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ORIGINAL PAPER

Biodiversity and conservation of terricolous lichens and bryophytes in continental lowlands of northern Italy: the role of different dry habitat types

Gabriele Gheza, et al. *[full author details at the end of the article]*

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Abstract
In dry habitats of European lowlands terricolous lichens and bryophytes are almost neglected in conservation practises, even if they may strongly contribute to biodiversity. This study aims at (a) testing the role of heathlands, acidic and calcareous dry grasslands for lichen and bryophyte diversity and conservation in lowland areas of northern Italy characterized by high human impact and habitat fragmentation; (b) detecting the effect of environmental drivers and vegetation dynamics on species richness and composition. Lichens, bryophytes, vascular plants, and environmental variables were recorded in 287 circular plots for 75 sites. Our results indicate that heathlands, acidic and calcareous dry grasslands host peculiar terricolous lichen and bryophyte communities that include several species of conservation concern. Thus, each habitat provides a complementary contribution to lichen and bryophyte diversity in continental lowland landscapes. Furthermore, in each habitat different factors drive species richness and composition with contrasting patterns between lichens and bryophytes. In terms of conservation, our results indicate that management of lowland dry habitats should act at both local and landscape scales. At local scale, vegetation dynamics should be controlled in order to avoid biodiversity loss due to vegetation dynamics and wood encroachment. At the landscape scale, patches of all the three habitats should be maintained to maximize regional diversity.

Keywords Bryophytes · Dry grasslands · Heathlands · Lichens · Natura 2000 network · Nature conservation

Introduction

Conservation efforts and protected areas are mainly targeted for “charismatic species”, leaving many overlooked taxa almost unprotected (Darbyshire et al. 2017; Rubio-Salcedo et al. 2013). This approach may lead to an unaware, but relevant, loss of biodiversity. Thus,

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the maintenance of these overlooked organisms is still a challenge in nature conservation and protection (Nascimbene et al. 2013).

Lichens and bryophytes, in particular terricolous species, are among the most neglected taxa, their diversity patterns being generally less explored than those of vascular plants. However, biodiversity patterns of these organisms have been increasingly studied in the last decade, due to the growing awareness of the importance that "biological soil crusts" play for biodiversity and ecosystem functioning in dry habitats (e.g. Büdel et al. 2014).

Most of the dry habitats occurring in the European Union are protected under the Natura 2000 Network (Council Directive 92/43/EEC). This is one of the most important tools for nature protection in Europe, covering over 18% of the terrestrial surface of the EU member States, and including most of the habitats of conservation concern. These habitats are mainly identified on the basis of the structure and composition of vascular plant vegetation, while lichens and bryophytes are only rarely mentioned to characterize their formal description. This is the case of habitats in which these organisms strongly contribute to characterize habitat physiognomy and biodiversity, as in boreo-arctic and alpine tundras (Natura 2000 code 4060), or in petrifying springs (Natura 2000 code 7220). However, there are additional habitat types in Europe in which terricolous lichens and bryophytes may substantially contribute to biodiversity and functioning, as in the following three types of open dry habitats in the lowlands (Gheza 2015; Gheza et al. 2016, 2018a, b, 2019): heathlands (Natura 2000 code 4030), acidic dry grasslands (Natura 2000 codes 2330 and 6210 acidophilous subtype), and calcareous grasslands (Natura 2000 codes 6110* and 6210*).

In the European lowlands, these lichen- and bryophyte-rich dry habitats are characterized by arid to semiarid oligotrophic soils and represent pioneer or intermediate stages of a succession that will lead to more complex plant communities. These habitats can still occupy rather large extents (Jentsch and Beyschlag 2003; Ketner-Oostra and Sýkora 2008), even if they are being increasingly fragmented due to anthropogenic activities. Though information is already available on biodiversity patterns and functional role of lichens and bryophytes for some of these habitats (e.g. Chytrý et al. 2001; Matt and Legg 2008; Jüriado et al. 2016; Ketner-Oostra et al. 2012; Gheza et al. 2016), current management policies adopted by the European Union do not deserve specific measures devoted to the conservation of lichens and bryophytes (e.g. ec.europe.eu/environment/nature/natura2000/management/habitats/models_eu.htm). One of the main threats for terricolous lichens and bryophytes in open dry habitats is related to vegetation dynamics leading to encroachment by woody species, that transforms open habitats into shrublands and forests (Borghesio 2004; Assini 2008; Brusa et al. 2019). Encroachment is mainly related to poor or no management (Brusa et al. 2019) and can also be accelerated by habitat fragmentation and lack of connectivity among fragments (Sengl et al. 2016). Conservation-oriented management is therefore crucial to preserve these habitats.

While most research focused on the description of diversity patterns in a single dry habitat type, only a few studies simultaneously tested differences among various habitats and explored the factors that may drive diversity patterns within each habitat (e.g. Jüriado et al. 2016). In particular, for continental lowlands, information is missing on the role of different dry habitat types for biodiversity and conservation of terricolous lichens and bryophytes. Also the drivers of their diversity have not been fully evaluated so far, thus hindering the development of suitable and targeted conservation practices.

With this study, we aim at (a) investigating the importance of heathlands, acidic and calcareous dry grasslands for lichen and bryophyte biodiversity and conservation in lowland areas of northern Italy characterized by high human impact and habitat fragmentation;

(b) detecting the effect of environmental drivers and vegetation dynamics on the diversity of such communities. We considered lichens and bryophytes separately, because these different taxonomic groups can have contrasting patterns in response to the same environmental conditions (Nascimbene and Spitale 2017; Gheza et al. 2018a). Overall, we addressed four questions: (1) Do lichen and bryophyte species richness and composition differ among heathlands, acidic dry grasslands and calcareous dry grasslands? (2) Which environmental factors drive the patterns of species richness and composition in these habitats? (3) Is vegetation dynamics a driver? (4) Are biodiversity patterns consistent between lichens and bryophytes?

Materials and methods

Study area

This study was carried out in the central-western Po Plain (northern Italy), in an area ranging from the surroundings of Turin (Piedmont region) to the boundary between the regions Lombardy and Veneto. Mean annual temperature ranges between 11 and 13.5 °C. Annual rainfall ranges between 600 and 1200 mm. Soil pH varies from very acidic and acidic (pH 4–5, north of the Po river) to subneutral (pH 6, surroundings of the Po river) and basophilic (pH 7, south of the Po river and north of the Po river in the easternmost part of the study area). Altitude varies beetween 70 and 400 m a.s.l.

In the study area lichen- and bryophyte-rich dry habitats include: (1) heathlands: open dry *Calluna vulgaris*-dominated heathlands on acidic clayey to sandy-pebbly soils, attributed to the Natura 2000 Habitat 4030 ("European dry heaths"); (2) acidic dry grasslands: grasslands on acidic substrates, attributed either to the Natura 2000 Habitats 2330 ("Inland dunes with open *Corynephorus* and *Agrostis* grasslands") or to an acidic facies of Habitat 6210 ("Seminatural dry grasslands and scrubland facies on calcareous substrates"); (3) calcareous dry grasslands: grasslands on calcareous substrates, attributed either to the Natura 2000 Habitat 6110* ("Rupicolous calcareous or basophilic grasslands of the *Alysso-Sedion albi*") or Habitat 6210* ("Seminatural dry grasslands and scrubland facies on calcareous substrates"). Habitats 2330 and 4030 are in these regions at the southernmost edge of their distributional range (Borghesio 2009; Assini et al. 2013; Gheza 2015; Probo et al. 2017).

In the investigated area, the three habitat types are often extremely fragmented, and located usually in marginal and unproductive areas that are not actively managed. They host frequently terricolous lichen and bryophyte communities which are species-poorer than in similar habitats in central Europe, but they also host species with a more Mediterranean distribution pattern (Gheza et al. 2016, 2019).

A preliminary survey was performed in order to identify all the areas with natural and semi-natural lichen- and bryophyte-rich dry habitats. This process led to the identification of 17 areas, 13 of which potentially hosting dry grasslands distributed along the main river valleys (Ticino, Sesia, Dora Baltea, Stura di Demonte, Po, Orba, Scrivia, Lambro, Adda, Brembo, Serio, Oglio) and in the Lomellina, and 4 hosting *Calluna* heathlands distributed in the Upper Plain (Vaude Canavesane, Baragge Biellesi-Vercellesi, Brughiere Lonatesi, Groane Milanesi). In these areas, lichen- and bryophyte-rich sites were preliminary identified by analyzing GIS maps and thanks to the cooperation with local botanists and Park managers. These sites were inspected during winters 2015–2016 and 2016–2017 in order to evaluate their suitability for this study. All the habitat patches attributable to the

Natura 2000 Habitats targeted by this research were considered as suitable. Overall, 39 acidic grasslands, 14 calcareous grasslands, and 22 heathlands were selected and investigated (Online Resource 1). For each site, data on mean annual temperature and precipitation were retrieved from the website of the Regional Environmental Agencies of Piedmont (http://www.arpa.piemonte.gov.it) and Lombardy (http://www.arpalombardia.it), using the values of the nearest meteorological station.

Sampling design and specimen identification

At each site, circular plots with a 3 m radius were placed regularly along a linear transect connecting the two furthest vertices of the habitat patch using Qgis (Qgis Development Team 2009). The number of plots was proportional to the size of the site area: 1 plot for sites between 100 and 1000 m^2, 2 plots between 1001 and 3000 m^2, 3 plots between 3001 and 5000 m^2, 5 plots between 5001 and 20,000 m^2, and 7 plots for areas larger than 20,000 m^2. This resulted in a total of 287 plots.

Vegetation was surveyed in each plot between April and June 2016 in grasslands and between May and July 2017 in heathlands. In each plot, the cover (%) and the mean height (cm) of the five vegetation layers (arboreal, higher-shrubby, lower-shrubby, herbaceous, cryptogamic) were recorded, as well as the cover (%) of each vascular plant, lichen, and bryophyte species. Most species were identified in the Laboratory of Flora, Vegetation and Ecosystem Services of the University of Pavia, where voucher specimens are stored. Several lichen specimens, identifiable only on the basis of chemical analyses, were checked by thin-layer chromatography for secondary metabolites, following the standard procedure described by Elix (2014). Identification of critical bryophyte specimens was checked by an expert bryologist. Nomenclature follows Nimis (2016) for lichens, and Cortini Pedrotti (2001, 2006) for bryophytes.

Within each plot, some soil features and parameters were also recordered: pH (measured in the field with a portable kit), texture (evaluated qualitatively according to the following five categories: clayey, loamy, sandy, sandy-pebbly, organic), depth (measured in cm).

The cover (%) of the different biological forms of vascular plant species was calculated for each plot, and the most frequent biological forms—therophytes, hemicryptophytes, phanerophytes—were considered in the analyses.

Since a Red List is available in Italy only for epiphytic lichens (Nascimbene et al. 2013), information about commonness and rarity of the lichen and bryophyte species in Italy were retrieved from Nimis (2016) and Cortini Pedrotti (2001, 2006) respectively. This information was used as a proxy for the conservation concern of the species that were splitted into two categories: common species, merging the categories “rather common”, “common”, “very common” and “extremely common” by Nimis (2016), and rare species, i.e. species that potentially are of conservation concern, merging the categories “extremely rare”, “very rare”, “rare” and “rather rare” by Nimis (2016). Lichen species found in this research but considered “absent” from the Po Plain by Nimis (2016) were merged in the category “extremely rare”. Species included in the Habitats Directive were also considered as species of conservation concern.

Statistical analyses

First of all, differences among the three habitat types in terms of environmental conditions (i.e. soil depth, pH, stoniness, mean annual temperature and precipitation, cover of shrub, herb and cryptogam layers) were tested with the Kruskal–Wallis test. The same test was used to analyze separately species richness of lichens and bryophytes, considering (1) all the species, (2) rare species, and (3) common species.

Secondly, significant differences were analyzed in species richness and composition among the three habitat types, using respectively General Linear Mixed Models (GLMM) and Permutational Multivariate Analysis of Variance (PERMANOVA). For the analyses related to species composition, the percentage cover values of the species recorded in the field were re-scaled as follows: 1 (cover 0.1–10%), 2 (cover 11–20%), 3 (cover 21–30%), 4 (cover 31–40%), 5 (cover 41–50%), 6 (cover 51–60%), 7 (cover 61–70%), 8 (cover 71–80%), 9 (cover 81–90%), 10 (cover 91–100%). Non-metric Multidimensional Scaling (NMDS) based on euclidean distance was then used to visualize the distribution of species pools among the habitat types. Furthermore, an indicator species analysis (ISA) (labdsv R package, Roberts 2019) with 9999 permutations was used to assess potential indicator species for each habitat type. Analyses were carried out for lichens and bryophytes separately.

Lastly, the effects of continuous environmental variables on lichens and bryophytes were tested, separately for each habitat type. GLMM models (Poisson distribution, with site as random factor) were performed by using species richness of lichens and bryophytes, respectively, and the PERMANOVA test using the species composition of the two groups as response variable (Online Resource 2). We reduced the redundancy among environmental and structural variables analyzing their correlation (corrplot R package, Wei and Simko 2017). Considering only the significant correlations (p-values < 0.01, Hmisc R package, Harrell 2018), we used a correlation value of 0.5 as threshold. P-values ranging between 0.05 and 0.1 were retained as indicative of marginal effects. Also in this case, we considered lichens and bryophytes separately. As descriptors of vegetation dynamics, we considered the occurrence and cover of different plant biological forms characterizing the target habitats. Annual herbs (therophytes) dominate pioneer stages and thus may indicate ongoing vegetation dynamics due to disturbance; perennial herbs (hemicryptophytes, geophytes) dominate early and intermediate stages and thus may indicate less active vegetation dynamics; woody species (chamephytes, phanerophytes) dominate more mature scrub and forest stages and thus may indicate very slow vegetation dynamics (Frey and Lösch 2010).

Statistical analyses were carried out with the softwares R (R Core Team 2015), package "glmmTMB" (Brooks et al. 2017), and PAST (Hammer et al. 2001).

Results

Overall, 33 lichen and 22 bryophyte species were found (Table 1). Among them, 4 species are included in the Habitats Directive (*Cladonia portentosa*, *Leucobryum glaucum*, *Sphagnum compactum*, *S. papillosum*) and 7 lichens are of conservation concern due to their rarity (*Cladonia coccifera*, *C. peziziformis*, *C. strepsilis*, *C. uncialis*, *Dibaeis baeomyces*, *Pycnothelia papillaria*, *Stereocaulon condensatum*). Only 3 bryophytes (14% of the bryophyte species) are considered rare in Italy, whereas 20 lichen species (61% of the

Table 1 List of all the lichen and bryophyte species recorded in this study

Taxon	Heathlands (4030)	Acidic dry grasslands (2330, 6210)	Calcareous dry grasslands (6110*, 6210*)	Rarity in Italy	Habitats directive
Blennothallia crispa	0	0	3	Very rare	
Cetraria aculeata	0	3	0	Extremely rare	
Cladonia caespiticia	1	0	0	Extremely rare	
Cladonia cariosa	0	5	0	Extremely rare	
Cladonia cervicornis	3	0	0	Extremely rare	
Cladonia chlorophaea	1	7	3	Very common	
Cladonia coccifera	16	20	0	Extremely rare	
Cladonia fimbriata	1	1	2	Common	
Cladonia foliacea f. *convoluta*	0	2	10	Very common	
Cladonia foliacea f. *foliacea*	0	62	0	Extremely rare	
Cladonia furcata	0	26	0	Rather rare	
Cladonia humilis	0	0	5	Extremely rare	
Cladonia peziziformis	6	8	0	Extremely rare	
Cladonia polycarpoides	2	21	0	Extremely rare	
Cladonia portentosa	1	12	0	Very rare	Annex V
Cladonia pulvinata	4	0	0	Extremely rare	
Cladonia pyxidata	0	23	0	Extremely common	
Cladonia rangiformis	1	74	12	Extremely common	
Cladonia rei	18	27	5	Rare	
Cladonia squamosa var. *squamosa*	0	9	0	Very rare	
Cladonia strepsilis	1	3	0	Extremely rare	
Cladonia symphycarpa	0	0	9	Rather common	
Cladonia uncialis subsp. *uncialis*	0	1	0	Extremely rare	
Cladonia verticillata	3	0	0	Extremely rare	
Dibaeis baeomyces	1	0	0	Very rare	
Enchylium tenax	0	0	7	Extremely common	

Table 1 continued

Taxon	Heathlands (4030)	Acidic dry grasslands (2330, 6210)	Calcareous dry grasslands (6110*, 6210*)	Rarity in Italy	Habitats directive
Gyalolechia fulgens	0	0	3	Rather common	
Placidium squamulosum	0	0	26	Rather common	
Psora decipiens	0	0	19	Rather rare	
Pycnothelia papillaria	1	0	0	Extremely rare	
Scytinium schraderi	0	0	2	Rather rare	
Stereocaulon condensatum	0	6	0	Extremely rare	
Toninia sedifolia	0	0	19	Very common	
Atrichum angustatum	1	0	0	Rather common	
Brachythecium albicans	0	1	9	Common	
Calypogeia arguta	3	0	0	Rather common	
Campylopus introflexus	18	28	0	Rather common	
Ceratodon purpureus	10	79	7	Common	
Dicranum scoparium	0	2	0	Common	
Didymodon fallax	0	0	76	Common	
Ditrichum heteromallum	1	0	0	Common	
Eurhynchium hians	2	0	0	Common	
Hypnum cupressiforme	13	14	0	Common	
Hypnum jutlandicum	4	0	0	Common	
Leucobryum glaucum	4	2	0	Common	Annex V
Polytrichastrum formosum	16	18	0	Common	
Polytrichum piliferum	7	78	0	Common	
Pseudocrossidium hornsuchianum	0	1	0	Common	
Racomitrium canescens	0	12	2	Common	
Rhynchostegium megapolitanum	0	0	21	Common	
Riccia ciliifera	0	12	3	Rather common	
Sphagnum compactum	3	0	0	Rather rare	Annex V
Sphagnum papillosum	1	0	0	Rather rare	Annex V
Syntrichia ruralis	0	1	24	Common	
Tortella tortuosa	0	3	76	Common	

For each habitat, the percentage frequency of occurrence is reported. The rarity according to Nimis (2016) and Cortini Pedrotti (2001, 2006) and the eventual presence in the Habitats Directive are also reported lichen species) are rare or very rare in Italy. *Campylopus introflexus*, an alien-invasive moss of neotropical origin, was found in several heathlands and acidic grasslands.

The pairwise comparisons showed that the three habitat types differ significantly for most of the environmental variables (Fig. 1). Climatic features (mean annual temperature, annual precipitation) differ slightly but significantly among the three habitat types. Soil pH differs between the three habitats as well: calcareous grasslands occur on alkaline soils, while both acidic grasslands and heathlands occur on acidic soils, but heathlands are generally found on more acidic soils than acidic grasslands. The lowest values of herb layer cover were found in acidic grasslands and the highest in heathlands, whereas cryptogam layer cover was perfectly specular, with highest values in acidic grasslands and lowest values in heathlands. Only stoniness, soil depth and cover of the shrub layer did not differ significantly between the two grassland types, but differed between them both and heathlands: in fact, heathlands are characterized by deeper soils and a better-developed shrub layer than grasslands.

Concerning lichens, the three habitats differed significantly in species richness, both considering the whole species pool and rare and common species separately (Fig. 2). Acidic grasslands are the richest habitat, while heathlands are the poorest one. For bryophytes, the three habitats differed significantly in terms of total species richness, while significant differences were not detected neither for richness of rare species between acidic grasslands and heathlands, nor for richness of common species in the two grassland types (Fig. 2).

According to the GLMMs, species richness was related to two habitat types (heathlands and acidic grasslands) for bryophytes and to the three habitat types for lichens (Table 2). The relationship was positive for acidic grasslands and negative for the other two habitat types. According to the PERMANOVA, the three habitats differed significantly in terms of overall, lichen and bryophyte composition ($p = 0.001$). The visual interpretation of the NMDS biplots confirmed this result, despite a partial overlap among the three habitats (Fig. 3). The total number of species was similar across the three habitats (Table 3).

The ISA revealed several indicator species specific for each habitat type (Table 4): 14 for heathlands (2 statistically significant), 25 for acidic grasslands (17 significant), and 16 for calcareous grasslands (14 significant). The alien-invasive moss *Campylopus introflexus* was significantly overrepresented in acidic dry grasslands.

According to the GLMMs, in heathlands the cover of hemicryptophytes was negatively related to species richness of both lichens and bryophytes, while mean annual temperature was negatively related only to lichens (Table 5). The cover of therophytes was marginally positively related to lichens, while temperature was negatively related to them; annual precipitation was marginally positively related to bryophytes (Table 5). In acidic grasslands, the cover of therophytes and a higher substrate pH were negatively related to lichens, whereas the cover of the shrub layer was positively related to them, and, in this habitat, bryophytes did not respond to the considered variables (Table 6). In calcareous grasslands, the cover of hemicryptophytes was negatively related to lichens, whereas higher values of substrate pH were positively related to them. Also in this habitat, bryophytes did not show significant to the variables quantified in this study (Table 7).

According to the PERMANOVA, in heathlands the cover of hemicryptophytes and phanerophytes and the mean annual precipitation were significantly related to both lichen and bryophyte composition, whereas the cover of therophytes was related only to bryophytes. Substrate pH and mean annual temperature were only marginally related to lichens and bryophytes, respectively (Table 5). In acidic grasslands, the cover of therophytes, hemicryptophytes and the shrub layer, as well as mean annual temperature were related to lichen communities, while substrate pH was related to both lichen and bryophyte assemblages (Table 6). In calcareous grasslands, annual precipitation and substrate pH were related to both lichen and bryophyte communities, while cover of therophytes and hemicryptophytes were related only to bryophytes (Table 7).

Discussion

Our results indicate that heathlands, acidic and calcareous dry grasslands host distinctive terricolous lichen and bryophyte communities which include several species of conservation concern. Thus, each habitat supports lichen and bryophyte diversity in continental lowland landscapes. However, in each individual habitat different factors appear to drive diversity with contrasting patterns between lichens and bryophytes (e.g. Grytnes et al. 2006; Löbel et al. 2006; Gheza et al. 2018a). This should be accounted for in conservation planning, to maximize and maintain diversity at the landscape level. In this context, plant vegetation dynamics play a crucial role, influencing both lichen and bryophyte species richness and composition across different habitat types. On the other hand, climatic factors (temperature, precipitation) may also play a role in determining community composition.

Heathlands, acidic and calcareous grasslands differ in vascular plant species composition and richness, as well as in vegetation structure, as shown by our data. Furthermore, we provide evidence of the occurrence of different lichen and bryophyte communities across these three habitats. Besides differences in species richness, indicating that dry acidic grasslands are the species-richest habitat, differences in species composition are remarkable. This supports the view that the recognition of these three habitats should include not only vascular plants, but also cryptogams.

The partial compositional overlap among both lichen and bryophyte communities of the three habitats is related to the frequent occurrence of a few species with very wide ecological requirements, which can be found on both acidic and calcareous soils, and in grasslands as well as in heathlands. These are the three lichens *Cladonia chlorophaea*, *C. rangiformis*, *C. rei* and the bryophyte *Hypnum cupressiforme*, which are ruderal and stress-

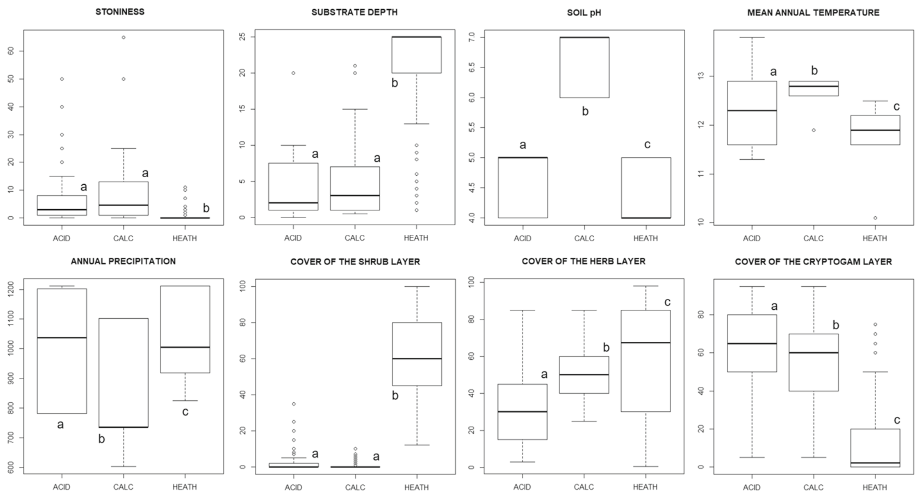

Fig. 1 Differences among the three habitats in terms of environmental variables. Different letters mark statistically significant differences according to the Kruskal–Wallis test

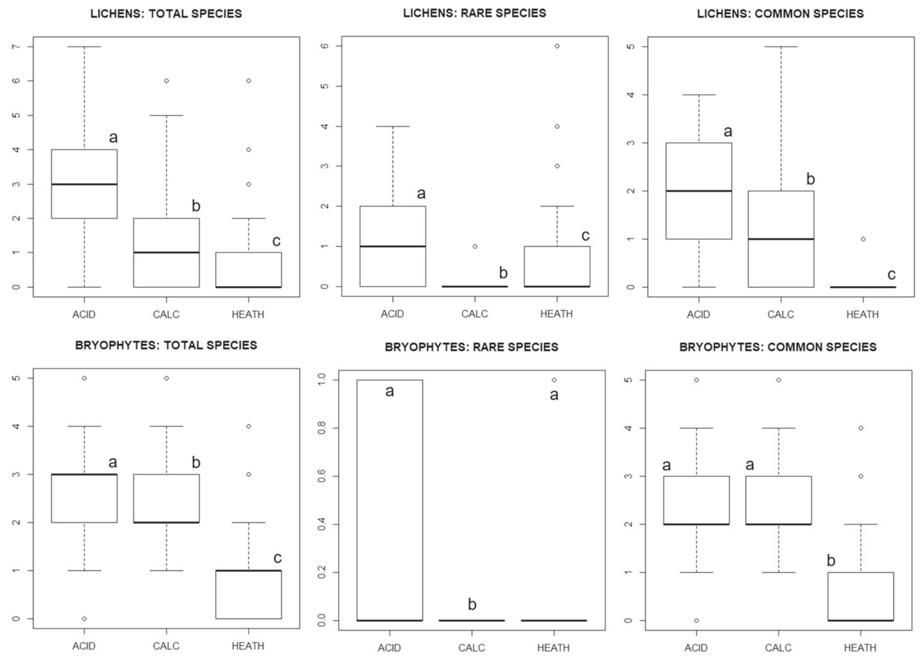

Fig. 2 Differences among the three habitats in terms of total, rare and common species richness. Different letters mark statistically significant differences according to the Kruskal–Wallis test

Table 2 Contribution of the three habitat types to the differences in species richness of lichens and bryophytes (GLMM); significant results are reported in bold

	Lichens		Bryophytes	
	Estimate	p	Estimate	p
Acidic dry grassland	**0.9268**	**3.02e−13**	**0.9028**	**< 2e−16**
Calcareous dry grassland	**− 0.7098**	**0.0033**	− 0.1452	0.253
Heathland	**− 1.7886**	**3.50e−14**	**− 1.1404**	**< 2e−16**

tolerant and can also establish both in natural sites and in sites with a certain degree of disturbance, where they may often dominate cryptogam communities (Paus 1997). Similarily to what happens with ruderal epiphytic species in forest habitats (Nascimbene et al. 2015), these species may drive floristic homogenization of cryptogam communities among the three studied habitats under high disturbance regimes. In this perspective, species-poor cryptogam communities dominated by the above mentioned species may be considered as a degraded succession of more diverse assemblages typical of more natural conditions. Moreover, they could be used as indicators of poor conservation status in habitat monitoring programs. Also the occurrence of extensive carpets of *Campylopus introflexus* can be used to indicate poor conservation conditions in acidic dry grasslands.

Vegetation dynamics revealed partially contrasting patterns between lichens and bryophytes. In dry habitats, the succession from pioneer to mature vegetation is mainly

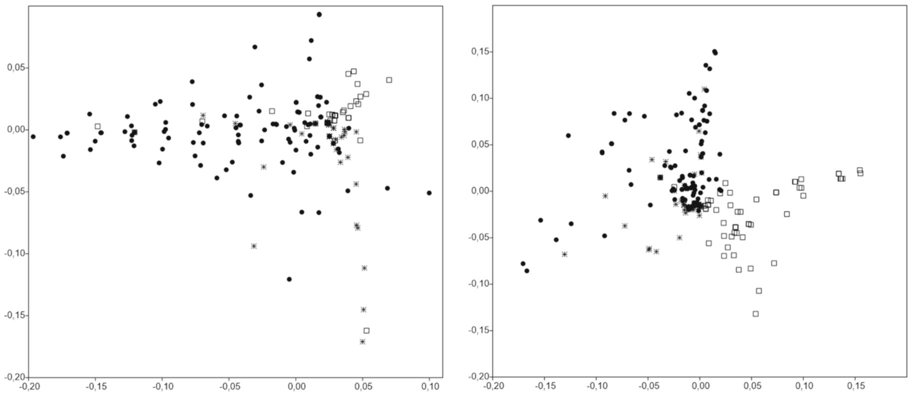

Fig. 3 NMDS scatterplots for lichen (left) and bryophyte (right) communities. Asterisks: heathlands; black dots: acidic dry grasslands; white squares: calcareous dry grasslands

Table 3 Number of total, exclusive and indicator species of lichens and bryophytes in the three dry habitats

	Lichens			Bryophytes		
	Total	Exclusive	Indicator	Total	Exclusive	Indicator
Heathlands	15	6	6	13	7	8
Acidic grasslands	18	8	16	13	2	9
Calcareous grasslands	14	9	11	8	2	5

linked to the increase of hemicryptophytes and, subsequently, of phanerophytes (Frey and Lösch 2010). However, even if vegetation succession is known to negatively affect terricolous cryptogams (Löbel et al. 2006), contrasting relationships among selected plant life forms and lichens and bryophytes across the investigated habitats may indicate that the effect of plant succession differently affects these two groups in different habitats. For example, the significant relationships revealed by our results suggest that hemicryptophytes could influence lichen communities in acidic grasslands and bryophytes in calcareous grasslands. In heathlands and calcareous grasslands, therophytes could influence bryophyte assemblages, whereas they could influence lichens in acidic grasslands. Despite these differences, the general pattern of our results indicates that the dynamics of plant vegetation outcompetes lichen and bryophyte communities, as suggested also by Ransijn et al. (2014). In particular, the increase in therophytes or hemicryptophytes is known to enhance grass encroachement (Friederich et al. 2011; Probo et al. 2017). This is particularly evident in heathlands, where *Molinia arundinacea* is the main hemicryptophyte with high cover values. Only in this habitat lichens and bryophytes have congruent patterns, being both negatively related to hemicryptophyte cover.

Climatic factors, i.e. precipitation and temperature, were related to both lichen and bryophyte composition, indicating that each habitat has the potential to host cryptogam communities composed of species with different climatic requirements (Nascimbene and Spitale 2017). In terms of conservation perspectives, this would imply that each habitat type should be protected under different climatic conditions to maximize the conservation

Table 4 Indicator species of the two groups of organisms in the three habitats; significant indicator species are reported in bold

	Lichens			Bryophytes		
	Species	INDVAL	p	Species	INDVAL	p
Heathlands	*Cladonia caespiticia*	0.87	1.0000	*Atrichum angustatum*	0.88	1.0000
	Cladonia cervicornis	2.63	0.1716	*Calypogeia arguta*	2.63	0.1714
	Cladonia pulvinata	**3.51**	**0.0507**	*Ditrichum heteromallum*	0.88	1.0000
	Cladonia verticillata	2.63	0.1628	*Eurhynchium hians*	1.75	0.1912
	Dibaeis baeomyces	0.88	1.0000	***Hypnum jutlandicum***	**3.51**	**0.0510**
	Pycnothelia papillaria	0.88	1.0000	*Leucobryum glaucum*	2.35	0.2413
				Sphagnum compactum	2.63	0.1760
				Sphagnum papillosum	0.88	1.0000
Acidic grasslands	*Cetraria aculeata*	3.47	0.0829	***Campylopus introflexus***	**17.07**	**0.0028**
	Cladonia cariosa	**5.21**	**0.0240**	***Ceratodon purpureus***	**65.45**	**0.0001**
	Cladonia chlorophaea	5.04	0.0938	*Dicranum scoparium*	1.74	0.3498
	Cladonia coccifera	**10.48**	**0.0456**	*Hypnum cupressiforme*	7.15	0.1406
	Cladonia foliacea	**60.86**	**0.0001**	***Polytrichastrum formosum***	**10.03**	**0.0480**
	Cladonia furcata	**26.09**	**0.0001**	***Polytrichum piliferum***	**71.82**	**0.0001**
	Cladonia peziziformis	4.98	0.1095	*Pseudocrossidium hornsuchianum*	0.87	1.0000
	Cladonia polycarpoides	**20.03**	**0.0001**	***Racomitrium canescens***	**10.66**	**0.0011**
	Cladonia portentosa	**11.36**	**0.0003**	***Riccia ciliifera***	**9.49**	**0.0009**
	Cladonia pyxidata	**22.61**	**0.0001**			
	Cladonia rangiformis	**63.54**	**0.0001**			
	Cladonia rei	**14.62**	**0.0098**			
	Cladonia squamosa	**8.69**	**0.0008**			
	Cladonia strepsilis	1.56	0.6354			
	Cladonia uncialis	0.87	1.0000			
	Stereocaulon condensatum	**6.09**	**0.0084**			
Calcareous grasslands	***Blennothallia crispa***	**3.45**	**0.0376**	***Brachythecium albicans***	**7.83**	**0.0021**
	Cladonia convoluta	**8.26**	**0.0021**	***Didymodon fallax***	**75.86**	**0.0001**
	Cladonia fimbriata	0.85	1.0000	***Rhynchostegium megapolitanum***	**20.69**	**0.0001**
	Cladonia humilis	**5.17**	**0.0093**	***Syntrichia ruralis***	**23.29**	**0.0001**

Table 4 continued

	Lichens			Bryophytes		
	Species	INDVAL	p	Species	INDVAL	p
	Cladonia symphycarpa	**8.62**	**0.0008**	***Tortella tortuosa***	**72.54**	**0.0001**
	Enchylium tenax	**6.89**	**0.0008**			
	Gyalolechia fulgens	**3.45**	**0.0399**			
	Placidium squamulosum	**25.86**	**0.0001**			
	Psora decipiens	**18.97**	**0.0001**			
	Scytinium schraderi	1.72	0.1998			
	Toninia sedifolia	**18.97**	**0.0001**			

Table 5 Factors related to richness (GLMM) and composition (PERMANOVA) of terricolous lichens and bryophytes in heathlands; significant factors are reported in bold

	Lichens				Bryophytes			
	Richness		Composition		Richness		Composition	
	Estimate	p	R^2	p	Estimate	p	R^2	p
Therophytes	**0.33512**	**0.0729**	0.02826	0.292	0.11655	0.1020	**0.02875**	**0.021**
Hemicryptophytes	**− 1.03212**	**2.50e–05**	**0.09199**	**0.005**	**− 0.44730**	**5.78e–05**	**0.04329**	**0.004**
Phanerophytes	0.03053	0.7790	**0.04927**	**0.042**	− 0.08716	0.4164	**0.02860**	**0.007**
Precipitation	0.19642	0.4855	**0.08708**	**0.007**	**0.23293**	**0.0696**	**0.16757**	**0.001**
Temperature	**− 0.61452**	**0.0331**	0.03666	0.162	0.24443	0.1740	**0.02123**	**0.099**
Substrate pH	0.19833	0.5082	**0.04613**	**0.077**	0.11458	0.2945	0.01977	0.146

of its region-specific species pool. Furthermore, temperature was related to cryptogams in heathlands and acidic grasslands, suggesting that the effects of climate warming could alter cryptogam assemblages in dry habitats, as already predicted for other habitat types (e.g. Nascimbene et al. 2018).

Within each habitat, substrate pH was only marginally related, likely reflecting the fact that its gradient is relatively low. However, while bryophyte richness is clearly independent from substrate pH, a contrasting pattern was detected for lichen richness between acidic and calcareous grasslands. In the former, lichen richness decreased at increasing soil pH, whereas in the latter, lichen richness increased with growing soil alkalinity. A likely explanation is that only few lichen species have a wide range of tolerance for substrate pH, while many species are either strictly acidophilous or strictly calciphilous (Nimis 2016). Therefore, at subneutral soil pH only few tolerant species can establish, whereas at the two extremes of the pH gradient also the more selective species occur, increasing lichen diversity. These results are consistent with Gould and Walker (1999), but partially in contrast with Löbel et al. (2006), who found an increase in lichen richness at increasing soil alkalinity. Soil pH is known to affect not only species richness and composition, but also

Table 6 Factors related to richness (GLMM) and composition (PERMANOVA) of terricolous lichens and bryophytes in acidic dry grasslands; significant factors are reported in bold

	Lichens				Bryophytes			
	Richness		Composition		Richness		Composition	
	Estimate	p	R^2	p	Estimate	p	R^2	p
Therophytes	**− 0.24039**	**0.0011**	**0.08045**	**0.001**	0.03213	0.6290	**0.01579**	**0.084**
Hemicryptophytes	0.07014	0.29711	**0.07931**	**0.001**	− 0.00540	0.9370	0.01482	0.140
Phanerophytes	− 0.00420	0.9405	0.00932	0.244	0.03396	0.5920	**0.01630**	**0.096**
Substrate pH	**− 0.10087**	**0.0808**	**0.03494**	**0.001**	− 0.03902	0.5440	**0.04443**	**0.001**
Temperature	0.02659	0.6693	**0.04423**	**0.001**	− 0.10839	0.1030	0.01001	0.324
Shrub layer	**0.11732**	**0.0197**	**0.01914**	**0.029**	0.06928	0.2460	0.00547	0.640

Table 7 Factors related to richness (GLMM) and composition (PERMANOVA) of terricolous lichens and bryophytes in calcareous dry grasslands; significant factors are reported in bold

	Lichens				Bryophytes			
	Richness		Composition		Richness		Composition	
	Estimate	p	R^2	p	Estimate	p	R^2	p
Therophytes	− 0.03733	0.8321	0.02980	0.221	0.15653	0.1060	**0.02830**	**0.043**
Hemicryptophytes	**− 0.52500**	**0.0094**	0.01961	0.532	−0.03579	0.7470	**0.06042**	**0.003**
Phanerophytes	0.00509	0.9704	0.03105	0.209	0.08896	0.2810	0.01718	0.187
Precipitation	− 0.09836	0.7144	**0.18268**	**0.001**	− 0.05328	0.6850	**0.17776**	**0.001**
Substrate pH	**0.44417**	**0.0782**	**0.12472**	**0.001**	− 0.01771	0.8840	**0.04837**	**0.003**
Herb layer	− 0.07858	0.6181	0.01886	0.517	0.01574	0.8890	0.01555	0.213

pigment and secondary metabolite production in terricolous lichens (Ochoa-Sueso et al. 2011; Zraik et al. 2018). Even if our results showed no significance for bryophytes, probably due to the small pH gradient within each habitat, these organisms are known to increase at increasing soil pH, both in species richness and cover, and not only in dry habitats but also in other ecosystems (Löbel et al. 2006; Oldén et al. 2016; Gheza et al. 2018a, b).

Management implications

Significant differences in richness and composition of lichen and bryophyte assemblages across the three habitats suggest that features of lichen and bryophyte communities (i.e. species richness and composition, and the occurrence of species of conservation concern) should be considered in habitat recognition. This would imply that habitat-specific conservation and monitoring have to target also cryptogams to preserve biodiversity in lowland dry habitats. Furthermore, the contrasting patterns between lichens and bryophytes should be considered, to maximize conservation effectiveness.

Conservation-oriented management of lowland dry habitats should be applied both on a local and a landscape level.

Small-scale vegetation dynamics of vascular plants should be controlled in order to avoid loss of lichen and bryophyte diversity due to vegetation dynamics and wood encroachment (Löbel et al. 2006). In particular, patches with pioneer vegetation stages should be actively maintained within each habitat type to maximize cryptogam diversity (Ketner-Oostra et al. 2012). This implies the restoration of patches of bare substrate by tree cutting, mowing, sod-cutting, topsoil removal/inversion (Chytrý et al. 2001; Allison and Ausden 2004; Ausden 2007; Matt and Legg 2008; van Andel and Aronson 2012; Glen et al. 2017). Sod-cutting and topsoil removal could be useful techniques also to remove the carpet-forming moss *Campylopus introflexus*, which is rapidly invading dry habitats in central Europe (Ketner-Oostra et al. 2012), and is widespread also in acidic dry grasslands of our study area. In heathlands, the uncontrolled increase of *Molinia arundinacea* is challenging the conservation of terricolous lichens and bryophytes. This tall grass should not be managed through extensive burning, which can foster its expansion (Brys et al. 2005; Jacquemyn et al. 2005; Probo et al. 2017). Grazing can be instead a good management tool to prevent grass encroachment (Kooijman and de Haan 1995), also combined with low-frequency burning (Borghesio 2009). However, in heavily human-impacted areas, as in our study area, where these habitats occur in fragmented patches even within agricultural and urbanized areas, grazing and burning could be impracticable. It should also be considered that grazing may have negative effects on terricolous lichens, mainly because of trampling (Silva et al. 2019). Therefore, mowing with subsequent removal of cut material could be an effective alternative technique applicable in these contexts.

At the landscape level, the maintenance of patches of all the three habitats is crucial to maximize regional diversity. This is especially urgent where these habitats occur only in fragmented and unconnected patches, since they are more prone to wood encroachment (Sengl et al. 2016) and alien species invasion (Assini 2008). Connectivity in such habitats could be improved by active management aimed at creating new habitat patches and expanding the existing ones (Ketner-Oostra et al. 2012), as aimed by currently active European projects, e.g. our LIFE Drylands project (https://www.lifedrylands.eu/) which is the first one in Italy devoted to such topic. Furthermore, mitigation of climate change effects could be achieved by preserving and enhancing microrefugia (Lenoir et al. 2017; Ellis 2020). In this case, microrefugia could be areas with favourable microtopographic features such as north slopes or concave sites that can enhance warming and dryness mitigation (Michalak et al. 2020).

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References

Allison M, Ausden M (2004) Successful use of topsoil removal and soil amelioration to create heathland vegetation. Biol Conserv 120:221–228

Ausden M (2007) Habitat management for conservation. Oxford University Press, Oxford

Assini S (2008) Habitat 2330 ("inland dunes with open *Corynephorus* and *Agrostis* grasslands"): problematiche di conservazione e ipotesi di intervento. Arch Geobot 14(1–2):23–28

Assini S, Mondino GP, Varese P, Barcella M, Bracco F (2013) A phytosociological survey of *Corynephorus canescens* (L.) P.Beauv. communities of Italy. Plant Biosyst 147(1):64–78

Borghesio L (2004) Biodiversity erosion in the Vauda nature reserve (Turin, Piedmont, NW Italy). Riv Piemont di Storia Nat 25:371–389

Borghesio L (2009) Effects of fire on the vegetation of a lowland heathland in North-western Italy. Plant Ecol 201:723–731

Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Maechler M, Bolker BM (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. Retrieved November 2019, from https://journal.r-project.org/archive/2017/RJ-2017-066/index.html

Brusa G, Dalle Fratte M, Zanzottera M, Cerabolini BEL (2019) Cambiamenti a lungo termine nell'uso del suolo nell'area di Malpensa e conseguenze sull'attuale presenza della brughiera. Pianura 38:72–85

Brys R, Jacquemyn H, De Blust G (2005) Fire increases aboveground biomass, seed production and recruitment success of *Molinia caerulea* in dry heathlands. Acta Oecol 28:299–305

Büdel B, Colesie C, Green TGA, Grube M, Làzaro Suau R, Loewen-Schneider K, Maier S, Peer T, Pintado A, Raggio J, Ruprecht U, Sancho LG, Schroeter B, Türk R, Weber B, Wedin M, Westberg M, Williams L, Zheng L (2014) Improved appreciation of the functioning and importance of biological soil crusts in Europe: the Soil Crust International Project (SCIN). Biodivers Conserv 23:1639–1658

Chytrý M, Sedláková I, Tichý L (2001) Species richness and species turnover in a successional heathland. Appl Veg Sci 4:89–96

Cortini Pedrotti C (2001) Flora dei muschi d'Italia I. Antonio Delfino Editore, Rome

Cortini Pedrotti C (2006) Flora dei muschi d'Italia II. Antonio Delfino Editore, Rome

Darbyshire I, Anderson S, Asatryan A, Byfield A, Cheek M, Clubbe C, Ghrabi Z, Harris T, Heatubun CD, Kalema J, Magassouba S, McCarthy B, Milliken W, de Montmollin B, Lughadha EN, Onana J-M, Saidou D, Sârbu A, Shresta K, Radford EA (2017) Important plant areas: revised selection criteria for a global approach to plant conservation. Biodivers Conserv 26:1767–1800

Elix JA (2014) A catalogue of standardized chromatographic data and biosynthetic relationships for lichen substances—third edition. Self-produced edition, Canberra. https://www.anbg.gov.au/abrs/lichenlist/Chem%2520Cat%25203.pdf

Ellis CJ (2020) Microclimatic refugia in riparian woodland: a climate change adaptation strategy. Forest Ecol Manag 462:118006

Frey W, Lösch R (2010) Geobotanik—Pflanze und vegetation in Raum und Zeit. Spektrum Akademische Verlag, Heidelberg

Friederich U, Gv O, Kriebitzsch WU, Selbmann K, Härdtle W (2011) Mechanisms of purple moor-grass (*Molinia caerulea*) encroachment in dry heathland ecosystems with chronic nitrogen inputs. Environ Pollut 159(12):3553–3559

Gheza G (2015) Terricolous lichens of the western Padanian Plain: new records of phytogeographical interest. Acta Bot Gallica 162(4):339–348

Gheza G, Assini S, Valcuvia Passadore M (2016) Terricolous lichen communities of *Corynephorus canescens* grasslands of Northern Italy. Tuexenia 36:121–142

Gheza G, Assini S, Marini L, Nascimbene J (2018a) Impact of an invasive herbivore and human trampling on lichen-rich dry grasslands: soil-dependent response of multiple taxa. Sci Total Environ 639:633–639

Gheza G, Nascimbene J, Mayrhofer H, Barcella M, Assini S (2018b) Two *Cladonia* species new to Italy from dry habitats in the Po Plain. Herzogia 31(1):293–303

Gheza G, Barcella M, Assini S (2019) Terricolous lichen communities in *Thero-Airion* grasslands of the Po Plain (Northern Italy): syntaxonomy, ecology and conservation value. Tuexenia 39:377–400

Glen E, Price EAC, Caporn SJM, Carroll JA, Jones LM, Scott R (2017) Evaluation of topsoil inversion in U.K. habitat creation and restoration schemes. Restor Ecol 25(1):72–81

Grytnes JA, Heegaard E, Ihlen PG (2006) Species richness of vascular plants, bryophytes and lichens along an altitudinal gradient in western Norway. Acta Oecol 29:241–246

Hammer Ø, Harper DAT, Ryan PD (2001) PAST: paleontological statistics software package for education and data analysis. Palaeontol Electron 4(1):1–9

Harrell FE (2018) Hmisc: harrell miscellaneous. R package version 4.1–1. Retrieved October 2019, fromhttps://CRAN.R-project.org/package=Hmisc

Jacquemyn H, Brys R, Neubert MG (2005) Fire increases invasive spread of *Molinia caerulea* mainly through changes in demographic parameters. Ecol Appl 15(6):2097–2108

Jentsch A, Beyschlag W (2003) Vegetation ecology of dry acidic grasslands in the lowland area of central Europe. Flora 198:3–25

Jüriado I, Kämärä M-L, Oja E (2016) Environmental factors and ground disturbance affecting the composition of species and functional traits of ground layer lichens on grey dunes and dune heaths of Estonia. Nord J Bot 34:244–255

Ketner-Oostra R, Sýkora KV (2008) Vegetation change in a lichen-rich inland drift sand area in the Netherlands. Phytocoenologia 38(4):267–286

Ketner-Oostra R, Aptroot A, Jungerius PD, Sýkora KV (2012) Vegetation succession and habitat restoration in Dutch lichen-rich inland drift sands. Tuexenia 32:245–268

Kooijman AM, de Haan MWA (1995) Grazing as a measure against grass encroachment in dutch dry dune grassland: effects on vegetation and soil. J Coast Conserv 1:127–134

Lenoir J, Hattab T, Pierre G (2017) Climatic microrefugia under anthropogenic climate change: implications for species redistribution. Ecography 40:253–266

Löbel S, Dengler J, Hobohm C (2006) Species richness of vascular plants, bryophytes and lichens in dry grasslands: the effects of environment, landscape structure and competition. Folia Geobot 41:377–393

Matt DG, Legg CJ (2008) The effect of traditional management burning on lichen diversity. Appl Veg Sci 11(4):529–538

Michalak JL, Stralberg D, Cartwright JM, Lawler JJ (2020) Combining physical and species-based approaches improves refugia identification. Front Ecol Environ 18(5):254–260

Nascimbene J, Spitale D (2017) Patterns of beta-diversity along elevational gradients inform epiphyte conservation in alpine forests under a climate change scenario. Biol Conserv 216:26–32

Nascimbene J, Nimis PL, Ravera S (2013) Evaluating the conservation status of epiphytic lichens of Italy: a red list. Plant Biosyst 147(4):898–904

Nascimbene J, Lazzaro L, Benesperi R (2015) Patterns of beta-diversity and similarity reveal biotic homogenization of epiphytic lichen communities associated with the spread of Black locust forests. Fungal Ecol 14:1–7

Nascimbene J, Nimis PL, Mair P, Spitale D (2018) Climate warming effects on epiphytes in spruce forests of the Alps. Herzogia 31(2):374–384

Nimis PL (2016) The Lichens of Italy—a second annotated catalogue. EUT, Trieste

Ochoa-Sueso R, Hernandez RR, Pueyo JJ, Manrique E (2011) Spatial distribution and physiology of biological soil crusts from semi-arid central Spain are related to soil chemistry and shrub cover. Soil Biol Biochem 43:1894–1901

Oldén A, Raatikainen KJ, Tervonen K, Halme P (2016) Grazing and soil pH are biodiversity drivers of vascular plants and bryophytes in boreal wood-pastures. Agr Ecosyst Environ 222:171–184

Paus SM (1997) Erdflechtenvegetation Nordwestdeutschlands und einiger Randgebiete. Bibl Lichenol 66:1–222

Probo M, Ascoli D, Lonati M, Marzano R, Lombardi G (2017) Restoration treatment to control *Molinia arundinacea* and woody alien species encroachement in *Calluna vulgaris* heathlands at the southern edge of their distribution. Biol Conserv 211:102–109

Qgis Development Team (2009) Qgis Geographic Information System. Open Source Geospatial Foundation. Retrieved May 2019, from https://qgis.osgeo.org

R Core Team (2015) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Ransijn J, Kepfer-Rojas S, Verheyen K, Riis-Nielsen T, Kappel Schmidt I (2014) Hints for alternative stable states from long-term vegetation dynamics in an unmanaged heathland. J Veg Sci 26(2):254–266

Roberts DW (2019) Package "labdsv" (Version 2.0–1). https://CRAN.R-project.org/package=labdsv

Rubio-Salcedo M, Martinez I, Carreno F, Escudero A (2013) Poor effectiveness of the Natura 2000 network protecting Mediterranean lichen species. J Nat Conserv 21:1–9

Sengl P, Magnes M, Wagner V, Erdös L, Berg C (2016) Only large and highly-connected semi-dry grasslands achieve plant conservation targets in an agricultural matrix. Tuexenia 36:167–190

Silva V, Catry FX, Fernandes PM, Rego FC, Paes P, Nunes L, Caperta AD, Sérgio C, Bugalho MN (2019) Effects of grazing on plant composition, conservation status and ecosystem services of Natura 2000 shrub-grassland habitat types. Biodivers Conserv 28:1205–1224

Van Andel J, Aronson J (2012) Restoration ecology—the new frontier. Wiley, London

Wei T, Simko V (2017) R package "corrplot": visualization of a correlation matrix (Version 0.84). Retrieved October 2019, from https://github.com/taiyun/corrplot/

Zraik M, Booth T, Piercey-Normore MD (2018) Relationship between lichen species composition, secondary metabolites and soil pH, organic matter, and grain characteristics in Manitoba. Botany 96:267–279

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Affiliations

Gabriele Gheza[1,2] · Silvia Assini[1] · Chiara Lelli[2] · Lorenzo Marini[3] · Helmut Mayrhofer[4] · Juri Nascimbene[2]

✉ Silvia Assini
silviapaola.assini@unipv.it

1 Department of Earth and Environmental Sciences, University of Pavia, Via S. Epifanio 14, 27100 Pavia, Italy

2 Department of Biological, Geological and Environmental Sciences, University of Bologna, Via Irnerio 42, 40126 Bologna, Italy

3 DAFNAE Department, University of Padova, Viale dell'Università 16, 35020 Legnaro, PD, Italy

4 Institute of Biology, Division of Plant Sciences, NAWI Graz, University of Graz, Holteigasse 6, 8010 Graz, Austria