

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

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Summary

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

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

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

4. *Synthesis*. In this work, we used a new approach for analysing a countrywide data set improving the ecological understanding of the dynamics regulating epiphytic communities. In particular, this study improves the understanding of the contribution of different components of diversity across two spatial scales and evaluates the relative importance of environmental predictors in explaining variation of each diversity component.

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

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Introduction

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

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

The relative importance of these components on the target community may have different implications for conservation ecology (Legendre, Daniel Borcard & Peres-Neto 2005). For instance, epiphytic lichen communities characterized by high rates of species replacement (i.e. trees strongly differ in lichen species composition) would require a number of protected sites to preserve the gene pools of the species. A high plot-level replacement rate may correspond to a low level of nestedness at a higher spatial scale, suggesting that effective conservation could be achieved by preserving a few scattered groups of trees hosting the target community. This approach has rarely been adopted in lichen ecology (e.g. Will-Wolf *et al.* 2006), and to our knowledge, no study has evaluated the effects of different drivers on the components of β -diversity and species similarity along both geographical and forest structure gradients at different spatial scales.

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

First, we analysed patterns of β -diversity components (species replacement, R and richness difference, D) and similarity (S) using the conceptual and methodological framework provided by Podani & Schmera (2011). We tested for the consistency of R and D and S across two spatial scales (within

individual plots, and within the whole forest) that are usually addressed by conservation studies. The contributions of β -diversity components and similarity may vary from plot to forest scale, reflecting dispersal dynamics (e.g. Sillett *et al.* 2000), substrate features and forest conditions. In general, we expected a mixed contribution of the three factors, but we hypothesized that species replacement would prevail in pair-wise comparisons among trees of different plots (due to dispersal limitations), while similarity would be most important in pair-wise comparisons among trees in the same plot, where distances between pairs were low. Because we operated within the same community, richness differences were expected to have a minor contribution, but may gain importance under more favourable conditions where the local species pool is richer.

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

Finally, we contrasted common species with species of conservation concern, testing whether patterns and drivers differed between these two groups. For each scale of observation (plot and forest), our analyses were based on three data sets, one including all tree pairs, one including only pairs of trees hosting species of conservation concern, and one including only pairs of trees without species of conservation concern.

Materials and methods

SAMPLING DESIGN AND DATA COLLECTION

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



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

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

Supporting Information) those classified as ‘very rare’ and ‘extremely rare’ in ITALIC, the reference Information System on Italian Lichens (Nimis & Martellos 2008).

MULTI-RESPONSE PERMUTATION PROCEDURES

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

SDR SIMPLEX

We used the SDR simplex approach (Podani & Schmera 2011) to estimate the relative importance of β -diversity and similarity in our presence/absence data matrices. The SDR partitions pairwise gamma diversity into additive components, which are calculated as three complementary indices measuring similarity, relative species replacement and relative richness difference for all pairs of trees. Calculations were computed using the computer program SDR Simplex (Podani 2001). In particular, the three indices were calculated as follows (see Podani & Schmera 2011 for more details).

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

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

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

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

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

Finally, species replacement (R) was given by

$$R = 2 * \min\{b, c\}/n \quad \text{eqn 3}$$

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

The analyses were conducted on three distinct data sets at both forest levels and at plot levels. Data sets were compiled based on the conservation status of the species (Fig. 2):

- 1 The c data set included only between-plot or between-forest pairs involving trees hosting species of conservation concern.
- 2 The o data set included only between-plot or between-forest pairs involving trees hosting species not of conservation concern.

Table 1. Descriptive statistics of *Lobaria pulmonaria* communities: response variables and environmental predictors (forest type mean \pm SD). The variable ‘number of tree species (NspTree)’ indicates the number of different tree species that occurred within plots and forest types

| 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_{ju} | Species turnover* (T data set) | 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_{jnc} | Species nestedness* (T data set) | 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 data set) | 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 data set) | 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 data set) | 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 data set) | 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 data set) | 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 data set) | 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 data set) | 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 data set) | 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 | | |
| Location, climate | S_O | Similarity (O data set) | 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 | | |
| | Lat | UTM WGS84 Latitude (m) | 4 653 261 \pm 379 818 | 471 8576 \pm 261 489 | 4 407 293 \pm 138 686 | 4 666 609 \pm 364 684 | 4 718 576 \pm 239 965 | 4 348 239 \pm 156 365 | | |
| | Long | UTM WGS84 Longitude (m) | 565 104 \pm 130 514 | 514 983 \pm 100 811 | 470 612 \pm 51 042 | 567 344 \pm 1 27 593 | 514 983 \pm 92 520 | 460 048 \pm 62 706 | | |
| | 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 248 | | |
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(continued)

Table 1. (continued)

| 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) | | |
| Forest structure | NspTree | Number of tree species (#) | 1.3 ± 0.8 | 2.2 ± 2.7 | 2.8 ± 1.8 | 2.1 ± 0.8 | 1.8 ± 1.4 | 3.1 ± 1.7 | | |
| | AvDistTree | Average distance between trees (m) | 4.7 ± 1.1 | 7.0 ± 1.4 | 5.4 ± 1.3 | 4.5 ± 1.4 | 6.7 ± 2.0 | 4.9 ± 1.2 | | |
| | NLargeTree | Number of large trees (trunk circumference >120 cm) | 36.6 ± 22.1 | 36.4 ± 13.3 | 8.1 ± 6.9 | 9.8 ± 6.5 | 9.1 ± 3.4 | 4.1 ± 3.7 | | |
| | StDevCirc | Standard deviation of the trunk circumference | 36.4 ± 15.7 | 47.1 ± 9.4 | 34.9 ± 17.5 | 32.8 ± 13.6 | 56.5 ± 9.9 | 20.1 ± 8.6 | | |

*Sensu Baselga (2012).

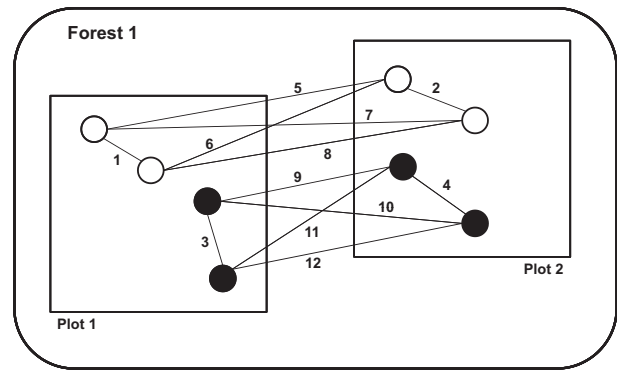


Fig 2. Schematic representation of tree-pair data sets used in this work. Two plots (1 and 2) are located within Forest 1. Black dots represent trees colonized by species of conservation concern, whereas white dots represent trees with other species. Six data sets were built using the similarity, relative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

3 The t data set included all the possible between-plot or between-forest pairs.

BETA DIVERSITY

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

$$\beta_{ju} = 2 \min(b, c) / a + 2 \min(b, c) \quad \text{eqn 4}$$

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

We measured nestedness as:

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

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

FRIEDMAN ANOVA AND KRUSKAL-WALLIS ANOVA

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

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

Finally, the nonparametric Kruskal–Wallis ANOVA was used to check the significance of the differences in species replacement, richness difference and similarity components among plot and forest level.

HIERARCHICAL PARTITIONING

We used hierarchical partitioning (HP) (Chevan & Sutherland 1991) to evaluate the relative importance of environmental predictors in explaining variation in β -diversity components (D and R) and similarity (S). Hierarchical partitioning jointly considers all possible models in a multiple regression and identifies the most likely causal factors. The analysis splits the variation explained by each variable into a joint effect together with the other explanatory variables and into an independent effect not shared with any other variable. The HP was conducted using the Hier. Part package (version 1.0–3; Walsh & Mac Nally 2008) implemented in R version 2.14.1 (R Development Core Team 2012). The estimated relative importance of each variable was represented by the size of its pure effect.

Results

LICHEN SPECIES IN *LOBARIA PULMONARIA*-DOMINATED COMMUNITIES OF ITALIAN FORESTS

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

MRPP

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

PATTERNS OF B-DIVERSITY COMPONENTS AND SIMILARITY

The SDR simplex analysis revealed that the structures of *L. pulmonaria*-dominated communities were nearly random,

Table 2. A-statistics (chance-corrected within-group agreement) after MRPP analysis on forest types at forest level. The P value is the significance of the pairwise delta value for differences between groups (ns = not 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} |

with a substantial equilibrium between β -diversity, nestedness and richness agreement (Fig. 3). Even when considering both spatial scales (plot and forest) and the disaggregated c and o data sets, the relative contributions of species replacement, richness difference and similarity were comparable. For most cases, the distributions of the components of diversity were consistent among spatial scales when analysed using KW-ANOVA (Table 3). Significant differences were only observed for β_{jtu} , β_{jne} and St, the former being higher at forest level, whereas the two latter showed a higher contribution at plot level.

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

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

HIERARCHICAL PARTITIONING OF INDEPENDENT EFFECTS OF ENVIRONMENTAL PREDICTORS OF B-DIVERSITY AND SIMILARITY COMPONENTS

Species replacement (R)

Both at both plot and forest levels, R was generally associated with forest structure predictors (Tables 5 and 6), with minor differences among the c, o and t data sets concerning the total amount of variation explained, the best predicting variables, and the percentage of variation for which they accounted. In particular, the average distance between trees was positively correlated with species replacement, especially at the forest level, where this factor was the best predictor both for the T and C data sets. Increasing the distance between trees from 2 to 8 m increased species replacement up to 55% (Fig. 4). For Ro (R for the o data set), the best variables at the forest level were the number of large trees with a modelled replacement increasing from 40% to 60%, along with an increase in the

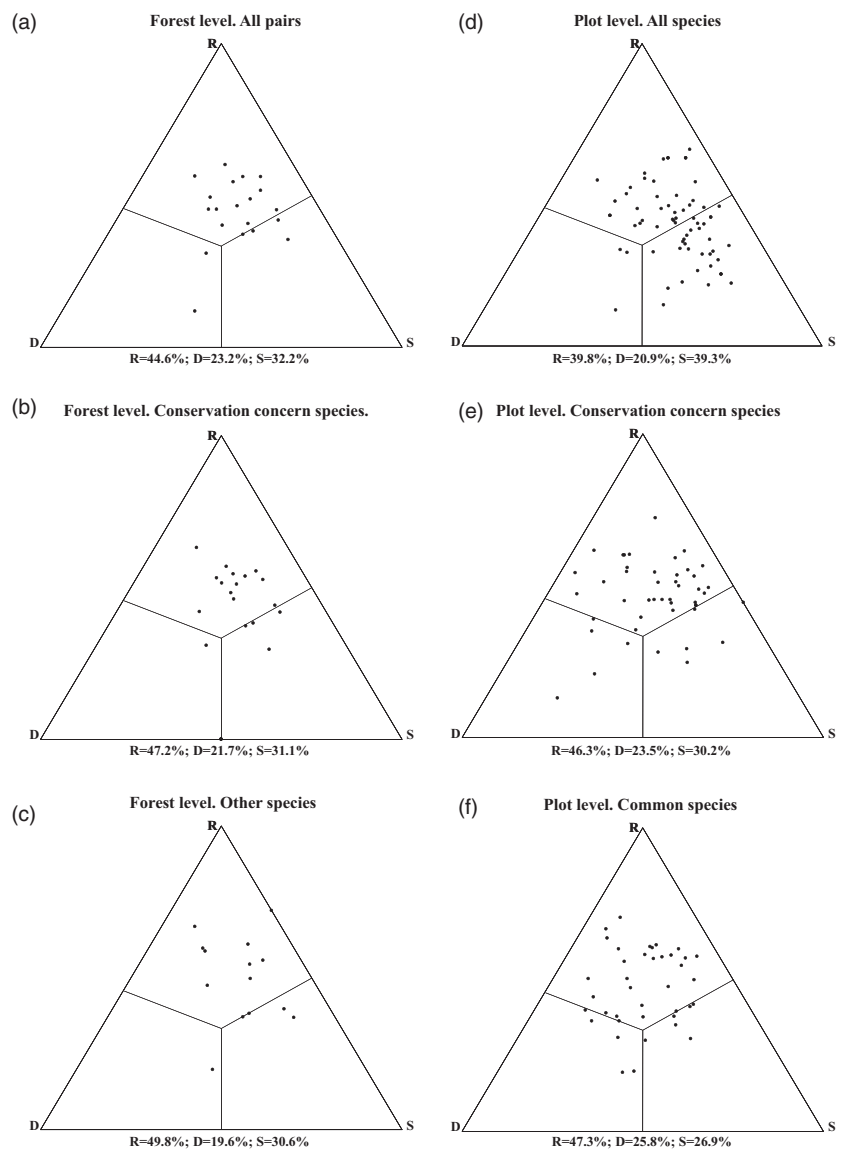


Fig 3. SDR simplex ternary plots for the *Lobaria pulmonaria* community data sets. The abbreviations *S*, *D* and *R* refer to relative similarity, richness difference, and species replacement, respectively. Dots represent pairs included in the data sets of each plot (left column) and forest (right column).

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

| | ANOVA K-W | <i>P</i> |
|---------------|-----------|----------|
| β_{jtu} | 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 |

number of large trees from 0 to 60, although the distance between trees was also relevant. Moreover, species replacement for lichens of conservation concern (Rc) was higher in

larger than in smaller forests. Species replacement between trees hosting species of conservation concern (Rc) was higher in disetaneous plots (i.e. with higher standard deviation of circumference), whereas only Ro was positively associated with a geographic predictor, being higher in northern than in southern plots.

Similarity (*S*)

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

Table 4. Friedman anova on similarity (*S*), relative species replacement (*R*) and relative richness difference (*D*) components of *Lobaria pulmonaria* communities. Comparisons were made between of pairs of trees including all lichen species (t), only pairs with species of conservation concern (c), and only pairs with other species not of conservation concern (o) in the same plots and forests

| | Plot level | | | Forest level | | |
|----|--------------|-------------------------|----------|--------------|-------------------------|-----------|
| | Average ± SD | χ^2 | <i>P</i> | Average ± SD | χ^2 | <i>P</i> |
| Rt | 44.4 ± 11.8 | 0.636 (<i>n</i> = 22) | 0.727 | 49.0 ± 7.5 | 2.426 (<i>n</i> = 12) | 0.297 |
| Rc | 47.4 ± 15.0 | | | 48.6 ± 9.5 | | |
| Ro | 48.7 ± 12.4 | 0.636 (<i>n</i> = 22) | 0.727 | 53.4 ± 11.4 | 2.783 (<i>n</i> = 12) | 0.249 |
| Dt | 19.8 ± 9.2 | | | 19.7 ± 6.8 | | |
| Dc | 25.2 ± 17.8 | 6.909 (<i>n</i> = 22) | 0.031* | 21.1 ± 6.7 | 1.167 (<i>n</i> = 12) | 0.558 |
| Do | 23.7 ± 12.0 | | | 17.2 ± 8.5 | | |
| St | 35.7 ± 11.3 | 15.700 (<i>n</i> = 20) | 0.0004* | 31.3 ± 10.3 | 45.129 (<i>n</i> = 68) | 0.000001* |
| Sc | 27.4 ± 14.6 | | | 30.3 ± 10.4 | | |
| So | 27.6 ± 11.5 | 18.778 (<i>n</i> = 18) | 0.00008* | 29.7 ± 12.7 | 31.600 (<i>n</i> = 45) | 0.000001* |
| Rt | 44.6 ± 11.0 | | | 39.8 ± 12.0 | | |
| Dt | 23.2 ± 9.9 | 9.143 (<i>n</i> = 14) | 0.010* | 20.9 ± 9.4 | 17.077 (<i>n</i> = 39) | 0.0002* |
| St | 32.3 ± 8.8 | | | 39.3 ± 11.9 | | |
| Rc | 47.2 ± 9.2 | 9.143 (<i>n</i> = 14) | 0.010* | 46.3 ± 11.9 | 17.077 (<i>n</i> = 39) | 0.0002* |
| Dc | 21.7 ± 7.1 | | | 23.5 ± 13.9 | | |
| Sc | 31.1 ± 9.3 | 9.143 (<i>n</i> = 14) | 0.010* | 30.2 ± 12.7 | 17.077 (<i>n</i> = 39) | 0.0002* |
| Ro | 49.8 ± 14.3 | | | 47.3 ± 12.8 | | |
| Do | 19.6 ± 10.4 | 9.143 (<i>n</i> = 14) | 0.010* | 25.8 ± 11.6 | 17.077 (<i>n</i> = 39) | 0.0002* |
| So | 30.8 ± 12.0 | | | 26.9 ± 10.8 | | |

**P* < 0.05. d.f. = 2 for all the comparisons.

Table 5. R^2 and hierarchical partitioning (HP) of independent effects (%) of statistically significant (*P* < 0.05) predictors on β -diversity variables for pairs of trees of the complete data set (t). Best predictors for each response variable are in bold; the signs (+, −) represent the direction of the correlations

| | Rt | Dt | St | β_{jtu} | β_{jne} | Rt | Dt | St | β_{jtu} | β_{jne} |
|-------------------|-----------------|-----------------|-----------------|---------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|
| 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 |
| Predictor | Forest level | | | | | Plot level | | | | |
| 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 (+) | 55.9 (−) |
| NLargeTree | | | | | | | 35.8 | | | 23.5 |
| StDevCirc | | 32.3 | | 29.6 | 25.2 | | | | | |

Richness difference (*D*)

Richness difference between trees was largely associated with geographic predictors, even though a contribution of forest structure variables (especially StDevCirc and NLargeTree) was also detectable (Tables 5 and 6). The Dc and Do at the forest level and Dt at the plot level decreased from *c.* 30% to *c.* 10% from western to eastern forests; the latter showed considerable uniformity of richness between trees (Fig. 6). A similar decrease also occurred with an increase in elevation,

which was the best predictor for Dt at the forest level and Dc at the plot level. An independent effect of rainfall, up to 43% of the total variation, drove Ro at the plot level.

Species turnover and nestedness *Sensu* Baselga (2012)

At the plot level, β_{jtu} and β_{jne} showed opposite and comparable patterns in relation with the average distance between trees (AvDistTree; *sensu* Baselga (2012)). This variable

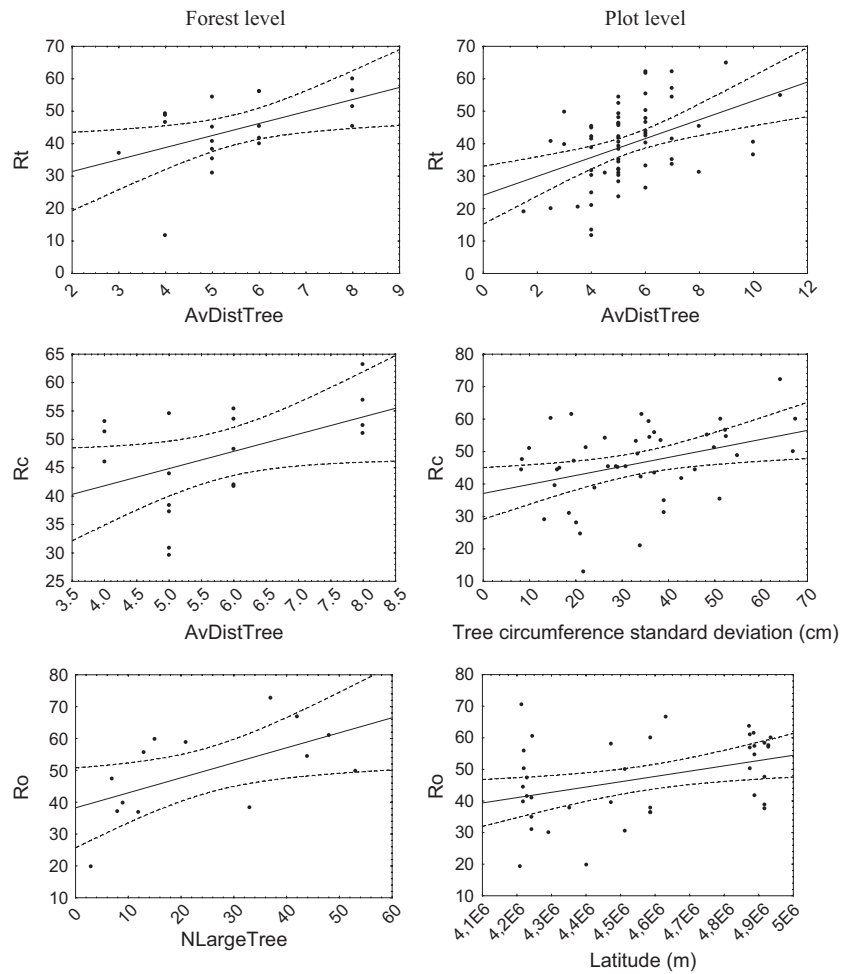


Fig. 4. Scatterplots of best predictors for lichen species replacement at forest and plot levels.

Table 6. R^2 and hierarchical partitioning (HP) of independent effects (%) of statistically significant ($P < 0.05$) predictors on β -diversity variables for pairs of trees with lichen species of Conservation Concern (c) and other species (o). Best predictors for each response variable are in bold; the signs (+, -) represent the direction of the correlations

| | 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 |
| Predictor | Forest level | | Plot level | | Forest level | | Plot level | | Forest level | | Plot level | |
| 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 | | | | |

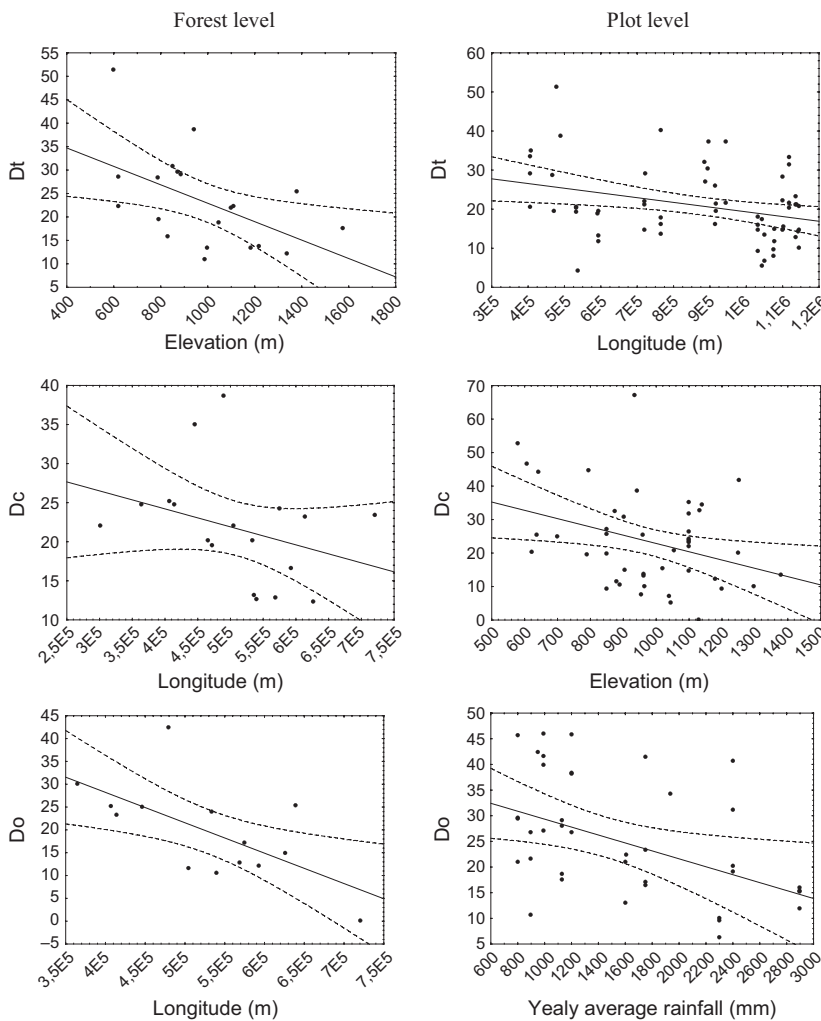


Fig. 5. Scatterplots of best predictors for lichen similarity at forest and plot levels.

accounted for most variation (37.6%) of β_{jne} also at forest level, whereas main differences of β_{jtu} at this scale were related to the habitat, being the species turnover higher in *Castanea* and *Fagus* than in *Quercus* forests (Fig. 7).

Discussion

The components of β -diversity and similarity contributed to shaping *L. pulmonaria* communities at both forest and plot scales across Italy, resulting in nearly random compositions, that is, the species set on each tree was a random sample from the available species pool. Consequently, the working hypothesis of a prevailing effect of replacement at the forest level due to dispersal limitations, versus a higher importance of similarity at the plot level, should be rejected. This pattern was consistent across the three data sets, indicating that species of conservation concern are subjected to the same processes ruling the whole community, although in some cases, the driving factors may differ. In the study conducted by Will-Wolf *et al.* (2006), who investigated the species turnover across spatial scales in the USA, the data sets coming from two different forest biomes with different lichen floras, had several similarities in lichen community structure and relation-

ships with environmental variables, corroborating the hypothesis that comparisons in term of community structure may give valuable insights into the generality of relations between community patterns and environmental variables across spatial scales and regions.

Despite the mixed contribution of the two β -diversity components and of similarity, at both spatial scales, species replacement was in general the main component. Species replacement is likely to gain importance in larger forests where, according to an area effect (Berglund & Jonsson 2001; Jönsson, Thor & Johansson 2011), the available species pool is expected to be richer than in smaller ones, as indicated by our results. This β -diversity component was mainly influenced by factors indicative of forest structure, being positively related with the distance between trees, which is likely to reflect dispersal dynamics and habitat conditions. This outline is also corroborated by the results on species turnover and nestedness *sensu* Baselga (2012), indicating that these components of β -diversity are basically driven by the same forest structure factors. The increase in species replacement is likely to increase the species pool of the community which in turn could benefit from the maintenance or the creation of relatively open-canopied forests (Jönsson, Thor & Johansson

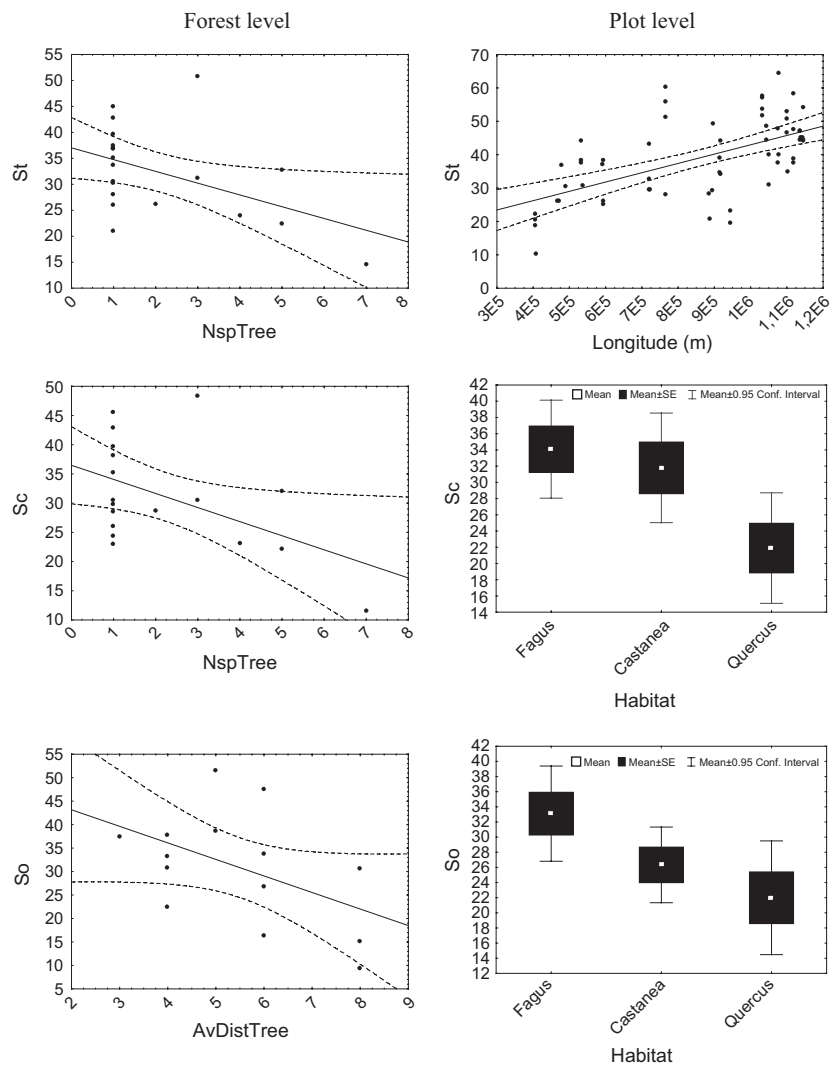


Fig. 6. Scatterplots of best predictors for lichen richness differences at forest and plot levels.

2011). This interpretation is supported by the tendency to have higher species replacement in chestnut forests, which are usually less dense than beech and oak forests. Two further factors related to forest structure influence patterns of species replacement: tree size heterogeneity, indicative of forest habitat heterogeneity and the presence of large old trees. In both cases, the increase in species replacement may reflect the positive effect of these factors on the available species pool (e.g. Jürriado *et al.* 2009; Brunialti *et al.* 2010). In particular, large old trees are known to be more lichen rich and to host more heterogeneous species assemblages than young trees (Nascimbene *et al.* 2009a). The consistent patterns of species replacement across both plot and forest scales may be due to the fact that we operated in homogeneously forested landscapes and within the same community. In this situation, unlike in fragmented landscapes, species dispersal is likely to be ruled by short-distance dynamics, and the available species pool is limited by the ecological requirements of species. However, the consistency of this pattern across scales may also reflect the importance of autogenic processes in shaping lichen communities. These processes are rarely addressed (e.g. Rogers 1990), and further research in this field could

better elucidate the background processes determining species replacement.

The contribution of pairwise similarity in shaping *L. pulmonaria* communities was higher at plot level when considering the t data set, but it was consistent across the two spatial scales when c and o disaggregated data sets were concerned. The drivers of similarity at the two spatial scales were different. At the forest scale, tree species diversity was far more important, while at the plot scale habitat type prevailed, with some differences between pairs with or without species of conservation concern. The importance of tree species for epiphytic lichens is well documented (e.g. Uliczka & Angelstam 1999; Nascimbene, Marini & Nimis 2009b; Lewis & Ellis 2010; Thor, Johansson & Jönsson 2010) and is mainly because of chemical and physical features of the bark (for a synthesis, see Ellis 2012). Our results suggest that increasing forest composition diversity should trigger an increase in the species pool of *L. pulmonaria* communities, including species of conservation concern. At the plot level, our results highlight the importance of habitat type. In particular, in oak-dominated plots, lichen assemblages between trees hosting species of conservation concern were less similar than in

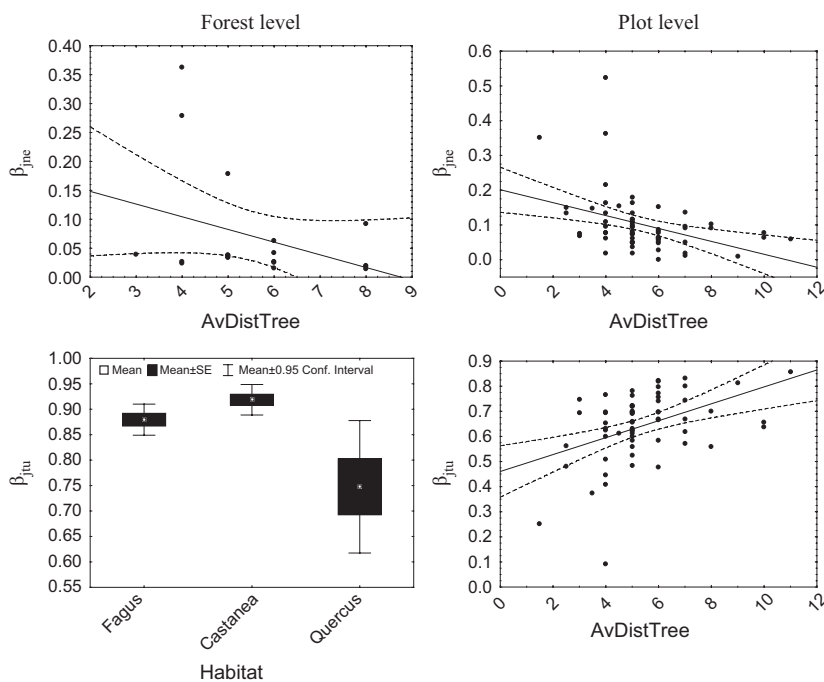


Fig. 7. Scatterplots of best predictors for species replacement (turnover, β_{jtu}) and nestedness (β_{jnc}) *sensu Baselga* (2012) for the t data set at forest and plot levels.

other habitats, while similarity between trees was higher in beech–silver fir plots. This is the only forest type in which this component, calculated for the whole data set (t), has even higher values than species replacement, indicating higher compositional homogeneity between trees than in the other forest types. These findings suggest that management practices to ensure lichen conservation should be tailored to habitat type. For example, in Italy, retention groups in oak forests should be larger than in other habitats, while in beech–silver fir forests, they could consist of a few trees which are likely to host similar assemblages of lichens. Furthermore, these results support the background idea of this study highlighting that the analysis of underlying processes structuring lichen communities may contribute relevant information for refining conservation measures. The analysis of species composition did not reveal differences among forest types suggesting that similar management could be applied to conserve *L. pulmonaria* communities across forest habitats. However, the analyses on β -diversity components and similarity revealed that some processes structuring *L. pulmonaria* communities may differ among habitats, such in the case of species similarity, supporting the need for habitat-specific management.

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

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

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

threatening natural ecosystems (Sutton, Reis & Bakr 2009; Gilliam *et al.* 2011) and are detectable in term of shifts in species composition of lichen communities (Geiser *et al.* 2010; Pinho *et al.* 2012).

Acknowledgements

We thank Prof. János Podani for introducing us to basic concepts of β -diversity and for helpful comments on a previous version of the manuscript. Prof. Pier Luigi Nimis is also acknowledged for his constructive remarks on the structure of the work. We are also grateful to two anonymous referees and to the associate Editor Frank Gilliam for their constructive suggestions that helped us in improving the effectiveness of our work.

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Received 29 July 2012; accepted 27 November 2012

Handling Editor: Frank Gilliam

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Lichenized and nonlichenized fungi considered in this study.