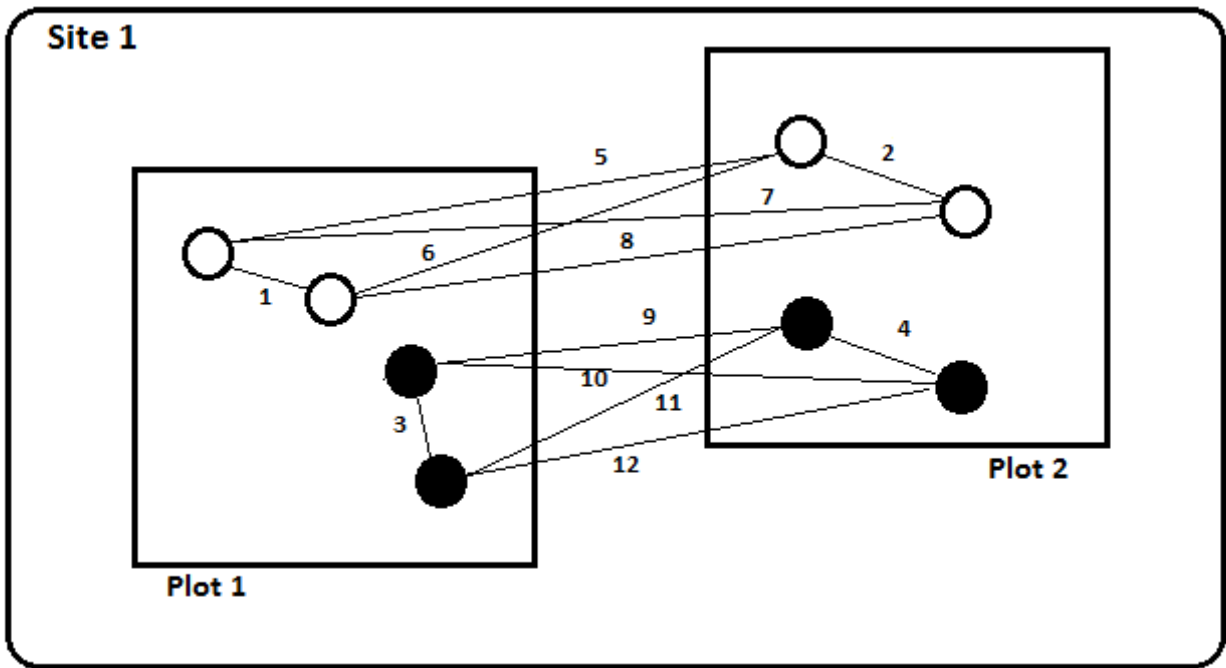
603 **Figure 1**



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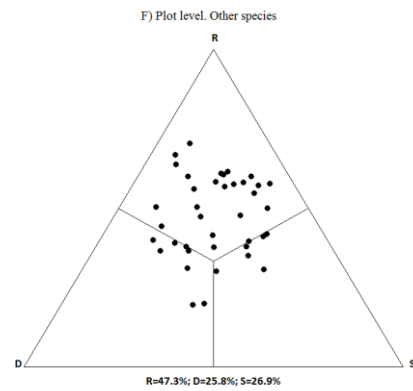
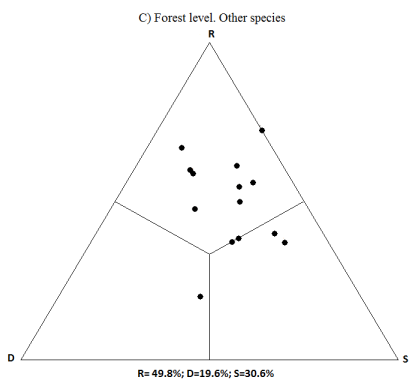
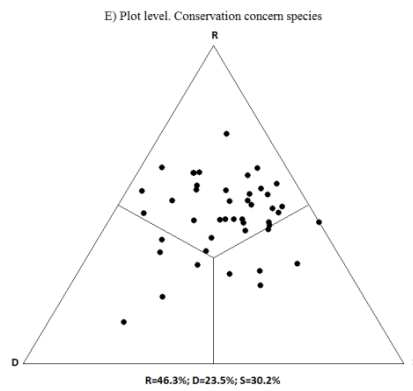
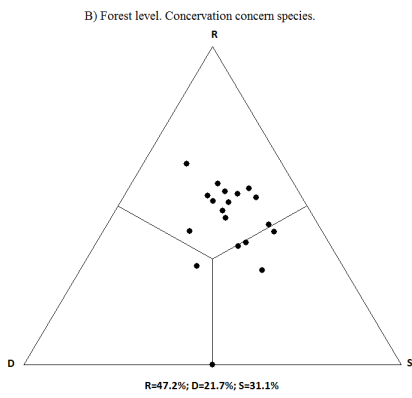
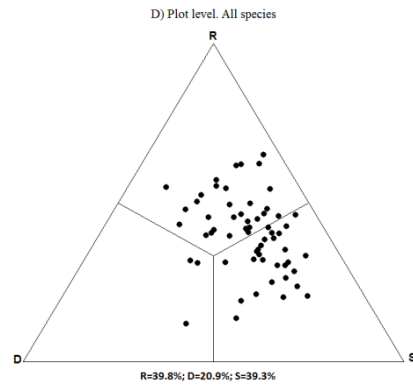
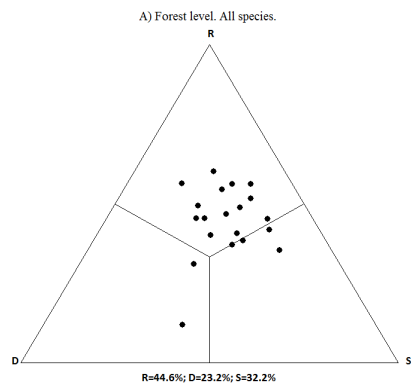
606 Figure 2



607

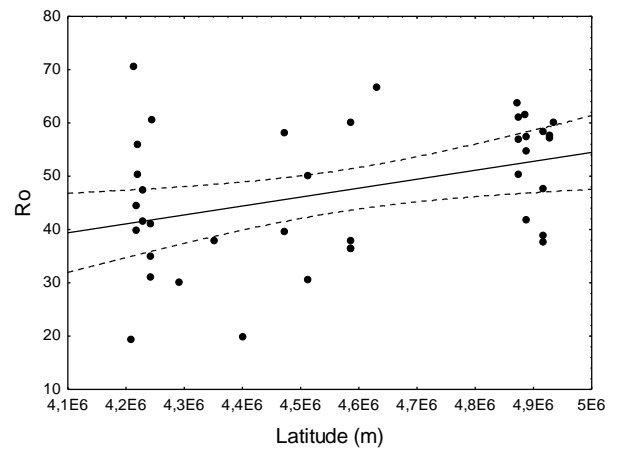
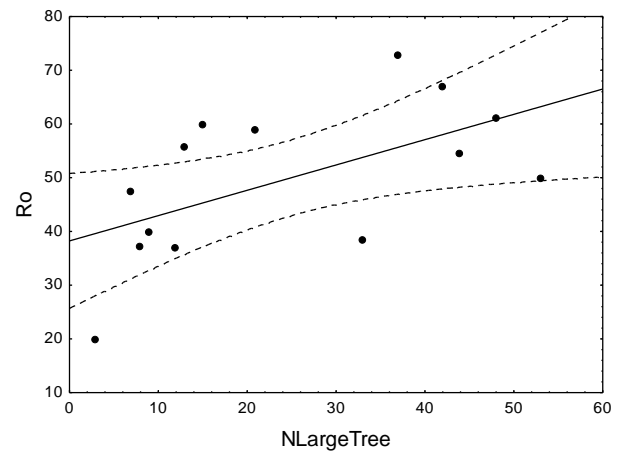
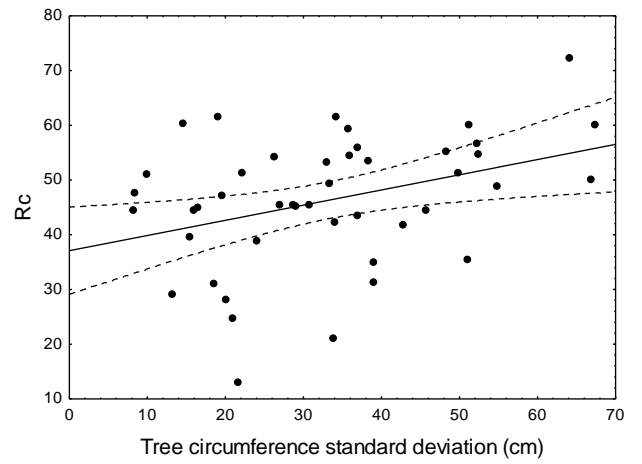
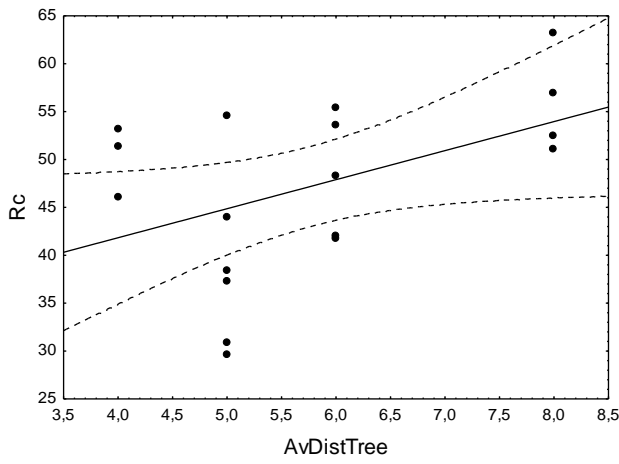
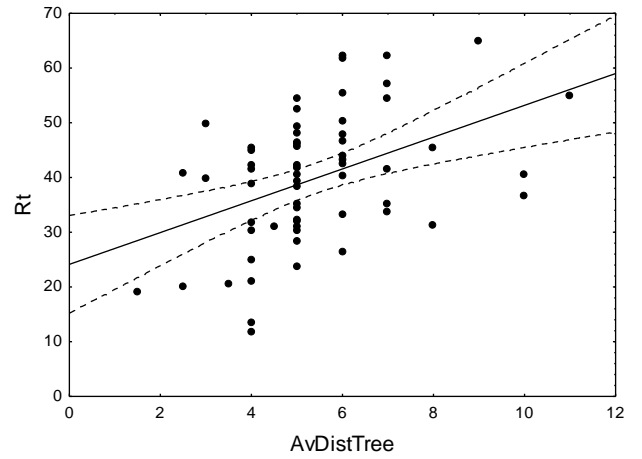
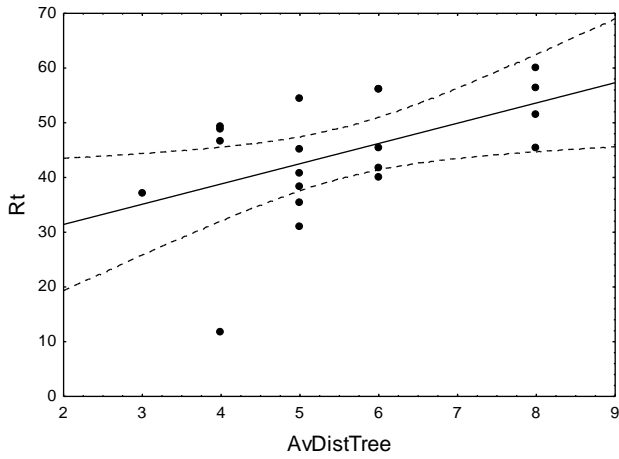
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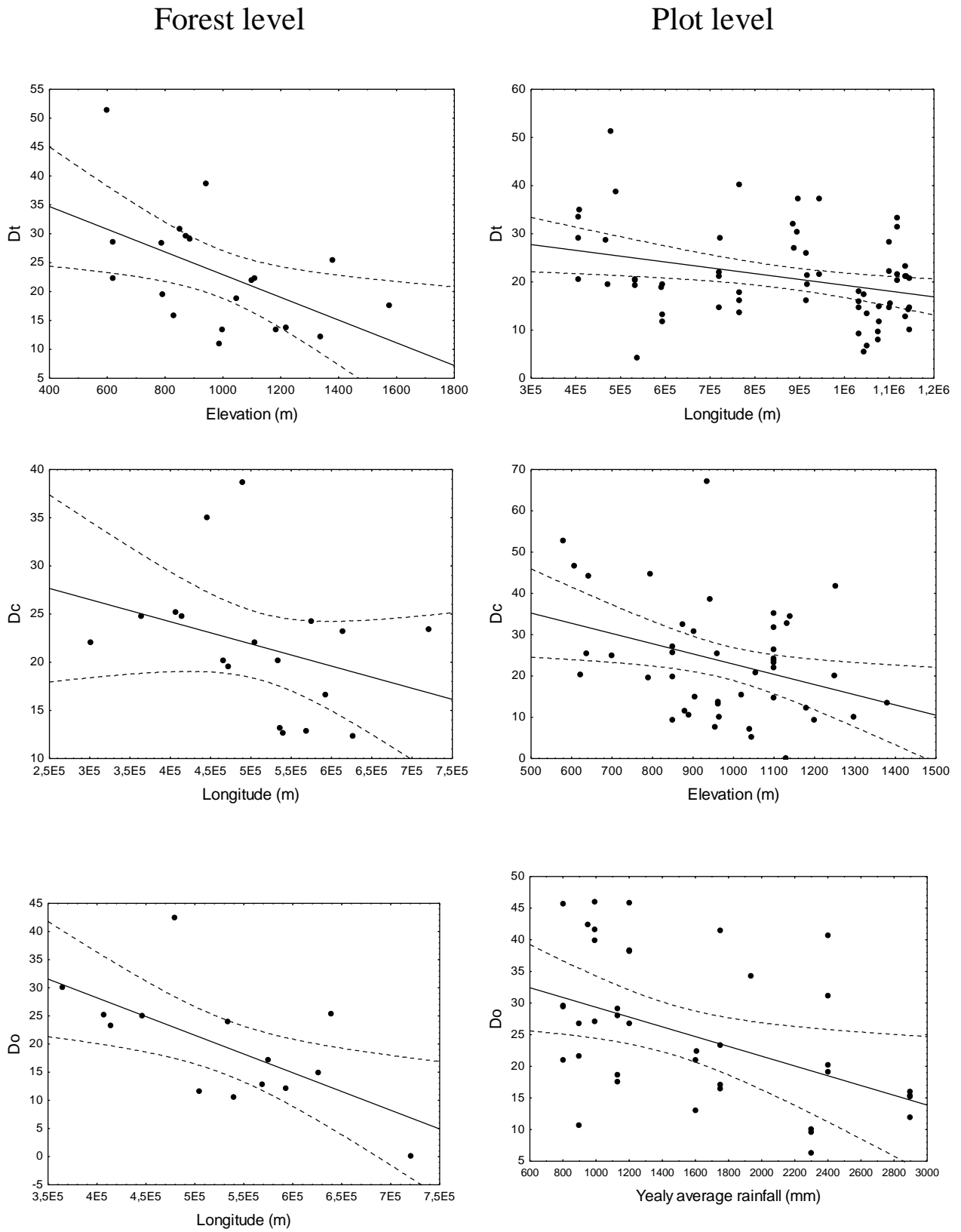
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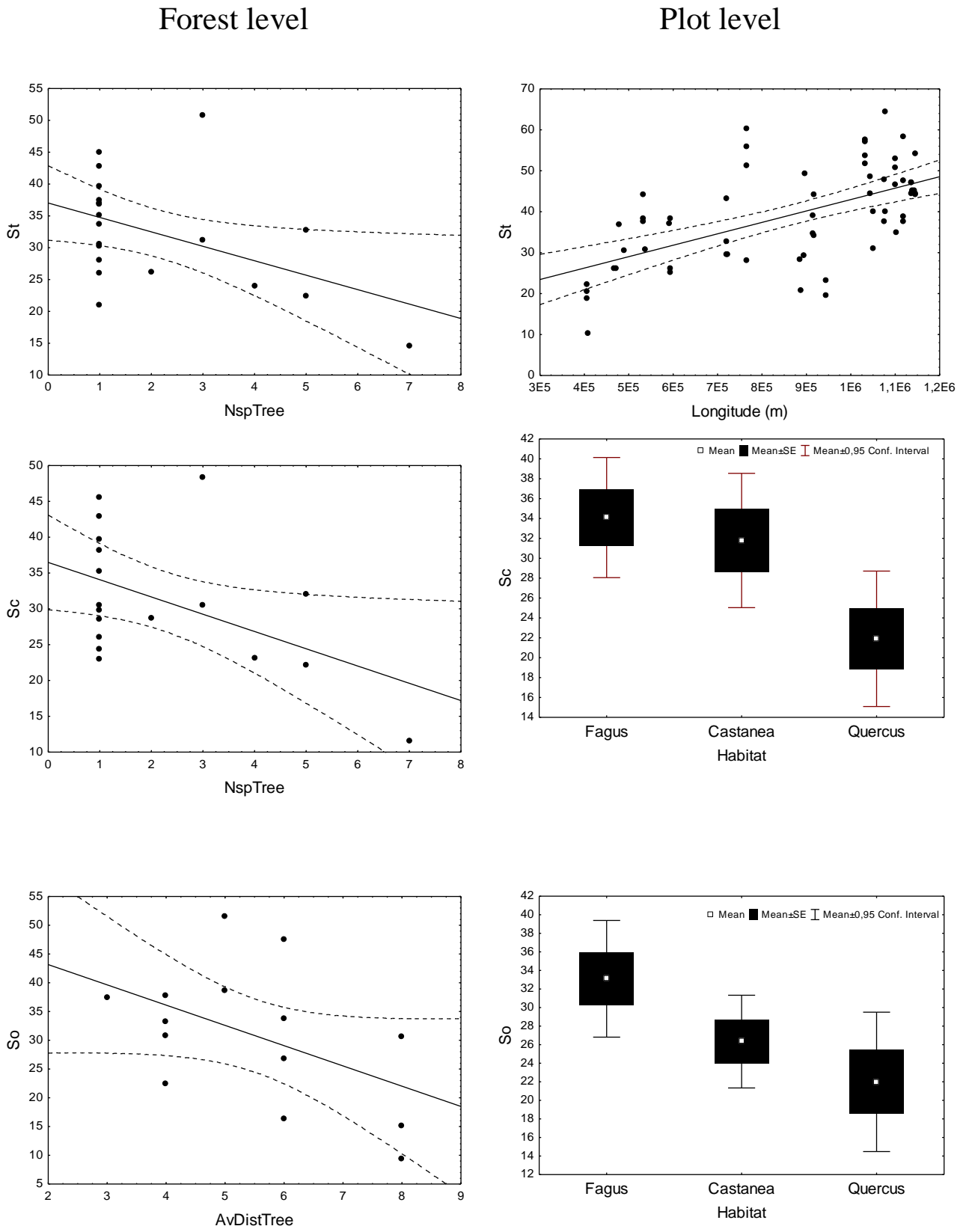


Forest level

Plot level

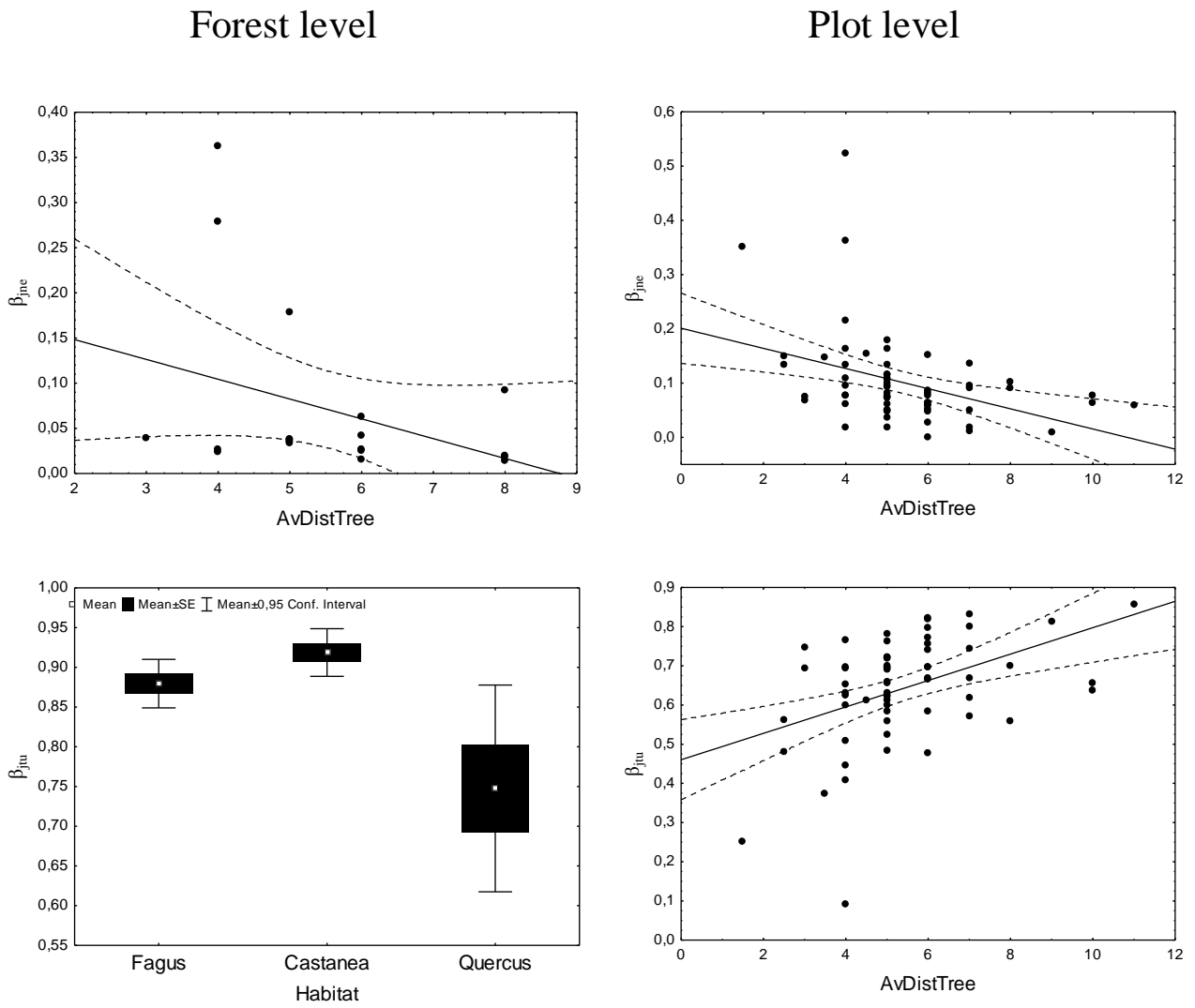






621 **Figure 7**

622



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