Cross Taxon Congruence Between Lichens and Vascular Plants in a Riparian Ecosystem

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Abstract: Despite that congruence across taxa has been proved as an effective tool to provide insights into the processes structuring the spatial distribution of taxonomic groups and is useful for conservation purposes, only a few studies on cross-taxon congruence focused on freshwater ecosystems and on the relations among vascular plants and lichens. We hypothesized here that, since vascular plants could be good surrogates of lichens in these ecosystems, it would be possible to assess the overall biodiversity of riparian habitats using plant data only. In this frame, we explored the relationship between (a) species richness and (b) community composition of plants and lichens in a wetland area located in central Italy to (i) assess whether vascular plants are good surrogates of lichens and (ii) to test the congruence of patterns of species richness and composition among plants and lichens along an ecological gradient. The general performance of plant species richness per se, as a biodiversity surrogate of lichens, had poor results. Nonetheless, the congruence in compositional patterns between lichens and vascular plants varied across habitats and was influenced by the characteristics of the vegetation. In general, we discussed how the strength of the studied relationships could be influenced by characteristics of the data (presence/absence vs. abundance), by the spatial scale, and by the features of the habitats. Overall, our data confirm that the more diverse and structurally complex the vegetation is, the more diverse are the lichen communities it hosts.

Keywords: biodiversity; co-correspondence analysis; conservation planning; surrogate taxon

1. Introduction

The growing impact of human-induced changes on natural ecosystems, such as land transformation and habitat degradation, is leading to the pressing need for straightforward methodologies for monitoring biodiversity in space and time [1–5]. Although broad-scale patterns of biodiversity are well documented, accurate descriptions of the distribution of biodiversity which down at fine spatial, temporal, or taxonomic scales are still missing, even for well-described groups, such as vascular plants or vertebrates [6].

Surrogacy can be defined as the relationship existing between a surrogate variable and an "objective" variable (also called "target variable" [7]). In ecology, cross-taxon congruence analysis can be expressed as the correlation in patterns of species richness and/or diversity [8] or, in a multi-species context, as community concordance (i.e., the relationship among compositional patterns of multiple taxonomic groups across sites [9,10]). More in general, cross-taxon congruence occurs when diversity and/or composition patterns of different biological groups covary spatially [11]. The interest in biological surrogates during the last decade has resulted in an increasing number of studies testing their effectiveness, in a multiplicity of locations and at different spatial scales [12]. Rodrigues and Brooks [13] pointed out that the use of surrogate taxa in conservation planning is substantially more effective than that of surrogates based on environmental data only. However, the effectiveness of the use of one taxon to predict community patterns for other taxonomic groups ultimately depends on its underlying mechanisms and on the strength of the relationship with, and among, such groups (e.g., [14–18]). Furthermore, the effectiveness of surrogate taxa as ecological indicators for biodiversity assessment also depends on other factors, such as the spatial scale of analysis and the choice of predictor variables [19]. The choice of the study scale is, in fact, also crucial to avoid spurious or undetected relationships among the collected variables and it could influence the time/cost of the sampling effort as well [20].

From an ecological perspective, the factors that affect cross-taxa relationships include the following: (1) a similar but independent response from two taxonomic groups to the same set of environmental conditions [9,21,22], (2) trophic interactions or functional interdependence [9], (3) a shared bio-geographical and evolutionary history at a large/global scale [23], and (4) species–energy relationships (e.g., [3]; for a summary see [24,25]). Thus, potential surrogate taxa should have the following properties [26,27]: (i) a well-known and stable taxonomy so that populations can be defined in a reliable way; (ii) a well understood biology and general life history; (iii) occur over a broad geographical range and breadth of habitat types at higher taxonomic levels (order, family) so that results will be broadly applicable; (iv) specialization of each population (at lower taxonomic levels, e.g., species, subspecies), within a narrow habitat, which is likely to make them sensitive to habitat change; (v) some evidence that patterns observed in the surrogate taxon do replicate in other taxa, which are more difficult to investigate in the overall biodiversity at different spatial scales. Since vascular plants play a crucial role in land management, they can be a convenient choice as surrogate taxa. Furthermore, plants are fundamental structural and functional components of terrestrial ecosystems, having the major role in net primary productivity. Vascular plants are widely used for depicting biodiversity hotspots to address the institution of natural reserves, to identify priorities for conservation actions, and, more in general, for environmental planning [28–31]. Since their sampling is relatively easy [32–34] and their taxonomy is sufficiently well described and standardized, they may reflect the diversity of other important, and less known and/or inconspicuous taxa, such as cryptogams.

Cryptogams, such as bryophytes and lichens, are rarely included in floristic and vegetation assessments for management and monitoring purposes due to difficulties encountered in their identification. Vascular plants are therefore of great interest to be used as a proxy for these groups of cryptogams. Some authors have tested the possible congruence between vascular plants and cryptogams for different habitats, locations, and spatial scales, but the results are fragmentary and conflicting [35]. For instance, contrasting results were observed in several studies using vascular plants as a surrogate group for lichens in forest ecosystems [36–39]. Vascular plants proved to be effective surrogate taxa to select sites for conservation purposes, especially if used in combination with other factors [37]. In contrast, another study showed that vascular plants can be ineffective as surrogate taxa for cryptogams [38], even though this could be explained by an over simplification of the forest structure as a consequence of human management. Contrasting patterns were also observed in the Mediterranean area, even though only a few studies tested for the congruence between vascular plants and cryptogams [19,34,40,41]. These studies highlighted a limited effectiveness of cross-taxon

estimates in a nature reserve in Tuscany, even though vascular plants may be useful surrogates of other organisms [34,42].

Despite the considerable amount of studies and meta-analyses on cross-taxon congruence [12], few examples deal with freshwater ecosystems: to the best of our knowledge, the effectiveness of vascular plants as a surrogate group for lichens has never been specifically addressed in riparian freshwater communities in the Mediterranean area. Though Heino [25] highlighted that cross-taxon congruence does not appear to be particularly relevant for conservation purposes in freshwater habitats, more recently Nascimbene et al. [43] strengthened the importance of riparian woods for lichen conservation in riparian forests, providing important evidence of their role as hotspots of biodiversity [44], as these fragile ecosystems are subjected to a high number of pressures and threats [45].

In this study, then, we hypothesized that if the composition of lichen communities was consistently correlated to that of riparian vascular plants, the latter can be used as surrogate group when assessing lichen diversity of riparian habitats.

Since plants are generally easier to identify in the field than lichens, they could be efficiently used in preliminary and cost-effective biodiversity assessments. This would allow the collection of large-scale datasets on biodiversity and ecological indicators of the quality of river edges within a relatively short period of time, if compared to that required to survey and identify lichen taxa as well.

To assess whether plant communities can be a suitable surrogate group for lichen community composition and diversity, we surveyed vascular plants and lichens from five different habitats, located along a strong gradient of water flood, on a stretch of the Tiber river (Arezzo, central Italy). We aimed at the following: (1) assessing cross-taxon congruence in composition between lichen and plant communities, (2) quantifying the effectiveness of plant communities as surrogates of lichen communities, and (3) assessing if the degree of cross-taxon congruence is consistent along an environmental gradient in the riparian habitat. The predictive strength of vascular plants was evaluated using both species richness and species composition. Furthermore, the degree of cross-taxon congruence in species composition was assessed considering presence/absence and abundance data. To the best of our knowledge, this is the first in-depth analysis reporting the congruence in composition between plants and lichens in freshwater habitats which considers the variation of different parameters (data type, variation in environmental gradient, and scale of species abundances).

2. Materials and Methods

2.1. Study Area and Sampling Design

The study area (Figure 1) is located in a stretch of 3 km from the Montedoglio dam along the Tiber river, (Arezzo, Tuscany, Italy). This area lays on alluvial lacustrine-fluvial deposits and is altered by human activities, such as gravel mines, which cause strong modifications to the original landscape. The construction of the dam and other infrastructures modified the track of Tiber several times [46]. The river regulation influenced the stream flux, leading to the disappearance of seasonal water availability, with consequent reduction of solid carriage due to rapid sedimentation [46]. Furthermore, the dam deep water temperature is a few degrees lower than in natural conditions (approximately 7.7 °C vs. 12 °C), reaching its natural temperature only some kilometers downstream [46]. Even in the presence of these disturbances, hygrophilous vegetation shows a high level of conservation and naturalistic value [47] and the study area has been included among the protected areas in the Region (ANPIL, Protected Natural Area of Local Interest).
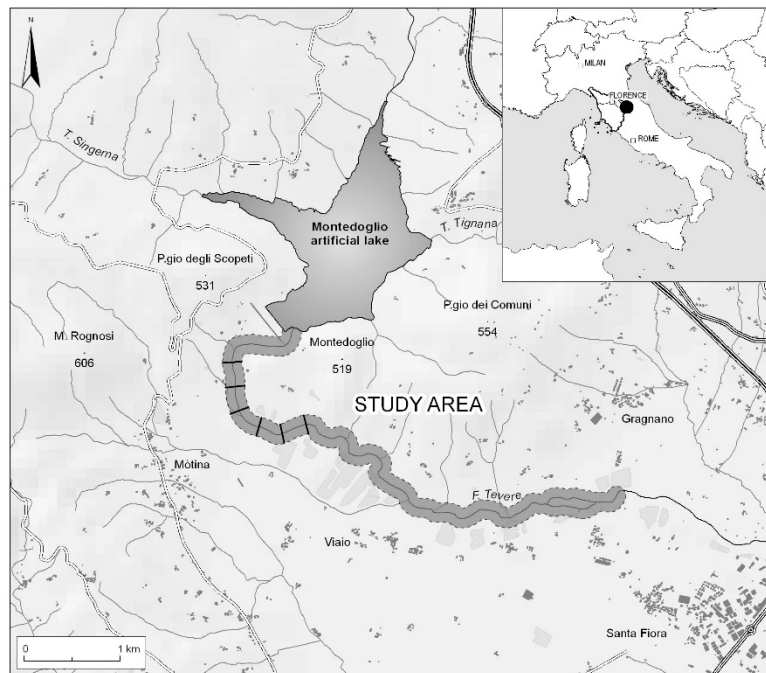
Figure 1. Location of the study area. Sampled transects are drawn as black lines.

Species richness and the composition of plant and lichen communities were surveyed along 12 transects (defined as "primary sampling units" following Lastrucci et al. [46]), each 5 m wide and with a variable length according to the width of the riparian zone (see Figure 1). These were randomly displaced along the riverside (6 on the left bank and 6 on the right one) and they were placed at 250 m from each other in order to avoid the effect of spatial autocorrelation.

Within each transect, "secondary sampling units" were delimited using a stratified random sampling. The strata corresponded to the five habitats previously identified and visually delimited through field survey. The following classification was adopted to characterize the sampled habitats (strata, see [46] for details):

- **(R) Flooded Banks**: Transitional area between the wet and dry river bed;
- **(GR) Dry Banks**: Composed by gravel and sand, mostly colonized by xerophilous vegetation;
- **(AR) Shrublands**: Thick shrublands dominated by *Salix eleagnos* and *Salix purpurea*;
- **(B) Riparian woods**: Woodlands dominated by *Populus nigra, Alnus glutinosa* and *Salix alba*;
- **(P) Swamps**: Depressions and river side branches with backwater and mud substrate; vegetation characterized by helophytes and hygrophilous species.

On the basis of the total area occupied by each habitat, a proportional number of randomly selected squared plots of 1 m^2 were sampled as follows: If the habitat area was lower than 25 m^2, three plots were sampled; when the habitat area was greater than 25 m^2, two more plots were added for each increase of 25 m^2 (e.g., for a habitat surface of 75 m^2, seven plots were displaced) for a total of 188 plots (Table 1). Presence and percentage coverages of vascular plants (proportion of the area occupied by a species on the plot total surface) and lichens (visual estimation of the % coverage on the plot) were recorded within each plot.

Table 1. Summary statistics of the analyzed dataset.

	Taxon	N° Sampled Plot	N° Sampled Species	Mean Species Richness	Min–Max
Whole dataset	Plants	184	193	10.57	2–21
	Lichens	184	45	2.79	0–15
Shrublands (AR)	Plants	47	95	10.61	2–21
	Lichens	47	33	3.91	0–15
Riparian woods (B)	Plants	58	98	11.05	4–21
	Lichens	58	34	3.29	0–12
Dry Banks (GR)	Plants	46	98	9.36	3–17
	Lichens	46	20	2.65	0–8
Swamps (P)	Plants	15	55	13.2	3–21
	Lichens	15	2	0.33	0–2
Flooded Banks (R)	Plants	18	59	9.77	2–18
	Lichens	18	4	0.72	0–4

Nomenclature followed Conti et al. [48] for vascular plants and Nimis and Martellos [49] for lichens.

2.2. Data Analyses

2.2.1. Congruence in Species Richness

The Spearman correlation coefficient (ρ) was used to measure congruence in species richness between plants and lichens, for the whole dataset and for each habitat. Similarly, patterns in species richness for the two groups were also compared using plot-based rarefaction curves [50]. Rarefaction curves were calculated, for plants and lichens, both collectively and for each sampled habitat type, using the "exact" formula proposed by Kobayashi [51] (but see [52]):

$$\overline{S_i} = S_n - \binom{n}{i}^{-1} \sum_{k \in G} \binom{n - n_k}{i}, i = 1, \ldots, n \tag{1}$$

where G is the set of species observed in the collection of n samples (plots), S_n is the total number of observed species, n_k is the number of samples containing at least one individual of species $k \in G$, and S_i is the expected species richness for the sub-sample i out of the total number of samples N. Since coordinates of each plot were not collected in the field, the application of spatially explicit rarefaction curves [53,54] was not possible.

The ratio between the species rarefaction curve for plants and for lichens was also calculated to compare patterns of rarefaction for the two taxa [18,52,55], both separately and collectively.

2.2.2. Congruence in Species Composition

Congruence in species composition was evaluated using three independent tests, as follows: (1) Mantel test, (2) co-correspondence analysis, and (3) differences in beta diversity between plants and lichens among habitats.

Mantel tests were performed using the non-parametric approach based on the Spearman rank correlation [56]. Monte Carlo randomizations based on 9999 permutations [57,58] were used to test for significance of the correlation between the two resemblance matrices. These were calculated using (a) the Bray–Curtis dissimilarity [59,60] for square rooted abundances of plants and lichens and (b) the Jaccard dissimilarity [59,60] for presence/absence data.

Co-correspondence analysis (hereafter Co-CA, see [10,61] for a full description of this method) was applied to quantify the ability of the plant community data in predicting lichen species composition. This method directly related the composition of two communities by maximizing the weighted

co-variance between weighted average (WA) species scores of one community (plants) and WA species scores of the other (lichens). Hence, Co-CA attempts to identify the ecological gradients that are common to both communities. Here we used the asymmetric, predictive form of Co-CA, which combines weighted averaging and the partial least squares approach (PLS; [62]). A leave-one-out cross-validatory fit (%) was performed to obtain the minimum number of axes to retain and to select the minimal adequate predictive models.

Co-CA was performed both on incidence and abundance-based matrices for the two taxa. In the latter case, a square root transformation was applied to plant and lichen species composition.

Finally, a procedure to test for differences in beta diversity among distinct sets of plots (also called *betadispersion*) was applied. This procedure creates a distribution of null values of the statistic test, which is compatible with the null hypothesis of no significant differences in multivariate dispersion between two or more groups. The test is based on any pairwise plot-to-plot dissimilarity matrix of choice and, given that, the beta diversity of a certain group of plots can be defined as the mean of the plot-to-plot dissimilarities within the groups [63,64]. A distribution of values of the test-statistic under the null hypothesis is then obtained by Mantel randomization of the dissimilarity matrix [65,66]. Differences in beta diversity between plant and lichen assemblages were tested for the whole set of plots, and for each sampled habitat separately, by comparing the average of the calculated dissimilarities (both the Bray–Curtis and the Jaccard matrices) between the two groups (plants and lichens) using the F-test described above. *P*-values were computed from 999 permutations of the plot-to-plot dissimilarities between the two groups.

All statistical analyses were performed using R 3.5.1 [67]. Plot-based rarefaction curves were calculated using R package 'vegan' [68], Co-CA was performed using R package 'cocorresp' [69], and beta dispersion was assessed using the R function 'betadispersion2', available in Bacaro et al. [66].

3. Results

3.1. Congruence in Species Richness

The total amount of species recorded in the 184 plots was 238, of which 193 were vascular plants and 45 were lichens (Table 1). Riparian woods (B) and dry banks (GR) showed the highest values of plant species richness (98), whereas shrublands (AR) and riparian woods (B) were the richest in lichens. Conversely, swamps (P) were characterized by the lowest number of both lichens and plants (Table 1).

When the whole dataset was considered, correlation in species richness resulted as not significant (Table 2). In contrast, when correlations were considered for each habitat separately, different patterns were observed. A moderate positive (but statistically significant) correlation was obtained between the two taxonomic groups in the AR habitat, while the opposite was observed for the P (swamps) habitat, for which we observed a negative (but significant) correlation coefficient (Table 2).

Table 2. Spearman correlations (ρ) between plant and lichen species richness for the whole set of data and for each habitat separately. (** $p < 0.01$; * $p < 0.05$).

Data	ρ
Whole Dataset	0.050
Shrublands (AR)	0.407 **
Riparian woods (B)	0.208
Dry Banks (GR)	0.011
Swamps (P)	−0.587 *

On average, rarefaction curves for both lichens and plant communities did not reach any asymptotic pattern (Figure 2a,b), except for lichens in habitat R and P. Furthermore, a completely different trend characterized the relationships between lichen and plant rarefaction curves. A general agreement characterized rarefaction curves for plant communities in the five habitats (Figure 2b).
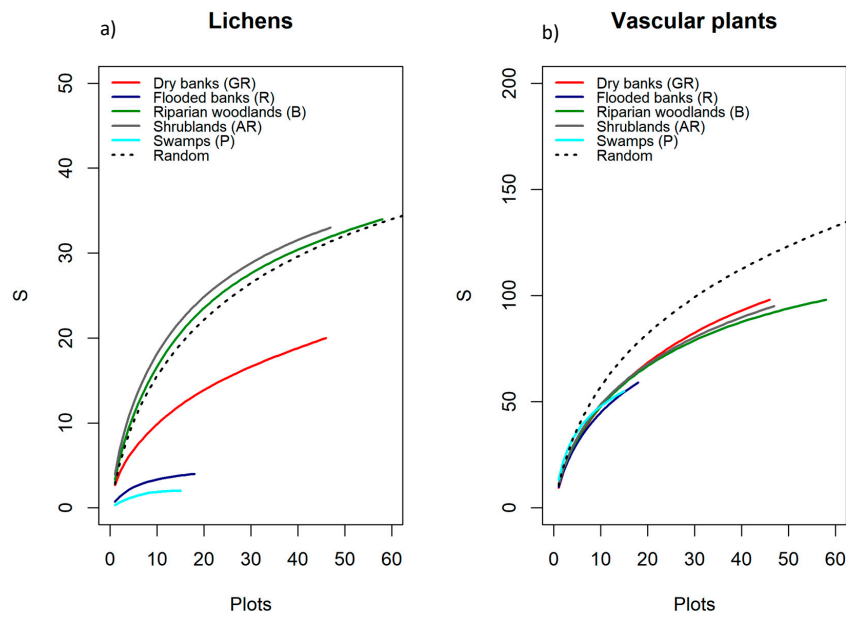
Figure 2. (**a**,**b**) Plot-based rarefaction curves calculated for lichens (**a**) and vascular plants (**b**), recorded from 184 plots sampled along the Tiber river for each riparian vegetation habitat vegetation types, showing the expected number of species, S, as a function of the number of plots. The plot-based rarefaction curve for the pooled sample of all the 184 plots is also shown (dashed line).

In plants, the random rarefaction curve is higher than the habitat-based rarefaction curves, suggesting that an equal contribution to the total complementarity is accounted for each habitat type. In contrast, lichens were characterized by a completely different pattern. Differences in species richness between AR and B (the richest communities) were higher than those between P and R habitats (the poorest communities). Furthermore, AR and B habitats displayed very diverse lichen communities since their rarefaction curves were higher than the random curve. The ratio between lichen and plant rarefactions (Lichens S/Plants S, Figure 3) suggested that both groups displayed some differences in species accumulation patterns across the five habitats and a decreasing trend was observed for R, GR, and AR; whereas the converse was observed in B and P.
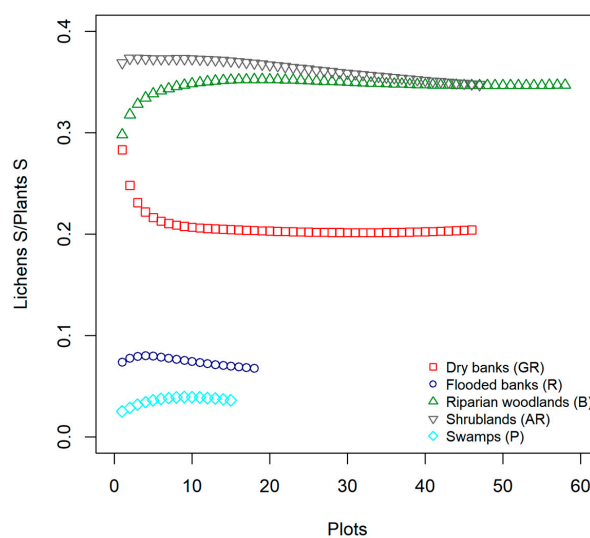
Figure 3. Ratio of lichens and plant rarefaction curves for the whole dataset and for each habitat explored separately.

3.2. Congruence in Species Composition

Mantel tests (Table 3) showed that lichen and plant dissimilarities were significantly and positively correlated along the whole gradient irrespective of the dissimilarity metric, with the exception of riparian woods (B) and swamp habitats (P) (Spearman ρ > 0.05).

Table 3. Correlation (Spearman's ρ) between the Bray–Curtis (log-transformed abundance data) and Jaccard dissimilarity matrices (occurrence data) of plants and lichens. *p*-values were calculated by using Monte Carlo randomization tests (999 permutations). Significant correlation coefficients are in bold. AR—Shrublands, B—Riparian woods, GR—Dry Banks, P—Swamps, R—Flooded Banks.

Dataset	Dissimilarity Metric	ρ	*p*
Whole Dataset	Bray–Curtis	0.238	**<0.001**
	Jaccard	0.153	**<0.001**
AR	Bray–Curtis	0.349	**<0.001**
	Jaccard	0.272	**<0.001**
B	Bray–Curtis	0.088	**0.007**
	Jaccard	0.039	0.171
GR	Bray–Curtis	0.346	**<0.001**
	Jaccard	0.202	**0.006**
P	Bray–Curtis	0.195	0.088
	Jaccard	0.267	0.052
R	Bray–Curtis	0.258	**0.038**
	Jaccard	0.339	**0.014**

Predictive Co-CA (Figure 4a,b) showed a moderate degree of congruence between plant and lichen composition and, more importantly, showed that plant communities significantly predict lichen composition. The first two Co-CA axes were significant, with a cumulative explained variance of ~11% and ~14% for presence/absence and abundance data, respectively (Table 4).

Table 4. Significance of Co-CA axes for lichens and plants considering both presence/absence and abundance data. Significant cross-validatory fit is shown in bold.

Co-CA Model	Axis	Cross-Validatory (%) Fit	*p*
Presence/Absence data	1	5.528	**0.01**
	2	5.486	**0.01**
	3	7.172	0.06
	4	6.965	0.17
Abundance Data	1	8.270	**0.01**
	2	5.970	**0.01**
	3	3.472	0.06
	4	2.552	0.24

The first Co-CA axis well describes the gradient from dry and xeric herbaceous plant communities (GR on the right) to shrubs and woody dominated plantCalibri communities (AR, B), while the second axis separates the ecotonal transitional area between wet and dry river bed (R, lower part of the graph) to the more stable and structured plant communities (AR and P, upper part of axis 2, Figure 4a,b. Appendix A presents the abbreviation list for lichens and vascular plant species).
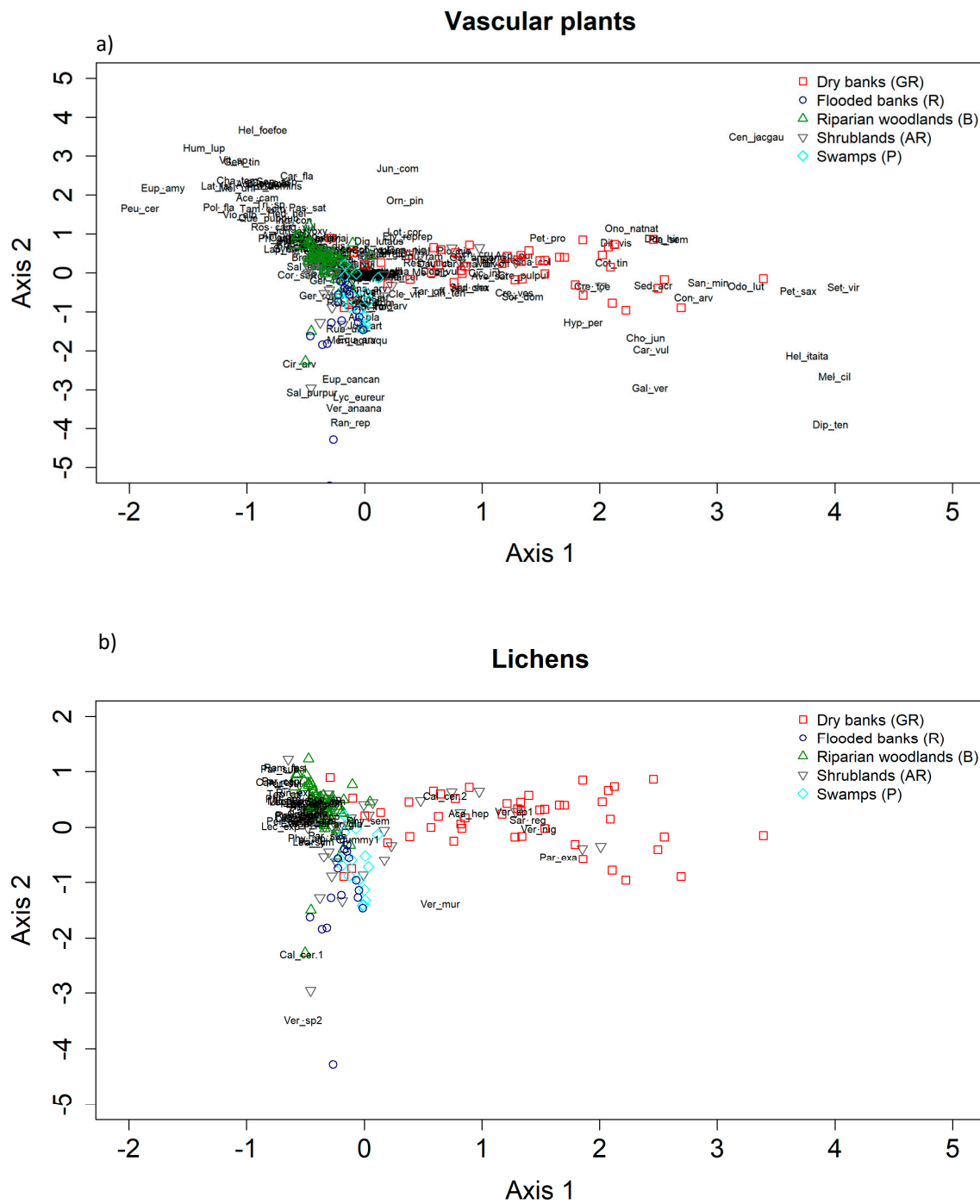
Figure 4. (**a**,**b**) Predictive Co-CA biplot of plant species composition (**a**) and lichen species composition (**b**) using abundance data. In each plot, species are positioned according to their loadings, with respect to normalized plot scores derived from the plant composition data. Symbols show the type of riparian vegetation habitat of each plot. The axes were rescaled to the same ranges so that sites occupy the same position in both plots. Explanations of species abbreviations are reported in Appendix A.

On average, beta diversity was slightly higher for plant than for lichen communities considering the whole dataset; these differences increased a bit considering each habitat separately (Table 5, Table 6). In particular, we observed similar values in plant dissimilarity values across all the habitats. Conversely, both the Jaccard and Bray–Curtis indices drastically decreased in lichens, moving from more structured habitats (AR, B) to those closer to (or in contact with) water (P, R). Notably, significant differences in

beta diversity between lichens and plant assemblages were observed both for the whole dataset (but only using presence/absence data) and for each habitat separately (Table 6).

Table 5. Mean beta diversity measures calculated for plants and lichens, separately. AR—Shrublands, B—Riparian woods, GR—Dry Banks, P—Swamps, R—Flooded Banks.

Dataset	Dissimilarity Measure	Average Beta Diversity Lichens	Average Beta Diversity Plants
Whole Dataset	Bray–Curtis	0.823	0.830
	Jaccard	0.664	0.885
AR	Bray–Curtis	0.807	0.679
	Jaccard	0.694	0.817
B	Bray–Curtis	0.781	0.680
	Jaccard	0.649	0.770
GR	Bray–Curtis	0.694	0.812
	Jaccard	0.501	0.860
P	Bray–Curtis	0.389	0.719
	Jaccard	0.249	0.783
R	Bray–Curtis	0.503	0.767
	Jaccard	0.337	0.834

Table 6. Differences in beta diversity between lichen and plant assemblages obtained using the following two measures of dissimilarity: Bray–Curtis dissimilarity (square root transformed species abundance data) and Jaccard dissimilarity (for presence/absence data). Analyses were carried out both for the whole set of 184 plots as well as for each habitat. *p*-values were obtained by Mantel randomization of the original plot-to-plot dissimilarity matrices (999 permutations); significant differences were highlighted in bold. AR–Shrublands, B–Riparian woods, GR–Dry Banks, P–Swamps, R–Flooded Banks.

Data set	Dissimilarity Metric	Source of Variation	Df	SSs	MSs	F Model	*p*
Whole Dataset	Bray–Curtis	Group	1	0.46	0.46	8.439	0.495
		Residuals	33670	1853.43	0.05		
	Jaccard	Group	1	411.94	411.94	10584	**0.001**
		Residuals	33670	1310.49	0.04		
AR	Bray–Curtis	Group	1	8.89	8.89	209.56	**0.001**
		Residuals	2160	91.66	0.04		
	Jaccard	Group	1	8.19	8.19	299.18	**0.001**
		Residuals	2160	59.16	0.02		
B	Bray–Curtis	Group	1	8.43	8.43	156.57	**0.001**
		Residuals	3304	177.91	0.05		
	Jaccard	Group	1	12.23	12.23	320.37	**0.001**
		Residuals	3304	126.16	0.03		
GR	Bray–Curtis	Group	1	7.16	7.16	161.63	**0.001**
		Residuals	2068	91.72	0.04		
	Jaccard	Group	1	66.46	66.46	1643.90	**0.001**
		Residuals	2068	83.61	0.04		
P	Bray–Curtis	Group	1	5.71	5.71	51.18	**0.001**
		Residuals	208	23.21	0.11		
	Jaccard	Group	1	15.00	15.00	302.83	**0.001**
		Residuals	208	10.30	0.04		
R	Bray–Curtis	Group	1	5.32	5.32	43.40	**0.001**
		Residuals	304	37.26	0.12		
	Jaccard	Group	1	18.90	18.90	324.15	**0.001**
		Residuals	304	17.72	0.05		

4. Discussion

The usefulness of surrogate taxon approaches is still controversial in ecological literature, with some studies showing strong cross-taxon congruence which is promising for their practical utilization, whereas others have found no congruence among taxa, limiting their use in conservation planning [23,70–75]. In a recent study on pattern of congruence among taxa in European Temperate Forests, Burrascano et al. [39] summarized the high variability in cross-taxon relationships and how the effect of spatial scale (grain and extent) could be pivotal for the observed variability. As an example, scarce relationships were observed between vascular plants and cryptogams in boreal forests [76,77], where bryophytes and lichens often constitute a major proportion of the species richness and biomass [78,79]. Disagreements in cross-taxon congruence are probably linked to differences among investigated studies in several key characteristics, such as the spatial scales, the study area location, and the analytical methods adopted [19], on which the effectiveness of congruence among two or more taxa depend.

4.1. Congruence in Species Richness

As pointed out by the cross-taxon correlation analysis we carried out between lichens and vascular plants richness, although the relationship resulted significant and positive in one of the five surveyed habitats (AR, shrublands) and negative in another one (P, Swamps), the overall performance of plant species richness per se as biodiversity surrogates of lichens was poor. Researchers working in various regions and using coarse grain plots (e.g., 50 × 50 m) obtained similar results and did not find any co-variation between the species richness of vascular plants and lichens [36,77]. In our study, many factors may have contributed to the general lack of species richness congruence and, among these, the small grain of the sampling units (1 m^2) may be considered one of them. Additionally, the functional characteristics of a particular taxon could be another factor affecting the degree of concordance among different taxonomic groups, along with the life history of the site. For instance, McMullin & Wiersma [80] recently pointed out that the relative richness and abundance of lichens can be effective indicators of forest continuity and diversity. In this study, the surveyed habitats are riparian woods and shrublands, which are not characterized by mature stands. Though lichens can rely only on these trees and shrubs as stable substrata to develop their thalli and build communities richer in species abundance and diversity than in the other three habitat types, lichen diversity is still limited.

In assessing congruence patterns, species richness has been often used instead of species composition considering it is much simpler and faster to collect in the field. In surrogacy studies, it is often discussed whether it is reasonable to use species richness of vascular plants as a proxy of total biodiversity [39,42,81,82], even though different patterns of co-variation in lichen composition are described in relation to the variation of composition of plants communities. Our results also confirm the role of methodological issues, such as the type of data used (presence/absence vs. abundances) in determining the strength of cross-taxon relationships. Specifically, we observed that the degree of congruence in compositional patterns between lichens and vascular plants can substantially vary across habitats and depends on the type of the data used, along with the characteristic of the vegetation (abundance vs. presence/absence). Recent studies showed how the use of two-three taxa instead of a single one may drastically increase surrogacy [83].

4.2. Congruence in Species Composition

In general, our findings describe different patterns of co-variation in lichen composition in relation to the composition variation of plants communities. Our results also confirm the role of methodological issues such as the type of data used (presence/absence vs. abundances) in determining the strength of cross-taxon relationships. Specifically, we observed that the degree of congruence in compositional patterns between lichens and vascular plants can substantially vary across habitats and depends on the type of the data used, along with the characteristic of the vegetation (abundance vs. presence/absence

data, species composition vs. variation in habitat characteristics). As for analysis at the species richness level discussed above, we showed a strong spatial structure of the data, which is also related to the spatial scale of the analysis. Specifically, at a coarser scale (i.e., along the ecological gradient), where environmental and structural gradients are more pronounced, especially for plant communities, these relationships display the strongest and clearest direction. On the other hand, at a finer scale, this signal seems to be hampered (see Table 3).

Nonetheless, studies at smaller grains (e.g., 1 × 1 m) have shown relatively strong correlations between vascular plants and lichens (see, for instance [71,84]). In general, our results corroborate previous evidence, especially those concerning the covariation in plant and lichen composition along the whole transitional gradient from river-to-land. In fact, it is well-known that the configuration and heterogeneity of habitats (e.g., variation in habitat types) of an area strongly influences the number of species found in that area [85]. Structurally complex and more mature habitats, indeed, provide more niches and diverse ways of exploiting the environmental resources, thus increasing species diversity [86]. However, a weak degree of association in community composition of vascular plants and cryptogams was evidenced in other studies from Australian [36], Canadian [84], and New Zealand forests [87] and dry grasslands in Sweden [88]. In relation to our data, a previous study pointed out that the five habitats can be well defined and characterized using plant communities [46]. The habitats host a specific set of plants, each with defined functional and structural features. Furthermore, our findings suggested a low compositional similarity, both among and within sampling units collected in the five habitats (see Tables 5 and 6). Based on these marked compositional differences, results of the Co-CA highlighted clear ordination patterns, as follows: For vascular plants, the marshlands indicator species group (P) is constituted mostly of water-related taxa, such as hydrophytes (*Potamogeton nodosus*), helophytes, or hygrophilous species (*Typha minima, Alisma plantago–aquatica, Epipactis palustris, Scirpoides holoschoenus, Lythrum salicaria, Lycopus europaeus*). Here, the few lichen species which are present are not exclusive to this habitat and are not represented at all in the Co-CA regions identified by (P) plots. The indicator species of the flooded banks (R) are mostly plants requiring a high ground water content (*Mentha aquatica, Veronica anagallis–aquatica*), species of cool and shaded habitats of the riparian forest fringes (*Petasites hybridus, Senecio aquaticus, Schedonorus giganteus*), or species resistant to trampling (*Agrostis stolonifera, Prunella vulgaris*). In this habitat, the recorded lichen species are those colonizing rocks, as the more stable substrate, and are mainly represented by the genus *Verrucaria*, which is known to comprehend amphibian taxa of both fresh and salt water and to develop thin partially or completely endolithic thalli.

The floristic component characterizing the dry banks (GR) is instead mostly composed of xerophilous vascular plant species such as *Bromus erectus, Sanguisorba minor, Ononis natrix, Plantago sempervirens*, and *Scabiosa columbaria*. These species are not strictly linked to the presence of water and indicate habitual long emersion times, which clearly differentiates this type of environment. Due to the instability of the substrate, characterized by sandy soil and pebbles, and the lack of shrubs or trees as substrate, the lichen communities are species poor and only few epilithic taxa were mainly surveyed, such as *Sargogye regularis* and *Verrucaria* spp.

The indicator species of riparian woods (B) are mostly trees which characterize the physiognomy of this habitat (*Populus nigra* and *Alnus glutinosa*) and a large number of shrubs, such as *Cornus sanguinea, Ligustrum vulgare, Fraxinus ornus*, and *Rubus caesius*. The presence of the invasive alien species *Robinia pseudoacacia* is also particularly significant [46]. Here, instead, lichens are mainly represented by epiphytic species, among which the few more generalist, nitrophilous taxa, such as *Xanthoria parietina, Lecidella elaeochroma*, and *Lecanora hagenii*, are frequently recorded.

A general consideration of the collected lichens relies on the fact that foliose macrolichens, such as those represented by the genera *Parmelia* and *Ramalina*, have been seldom surveyed across the five habitats. This might likely be due to the young forest/shrubs stands, in which the large foliose lichens did not have still time to develop conspicuously. The surveyed communities are mainly characterized

by crustose species, which easily develop on the rather smooth bark of the tree and shrub species, such as those of the genera *Lecanora, Lecidella*, and *Calopaca*.

Finally, in our analysis we observed that the degree of cross-taxon congruence in species composition does not change strongly, regardless of the type of predictor variable used (abundance vs. presence/absence). Although it has been suggested that abundance data provide relatively detailed information concerning composition and structure of the communities [19,89], the collection of this type of data is labour and cost intensive. On other hand, the presence/absence data are less precise but much more cost effective. Our results showed that presence/absence data, for almost all the selected methodologies, provided similar results than those achieved by using abundances even if, on average, relationships were strongest when abundances were considered [19,90].

5. Conclusions

Recently, a new impulse to the study of cross-taxon relationship has been promoted, especially for nature conservation purposes [91]. Monitoring programs often use plants as general indicators of the conservation status of habitats, though plant species richness may be a poor indicator for the richness of other species groups, as also demonstrated and discussed above. Nevertheless, the use of plants in this context may represent a cost-effective approach to estimate environmental conditions [90,92] and habitat quality [93]. Our study strengthens the idea that cross-taxon congruence between plants and lichens is strongly habitat dependent. For sure it may provide useful information for biodiversity managers, although its use in real conservation contexts is far to be reliable. In conclusion, as emerged from this study, a stand-alone vegetation-driven conservation planning approach is likely to be ineffective to protect lichens diversity overall. In order to be effective, a detailed habitat-based assessment should be performed. This study then confirmed that cross-taxon congruence patterns are highly complex; thus, it is crucial to increase the spatial scale of the observations along with performing taxon-specific assessments.

Author Contributions: G.B. and L.L. conceived of the presented idea. E.T. performed computations. S.M. (Simona Maccherini) and M.M. verified the analytical methods. LL, T.G., R.B., V.G. collected the data, D.D.R., R.N., F.P., S.M. (Stefano Martellos), L.M. discussed the results and contributed to the final manuscript.

Conflicts of Interest: The authors declare no conflict of interest.

Appendix A

Table A1. Abbreviation list of Lichens and Vascular Plants, as presented in the Co-Correspondence analysis (Fig. IV, Bacaro et al. 2019).

Lichens		Vascular plants	
Species	*Abbr.*	*Species*	*Abbr.*
Acarospora heppi	*Aca_hep*	*Acer campestre*	Ace_cam
Arthrosporum populorum	*Art_pop*	*Acer opalus subsp. obtusatum*	Ace_opaobt
Caloplaca cerina	*Cal_cer*	*Achillea millefolium*	Ach_mil
Caloplaca cerinella	*Cal_cer.1*	*Aegopodium podagraria*	Aeg_pod
Caloplaca cfr. cerinelloides	*Cal_cer.2*	*Agrimonia eupatoria*	Agr_eup
Caloplaca pyracea	*Cal_pyr*	*Elymus caninus*	Ely_can
Candelaria concolor	*Can_con*	*Elymus repens subsp. repens*	Ely_reprep
Candelariella reflexa	*Can_ref*	*Agrostis stolonifera*	Agr_sto
Candelariella xanthostigma	*Can_xan*	*Ajuga chamaepitys*	Aju_cha
Evernia prunastri	*Eve_pru*	*Alisma plantago-aquatica*	Ali_pla
Graphys o Arthonia cfr.	*Gra_cfr*	*Alnus cordata*	Aln_cor
Hyperphyscia adglutinata	*Hyp_adg*	*Alnus glutinosa*	Aln_glu
Lecanora carpinea	*Lec_car*	*Amorpha fruticosa*	Amo_fru
Lecanora cfr. expallens	*Lec_exp*	*Anagallis arvensis*	Ana_arv
Lecanora chlarotera	*Lec_chl*	*Anagallis foemina*	Ana_foe
Lecanora hagenii	*Lec_hag*	*Cota tinctoria*	Cot_tin
Lecanora symmicta	*Lec_sym*	*Anthyllis vulneraria*	Ant_vul
Lecidella elaeocroma	*Lec_ela*	*Helosciadium nodiflorum*	Hel_nod

Table A1. *Cont.*

Lichens		Vascular plants	
Species	*Abbr.*	*Species*	*Abbr.*
Lepraria sp.	*Lep_sp.*	*Artemisia vulgaris*	Art_vul
Micarea cfr. prasina	*Mic_pra*	*Asperula purpurea*	Asp_pur
Parmelia caperata	*Par_cap*	*Avena sativa*	Ave_sat
Parmelia glabratula	*Par_gla*	*Barbarea vulgaris*	Bar_vul
Parmelia subaurifera	*Par_sub*	*Bidens frondosa*	Bid_fro
Parmelia subrudecta	*Par_sub.1*	*Bidens tripartita*	Bid_tri
Parmelia sulcata	*Par_sul*	*Brachypodium rupestre*	Bra_rup
Parmelia tiliacea	*Par_til*	*Brachypodium sylvaticum*	Bra_syl
Pertusaria albescens	*Per_alb*	*Bromus erectus*	Bro_ere
Phaeophyscia orbicularis	*Pha_orb*	*Bromus madritensis*	Bro_mad
Phlyctis argena	*Phl_arg*	*Calystegia sepium subsp. sepium*	Cal_sepsep
Physcia adscendens	*Phy_ads*	*Carex hirta*	Car_hir
Physcia aipolia	*Phy_aip*	*Carex distans*	Car_dis
Physcia semipinnata	*Phy_sem*	*Carex flacca*	Car_fla
Physconia distorta cfr.	*Phy_dis*	*Carex otrubae*	Car_otr
Ramalina fastigiata	*Ram_fas*	*Carex pendula*	Car_pen
Ramalina sp.	*Ram_sp.*	*Carlina corymbosa*	Car_cor
Rinodina exigua	*Rin_exi*	*Carlina vulgaris*	Car_vul
Sarcogine regularis	*Sar_reg*	*Catapodium rigidum*	Cat_rig
Scoliciosporum sp.	*Sco_sp.*	*Centaurea jacea subsp. gaudini*	Cen_jacgau
Tephromela atra	*Tep_atr*	*Centaurea nigrescens*	Cen_nig
Verrucaria cfr. muralis	*Ver_mur*	*Cephalaria transsylvanica*	Cep_tra
Verrucaria nigrescens	*Ver_nig*	*Chaerophyllum temulum*	Cha_tem
Verrucaria tallo continuo marrone	*Ver_sp1*	*Chara vulgaris*	Cha_vul
Verrucaria tallo nero acquatica	*Ver_sp2*	*Chondrilla juncea*	Cho_jun
Xanthoria parietina	*Xan_par*	*Cichorium intybus*	Cic_int
Parmelia exasperata	*Par_exa*	*Cirsium arvense*	Cir_arv
		Cirsium creticum subsp. triumfetti	Cir_cretri
		Cirsium vulgare	Cir_vul
		Clematis vitalba	Cle_vit
		Colutea arborescens	Col_arb
		Convolvulus arvensis	Con_arv
		Cornus sanguinea	Cor_san
		Emerus major subsp. major	Eme_majmaj
		Corylus avellana	Cor_ave
		Crepis foetida	Cre_foe
		Crepis pulchra subsp. pulchra	Cre_pulpul
		Crepis vesicaria	Cre_ves
		Cruciata glabra	Cru_gla
		Cruciata laevipes	Cru_lae
		Dactylis glomerata	Dac_glo
		Daucus carota	Dau_car
		Digitalis lutea subsp. australis	Dig_lutaus
		Diplotaxis tenuifolia	Dip_ten
		Dorycnium hirsutum	Dor_hir
		Echinochloa crusgalli	Ech_cru
		Echium vulgare	Ech_vul
		Epilobium hirsutum	Epi_hir
		Epipactis cfr. helleborine	Epi_hel
		Epipactis palustris	Epi_pal
		Equisetum arvense	Equ_arv
		Equisetum palustre	Equ_pal
		Equisetum ramosissimum	Equ_ram
		Eupatorium cannabinum subsp. cannabinum	Eup_cancan
		Euphorbia amygdaloides	Eup_amy
		Euphorbia platyphillos	Eup_pla
		Schenodorus arundinaceus	Sch_aru
		Schedonorus giganteus	Sch_gig
		Fontinalis antipyretica	Fon_ant
		Fraxinus ornus subsp. ornus	Fra_ornorn
		Galega officinalis	Gal_off
		Galeopsis angustifolia subsp. angustifolia	Gal_angang
		Galium mollugo subsp. erectum	Gal_molere
		Galium aparine	Gal_apa
		Galium palustre subsp. palustre	Gal_palpal
		Galium verum	Gal_ver
		Genista tinctoria	Gen_tin
		Geranium columbinum	Ger_col
		Geranium robertianum	Ger_rob
		Geranium rotundifolium	Ger_rot
		Hedera helix	Hed_hel
		Helichrysum italicum subsp. italicum	Hel_itaita
		Helleborus bocconei subsp. bocconei	Hel_bocboc
		Helleborus foetidus subsp. foetidus	Hel_foefoe
		Humulus lupulus	Hum_lup

Table A1. *Cont.*

Lichens		Vascular plants	
Species	*Abbr.*	*Species*	*Abbr.*
		Hypericum perforatum	Hyp_per
		Inula conyzae	Inu_con
		Dittrichia viscosa	Dit_vis
		Juglans regia	Jug_reg
		Juncus articulatus	Jun_art
		Juncus fontanesii subsp. fontanesii	Jun_fonfon
		Juncus inflexus	Jun_inf
		Juniperus communis	Jun_com
		Juniperus oxycedrus subsp. oxycedrus	Jun_oxyoxy
		Knautia arvensis	Kna_arv
		Lapsana communis subsp. communis	Lap_comcom
		Lathyrus latifolius	Lat_lat
		Lathyrus sylvestris subsp. sylvestris	Lat_sylsyl
		Leucanthemum vulgare subsp. vulgare	Leu_vulvul
		Ligustrum vulgare	Lig_vul
		Linum tenuifolium	Lin_ten
		Lonicera etrusca	Lon_etr
		Lotus corniculatus	Lot_cor
		Lycopus europaeus subsp. europaeus	Lyc_eureur
		Lysimachia nummularia	Lys_num
		Lythrum salicaria	Lyt_sal
		Melica ciliata	Mel_cil
		Melica uniflora	Mel_uni
		Melilotus albus	Mel_alb
		Melilotus officinalis	Mel_off
		Mentha aquatica subsp. aquatica	Men_aquaqu
		Mentha spicata	Men_spi
		Molinia caerulea subsp. arundinacea	Mol_caearu
		Nasturtium officinale subsp. officinale	Nas_offoff
		Odontites luteus	Odo_lut
		Odontites vulgaris	Odo_vul
		Ononis natrix subsp. natrix	Ono_natnat
		Ornithopus pinnatus	Orn_pin
		Pastinaca sativa	Pas_sat
		Petasites hybridus subsp. hybridus	Pet_hybhyb
		Petrorhagia prolifera	Pet_pro
		Petrorhagia saxifraga	Pet_sax
		Peucedanum cervaria	Peu_cer
		Peucedanum verticillare	Peu_ver
		Helminthotheca echioides	Hel_ech
		Picris hieracioides	Pic_hie
		Plantago sempervirens	Pla_sem
		Plantago lanceolata	Pla_lan
		Plantago major	Pla_maj
		Poa compressa	Poa_com
		Polygala flavescens	Pol_fla
		Persicaria maculosa	Per_mac
		Populus alba	Pop_alb
		Populus nigra	Pop_nig
		Potamogeton nodosus	Pot_nod
		Potentilla reptans	Pot_rep
		Primula vulgaris subsp. vulgaris	Pri_vulvul
		Prunella vulgaris subsp. vulgaris	Pru_vulvul
		Prunus avium subsp. avium	Pru_aviavi
		Prunus domestica subsp. domestica	Pru_domdom
		Prunus domestica subsp. insititia	Pru_domins
		Prunus spinosa subsp. spinosa	Pru_spispi
		Pulicaria dysenterica	Pul_dys
		Quercus cerris	Que_cer
		Quercus pubescens subsp. pubescens	Que_pubpub
		Ranunculus lanuginosus	Ran_lan
		Ranunculus repens	Ran_rep
		Reseda lutea subsp. lutea	Res_lutlut
		Robinia pseudacacia	Rob_pse
		Rosa canina	Ros_can
		Rubus caesius	Rub_cae
		Rubus ulmifolius	Rub_ulm
		Salix alba	Sal_alb
		Salix eleagnos subsp. eleagnos	Sal_eleele
		Salix purpurea subsp. purpurea	Sal_purpur
		Salix triandra	Sal_tri
		Sanguisorba minor	San_min

Table A1. *Cont.*

Lichens		Vascular plants	
Species	*Abbr.*	*Species*	*Abbr.*
		Scabiosa columbaria	Sca_col
		Schoenus nigricans	Sch_nig
		Scirpoides holoschoenus	Sci_hol
		Scrophularia canina	Scr_can
		Sedum acre	Sed_acr
		Sedum sexangulare	Sed_sex
		Senecio aquaticus	Sen_aqu
		Setaria viridis	Set_vir
		Solanum dulcamara	Sol_dul
		Sonchus arvensis	Son_arv
		Sonchus asper	Son_asp
		Sorbus domestica	Sor_dom
		Sparganium erectum subsp. erectum	Spa_ereere
		Spartium junceum	Spa_jun
		Succisa pratensis	Suc_pra
		Symphytum tuberosum subsp. angustifolium	Sym_tubang
		Tamus communis	Tam_com
		Taraxacum gr. officinale	Tar_off
		Thalictrum flavum	Tha_fla
		Torilis arvensis	Tor_arv
		Trifolium sp.	Tri_sp.
		Tussilago farfara	Tus_far
		Typha minima	Typ_min
		Ulmus minor	Ulm_min
		Verbascum thapsus subsp. thapsus	Ver_thatha
		Veronica anagallis-aquatica subsp. anagallis-aquatica	Ver_anaana
		Viola alba	Vio_alb
		Vitis sp.	Vit_sp.

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