

comparison with the communities found in the remnant habitats. Historical comparisons have been successfully applied only within urban environments, where site-referred historical data could be more easily retrieved (Rose and Hawksworth, 1981; Isocrono et al., 2007). When this information is available, historical comparison is a powerful tool to evaluate changes in biodiversity (Biesmeijer et al., 2006; Mac Nally et al., 2009), despite some limitations, related to heterogeneity of available datasets or differences in the sampling effort (e.g. Kosior et al., 2008; Newbold, 2010). In this study, we used historical information on the epiphytic lichen biota which was hosted in native oak forests in a region in Northern Italy. These data provide an exceptional framework to identify shifts in lichen communities due to the changes in land use which occurred during the last two centuries.

Specifically this study had two main objectives: (1) to check if epiphytic lichens historically recorded (1851–1894) in a region formerly covered by large native oak forests are still present in the remnant forests, and (2) to compare the epiphytic lichen communities inhabiting the remnants, with those found in the habitats that have replaced the native forests (black-locust forests and isolated trees in agrarian landscapes).

2. Materials and methods

2.1. Study area

The study was carried out in the Montello area, an elliptical shaped hill placed in the northern part of the Venetian plain (NE-Italy, Veneto, Treviso), extending over a 5000 ha surface with its main axis (13 km) NNE–SSW oriented (Fig. 1). The mean elevation is 200 m (maximum 369 m) and it is 100 m higher than the surrounding plain (Ferrarese and Sauro, 2005). The climate is temperate to humid subtropical with a mean annual temperature of 12.9 °C, January being the coldest month (mean temperature 3–4 °C) and July being the warmest one (mean temperature 22.7 °C). Mean annual rainfall is 1100 mm, with maxima in spring and autumn.

2.2. Historical landscape and forest management

For centuries the Montello area was covered by a continuous oak [*Quercus robur* L. and *Q. petraea* (Matt.) Liebl.] forest. However, similarly to what occurred over much of the hilly and lowland deciduous forests in Northern Italy, since the end of the 19th and during the 20th centuries native oak forests were subjected to severe cutting for agriculture land reclamation.

The first written information on the forest of Montello is available in a document dated 994 (Favero, 1875). From 1389 to 1797 the forest was owned by Venice republic and was used for providing the wood for the huge naval arsenal. The management was based on selective cutting resulting in a continuous, pure multilayered oak forest (Favero, 1875; Susmel, 1994). After the decline of Venice the forest was owned by the Austro-Hungarians until 1866. In this period, the intensity of the exploitation increased mainly due to illegal cutting by the local population. The intense disturbance promoted also the establishment of black locust (*R. pseudoacacia*), which was favoured by man because of its fast growth and good wood quality for firewood and agricultural uses. In 1892, the local stakeholders declared the total destruction of the native forest and the conversion of the whole area into a farmland (Bertolini, 1905). However, due to non-optimal conditions for agriculture, the conversion was not completed and part of the area remained covered by forests which were overexploited and greatly disturbed during the First World War. Between 1950 and 1970 the area was largely abandoned while in the surrounding region both industries and agriculture greatly developed. From 1954 to 2004 the total forested area progressively increased (Ferrarese and Castiglioni, 2005), being mainly related to the rapid spread of black locust, which prevented the re-establishment of the native oak forest.

2.3. Current landscape and management

Currently, Montello appears like an island surrounded by the anthropogenic landscape of the Venetian plain with diffuse agriculture and secondarily urbanization. In this area there are only minor industrial

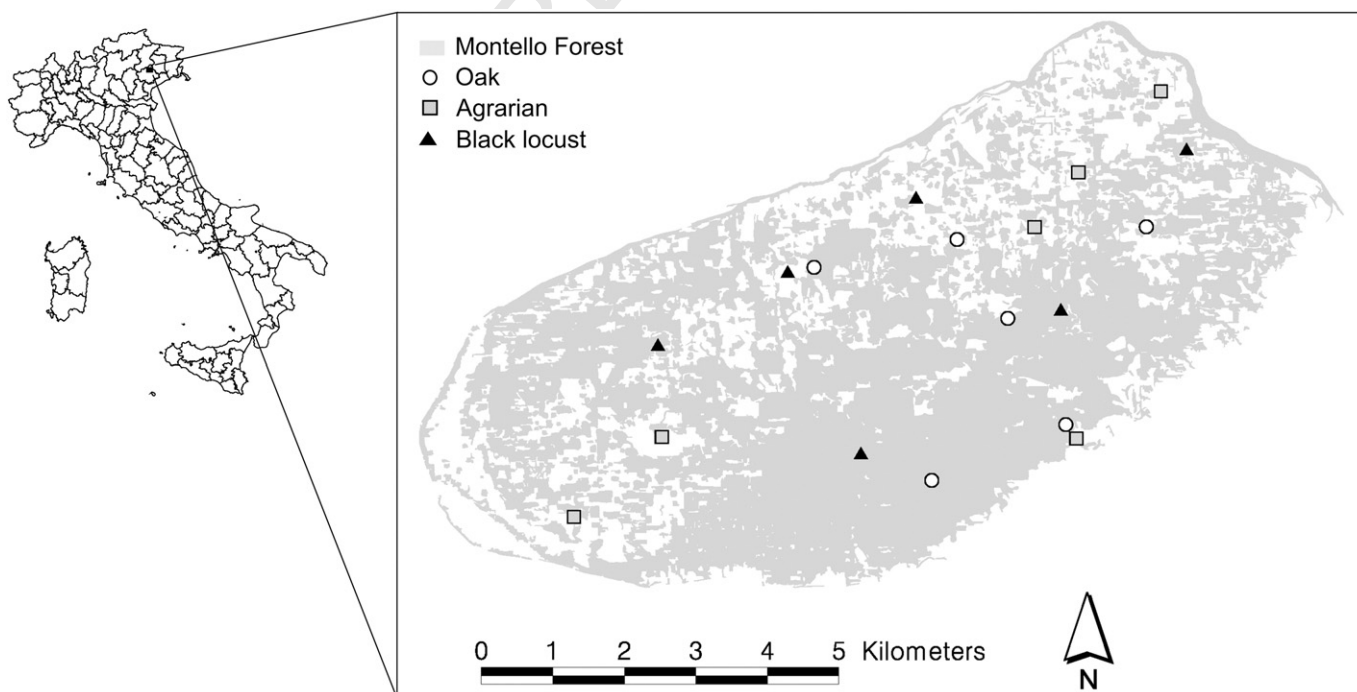


Fig. 1. Geographic position of the study area in north-eastern Italy. In the detailed map, the position of the 18 sampling plots surveyed for comparing currently available habitats (oak forest, agrarian habitat, and black-locust forest) for epiphytic lichens is reported.

activities which developed in the last 3–4 decades, resulting in relatively high levels of lichen diversity and in moderate or low degrees of air pollution even in the past years when some areas of the Veneto region were affected by high levels of SO_x pollution (Cislaghi and Nimis, 1997; Nimis et al., 1991).

Forty percent of the Montello area is managed for extensive agriculture, including arable fields, hay meadows, and vineyards, while the remnant 60% is covered by forests. The forest landscape may be described as a rather continuous black-locust matrix with interspersed oak-dominated patches. Pure black-locust formations are, therefore, the main forest type, representing over 90% of the forested area. They are private forests managed with short-rotation cycles (15–30 years), mainly for firewood production. Of the original c. 5000 ha of the oak forest present in the 19th century, only a few remnant patches (total area 106 ha) remained in the central part of the hill. They are non-intensively managed with occasional cutting by the owners. Additional minor formations are chestnut forests and artificial conifer plantations. Since 2000, Montello has been included in the Natura 2000 network (IT 3240004).

2.4. Comparison between historical and current lichen data

Information on the epiphytic lichen biota hosted in the past in the oak forest of Montello was retrieved from two main sources. The analytical lichen flora of Veneto by Saccardo (1894) includes all the records which were known for the region until that date. From this checklist we compiled the records for which it was clearly stated the provenance from Montello. Further information was retrieved from the herbarium BASSA which hosts the specimens collected by Massalongo and Beltramini during their field trip in August 1851 (Nascimbene, 2007). We included only species for which the note on the collecting site was completed by a precise comment on the habitat (oak forests). Despite the fact that in a comment to their field work Massalongo and Beltramini stated that the Montello was a relatively lichen poor area (Nascimbene, 2007) this dataset is not proposed here as an exhaustive checklist.

In 2009, we carried out accurate floristic surveys in all (n = 43) the oak remnant formations (total area 106 ha), checking if the species sampled between 1851 and 1894 were still present in the remnant forests. The minimum, mean and maximum patch size was 0.369, 2.47 and 12.6 ha, respectively. We carefully explored all the microhabitats potentially hosting the species historically recorded, including the base of the trunks which are often covered by mosses and are potentially suitable for example for some *Peltigera* species.

We retrieved the current rarity status of each species included in the historical list. Nimis and Martellos (2008) have estimated the rarity of the species at the national level on the basis of: a) number of samples in the TSB lichen herbarium, b) number of literature records, and, c) expert judgement. Eight commonness-rarity classes were used, from extremely rare to extremely common. The 'extremely rare' status is given only to taxa known from less than 5 localities in Italy, or to those that were not mentioned in the literature in the last 50 years. Recently-described or dubious taxa are excluded from this category. Extremely rare species are roughly compared to threatened species (Nimis and Martellos, 2008) according to the IUCN criteria (2001) and therefore targeted for conservation purposes at the national level. Nomenclature of lichens follows Nimis and Martellos (2008).

2.5. Comparison between currently available habitats for epiphytic lichens

A second lichen survey was performed to compare the three main habitats which are currently available for the establishment of epiphytic lichen communities: (1) isolated, mainly subneutral-barked (e.g. *Juglans regia* L.), trees in agrarian landscapes providing well-lit conditions, (2) pure black-locust forests providing moderately shaded

conditions, and (3) remnant oak forests not including black-locust trees, providing shaded conditions and subacidic–acidic substrates. For each of the three habitat types, six 30 × 30 m plots were selected in different parts of the hill in order to encompass the variability of each habitat in the study area (Fig. 1). The minimum distance between plots of the same habitat was 500 m to reduce spatial dependence. The borders of the forest plots were at least 50 m far from the forest edge. Agricultural plots were selected where at least six trees with DBH > 15 cm could be found within a 900 m² area. In each plot, 6 trees with DBH > 15 cm were selected for lichen survey by random sampling, for a total of 108 trees (36 in each habitat type). In black-locust and oak forests only black-locust and oak trees were respectively used for the lichen survey. In agricultural habitats lichens were mainly surveyed on *J. regia* L. (70%), and on *Prunus avium* L., *Pyrus* sp., and *Quercus* sp. The lichen inventory followed the guidelines proposed by Stofer et al. (2003) for the Forest BIOTA project, which are based on the European guidelines for lichen monitoring (Asta et al., 2002). Lichen diversity was sampled using four standard frames of 10 × 50 cm as sampling grids, subdivided into five 10 × 10 cm quadrats, which were attached to the tree trunk at the cardinal points with the lower side at 100 cm from the ground. All lichen species inside the frames were listed and their frequency was computed as the number of 10 × 10 cm quadrats in which the species occurred. Nomenclature of lichens follows Nimis and Martellos (2008).

2.6. Data analysis

The comparison between historical and current lichen data was done only qualitatively as the historical records were not precisely localized. We, therefore, estimated species extinctions at the regional level.

Concerning the comparison between currently available habitats, one-way analysis of variance (ANOVA) was applied to test the effect of habitat type on species richness. The analysis was performed using the cumulative number of species per plot (sum of the species found on the six trees) and mean number of species per tree, separately. In both cases we used the plot as replicate to avoid pseudo-replication. After the ANOVA, a Tukey's honest significance test for multiple comparison was applied to detect differences between the three habitat types (P < 0.05). To test the influence of habitat type on species composition, ordination methods were applied. The response variable was the species by plot matrix based on species frequencies. A preliminary Detrended Correspondence Analysis (DCA) was performed. The largest DCA gradient length, expressed in the standard deviation (SD) units of species turnover, of the first four DCA axes was 3.23. Thus, the use of linear-based ordination models was appropriate for these data (Ter Braak and Šmilauer, 2002). First, a Principal Component Analysis (PCA) was performed to extract the variability related to species composition. Second, a Redundancy Analysis (RDA) was performed, using habitat type as a factor. RDA tested if the three habitat types differed in species composition using a Monte Carlo permutation test (n = 1000). We ran both PCA and RDA to evaluate how much variation in species composition data was explained by habitat type. For these analyses we used the CANOCO package (Version 4.5, Ter Braak and Šmilauer, 2002).

3. Results

3.1. Historical vs. current lichen records

The historical list included 30 species and 1 lichenicolous fungus (*Sphinctrina turbinata*) (Table 1). They were mainly crustose (55%) and foliose (35%) species reproducing by ascospores (77%), or soredia (16%). Fifty-five percent of the species had chlorococcoid green algae, 29% cyanobacteria, and 26% trentepholioid algae as photobiont. Five species were extremely rare at the national level.

Table 1

Comparison of species found in the oak forest during the period 1851–1894 and in 2009. For each species the photobiont type and the current rarity status at the national level are reported according to Nimis and Martellos (2008). Photobiont: Ch = green algae other than trentepohlia; Cy = cyanobacteria; Tr = trentepohlioid alga.

Species found between 1851 and 1894	2009	Photobiont	Nationally rare
Acrocordia gemmata (Ach.) A.Massal.	Extinct	Tr	
Arthonia cinereopruinosa Schaer.	Extinct	Tr	+
Arthonia cinnabarina (DC.) Wallr.	Extinct	Tr	
Arthonia elegans (Ach.) Almq.	Extinct	Tr	
Arthonia pruinata (Pers.) A.L.Sm.	Extinct	Tr	
Arthonia radiata (Pers.) Ach.	Extinct	Tr	
Bacidia rosella (Pers.) De Not.	Extinct	Ch	
Calicium abietinum Pers.	Extinct	Ch	
Degelia plumbea (Lightf.) M.Jørg. & P.James	Extinct	Cy	
Flavoparmelia caperata (L.) Hale	Confirmed	Ch	
Fuscopannaria leucophaea (Vahl) M.Jørg.	Extinct	Cy	
Gomphillus calycioides (Duby) Nyl.	Extinct	Ch	+
Lecanographa amylacea (Pers.) Egea and Torrente	Extinct	Tr	
Lecidea exigua Chaub.	Extinct	Ch	
Leptogium corticola (Taylor) Tuck.	Extinct	Cy	+
Leptogium cyanescens (Rabenh.) Korb.	Extinct	Cy	
Lobaria pulmonaria (L.) Hoffm.	Extinct	Ch/Cy	
Nephroma resupinatum (L.) Ach.	Extinct	Cy	
Pannaria rubiginosa (Ach.) Bory	Extinct	Cy	+
Parmotrema perlatum (Huds.) M.Choisy	Confirmed	Ch	
Peltigera canina (L.) Willd.	Extinct	Cy	
Peltigera horizontalis (Huds.) Baumg.	Extinct	Cy	
Peltigera polydactyla (Neck.) Hoffm.	Extinct	Cy	
Pertusaria amara (Ach.) Nyl.	Extinct	Ch	
Pertusaria hymenaea (Ach.) Schaer.	Extinct	Ch	
Pertusaria leioplaca DC.	Extinct	Ch	
Pertusaria pertusa (Weigel) Tuck.	Extinct	Ch	
Pyrenula nitida (Weigel) Ach.	Extinct	Tr	
Pyrgidium montelicum (Beltr.) Tibell	Extinct	Ch	+
Ramalina farinacea (L.) Ach.	Extinct	Ch	
Sphinctrina turbinata (Pers. Fr.) De Not.	Extinct	Tr	

Only two species out of 31 were found again in 2009 (*Flavoparmelia caperata* and *Parmotrema perlatum*). Both species are still common in Italy. *P. perlatum* is more frequent in areas with suboceanic climate, such as the Tyrrhenian side of the peninsula, while in the north it is restricted to remnant humid forests (Nimis and Martellos, 2008).

3.2. Current lichen diversity

Forty-seven species were found in the 18 plots (Appendix). Cumulative species richness as well as mean species richness was highest in agrarian stands and lowest in oak forests, black-locust forests being in an intermediate position (Fig. 2). Also the overall number of species increased from oak to black-locust forests and agrarian stands (16, 19, and 37). Thirteen percent of the species occurred in all the habitat types, being however more frequent in black-locust forests and agrarian stands, such in the case of the two nitrophytic species *Candelaria concolor* and *Phaeophyscia chloantha*.

In the PCA ordination (Fig. 3a), the two axes represented 64.3% of the total variation in species composition (43.4% axis 1 and 20.9% axis 2). Plots belonging to different habitats were clearly separated, indicating major differences in species composition. Black-locust forests were in an intermediate position between oak forests and agrarian stands. In the RDA ordination, which was constrained to the habitat types (Fig. 3b), the two axes represent 52.6% of the total variation (38.4% axis 1 and 14.4% axis 2), i.e. the constrained ordination explained a large proportion of variation in species composition. A high number of species was related to agrarian stands. However, each habitat included some associated species, such in the case of *Catillaria nigroclavata* and *Hyperphyscia adglutinata* for black-locust forests, and *Arthonia spadicea*, *Lepraria lobificans*, and *P. perlatum* for oak forests. The forest species *Dimerella pineti* is shared between black-locust and oak forests.

4. Discussion

Our study found severe species extinction comparing the available historical records with those found on the remnant habitats. Amongst the species historically recorded in native forests, there is a large incidence of lichens with cyanobacteria and *Trentepohlia* as photobiont. These lichens, which in Europe have an oceanic-suboceanic distribution, are considered old-growth specialists extremely sensitive to intensive forest management (e.g. Campbell and Fredeen, 2004; Kuusinen, 1996), and human impact (e.g. Gauslaa et al., 2007; Geiser and Neitlich, 2007; Richardson and Cameron, 2004; Wolseley and Aguirre-Hudson, 1997). In Italy, they are mainly restricted to the western side of the peninsula and to the rainiest areas of the Alps where they are associated with humid and scarcely disturbed forests (Nascimbene et al., 2007, 2009; Nimis and Tretiach, 1995).

In our study region, the continuous native oak forest was transformed into either black-locust formations or arable lands, while only a few remnant patches are still preserved. According to Belinchón et al. (2009), destruction and fragmentation of forest habitats represent one of the most important threats for epiphytic lichens. The loss of the native habitat, the subsequent invasion by black locust and the agricultural management, were probably the most influential factors which affected and modified the composition of lichen communities (Aragón et al., 2010; Loppi and De Dominicis, 1996; Van Herk et al., 2003), causing the local extinction of most of the species historically recorded and the establishment of lichen communities composed by eutrophication-tolerant species. Air pollution might potentially have contributed to this process but the relatively high values of lichen diversity found in this area by Nimis et al. (1991), indicating low impact of SOx pollution, allowed us to hypothesize that metapopulation processes are likely to be more important than air pollution in our specific case. This hypothesis is also corroborated by the fact that some of the species still found in the remnant oak forests, such as *A. spadicea* and *P. perlatum* are strongly sensitive to air pollution (Nimis, 1993). The historical and current pollution conditions of our study region are significantly different from that in central and eastern Europe, where large industrial areas related to metal and coal mining and transformation developed since the end of 19th century, producing severe impacts on epiphytic lichens and causing the extinction of many species even in remote forested areas which were greatly impacted by a long-distance acidic deposition. Despite high and diffuse anthropization, the landscape of north-eastern Italy is still dominated by agriculture mixed with small industries which mainly developed in the last 3–4 decades.

Considering the habitats currently available to epiphytic lichens, remnant oak forests host lichen communities which clearly differ in species composition from both agrarian habitats and black-locust forests. Oak remnants hosted only a few species which were found in native forests and were the lichen poorest habitat in the study region. Aragón et al. (2010) have demonstrated that in oak forests, management intensity was the main predictor affecting the total epiphytic richness, suggesting that our small remnants could be influenced by past intensive management, resulting in species poor lichen communities. However, it is noteworthy that these communities were mainly composed by sub-acidophytic, shading tolerant, and nitrogen intolerant species (Nimis and Martellos, 2008), indicating that in this habitat the current level of eutrophication through nutrient deposition from the surrounding agrarian landscape is still low (Loppi and De Dominicis, 1996; Van Herk et al., 2003). Agrarian habitats were the species richest habitat. However, they hosted lichen assemblages dominated by lichens preferring well-lit and dry conditions, most of which are related to eutrophicated substrates (Nimis and Martellos, 2008). Despite the fact that eutrophication could cause impoverishment and shifts in species composition (Aragón et al., 2010; Loppi and De Dominicis, 1996), several nitrophytic lichens are enhanced by high levels of N deposition, resulting in relatively species rich communities (Loppi and Nascimbene, 2005).

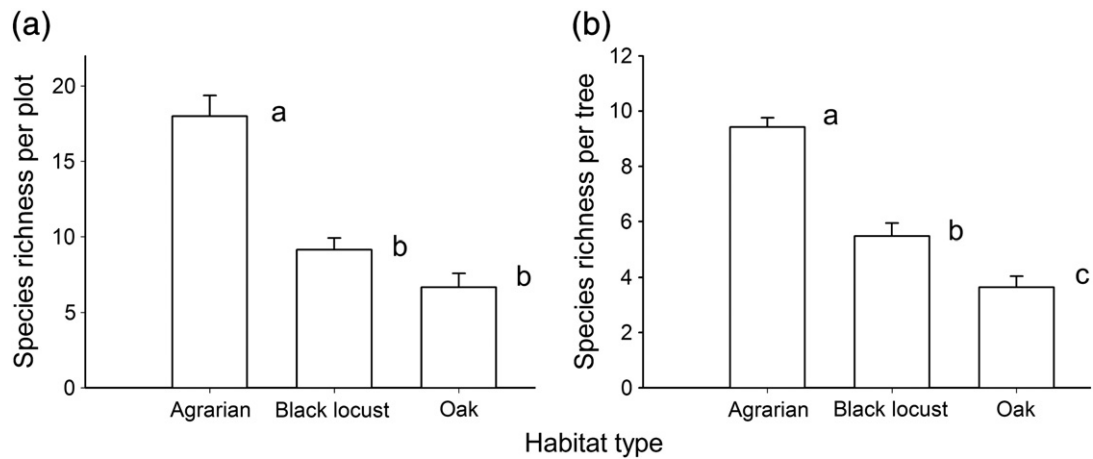


Fig. 2. Results of the one-way ANOVA and Tukey's honest significance test for multiple comparisons. We tested both (a) the cumulative number of species per plot and (b) the mean number of species per tree. We used the 18 plots as replicates in both analyses. Bars indicate mean with SE while different letters mark significant differences at $P < 0.05$.

2010). The ecological requirements of the species found in black-locust forests were similar to those inhabiting agrarian stands. The presence of a few forest lichens, such as *D. pineti*, which was mainly associated with oak remnants, or the rare *Agonimia allobata*, which was recently found in the region within riparian forests (Nascimbene et al., 2008), indicates a potential of these alien formations for hosting specific lichen communities. In this perspective, further research is needed to clarify if there is a succession during the rotation cycle (see e.g. Rogers and Ryel, 2008), with a shift from open habitat to forest habitat communities, and if a prolonged rotation cycle could allow black-locust stands to be suitable surrogates for richer forest lichen assemblages.

4.1. Management implications

Our study indicated that the loss of the native oak forest with the subsequent invasion by black locust was probably the major cause of local extinction of several rare lichen species. The few remnant oak forests were species poor and mainly composed of common species.

Since oak forests are targeted amongst the habitats of conservation concern in Europe (e.g. see Council Directive 92/43/EEC), future forest management should aim at restoring a more natural forest composition, favouring the spread of oaks and other native trees in lowland systems which are included in the Natura 2000 network. This might be expected to produce positive effects on lichen communities, providing more habitat area and more buffered conditions enhancing the establishment of forest species. The invasiveness of black locust is the main constraint to restoring large oak forests in the study area due to its fast vegetative reproduction. Since an inversion of the ratio between oak and black-locust forests does not seem realistic even in the long term, it should be investigated if some changes in the management of black-locust forests could be introduced to promote more conservation-oriented practices. These problems are likely to be common also in other lowland and hilly regions throughout Northern Italy, involving Natura 2000 sites (e.g. Motta et al., 2009). For this reason, a national strategy for biodiversity conservation and monitoring of lowlands forests should provide the framework for local restoration projects.

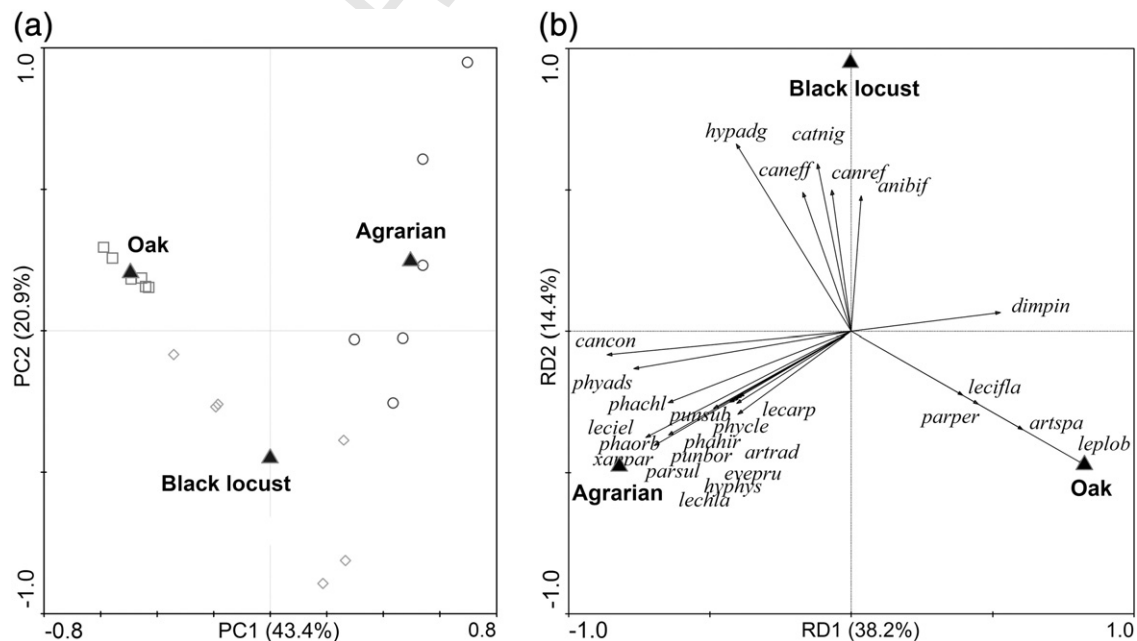


Fig. 3. (a) PCA ordination diagram of the 18 plots against the first two Principal Components and (b) RDA ordination diagram of lichen species occurring in the 18 plots against the first two canonical axes constrained by habitat type. In parentheses the explained variation by each axis is reported. In the RDA plot, only species with a fit-range above 10% are shown. ▲ Categorical variables; † Species. Abbreviations as in Appendix.

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Appendix A

Species found in the 18 plots. Frequency in each habitat type is expressed as the proportion of plots in which the species occurred. BL = Black-locust forests; O = Oak forests; A = Agrarian. * marks nitrophytic species, while ° marks shading tolerant species according to Nimis and Martellos (2008).

Species	Abbreviations	Frequency (%)		
		BL	A	O
Agonimia allobata (Stizenb.) P.James°	agoal	16.7	0	0
Anisomeridium biforme (Borrer) R.C.Harris	anibif	33.3	0	16.7
Arthonia radiata (Pers.) Ach.	artrad	0	33.3	0
Arthonia spadicea Leight.°	artspa	0	0	100
Arthrosporum populorum A.Massal.	arpopu	0	16.7	0
Caloplaca cerinella (Nyl.) Flagey*	calcer	0	33.3	0
Caloplaca ferruginea (Huds.) Th.Fr.	calfer	0	16.7	0
Caloplaca obscurella (Körb.) Th.Fr.	calobs	16.7	0	0
Caloplaca pyracea (Ach.) Th.Fr.	calpyr	0	50	0
Candelaria concolor (Dicks.) Stein*	cancon	100	100	16.7
Candelariella efflorescens auct. eur.*	caneff	83.3	50	0
Candelariella reflexa (Nyl.) Lettau*	canref	50	50	16.7
Candelariella xanthostigma (Ach.) Lettau	canxan	50	66.7	16.7
Catillaria nigroclavata (Nyl.) Schuler	catnig	83.3	83.3	0
Cladonia coniocraea (Flörke) Spreng.	clacon	0	0	33.3
Dimerella pineti (Ach.) Vezda°	dimpin	66.7	0	100
Evernia prunastri (L.) Ach.	evepru	0	33.3	0
Flavoparmelia caperata (L.) Hale	flacap	0	66.7	33.3
Flavopunctelia flaventior (Stirt.) Hale	flafla	0	16.7	0
Hyperphyscia adglutinata (Flörke) H. Mayrhofer & Poelt*	hypadg	100	100	0
Hypogymnia physodes (L.) Nyl.	hyphys	0	33.3	0
Lecania cyrtella (Ach.) Th.Fr.	leccyr	16.7	33.3	0
Lecanora carpinea (L.) Vain.	leccar	0	33.3	0
Lecanora chlorotera Nyl.*	lechla	0	50	16.7
Lecanora sambuci (Pers.) Nyl.	lesamb	0	33.3	0
Lecidella elaeochroma (Ach.) M.Choisy	leciel	16.7	83.3	0
Lecidella pulveracea (Schaer.) P.Syd.	lecifla	0	0	33.3
Lepraria incana (L.) Ach.°	lepinc	0	0	16.7
Lepraria lobificans Nyl.°	leplob	0	0	100
Melanelixia fuliginosa (Duby) O. Blanco. A. Crespo. Divakar. Essl. D. Hawksw. & Lumbsch	melful	0	33.3	0
Melanelixia subaurifera (Nyl.) O. Blanco. A. Crespo. Divakar. Essl. D. Hawksw. & Lumbsch	melsub	0	16.7	0
Normandina pulchella (Borrer) Nyl.	norpul	66.7	33.3	83.3
Parmelia sulcata Taylor	parsul	0	33.3	0
Parmelina tiliacea (Hoffm.) Hale	partil	0	16.7	0
Parmotrema perlatum (Huds.) M.Choisy	parper	0	0	50
Phaeophyscia chloantha (Ach.) Moberg*	phachl	66.7	100	16.7
Phaeophyscia hirsuta (Mereschk.) Essl.*	phahir	16.7	66.7	0
Phaeophyscia orbicularis (Neck.) Moberg*	phaorb	16.7	100	0
Phaeophyscia pusilloides (Zahlbr.) Essl.	phapus	0	16.7	0
Physcia adscendens (Fr.) H.Olivier*	phyads	83.3	100	0
Physcia clementei (Turner) Maas Geest.	phycle	0	50	0

Appendix A (continued)

Species	Abbreviations	Frequency (%)		
		BL	A	O
Physconia distorta (With.) J.R.Laundon*	phydis	0	16.7	0
Physconia perisidiosa (Erichsen) Moberg	phyper	0	16.7	0
Pseudevernia furfuracea (L.) Zopf v. furfuracea	psefur	0	33.3	0
Punctelia borrieri (Sm.) Krog	punbor	16.7	50	16.7
Punctelia subrudecta (Nyl.) Krog	punsub	0	33.3	0
Xanthoria parietina (L.) Th.Fr.*	xanpar	16.7	100	0

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