Habitat loss, extinction debt and climate change threaten terricolous lichens in lowland open dry habitats

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A B S T R A C T

Habitat loss is the main driver of biodiversity decline worldwide. An immediate consequence can be extinction debt, i.e. time-delayed extinction of species following habitat loss. We tested extinction debt in terricolous lichen communities in 45 patches of lowland open dry habitats in the western Po Plain (northern Italy) considering richness of four species groups: total, red-listed, rare, and common species. The distance from the currently nearest patch and the annual precipitation correlated – negatively and positively, respectively – with all the groups. Total, red-listed, and rare species were positively related to the oldest available patch extent (1954). Common species were positively related to the current (2020) patch extent. Total and red-listed species were negatively related to the extent difference (1954–2020). Results reveal an extinction debt which has not yet been completely paid and that could be exacerbated by climate change. To counteract this trend, management should conserve habitat patches with the highest species richness, improve connectivity between habitat patches, and provide suitable microrefugia for species with different ecological requirements.

1. Introduction

Habitat loss is the main driver of biodiversity decline and species extinction worldwide (Tilman et al., 1994; Pykälä 2019). Caused mainly by human activities like land use change and land consumption, the reduction, fragmentation, degradation and finally disappearance of natural and semi-natural habitats are the facets of this phenomenon, all impacting on diversity patterns of many different taxa (Hooftman et al., 2015; Niemandt and Greve 2016; Pykälä 2019). A treacherous consequence of such process is the extinction debt, i.e. the time-delayed extinction of species following environmental perturbations like habitat loss (Tilman et al., 1994; Kuussaari et al., 2009). This happens when the habitat extent has decreased, but residual species survive because the community has still to reach its equilibrium with the new habitat extent (Kuussaari et al., 2009). This implies that (1) where extinction debt has not yet been fully paid, present-day diversity mainly reflects the past habitat extent, and (2) several species are doomed to go extinct within a relatively short time (Kuussaari et al., 2009) if no conservation actions are applied. Although restoring initial conditions can become impossible when habitat loss is fast, when the process is

gradual and extinction debt is detected before the new equilibrium is reached, mitigation actions can be carried out to counteract its effects on biodiversity.

Habitat loss and extinction debt are expected to be exacerbated by the effects of climate change (Hannah et al., 2006; Dullinger et al., 2012; Talluto et al., 2017; Pires et al., 2018; Rumpf et al., 2019), which is recognized among major global threats to biodiversity (Bellard et al., 2012; Garcia et al., 2014). Anthropogenic climate change is in fact rapidly impacting the physiology, phenology, and distribution of multiple taxa (Hannah et al., 2006; Summers et al., 2012) and ecosystem functioning (Grimm et al., 2013; Pires et al., 2018), both directly and due to indirect effects. Its negative impact on biodiversity is not limited to warming, but also includes modifications of precipitation regimes and, therefore, water availability (Hannah et al., 2006), as well as anomalous extreme weather events able to alter climate patterns or destroy natural habitats.

Open dry habitats, i.e. acidic and calcareous dry grasslands and *Calluna vulgaris*-heathlands, are amongst the most threatened terrestrial habitats in Europe, having suffered most severe impacts due to abandonment and lack of proper management (Fagúndez 2013; Habel et al.,

2013; Janssen and Rodwell, 2016; Brusa et al., 2019). Preserving open dry habitats is crucial for biodiversity conservation, since they support a partially unique and high diversity of vascular plants, cryptogams, and several animal taxa (Dengler et al., 2014; Chatters 2021). They are also the most relevant habitats for terricolous lichens in temperate lowlands of the continent (Paus 1997; Bültmann 2005; Sparrius 2011; Leppik et al., 2013; Gheza et al., 2020, 2021). This implies that the loss of such habitats is likely to foster the local extinction of several species, as already observed in Central Europe (e.g. Leppik et al., 2013).

Among the main taxa contributing to biodiversity and ecosystem functioning in such habitats, lichens dwelling on soil are the most vulnerable to habitat loss (Scheidegger and Clerc 2002; Boch et al., 2016). Furthermore, vascular plants and bryophytes are more competitive and have faster growth and dispersion abilities, being therefore more efficient in colonizing substitution habitats (Tikka et al., 2001; García de León et al., 2017; Schmid et al., 2017). Substitution habitats are of paramount importance also for lichens (Leppik et al., 2013), but colonization can occur only when propagule sources are preserved in the surroundings. Due to their inconspicuous size and relatively limited dispersal, many lichens are expected to persist for a more or less long time even under a severe decrease of suitable habitat – provided that microsites with suitable microhabitats endure (i.e. microrefugia; Ellis and Eaton 2021; Di Nuzzo et al., 2022).

To date, extinction debt dynamics have been detected in dry grasslands for vascular plants (Helm et al., 2006; Cousins 2009; Krauss et al., 2010; Piqueray et al., 2011) and in forest habitats for epiphytic lichens (Ellis and Coppins 2007; Ranius et al., 2008), but this topic has never been studied for terricolous lichens in dry habitats. On the other hand, detrimental effects of climate change on terricolous lichens are increasingly highlighted not only in high-altitude environments (e.g. Allen and Lendemer 2016; Di Nuzzo et al., 2021; Vallese et al., 2022), but also in lowland dry habitats (Gheza et al., 2020, 2021), corroborating the hypothesis of a combined effect with habitat loss.

The western Po Plain offers the opportunity to study such dynamics under severe conditions, being one of the most human-impacted areas of Europe, where land consumption exceeds the European average (ISPRA 2021) and, therefore, loss of natural and semi-natural habitats is widespread and fast. It is also an area where climate change is expected to impact severely, especially on precipitation regimes, causing increasingly frequent drought periods (Baronetti et al., 2022; Straffelini and Tarolli 2023). In spite of such threats, scattered remnants of lichen-rich open dry habitats still persist, mainly in the few protected areas. Within this environmental context, the main local factors impacting lichen diversity – i.e. vegetation dynamics, mechanical disturbance, soil properties – have already been investigated (Gheza et al., 2018, 2020, 2021), while the role of factors acting across timespans at a larger spatial scale (e.g. landscape tansformation and climate change) have not yet been explored.

In this work, we show that by using complete species lists of fragments of lichen-rich dry grasslands and heathlands and estimates of their current and past extent it is possible to unravel extinction debt dynamics that are related to habitat loss and fragmentation (Kuussaari et al., 2009). If the results reveal a positive relationship between current species richness and the past extent of the fragments, this would suggest the existence of an extinction debt not yet fully paid, since current species richness would reflect the past arrangement of the landscape (Kuussaari et al., 2009). An accurate quantification of the lost species would not be possible without historical data (Kuussaari et al., 2009), however detecting such extinction debt would offer a chance for setting adequate conservation measures aimed at preserving the remnant species. Moreover, if climate (i.e. temperature and precipitation) would influence species richness patterns across our study area, this would imply that climate change could exacerbate the effects of habitat loss potentially accelerating the payment of the extinction debt. This would substantially decrease time and possibilities for conservation.

2. Materials and methods

2.1. Study area

We selected an environmentally homogeneous study area, i.e. the Ticino river valley (northwestern Italy) and its surroundings. This study area includes the actual river valley, the main heathlands of the western upper plain of Lombardia, which are located along the edge of the river valley, and the last remnants of inland sand dunes in the Lomellina, which are also near the edge of the river valley (Fig. 1; Supplementary File 1). This is a unique case study within the human-impacted landscape of the Po Plain, thanks to its long history of nature protection: the Lombardy and Piedmont Parks of the Ticino River Valley were established in 1974 and 1978 respectively, in a territory where many wide private hunting estates occurred. This allowed the continuous conservation of natural and semi-natural habitats on a wide scale in the whole of the river valley, that was appointed as a "MAB Biosphere Reserve" in 2002.

Prior to the 21st century, open dry habitats were widespread (Biroli, 1808; Nocca and Balbis, 1823; Cozzi, 1917; Giacomini, 1958; Brusa et al., 2019) as remnants of very ancient open habitats maintained by human action, but likely with a natural origin, like those occurring in Central Europe (Feurdean et al., 2018). The recent history of the study area can elucidate the swift decline of such habitats. The whole area underwent a massive deforestation during WWII (Tomaselli and Gentile 1971). This maintained wide extents of open habitats, together with practices of subsistence economy, e.g. herding, which had a major role in maintaining heathlands until the 1950s (Giacomini, 1958; Brusa et al., 2019). Soon after, the decline of these habitats began, mainly due to reforestation, abandonment, and increasing land reclamation for agriculture, urbanization and infrastructures (Brusa et al., 2019). Grasslands located at the bottom of the river valley also suffered from the regimentation of the rivercourse, which have totally or almost completely hindered the natural river dynamics, preventing the reappearance of pioneer mineral soil patches following the modifications of the course after extraordinary floods. Inland sand dunes, located outside the river valley, were mostly destroyed by land reclamation since an even older time (Boni 1947; Bertossi 1950; Corbetta 1968), and are nowadays almost fully lost, except in the few sites that were included in this study (Assini 2007; Gheza 2015; Gheza et al., 2019). The widest extensions of open dry habitats in the study area lasted mainly in formerly or still enclosed lands, especially within military areas, like in the surroundings of the two airports of La Promessa (abandoned since WWII) and Malpensa, and at the inland dune sites of Remondò.

The last remnants of open dry habitats at present days all occur on shallow, oligotrophic, acidic, sandy-pebbly soils, which allowed to have homogeneous soil features, that are relevant drivers of terricolous lichen assemblages (Gheza et al., 2020, 2021), in all our study sites. They are habitats of conservation concern at European level and protected under the Directive 92/43/EEC (Habitats Directive) as Habitats 2330 "Inland sand dunes with open *Corynephorus* and *Agrostis* grasslands" (Assini 2007; Assini et al., 2013; Gheza et al., 2019), 4030 "European dry heaths" (Cerabolini et al., 2017) and 6210 (*)-acidophilous subtype "Semi-natural dry grasslands and scrubland facies on calcareous substrates (*Festuco-Brometalia*) (*important orchid sites)" (Gheza et al., 2019; Assini et al., 2024). They often occur in mixed patches along the river valley, especially in its upper part, whereas on the inland dunes only *Corynephorus* grasslands occur (Supplementary File 1).

Climate is temperate-continental (Rivas-Martínez et al., 2004). A slight climatic gradient exists from the upper river valley, with higher annual precipitation (1190 mm/year) and lower mean annual temperature (13.1 °C), towards the lower river valley, with lower precipitation (782 mm/year) but higher temperature (14.1 °C). The Lomellina is more similar to the lower valley (863-841 mm/year, 13.8 °C). Climatic data were retrieved from the CHELSA database (Karger et al., 2017; 2018).
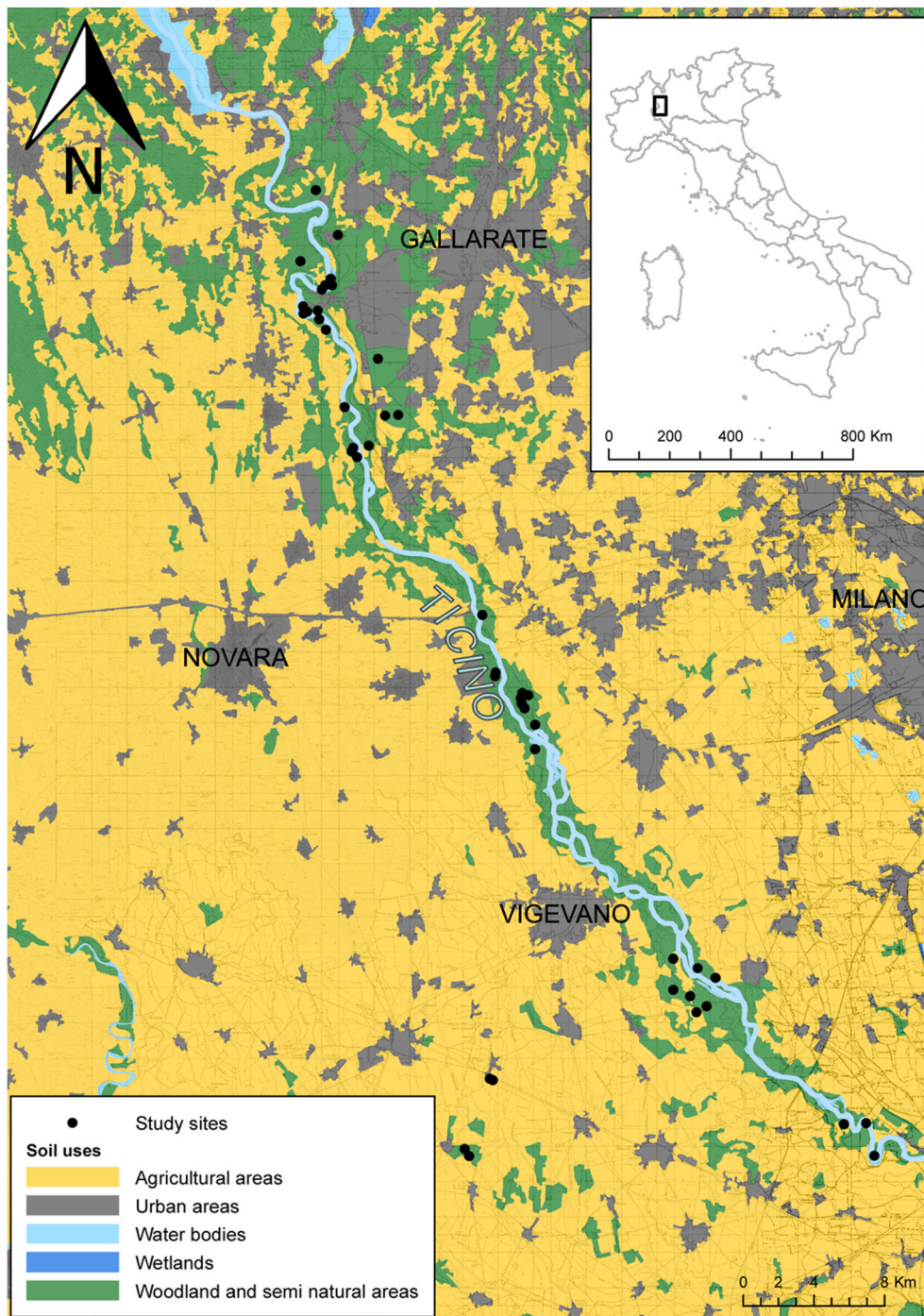
Fig. 1. Study area and study sites (black dots) in the western Po Plain (Northern Italy).

2.2. Lichen inventories

Forty-five sites hosting lichen-rich open dry habitats with homogeneous soil features and different areas were found during a decade of field explorations carried out by the authors in the study area (Supplementary File 1). By selecting these specific sites, it was possible to standardize some of the most relevant factors, i.e. soil pH (acidic in all the sites) and texture (sandy-pebbly in all the sites), land use history, and protection, focusing the analysis on the effects of habitat patch size and climate.

Each site was visited 3 to 9 times in the period 2012–2021 (Gheza 2015, 2018a; Gheza et al., 2018, 2019, 2020). The accurate investigation of all the sites resulted in complete lists of terricolous lichens. All the

sites were surveyed again once in winter 2021–2022, to verify the persistence of the species; only the species found during this last survey were considered here.

Specimens were identified in the laboratory with standard lichenological procedures, using the keys by Nimis and Martellos (2004) and Gheza (2018b). Several *Cladonia* specimens were resolved by means of TLC with solvents A, B or B', and C (Elix, 2014). Voucher specimens are deposited in the First Author's private herbarium.

Lichen nomenclature follows ITALIC 7.0 (Nimis and Martellos 2023).

2.3. Environmental variables

Given the aforementioned homogeneity in substrates and land use

history, we were able to investigate the effects of habitat loss, i.e. decrease in the habitat patch size, and climate, while minimizing the other sources of variation. The estimate of the decrease of open dry habitats was based on the orthophotos available for the study area analyzed by means of Q-GIS (QGIS.org, 2022). The oldest available orthophotos, used to infer the past extent of habitat patches, dated back to 1954 (aerial photography "GAI flight", coordinated by the IGM and carried out by the "Gruppo Aereo Italiano", with frames taken mainly at about 5.000 m height, resulting in a scale of about 1:30.000 – WMS service, Regione Lombardia). In the 1954 orthophotos, due to the poor quality, dry grasslands and heathlands were indistinguishable from each other. However, such vegetation types can be considered as a continuum, since, due to their similar ecological requirements, they are often found in intermixed patches in the study area, with heathlands representing a dynamic stage succeeding the grasslands. This is also coherent with the fact that many lichen species are shared between these habitat types (Gheza 2015, 2018a; Gheza et al., 2020). The current extent of the habitat patches was checked in the field in winter 2021–2022 and then reported on the 2020 orthophotos (Satellite images, data @2020 Google).

We calculated the following predictive variables: the extents of each habitat patch in 1954 and 2020, describing the oldest information available and the current situation; the percent difference in area between 1954 and 2020; the current distance of each habitat patch from the nearest other patch, measured on the orthophoto of 2020. The area extents variables ranged between several orders of magnitude, therefore these variables were log-scaled to avoid bias due to outliers (Zuur et al., 2009).

Since climate is known to affect terricolous lichen communities (Gheza et al., 2020; 2021; Di Nuzzo et al., 2021; Vallese et al., 2022), we also considered total annual precipitation and mean annual temperature, whose mean values were extracted from the CHELSA database (Karger et al., 2017; Karger et al., 2018), which makes available the historic data series from 1981 to 2010.

Correlation between the variables listed above was assessed by means of the Pearson's correlation coefficient (Supplementary File 2). Precipitation and temperature were highly correlated (r > 0.7), therefore only that considered as the most ecologically meaningful one was selected to be used in the models (cf. Porro et al., 2020), i.e. precipitation.

The following variables were therefore retained for the analyses: (1) area extent of the patch in 1954; (2) area extent of the patch in 2020; (3) percent difference in area extent of the patch between 1954 and 2020; (4) current distance of each patch from the nearest other patch; (5) annual precipitation.

For the subsequent statistical analyses, all the considered explanatory variables were standardized to a mean of zero and a standard deviation of one (Quinn and Keough 2002; Zuur et al., 2007).

2.4. Data analysis

We tested the effects of the five variables listed above on: (1) total species richness, i.e. all the species recorded in each patch; (2) red-listed species (Gheza et al., 2022); (3) rare species, i.e. species considered "extremely rare" to "very rare" in the Submediterranean ecoregion (Nimis and Martellos 2023; Martellos et al., 2020); (4) common species, i.e. species considered "common" to "rather rare" in the Submediterranean ecoregion (Nimis and Martellos 2023; Martellos et al., 2020). Both red-listed and rare species included taxa of conservation concern, but there was only a partial overlap between them, since red-listed species were assessed at a national level, whereas rare species were evaluated under a phytoclimatic perspective, which is more local and homogeneous; therefore, these two categories could be expected to provide different information.

Data distribution was preliminary tested by the Shapiro-Wilk test. Total richness and common species values followed a normal

distribution, whereas red-listed and rare species values followed a Poisson distribution; thus, we used Generalized Linear Models (GLMs; McCullagh and Nelder, 1989) with a normal distribution for the first case and a Poisson distribution for the second.

For each dependent variable (i.e. total species richness, red-listed, rare, and common species) we built five candidate models based on different ecological hypotheses (Symonds and Moussalli 2011). Among the five candidate models, the best model/s were identified using the Akaike Information Criteria (AIC; Burnham and Anderson, 2002). When more than one model was included in a range of ΔAIC <2 from the lowest AIC model, we considered them as having a similar importance in explaining underlying relationships between dependent variables and predictors. If a model had an AIC comparable with the one of the null model, i.e. ΔAIC <2, it was considered describing not relevant relationships.

For all the best models, the 95% upper and lower confidence intervals of beta coefficients were estimated. Residuals normality of the best linear models and dispersion of the best Poisson models were assessed by means of a Kolmogorov-Smirnov test and a Dispersion Test respectively (Marsaglia et al., 2003). Predictive ability of all models was evaluated by means of a Pearson Correlation Test. For all the best models, we tested the residual spatial autocorrelation by means of the Moran I test (Zuur et al., 2007; Bivand et al., 2008).

All the analyses were performed with R version 4.2.2 (2022-10-31) "Innocent and Trusting" (R Core Team, 2019), using functions of the following packages: spdep (function: moran. test; Bivard and Wong 2018), ggplot2 (function: ggplot; Wickham 2016), AER (function: dispersiontest; Kleiber and Zeileis 2020) and fitdistrplus (function: descdist; Delignette-Muller and Dutang 2015).

The dataset is available as Supplementary File 1.

3. Results

Overall, we recorded 23 terricolous lichen species (Table 1), mostly belonging to the genus *Cladonia*. The most frequent were *Cladonia rangiformis*, *C. foliacea*, *C. polycarpoides*, *C. rei*, and *C. chlorophaea*. The richest site hosted 13 species, whereas the two poorest sites hosted only 1 species. On average, we found 6.29 ± 3.29 species per site, with 0.98 ± 1.25 red-listed, 1.78 ± 1.99 rare and 4.51 ± 1.78 common species per site.

Table 1

List of the 23 species recorded in the 45 study sites, with their number of occurrences, rarity (simplified from Nimis and Martellos 2023, see text), and red-list category (when applicable; Gheza et al., 2022).

Species	Occurrences	Rarity	Red List
Cetraria aculeata (Schreb.) Fr.	3	Rare	–
Cladonia caespiticia (Pers.) Flörke	3	Common	NT
Cladonia cariosa (Ach.) Spreng.	6	Rare	–
Cladonia cervicornis (Ach.) Flot.	6	Rare	–
Cladonia chlorophaea (Sommerf.) Spreng.	23	Common	–
Cladonia coccifera (L.) Willd.	19	Rare	–
Cladonia conista (Nyl.) Robbins	5	Rare	DD
Cladonia cryptochlorophaea Asahina	3	Rare	NT
Cladonia foliacea (Huds.) Willd.	38	Common	–
Cladonia furcata (Huds.) Schrad.	18	Common	–
Cladonia peziziformis (With.) J.R. Laundon	7	Common	NT
Cladonia polycarpoides Nyl.	29	Common	–
Cladonia portentosa (Dufour) Coëm.	12	Rare	NT
Cladonia pulvinata (Sandst.) Herk & Aptroot	8	Rare	DD
Cladonia pyxidata (L.) Hoffm.	13	Common	–
Cladonia ramulosa (With.) J.R. Laundon	1	Rare	–
Cladonia rangiformis Hoffm.	43	Common	–
Cladonia rei Schaer.	29	Common	–
Cladonia strepsilis (Ach.) Grognot	6	Rare	VU
Cladonia uncialis (L.) F.H. Wigg.	5	Rare	–
Cladonia verticillata (Hoffm.) Schaer.	1	Rare	–
Dibaeis baeomyces (L. f.) Rambold & Hertel	1	Rare	–
Stereocaulon condensatum Hoffm.	4	Rare	–

All the computed models showed AIC values significantly lower than the corresponding null models' AIC.

The model with the lowest AIC (207.04) for the total richness included patch extent in 1954 and annual precipitation with a positive effect, and difference of extent between 1954 and 2020 and distance from the nearest patch with a negative effect (Fig. 2). All variables' 95% confidence intervals did not include zero (Tables 2 and 3). Shapiro-Wilk test confirmed residuals normality (p-value = 0.44), while Pearson correlation test estimated a correlation of 0.76 between observed and predicted data (p-value <0.001). No residuals' spatial autocorrelation was evidenced (Moran's I = 0.178, p-value = 0.14).

The model with the lowest AIC (94.27) for the number of red-listed species included patch extent in 1954 and annual precipitation with a positive effect, and difference of extent between 1954 and 2020 and distance from the nearest patch with a negative effect (Fig. 3). All variables' 95% confidence intervals did not include zero (Tables 2 and 4). No significant model over- or underdispersion was detected by the Dispersion Test (p-value = 0.67, dispersion = 0.90), while Pearson correlation test estimated a correlation of 0.86 between observed and predicted data (p-value <0.001). No residuals' spatial autocorrelation was evidenced (Moran's I = 0.180, p-value = 0.13).

The models with the two lowest AICs (137.73 and 138.22) for the number of rare species both included patch extent in 1954 and annual precipitation with a positive effect, and distance from the nearest patch with a negative effect (Fig. 4), all with 95% confidence intervals not overlapping zero. Only one of the models included difference of extent between 1954 and 2020 with a negative effect, but with confidence intervals including zero (Tables 2 and 5). For both models, no significant model over- or underdispersion was detected by the Dispersion Test (p-values = 0.14 and 0.17, dispersion = 1.25 and 1.24). Pearson correlation test estimated a correlation of 0.77 and 0.78 respectively between observed and predicted data (both p-values <0.001). No residuals' spatial autocorrelation was evidenced (Moran's I = 0.211 and 0.209, p-values = 0.13 and 0.11).

The models with the two lowest AICs (161.78 and 161.94) for the number of common species both included patch extent in 2020 and annual precipitation with a positive effect, and distance from the nearest patch with a negative effect (Fig. 5), all with 95% confidence intervals not overlapping zero. Only one of the models included difference of extent between 1954 and 2020 with a positive effect, but with confidence intervals including zero (Tables 2 and 6). For both models, Shapiro-Wilk test confirmed residuals normality (p-value = 0.10 and
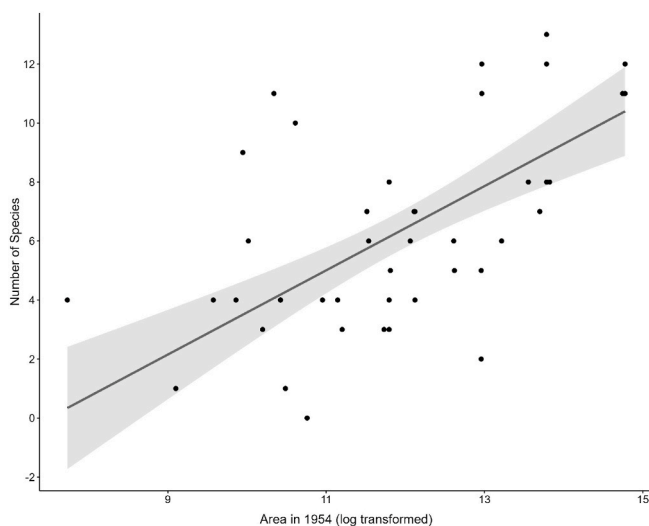
Table 2

All the models computed for each analysis, sorted by AIC; best models (ΔAIC <2) in bold. Model type and sample size are reported for each analysis. Area_1954 = area extent of the patch in 1954; area_2020 = area extent of the patch in 2020; area_delta = percent difference in area extent of the patch between 1954 and 2020; near_2020 = current distance of each patch from the nearest other patch; precipitation = annual precipitation.

Model	AIC
Total species richness (gaussian glm; n = 45)	
~ area_1954 + area_delta + precipitation + near_2020	**207.04**
~ area_1954 + precipitation + near_2020	210.45
~ area_2020 + area_delta + precipitation + near_2020	210.57
~ area_2020 + precipitation + near_2020	214.97
~ area_delta + precipitation + near_2020	233.46
~1 (null model)	237.97
Red-listed species richness (Poisson glm; n = 45)	
~ area_1954 + area_delta + precipitation + near_2020	**94.27**
~ area_1954 + precipitation + near_2020	96.95
~ area_2020 + area_delta + precipitation + near_2020	101.04
~ area_2020 + precipitation + near_2020	103.76
~ area_delta + precipitation + near_2020	122.69
~1 (null model)	132.31
Rare species richness (Poisson glm; n = 45)	
~ area_1954 + precipitation + near_2020	**137.73**
~ area_1954 + area_delta + precipitation + near_2020	**138.22**
~ area_2020 + area_delta + precipitation + near_2020	151.56
~ area_2020 + precipitation + near_2020	163.17
~ area_delta + precipitation + near_2020	173.12
~1 (null model)	186.32
Common species richness (gaussian glm; n = 45)	
~ area_2020 + precipitation + near_2020	**161.78**
~ area_2020 + area_delta + precipitation + near_2020	**161.94**
~ area_1954 + area_delta + precipitation + near_2020	169.14
~ area_1954 + precipitation + near_2020	170.35
~ area_delta + precipitation + near_2020	177.61
~1 (null model)	182.54

Table 3

Best AIC model for overall species richness. For each model, the estimates (β), the standard errors (SE), t-value (t), the lower (LCI) and upper (UCI) 95% confidence intervals are displayed. Variables with confidence intervals not overlapping 0 reported in bold.

Variable	Estimate ±SE	t	LCI	UCI
Intercept	6.29 ± 0.33	18.82	5.63	6.94
area_1954	**2.31 ± 0.39**	**5.93**	**1.54**	**3.07**
area_delta	**−0.89 ± 0.39**	**−2.26**	**−1.67**	**−0.12**
precipitation	**1.32 ± 0.34**	**3.87**	**0.65**	**2.00**
near_2020	**−1.05 ± 0.34**	**−3.06**	**−1.72**	**−0.38**

0.33). Pearson correlation test estimated a correlation of 0.69 and 0.72 respectively between observed and predicted data (both p-values <0.001). No residuals' spatial autocorrelation was evidenced (Moran's I = 0.167 and 0.070, p-values = 0.16 and 0.30).

4. Discussion

Our results showed the expected correlations of the past extent of open dry habitat patches, climate (i.e. annual precipitation) and the distance from the nearest dry habitat patch with the main components of species richness of terricolous lichen communities, i.e. the numbers of total, red-listed, rare and common species.

Past extent of the habitat patch and annual precipitation correlated positively and significantly with the number of total, red-listed and rare terricolous lichen species, whereas the area difference between 1954 and 2020 correlated negatively and significantly with total and red-listed species, and the distance from the nearest lichen-rich open dry habitat patch correlated negatively and significantly with total, rare and common species. The congruency of most of the results across these
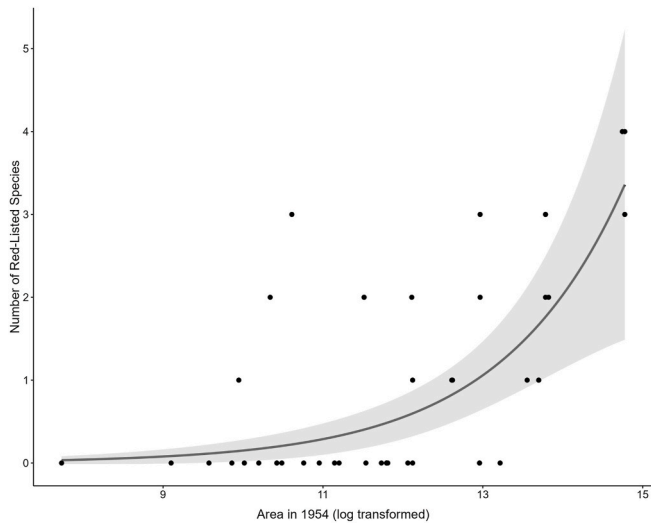

Fig. 2. Effect of patch area in 1954 (log transformed) on total species richness. Black dots represent observed data. The grey area corresponds to 95% confidence intervals.

Fig. 3. Effect of patch area in 1954 (log transformed) on red-listed species richness. Black dots represent observed data. The grey area corresponds to 95% confidence intervals.

Table 4
Best AIC model for red-list species richness. For each model, the estimates (β), the standard errors (SE), z-value (z), the lower (LCI) and upper (UCI) 95% confidence intervals are displayed. Variables with confidence intervals not overlapping 0 reported in bold.

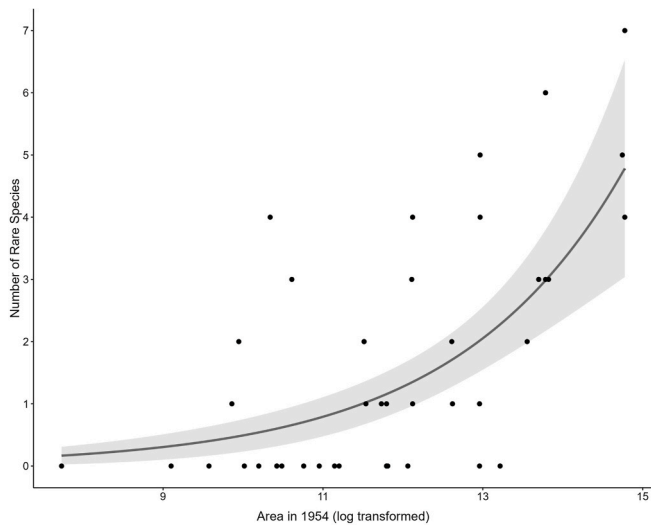| Variable	Estimate ±SE	z	LCI	UCI
Intercept	−0.66 ± 0.25	−2.62	−1.21	−0.21
area_1954	**1.05 ± 0.20**	**5.17**	**0.66**	**1.47**
area_delta	**−0.60 ± 0.25**	**−2.46**	**−1.06**	**−0.06**
precipitation	**0.85 ± 0.24**	**3.45**	**0.41**	**1.38**
near_2020	−0.26 ± 0.15	−1.71	−0.59	0.02

Fig. 4. Effect of patch area in 1954 (log transformed) on rare species richness. Black dots represent observed data. The grey area corresponds to 95% confidence intervals.

groups suggests that the pattern is clear and impacting on multiple components of lichen communities, highlighting the contribution given by species of conservation concern, i.e. red-listed and rare, to the overall diversity. On the other hand, only for the common species the best model included the current extent of the habitat patch with a positive

Table 5
Best AIC models for rare species richness. For each model, the estimates (β), the standard errors (SE), z-value (z), the lower (LCI) and upper (UCI) 95% confidence intervals are displayed. Variables with confidence intervals not overlapping 0 reported in bold.

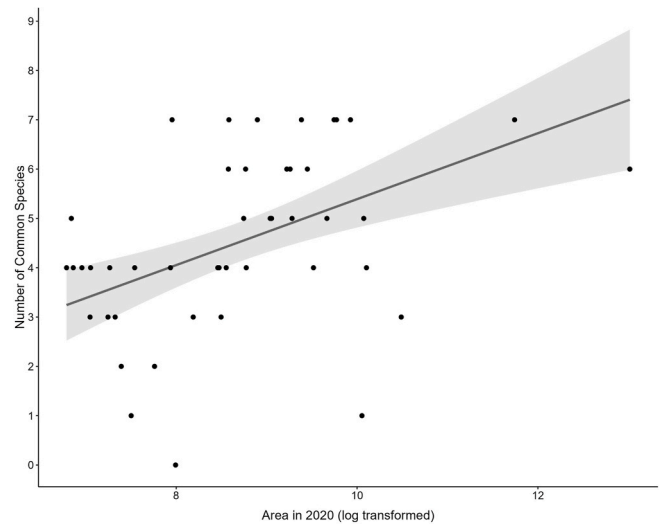| Variable	Estimate ±SE	z	LCI	UCI
Intercept	0.19 ± 0.15	1.26	−0.13	0.48
area_1954	**0.77 ± 0.13**	**6.06**	**0.53**	**1.03**
precipitation	**0.45 ± 0.15**	**2.96**	**0.16**	**0.76**
near_2020	**−0.23 ± 0.12**	**−1.90**	**−0.47**	**−0.01**
Intercept	0.20 ± 0.15	1.30	−0.12	0.48
area_1954	**0.86 ± 0.15**	**5.86**	**0.58**	**1.15**
area_delta	−0.27 ± 0.20	−1.34	−0.62	0.18
precipitation	**0.45 ± 0.15**	**2.97**	**0.16**	**0.75**
near_2020	**−0.25 ± 0.12**	**−2.10**	**−0.51**	**−0.03**

Fig. 5. Effect of patch area in 2020 (log transformed) on common species richness. Black dots represent observed data. The grey area corresponds to 95% confidence intervals.

Table 6
Best AIC models for common species richness. For each model, the estimates (β), the standard errors (SE), t-value (t), the lower (LCI) and upper (UCI) 95% confidence intervals are displayed. Variables with confidence intervals not overlapping 0 reported in bold.

Variable	Estimate ±SE	t	LCI	UCI
Intercept	4.51 ± 0.20	22.11	4.11	4.91
area_2020	**0.88 ± 0.21**	**4.16**	**0.47**	**1.30**
precipitation	**0.51 ± 0.21**	**2.81**	**0.18**	**0.99**
near_2020	**−0.76 ± 0.21**	**−3.60**	**−1.18**	**−0.35**
Intercept	4.51 ± 0.20	22.29	4.11	4.91
area_2020	**0.98 ± 0.22**	**4.39**	**0.54**	**1.42**
area_delta	0.29 ± 0.22	1.29	−0.15	0.72
precipitation	**0.53 ± 0.21**	**2.55**	**0.12**	**0.94**
near_2020	**−0.75 ± 0.21**	**−3.55**	**−1.16**	**−0.34**

effect, suggesting that richness in this group could be driven by faster dynamics involving more prompt responses to cope with environmental changes and/or better (re)colonization abilities of such species, which in some cases could be seen as generalists (e.g. *Cladonia foliacea*, *C. rangiformis*, *C. rei*; cf. Paus 1997; Bültmann 2005).

The past extent of the habitat patch is therefore the most relevant driver of terricolous lichen species richness in lowland open dry habitats, being positively correlated with richness of total, red-listed and rare species. This explains the occurrence of richer communities in several

sites that are currently small, but were much larger in the 1950s. Contrariwise, sites that are large at present but were smaller in the past – including sites that were enlarged only in recent decades – are poorer in terricolous lichens, as well as sites that were already small in the 1950s (cf. Supplementary File 1). Such pattern reveals an extinction debt that has only been partially paid (Kuussaari et al., 2009), suggesting that there is still time left to save the remnant lichen richness. A similar pattern was already detected in open dry habitats for vascular plants (Helm et al., 2006; Cousins 2009; Krauss et al., 2010; Piqueray et al., 2011), but our research is the first that provides evidence of extinction debt in terricolous lichens in such habitats, at the best of our knowledge. This similarity was not obvious *a priori*, since lichen physiology and ecology are very different from vascular plants, and therefore also their colonization and extinction patterns could be expected to differ (García de León et al., 2017). Furthermore, more competitive species tend to disappear before less competitive ones (Tilman et al., 1994), and therefore extinction debt in lichens could be more delayed than in vascular plants.

The distance from the nearest other patch was included in the best model with a negative effect for total, rare and common species richness. This could suggest a role of habitat fragmentation in the impoverishment of terricolous lichen communities, since close habitat patches are likely to descend from the same, formerly wide patch, whereas distant patches are more likely to descend from already separate habitat patches and are more prone to be affected by long-term isolation. Habitat fragmentation is known to severely impact biodiversity in open habitats, due to both the decrease of suitable habitat and the increase of edge-effect (Angold 1997; Wesche et al., 2005; Piessens et al., 2006; Reitalu et al., 2009; Niemandt and Greve 2016). Habitat fragmentation can also exacerbate species disappearance, since extinction debt becomes even more difficult to detect and counteract in strongly fragmented habitats (Cousins 2009). However, the study of this topic has been addressed in such habitats mainly for vascular plants (Cousins 2009; Niemandt and Greve 2016), and was poorly developed for terricolous lichens so far.

Annual precipitation was positively related with total lichen richness, as already reported from our study area for both taxonomic and functional diversity (Gheza et al., 2020, 2021). Such a correlation has been demonstrated from several different environmental contexts (e.g. Eldridge and Tozer 1997; Rai et al., 2015), sometimes referring to the positive role of water availability in general, not only of that directly derived from precipitation (Zedda and Rambold, 2015). The strong significant negative correlation between precipitation and temperature may suggest that the positive correlation with precipitation could carry with itself also a negative correlation with temperature. The real effect of each of these two climatic variables is difficult to disentangle, since they go hand-in-hand in the study area. However, the negative effect of warming on terricolous lichen communities is strongly supported by several recent works (Escolar et al., 2012; Di Nuzzo et al., 2021; Vallese et al., 2022). The combined effect of decreasing precipitation and increasing temperature could therefore be even more detrimental to terricolous lichens.

Since climate clearly plays a role in driving terricolous lichen diversity, the perturbations caused by climate change on precipitation regimes and temperatures are likely to impact on their communities. Under this perspective, the combined effect of habitat loss and climate change, which impacts negatively on biodiversity and can often be difficult to detect explicitly (e.g. Hannah et al., 2006; Mantyka-Pringle et al., 2012; Segan et al., 2016), strongly threatens terricolous lichens.

5. Implications for conservation

Active maintenance and restoration of remnants of dry grasslands and heathlands are warranted to support terricolous lichen diversity, given the evidenced negative effects of habitat loss and climate change. Restoration, protection, and long term-management of the sites with the highest species richness would be the best practices, even when in such

locations the current habitat extent is small. This approach may at least partially counteract extinction debt, if realized before the communities reach the new equilibrium with the current habitat extent and the extinction of further species.

Fostering the occurrence of microrefugia (Ellis and Eaton 2021; Di Nuzzo et al., 2022) could also be useful. In these open dry habitats, maintaining a mosaic of open vegetation in different dynamic stages (Gheza et al., 2020, 2021) or heterogeneous microtopographic features, e.g. dunes (Veres et al., 2020, 2021), can be effective tools to provide different microhabitats that can act as microrefugia for species with slightly different ecological requirements.

Habitat fragmentation could also be counteracted by fostering connectivity between habitat patches, using both already existing and newly created patches as 'stepping stones'. However, the poor knowledge on colonization abilities and recolonization lag in terricolous lichens currently hinders the assessment of the effectiveness of this latter method for such organisms.

Some of the patches with the highest species richness were located in enclosed lands both on former or still active military grounds and private estates. Enclosed lands can effectively contribute to improve the conservation of such habitats at the landscape scale (Ellwanger and Reiter 2019; Schellenberg and Bergmeier 2020), in a perspective of area-based conservation, a concept which includes not only protected areas, but also such types of private areas (Hoffmann 2022).

Finally, this study also highlights that exhaustive species inventories are fundamental in conservation as a tool to track biodiversity patterns. They allow to test and improve sampling techniques (Vondrák et al., 2018), confirm the validity of ecological patterns (Gheza et al., 2023), and detect diversity hotspots (Nascimbene et al., 2022; Vondrák et al., 2022), which are crucial to preserve. Therefore, the compilation of such inventories, far from being a stamps' collector pastime, is a crucial activity to support effective biodiversity conservation, and should be much more emphasized in current conservation literature.

Competing interests

The authors have no relevant financial or non-financial interests to disclose.

CRediT authorship contribution statement

Gabriele Gheza: Writing – review & editing, Writing – original draft, Investigation, Formal analysis, Data curation, Conceptualization. **Zeno Porro:** Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Data curation. **Matteo Barcella:** Writing – review & editing, Data curation. **Silvia Assini:** Writing – review & editing, Resources, Funding acquisition. **Juri Nascimbene:** Writing – review & editing, Resources, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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