Chronicle of a death foretold: The vanishing of an emblematic cultural landscape results in the loss of its unique plant communities

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ABSTRACT

Badlands are peculiar geomorphological formations shaping landscapes of high ecological and cultural value. In the last decades, land reclamation for agricultural purposes and the cessation of traditional land use, such as sheep grazing, led to their decline in extent in many areas. To quantify the changes in badland-related plant communities, we resurveyed badland vegetation in a site of the Crete Senesi (Siena, central Italy) after 16 years (2006–2022), using 48 quasi-permanent vegetation plots and by means of uni- and multivariate analysis of variance. We found an increase in the total vegetation cover of plant communities growing in former bare soil and sparsely vegetated areas, in line with an overall decrease in the extent of bare soil surfaces in the study area, which we highlighted through the analysis of multitemporal satellite images. Pioneer vegetation characterized by the endemic plant *Artemisia caerulescens* subsp. *cretacea* changed into ruderal annual grasslands, while former bare soils were colonized by such pioneer

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vegetation. In contrast, perennial grasslands remained stable. Grasslands with shrubs became more similar to perennial grasslands in species composition. Species richness increased in former bare soils, and using the total vegetation cover as a proxy for successional stages, we found that Shannon diversity and evenness peaked at about 90% of total cover. In all the stages of colonization, short distance dispersal species prevailed, both therophytes (*Avena sterilis, Parapholis strigosa*) and perennials (*Artemisia caerulescens* subsp. *cretacea, Bromopsis erecta*). Long distance dispersal species (*Galatella linosyris*) started colonizing at about 60% of total vegetation cover, and at high vegetation cover all the functional groups coexisted. Our results confirm that the badland landscapes of southern Tuscany and specialist plant diversity adapted to badlands are vanishing after a diminishing of active land management, suggesting the current ineffectiveness of the Natura 2000 network in their conservation.

1. Introduction

Land use change is one of the main drivers of biodiversity loss worldwide. Over the last century, European semi-natural habitats have declined by about 90% compared to their historical extent (EEA, 2016). The decline of these habitats has resulted in an increase of their conservation interest. Besides, ecosystem services such as cultural and scenic value, water retention, and storage of genetic diversity are gradually lost (Torralba et al., 2018; Bengtsson et al., 2019). Due to their dependence on human management, semi-natural habitats have recently been proposed to be caught in a socio-ecological vortex of extinction (Herzon et al., 2022).

The dramatic shifts that semi-natural habitats are undergoing make their monitoring urgent. Quantifying vegetation change over time is pivotal for defining conservation and restoration actions aimed at protecting semi-natural habitats. Measuring temporal vegetation change has always aroused great interest by plant ecologists, who have long used vegetation resampling to ascertain differences between two sampling dates (Loeb, 1990). A critical issue that needs to be addressed when conducting vegetation resurvey studies is the accuracy of plot relocation. However, even approximate plot relocations can provide robust results (Kopecký and Macek, 2015). Although the methodological pitfalls of plant community resampling are well known (Cain, 1936; Loeb, 1990; Verheyen et al., 2018), resurveying permanent or non-permanent plots is still crucial for understanding the effects of different drivers for an effective management and conservation of natural resources (Kapfer et al., 2017; de Bello et al., 2020).

The Italian peninsula is characterized by the presence of peculiar semi-natural habitats, generally known as badlands, resulting from the severe erosion of Plio-Pleistocene marine clays (Torri et al., 2000). These are classified in two types: "calanchi", which are knife-edge rill-gully erosion spots developing on hillslopes and are the most common type of badland, and the rarer "biancane", which are small dome-shaped remnants of intensely digitated, gully and pipe erosion spots, resembling a miniature clay hill (Calzolari and Ungaro, 1998; Phillips, 1998), present in Italy only in Tuscany, Basilicata and Calabria (Bazzoffi et al., 1997). Because of their harsh features, badlands are typically either reclaimed or left aside. However, the acknowledgment of their value for biodiversity led to their protection through national parks in some areas of the World (e.g., https://www.nps.gov/badl/index.htm).

Biancana badlands are a typical element of the cultural landscape of southern Tuscany. They host plants endemic to peninsular Italy, such as *Artemisia caerulescens* subsp. *cretacea*, and several plant communities of high conservation interest, such as *Bromopsis erecta* grasslands (*Bromion erecti* Koch 1926) (Chiarucci et al., 1995; Maccherini et al., 2000). The latter are protected under the European Habitats Directive, code "Habitat 6210(*) – Semi-natural dry grasslands and scrubland facies on calcareous substrates (*Festuco-Brometalia*) (*important orchid sites)" (European Commission, 1992). Recently, badland specialist pioneer plant communities with *Artemisia caerulescens* subsp. *cretacea* and *Parapholis* spp. have also been proposed for inclusion in the Annex I of the Habitats Directive (Casavecchia et al., 2021). Over the last 25–30 years, some of the Tuscan biancana badlands have been protected in order to preserve their biodiversity and their cultural and geomorphological landscapes. However, appropriate management strategies are still not defined (Marignani et al., 2007; Marignani et al., 2008a; b). Rural abandonment and the lack of management practices have contributed to the loss of eroded areas due to the encroachment of vegetation by natural succession, resulting in the loss of species and geomorphological units of high conservation, ecological, and cultural value (Torri et al., 2013). Unlike elsewhere in Italy, Tuscan badlands are perceived by both local authorities and local people as a disappearing cultural element of great conservation concern, substantially contributing to the maintenance of the typical landscape of southern Tuscany and of its biodiversity (Phillips, 1998). Until 40 years ago, biancana badlands were extremely widespread in the "Crete Senesi" and "Val d'Orcia" areas, two cultural landscapes of southern Tuscany. Here, they were included in the UNESCO World Heritage list as a valuable cultural landscape (Fresta, 2011).

Local-scale (plot level) variables play a major role in determining the patterns of species composition in the vegetation of biancana badlands. Soil electrical conductivity (EC) is the most important factor determining the persistence of annual grassland communities supporting the endemic species *Artemisia caerulescens* subsp. *cretacea*, together with the maintenance of soil sedimentation from the southern slopes of biancana badlands (Maccherini et al., 2011; Torri et al., 2018).

The origins of Tuscan biancana badlands date back to the demographic expansion of the Middle Ages (Torri et al., 2018). In the second half of the 19th century, such geomorphological formations and the vegetation they host have undergone a process of disappearance. Until recently, this process was mainly due to the destruction of "biancane" to reclaim arable land. This process was partially slowed down by the spread of sheep farming in the 1970's, since sheep trampling promotes erosion phenomena in badlands (Gallart et al., 2013). Between 1954 and 2005, bare soil and sparse and discontinuous herbaceous cover decreased by more than 60%, from 82 ha to 25 ha, in the most important remnants of Tuscany (Torri et al., 2013). Bare soil and sparsely vegetated areas were encroached by
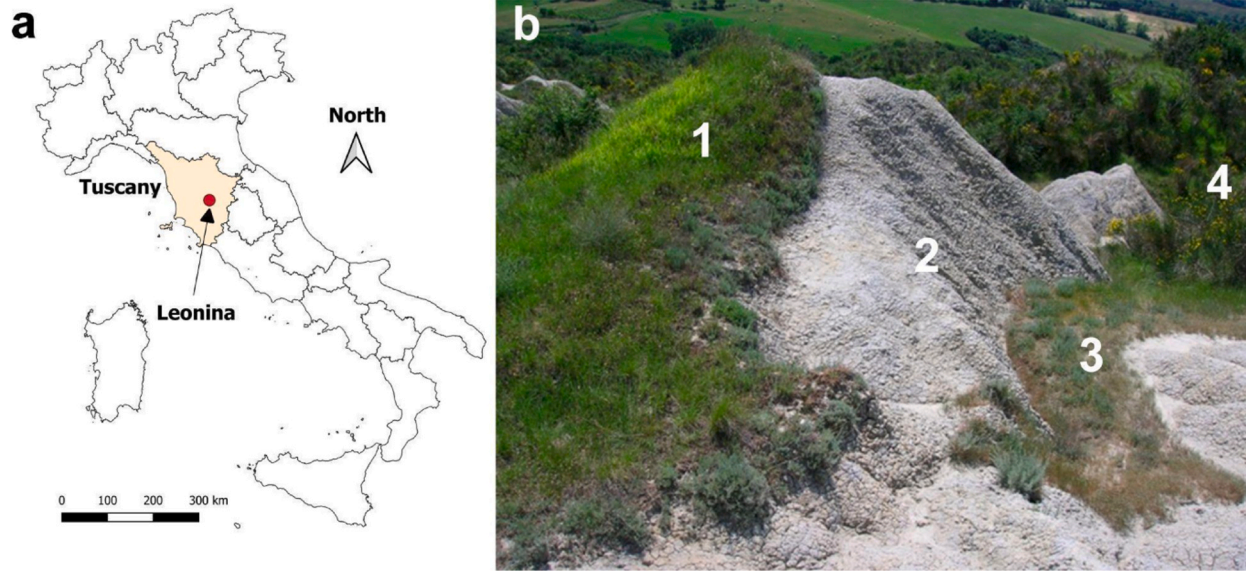
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Fig. 1. a) Location of the study area in Italy and Tuscany; b) biancana in the Leonina field with different vegetation types developing on soils with different salinity and erosion rates: 1) upper part of a biancana with perennial *Bromopsis erecta* grassland; 2) bare soil with little or no vegetation on a southern biancana slope; 3) biancana pediment with *Artemisia caerulescens* subsp. *cretacea* and *Parapholis* spp. pioneer vegetation; 4) *Spartium junceum* shrubland.

generalist ruderal species, such as *Avena* spp. and *Dactylis glomerata* (Torri et al., 2013). The decrease in extent of eroded spots of biancana badlands leads to a loss of biodiversity due to the disappearance of the highly specialized plant communities that occupy the peculiar ecological niches created by the combination of erosion and sedimentation processes.

Seed dispersal is a critical process for species colonization and community assembly during vegetation succession in badlands, particularly in the light of their very species-poor germinable seed bank, especially in bare soil areas (Maccherini et al., 2019). The lack of vegetation on badland slopes, which is essential for the survival of the most characteristic feature of biancanas, is attributed by the literature to the high erosion rates that remove seeds, litter or entire plants or that act indirectly by changing those soil properties to which seed germination and seedling establishment are sensitive (Gallart et al., 2013). Understanding the functional aspects of vegetation succession in terms of plant dispersal mode and life forms can add an important piece of knowledge on the ecology of remnant biancana badlands. This aspect has so far only been described, but never quantified.

As badlands are disappearing, it is urgent to monitor the evolution of their plant communities to define effective conservation strategies. While several resampling studies are available for a wide range of ecosystems worldwide (Taverna et al., 2005; Meyer et al., 2013; Pedrotti et al., 2014; Frate et al., 2018; Fanfarillo et al., 2019; Lelli et al., 2021; Schüle et al., 2023), to the best of our knowledge there is no information on the temporal trends of badland plant communities obtained using this approach. Therefore, in this study we investigated the spatial and temporal changes of plant communities that occurred over 16 years in one of the most important remnants of biancana badlands in central Italy (Leonina site, Siena, Tuscany). We aimed to answer the following research questions: i) has the diversity of plant communities of the Leonina biancana badlands changed? ii) which communities have undergone the most significant changes? iii) which environmental processes have been responsible for the changes? Moreover, we questioned which is the role of species with different dispersal and life strategies in the vegetation succession that leads to badland disappearance.

2. Materials and methods

2.1. Study site

The study area is located in the Municipality of Asciano, within the cultural landscape of the "Crete Senesi", southeast of Siena, central Italy (centroid coordinates, WGS84: 43°16′35′′ N, 11°25′56′′ E) (Fig. 1a). It is included in the Natura 2000 network, and namely in the Special Area of Conservation (SAC) "Crete di Camposodo e Crete di Leonina" (IT5190004) (Italian Ministry for the protection of land and sea, 2016). The elevation ranges between 200 and 250 m a.s.l. The hilly parts of the landscape are characterized by outcrops mainly composed of Pliocene marine sediments, while the valleys are characterized by more recent fluvial deposits. The climate is transitional between sub-humid and subarid, with a mean annual temperature around 13 °C and a mean annual rainfall between 700 and 800 mm. The precipitation regime has a Mediterranean character, with a minimum during summer months (Tuscany Region, 2022a).

The biancana badlands of the Crete Senesi are characterized by cascades of small domes/hummocks with base diameters ranging from 2 to over 20 m, generally protruding 3–10 m above gently sloping pediments. In some cases, protrusion can reach more than 20–30 m. The pediment can be either absent or extend up to 10–15 m from the slopes of the eroded hummocks (Calzolari and Ungaro, 1998). Differently developed biancana soils are spatially distributed in patches and soil diversity is reflected in the distribution of different vegetation types (Chiarucci et al., 1995) (Fig. 1b). The pioneer vegetation of the biancana micro-pediments is characterized by halotolerant species such as *Artemisia caerulescens* subsp. *cretacea*, *Hordeum marinum*, *Parapholis incurva*, *Parapholis strigosa*, and *Scorzonera laciniata*. On less salty and less eroded soils, grasslands with *Galatella linosyris*, *Bromopsis erecta*, *Dactylis glomerata*, *Phleum nodosum*, and *Plantago lanceolata* occur. The biancana domes and ESE-facing slopes host dry grasslands dominated by *Bromopsis erecta*, *Galatella linosyris*, and *Linum corymbulosum*. With increasing soil stability and water availability, *Bromopsis erecta* becomes more abundant and is often accompanied by shrubs. Wetter and cooler sites host dense *Thinopyrum acutum* grasslands. Shrublands are dominated by *Crataegus monogyna*, *Prunus spinosa*, *Pyrus spinosa*, *Spartium junceum* and *Ulmus minor*. Mixed deciduous oak woods with *Quercus pubescens* and *Quercus cerris* are also present (Torri et al., 2018).

2.2. Historical and recent vegetation data

In late May 2022, we revisited 48 plots previously sampled in late May 2006 according to a stratified random sampling design based on land cover classes and the partition of the biancana field in four zones (Maccherini et al., 2011). The 48 plots were re-sampled using the same methods, after having been relocated using their geographical position with a GPS device (quasi-permanent plots *sensu* Kapfer et al., 2017). For each of the 4 zones identified in 2006 in the biancana field, we sampled four 1 × 1 m quadrats (plots) in each of the following land cover classes: i) bare soil with little or no vegetation; ii) sparsely and discontinuous herbaceous cover; iii) grasslands; and iv) grasslands with shrubs (shrub cover <20%) (4 zones × 4 land cover classes × 4 plots). The percentage cover of vascular plants in each plot was estimated using the point-quadrat method (Moore and Chapman, 1986), with a density of 100 pins/m^2. This method reduces the differences between observers since it is more accurate than the visual estimation of percentage covers to record species abundance, and it is considered especially adequate for open habitats (Lepš, 1987; Kent, 2011). Starting from the data published by Maccherini et al. (2011), we harmonized species nomenclature after consulting Pignatti (1982) and Pignatti et al. (2017-2019), according to the updates by Bartolucci et al. (2018) and Galasso et al. (2018).

2.3. Environmental data

Based on the data from the closest climate stations (Tuscany Region, 2022a), we assessed climatic shifts for the period 2005–2022 in terms of annual rainfall, mean annual temperature, summer days (SU30), number of extremely heavy precipitation days (R20), and aridity (De Martonne, 1926; Zhang et al., 2011) (Supplementary Data – Fig. S1).

Since soil EC is one of the main drivers of diversity of plant communities in biancana badlands, besides being important in defining the very first stages of soil development (Torri et al., 2018), we retrieved such information for 48 plots sampled in the study area in 2006 from Maccherini et al. (2011). Soil EC ($EC_{1:2,5}$, dS m^{-1}) was measured using the pre-calibrated electronic probes WTW I 340 multimeter WTW® (Weilheim, Germany). The extent of bare soil in the Leonina biancana field was identified by photo-interpretation of aerial orthophotos at six years (2002, 2007, 2010, 2013, 2016, 2019 - Tuscany Region, 2022b), with a minimum mapping unit of 10 m^2. The landscape analyses were carried out in QGIS v. 3.20.3 (QGIS Development Team, 2021).

2.4. Data analysis

To analyse climatic trends over the 16 years between the two surveys, we built a series of linear regression models using mean annual temperature, annual rainfall, SU30, and R20 as response variables and year as a predictor, using the function *lm* in the package *stats* of R (R Core Team, 2022). As soil salinity is known to decrease with increasing vegetation cover (Bertness et al., 1992; Crain and Bertness, 2006; Thiam et al., 2021), we built a linear regression model with soil salinity as a response variable and the total vegetation cover as a predictor. The statistical significance of the linear trend models was assessed by means of ANOVA tests (999 permutations) using the *anova* function in the *stats* package. We also plotted the extent of bare soil surfaces from 2002 to 2019 (2002, 2007, 2010, 2013, 2016, 2019) in the Leonina biancana field.

The multivariate temporal trend of plant communities for different land use classes was analysed using redundancy analysis (RDA) with untransformed percent cover data for each species. We tested the following hypotheses: there were no directional changes of species composition in time that are either common to all the land cover classes or specific to one land cover class (effect of the factor "year of observation"); the individual land cover classes did not differ in their temporal dynamic (effect of the interaction "year of observation" × "land cover class"). Significance of the multivariate analyses was tested using Monte Carlo permutation tests (499 permutations). Multivariate analyses were performed in the CANOCO 5 software (Ter Braak and Smilauer, 2012).

Plant species richness and total vegetation cover (%) were calculated for: i) each plot; ii) each year of observation (2006 and 2022); and iii) each land cover class. We also calculated the Shannon-Wiener diversity (*H*-Shannon's entropy), and the Pielou's evenness index (*J*) for each plot (function *diversity* in the *vegan* package of R) (Oksanen et al., 2022), according to Eqs. 1 and 2:

$$H = -\sum_{i=1}^{N} p_i \ln \quad p_i \tag{1}$$

$$J = \frac{H}{\ln \quad N} \tag{2}$$

where p_i is the relative abundance of element (species) *i* and *N* is the total number of different elements considered. Moreover, we calculated Shannon-Wiener diversity and Pielou's evenness indexes including bare soil and its abundance as an additional element (H_b and J_b, respectively). This allowed keeping constant the reference surface for the calculation of the two indexes, which is otherwise smaller with increasing abundance of bare soil in the plot.

To quantify vegetation changes, we first analysed the following univariate attributes: i) plant species richness; ii) total vegetation cover; iii) Shannon's diversity index; iv) Pielou's evenness index. These attributes were used as response variables in two-way repeated measures ANOVAs using GLM, where the explanatory factors were year of observation (two fixed levels: 2006 and 2022) and land cover class (four fixed levels: bare soil with little or no vegetation, sparsely and discontinuous herbaceous cover, grasslands, and grasslands with shrubs). The number of species was square root-transformed and the total vegetation cover values were log (x + 1) transformed to improve the normality of the data. When the factor "year" or the interaction "year × land cover class" was significant, we performed pairwise comparisons to test the effect of the factor "year" on the response variables, separately for each land cover class. We used the Bonferroni correction for multiple comparisons. We set alpha at 0.05. Univariate data were analysed using SPSS 13.0 for Windows (SPSS Inc, 2004).

To explore the colonization patterns of plant species along the stages of ecological succession, we classified each species into four functional groups (FGs) (Supplementary Data, Table S1) based on their i) dispersal strategy: short-distance dispersal (SDD) *vs* long-distance dispersal (LDD) (*Allium* type *vs Bidens* type, *Cornus* type, and *Epilobium* type *sensu* Sádlo et al., 2018); ii) Raunkiær's life form: therophyte (T) *vs* perennial (nT). The resulting combinations were four: i) short-distance dispersal therophyte (SDD/T); ii) short-distance dispersal perennial (SDD/nT); iii) long-distance dispersal therophyte (LDD/T); iv) long-distance dispersal perennial (LDD/nT). We calculated the cumulative cover of the four FGs for each plot. Life forms were retrieved from Pignatti et al. (2017-2019). Only taxa identified to the species level were classified into FGs and used in the related analyses. Since there is no classification of the Italian flora based on dispersal strategies, we used the one by Sádlo et al. (2018) for the Czech flora. We could find most of the species occurring in our dataset, and as for the few missing species we attributed to them the dispersal strategy of a similar species from the same genus.

To explore the patterns of colonization by plant species along vegetation succession, we calculated the cover of each FG and of the most abundant species for all the plots. We plotted the values of the calculated attributes, averaged on moving windows of 10 values,

against the total vegetation cover, obtaining curves describing the patterns of change of FGs, H, J, H_b, and J_b along the ecological succession. The same operation was done using the cover values of the seven most abundant species, i.e., *Brachypodium rupestre, Xeranthemum cylindraceum, Bromopsis erecta, Galatella linosyris, Parapholis strigosa, Artemisia caerulescens* subsp. *cretacea*, and *Avena sterilis*. The results obtained through this procedure are comparable to those that may be obtained through annual observations in permanent sampling plots.

3. Results

3.1. Community composition

In total, we recorded the presence of 136 taxa: 88 in 2006 and 118 in 2022. The most frequent species in both years were *Avena sterilis, Galatella linosyris, Dactylis glomerata, Gaudinia fragilis,* and *Xeranthemum cylindraceum.*

The RDA analysis (Fig. 2) showed that the factor "year of observation" explained 13% of the variation in species composition ($p < 0.01$), while the factor "year of observation" × "land cover class" explained 9.5% of the variation ($p < 0.01$). This means that the examined plant communities changed in composition from 2006 to 2022 and that these changes were dependent on the land cover class analysed. Grasslands were the most stable communities, i.e., they underwent the least changes. Grasslands with shrubs showed a shift towards grasslands. A slightly bigger change was shown by the sparsely vegetated areas, where there was an increase in *Avena sterilis* and *Anisantha madritensis*, and by the bare soil, which moved towards the sparsely vegetated communities characterized by *Artemisia caerulescens* subsp. *cretacea* and *Parapholis strigosa.*

3.2. Changes in species richness, diversity indexes, and functional groups

Both species richness and the total vegetation cover per plot increased significantly from 2006 to 2022. Pairwise comparisons showed that species richness increased significantly only in bare soil. Total vegetation cover increased in both bare soil (with the loss of 5 plots without vegetation, i.e., 100% bare soil) and in sparsely vegetated areas. However, the number of species per plot increased only in bare soil. We did not observe significant changes in Shannon's diversity index and Pielou's evenness (Fig. 3, Table S2).

Shannon diversity showed two initially rising curves with a maximum at a total vegetation cover of about 90% (Fig. 4a). The H_b curve had a monotonically increasing slope, while the H curve showed a slight decrease between 40% and 60% vegetation cover. Both the indexes reach a maximum at about 90% cover, before a slight decline occurs corresponding to 100% total cover.

The evenness indexes J and J_b showed similar trends to Shannon diversity in relation to total vegetation cover, in particular the
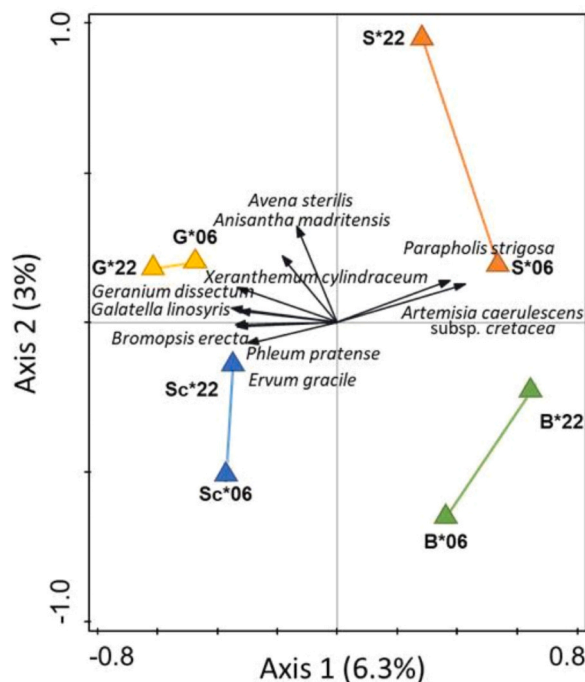

Fig. 2. Redundancy analysis (RDA) diagram showing species, land cover classes, and years for the plant communities of the Leonina biancana field. Compositional changes within the different land cover classes over 16 years are drawn as trajectories. Land cover classes (classified in the year 2006): B = bare soil with little or no vegetation; S = sparse and discontinuous herbaceous cover; G = grasslands; Sc = grasslands with shrubs (shrub cover < 20%).
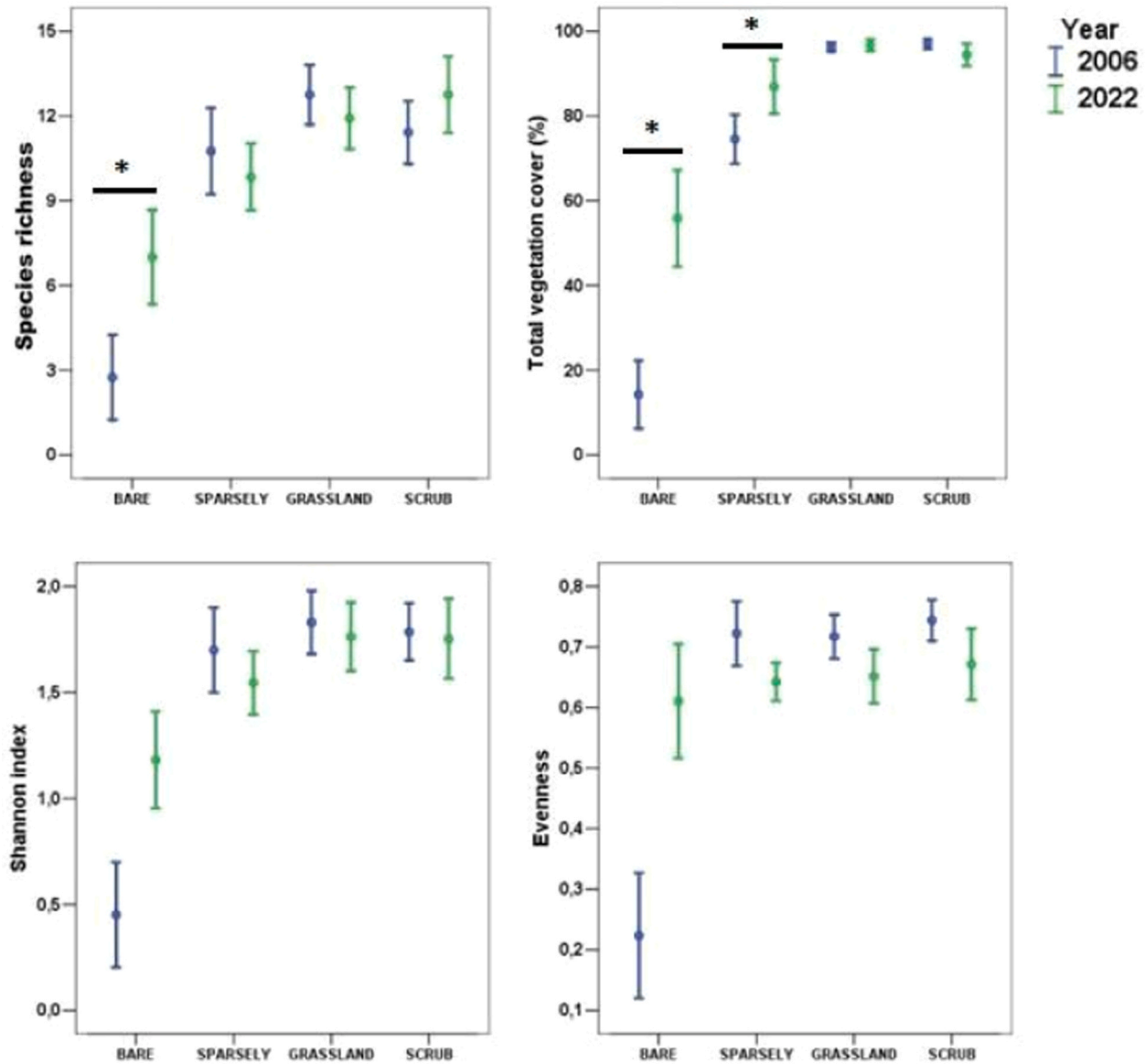
Fig. 3. Error bar charts (mean ± standard error) showing differences in species richness, total vegetation cover (%), Shannon diversity, and evenness for each land cover class for the two years of observation. Asterisks indicate significant differences between the two years for each land cover class at p < 0.05 (ANOVA model). Land cover classes (classified in the year 2006): Bare = bare soil with little or no vegetation; Sparsely = sparsely and discontinuous herbaceous cover; Scrub = grasslands with shrubs (shrub cover < 20%).
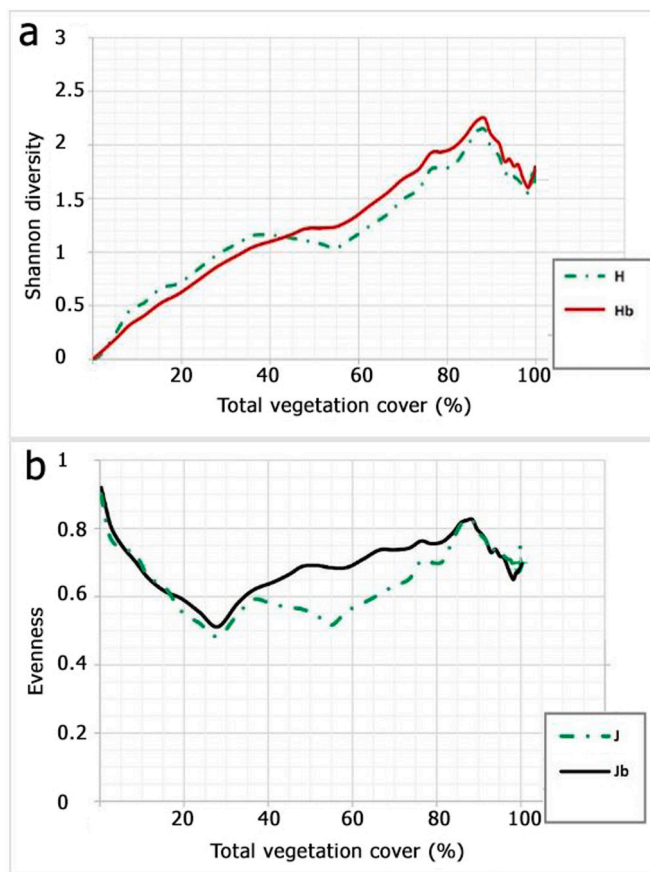
Fig. 4. Trends of a) Shannon diversity and b) Evenness in relation to the total vegetation cover.); H = Shannon diversity (only plant species); H_b = Shannon diversity (bare soil + plant species); J_b = Pielou's evenness (bare soil + plant species); J = Pielou's evenness (only plant species).

same peak at 90% cover (Fig. 4b). Each evenness curve shows an absolute maximum at zero cover (where $J=J_b=1$) and a minimum at about 30% cover (Fig. 4b). The J_b curve is smoother than the J curve, similar to the corresponding H_b curves, which are generally smoother than the H curve.

The variation in abundance of the four FGs and of the most abundant species with respect to the total vegetation cover (Fig. 5a,b) shows that all the stages of colonization are characterized by an increase of SDD species, both therophytes and perennials. However, this increase is due to pioneer species like *Artemisia caerulescens* subsp. *cretacea* (SDD/nT) and *Parapholis strigosa* (SSD/T) until about 50–60% of total vegetation cover, and to species of more stable morphologies at higher total vegetation covers, especially *Avena sterilis* (SSD/T) and *Bromopsis erecta* (SSD/nT). LDD species like *Galatella linosyris* (LDD/nT) start increasing at about 60% of total vegetation cover. From about 90% cover, all the functional groups reached high abundance with oscillating levels, without further clear trends. Remarkable is the sharp increase in abundance of *Avena sterilis* and *Bromopsis erecta* at very high vegetation covers.

3.3. Trends in environmental data

Analysis of climatic trends in the study area revealed a significant increase in mean annual temperature and SU30. Increasing trends in annual rainfall, R20, and aridity index (and thus a decrease of aridity) were also observed, but these were not statistically significant (Supplementary Data, Fig. S1).

We found a high and significant negative predictive power of total vegetation cover on EC in the year 2006 (Fig. 6).

The temporal analysis of the changes in bare soil cover showed a decrease in extent of eroded areas over the years, which passed from 30476 m^2 in 2002 to 9302 m^2 in 2019, with a loss of almost 70% of the eroded surfaces (Fig. 7).

4. Discussion

Our study revealed significant changes in the plant communities developing in the Leonina badlands after 16 years.

These changes mainly concerned two types of land use: bare soil and sparsely vegetated areas. In terms of species shifts, we highlighted how the areas that were characterized by bare soil in 2006 were subject to an increase in the percentage cover of badland
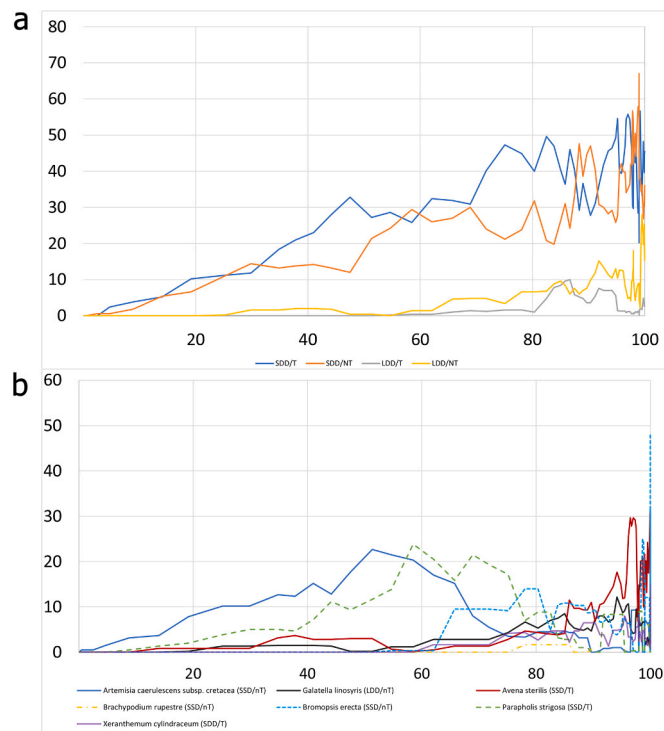
Fig. 5. Trends of abundance (% cover) of a) plant functional groups and b) the seven most abundant species in relation to the total vegetation cover. SDD = short distance dispersal; LDD = long distance dispersal; T = therophyte; nT = perennial.
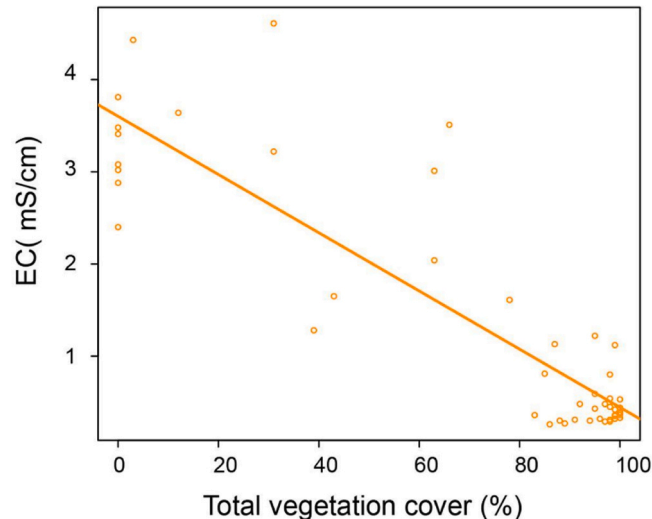

Fig. 6. Linear regression of total vegetation cover against soil electrical conductivity (EC). $R^2 = 0.78$; $p < 0.001$. Data are referred to the year 2006.

pioneer species such as *Artemisia caerulescens* subsp. *cretacea* and *Parapholis strigosa*. Sparsely vegetated areas, previously characterized by pioneer vegetation, changed their trajectory towards a different vegetation type with a decrease in *Artemisia caerulescens* subsp. *cretacea* and an increase in the percentage cover of annual ruderal grasses such as *Avena sterilis* and *Anisantha madritensis*. This is consistent with previous evidence on the dynamics of Leonina biancana badland vegetation in the period 1954–2005, which highlighted how bare soil and sparse vegetation, analysed as a whole class, were colonized by ruderal grasses (*Avena* spp., *Anisantha madritensis*) at the expense of characteristic vegetation with *Artemisia caerulescens* subsp. *cretacea* (Torri et al., 2013). Our analysis, which considered the two land cover classes separately, revealed more details about the dynamics of badland plant communities, suggesting that pioneer vegetation can colonize new areas in former bare soil, and can thus be maintained if eroded spots are present.
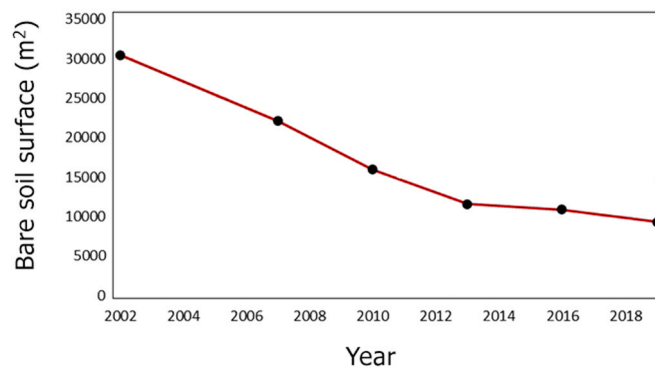
Fig. 7. Changes in the extent of bare soil surfaces from 2002 to 2019 in the Leonina biancana field. Data obtained by photo-interpretation of aerial orthophotos (Tuscany Region, 2022b), with a minimum mapping unit of 10 m^2, in QGIS v. 3.20.3 (QGIS Development Team, 2021).

Consequently, bare surfaces such as the southern steep slopes of biancane, rich in salt and prone to severe erosion, and those parts of the pediment that are close to the southern slope, represent the most important elements for the conservation of badland-specialist plant communities. Vegetation encroachment can thus modify one of the most peculiar morphologies of biancana badlands (Roveri et al., 2014). The colonization of bare surfaces by vegetation causes a strong increase of soil pore connectivity (Torri et al., 2018). This promotes the penetration and diffusion of water into marine sediments, favoring sodium removal and a decrease of EC (Calzolari, 1993; Calzolari et al., 1996; Bierbaß et al., 2014; Torri et al., 2018), consistently with our results. Moreover, the presence of roots improves soil resistance to erosion through the formation of water-stable aggregates and an increased porosity (Torri et al., 2002, 2018; De Baets et al., 2008). Consequently, when disturbance elements such as browsing, trampling, and burning are missing, the whole system stabilizes and plant communities change towards less pioneer types. Progressively, *Artemisia caerulescens* subsp. *cretacea* and other pioneer species are replaced by species such as the perennial grasses *Brachypodium rupestre* and *Bromopsis erecta* and the annual grasses *Avena sterilis* and *Gaudinia fragilis*.

Grasslands did not change their composition, at least over the period examined. This pattern is well described by previous studies of alpine vegetation, which suggest that closed grasslands are more stable than open communities due to a higher inertia in community composition (Lelli et al., 2022). Moreover, seminatural calcareous dry grasslands of southern Tuscany, and especially those dominated by *Bromopsis erecta*, were found to be resistant to shrub encroachment at mid-term scales (Maccherini and Santi, 2012; Maccherini et al., 2018). *Bromopsis erecta* is also known to be favored by global warming (Poniatowski et al., 2018), so that increasing temperatures in the study area might also explain the resistance of such grasslands. The observed grassland resistance is inconsistent with other results from Europe, where shrub encroachment due to secondary succession is a widespread phenomenon (Calaciura and Spinelli, 2008; Schüle et al., 2023).

The patterns of H and H$_b$ show similar trends with increasing vegetation cover. They reach a maximum before 90% cover, and then decrease by about 17%. The increase in both H and H$_b$ with increasing vegetation cover, and their sudden decrease when the latter reaches 90% suggests that Shannon diversity increases until one species, in our case grasses like *Avena sterilis* and *Bromopsis erecta*, becomes dominant. This is consistent with well-known trends in grassland vegetation dynamics observed previously in our study area (Maccherini et al., 2000). However, H tended to decrease slightly between 40% and 60% total cover. Such cover is typically of pioneer plant communities of pediments, which are characterized by reduced species richness and consequently lower Shannon diversity. Few halotolerant species can colonize such harsh environments due to the salinity and the intense sediment deposition from the biancana slope (Maccherini et al., 2011). With time, other species slowly colonize the pediments, vegetation cover increases and, as also highlighted by our results, salinity decreases. Thus, the succession goes on causing a new increase of H. J and J$_b$ had trends similar to those of Shannon indexes. However, J, but not J$_b$, showed a slight decrease between 40% and 60% cover, similar to H. This can be explained by the fact that such covers are those of pioneer plant communities, hosting few species. Such successional stages are also characterized by high amounts of bare soil, which is why J$_b$, contrarily to J, kept increasing between 40% and 60% cover. When the amount of bare soil becomes less important (>60% of vegetation cover), J starts to increase again and at 90% cover it reaches the same levels as J$_b$. At this cover, both the evenness indexes reach their maximum if we exclude the bare soil stage. A decrease in both J and J$_b$ can then be observed, due to the dominance of perennial grasses in closed grassland communities. The trends shown here by the evenness are consistent with those observed in other ecosystems along vegetation succession, such as abandoned croplands and mines (Zhang, 2005; Norman et al., 2006).

The patterns of FGs and species abundances showed that the colonization of bare soil starts with badland specialist vegetation characterized by SDD species, and especially *Artemisia caerulescens* subsp. *cretacea* and *Parapholis strigosa*. These plant communities, which are the most unique of badlands in terms of species composition and have a high conservation value, disappeared as vegetation cover increased. This was especially due to the colonization by *Avena sterilis*, consistently with previous evidence (Torri et al., 2013). When vegetation reaches 90% total cover, the competition between plant species becomes high and no clear trends can be observed, but oscillations in abundance of all the FGs (Huisman and Weissing, 2001). LDD species had a minor role in the ecological succession, consistently with their reduced abundance in the dataset. This means that the process of disappearance of bare soil and badland-specialist plant communities is mainly due to the colonization by species that are present in the immediate surroundings. As

erosion rates decrease, pioneer plant communities colonize bare soil, ruderal annual grasslands replace pioneer plant communities, and perennial grasslands replace ruderal annual grasslands, until the disappearance of the biancana.

We observed a general decrease in the extent of bare soil surfaces over the years. Consistently, annual rainfall and extreme precipitation events, which are important drivers of erosion in Mediterranean badlands (García-Ruiz et al., 2013), did not increase significantly over time. However, we observed a significant warming, which is often associated with an increase in soil erosion (Ma et al., 2021). Overall, revegetation processes seem to be the main factors limiting soil erosion in our study site. Consequently, land management could be the most important driver for maintaining badlands in the study area. This is important in view of the conservation of such unique ecosystems, which cannot be maintained through passive protection by the SAC. Indeed, active management is necessary for the conservation of biodiversity in many other secondary habitats in Europe (Halada et al., 2011; Kettermann et al., 2022).

5. Conclusions

For the first time, our work highlighted how the decline of the biancana badlands of southern Tuscany, resulting from the progressive recolonization of eroded areas by vegetation, is leading to the loss of unique habitats and associated plant communities. This is particularly due to the reduction in extent of bare soil surfaces, with evidence of vegetation succession that will lead to the disappearance of communities supporting endemic species like *Artemisia caerulescens* subsp. *cretacea*. Such communities currently resulted to shift in space, colonizing bare soil and being replaced by ruderal grasslands where they were formerly present. Moreover, the observed processes are causing the loss of a cultural landscape of great value at the global level. On the other hand, Natura 2000 habitats like *Bromopsis erecta* grasslands appeared stable in the resurveyed sites at least in the 16 years of observation, contrarily to elsewhere in Europe. Considering that the study area is included in a SAC due to the presence of badlands themselves and that seminatural vegetation needs human management to be maintained, the conservation measures applied till now seem insufficient for biodiversity conservation. Active management fostering erosion rates should be carried out instead, both non-recurring (prescribed cutting and burning in small sectors) and recurring (reintroduction of grazing).

CRediT authorship contribution statement

E.F.: Conceptualization, Methodology, Investigation, Writing – original draft, Writing – review & editing. **S.M.:** Conceptualization, Methodology. **D.T.:** Conceptualization, Methodology, Investigation, Writing – original draft, Writing – review & editing. **C.A.:** Investigation, Writing – review & editing. **G. Bo:** Investigation, Writing – review & editing. **G.C.:** Investigation, Writing – review & editing. **S.C.:** Investigation, Writing – review & editing. **A.C.:** Investigation, Writing – review & editing. **P. D.G.:** Investigation, Writing - review & editing. **L.d.S.:** Investigation, Writing – review & editing. **T.F.:** Investigation, Writing – review & editing. **D.F.:** Investigation, Writing – review & editing. **J.F.:** Investigation, Writing – review & editing. **A.G.:** Investigation, Writing – review & editing. **L. L.:** Investigation, Writing – review & editing. **M. Mu.:** Investigation, Writing – review & editing. **L. P.:** Investigation, Writing – review & editing. **A.S.:** Investigation, Writing – review & editing. **M.T.:** Investigation, Writing – review & editing. **S.M.:** Investigation, Supervision, Writing – original draft, Writing – review & editing. **G. Ba.:** Writing – review & editing. **M.Ma.:** Writing – review & editing. **Duccio Rocchini** : Writing - review & editing.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Emanuele Fanfarillo reports financial support was provided by the Italian Botanical Society.

Data Availability

Data will be made available on request.

Data availability

Full data will be made available on request. Species mean percentage covers in 2006 and 2022 per each land cover class are available in Table S3.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2023.e02655.

References

Bartolucci, F., Peruzzi, L., Galasso, G., Albano, A., Alessandrini, A., Ardenghi, N.M.G., et al., 2018. An updated checklist of the vascular flora native to Italy. Plant Biosyst. 152 (2), 179–303. https://doi.org/10.1080/11263504.2017.1419996.

Bazzoffi, P., Boscagli, A., Brandi, G., Busoni, E., Calzolari, C., Chiarucci, A., et al., 1997. Badland processes and significance in changing environments. Suppl. di Geogr. Fis. e Din. Del. Quat. 3, 151–166.

Bengtsson, J., Bullock, J.M., Egoh, B., Everson, C., Everson, T., O'Connor, T., O'Farrell, P.J., Smith, H.G., Lindborg, R., 2019. Grasslands - More important for ecosystem services than you might think. Ecosphere 10, e02582. https://doi.org/10.1002/ecs2.2582.

Bertness, M.D., Gough, L., Shumway, S.W., 1992. Salt tolerances and the distribution of fugitive salt marsh plants. Ecology 73 (5), 1842–1851. https://doi.org/10.2307/1940035.

Bierbaß, P., Wündsch, M., Michalzik, B., 2014. The impact of vegetation on the stability of dispersive material forming biancane badlands in Val d'Orcia, Tuscany, Central Italy. Catena 113, 260–266. https://doi.org/10.1016/j.catena.2013.08.003.

Cain, S.A., 1936. The composition and structure of an oak woods, cold spring harbor, Long Island, with special attention to sampling methods. Am. Midl. Nat. 17, 725–740. https://doi.org/10.2307/2420095.

Calaciura, B., Spinelli, O., 2008. Management of Natura 2000 Habitats Semi-Natural Dry Grasslands (*Festuco-Brometalia*) 6210. European Commission, Brussels.

Calzolari, C., Ungaro, F., 1998. Geomorphic features of a badland (biancane) area (Central Italy): characterisation, distribution and quantitative spatial analysis. Catena 31, 237–256. https://doi.org/10.1016/S0341-8162(97)00046-5.

Calzolari, C., Ristori, J., Sparvoli, E., 1993. Soils of Biancana badlands: distribution, characteristics and genesis in Beccanello farm (Tuscany, Italy). Quad. di Sci. Del. Suolo 3, 119–142.

Calzolari, C., Torri, D., Del Sette, M., Maccherini, S., Bryan, R., 1996. Evoluzione dei suoli e processi di erosione su biancane: il caso delle biancane de La Foce (Val d'Orcia, Siena). Boll. Soc. Ital. Sci. Suolo 8, 185–203.

Casavecchia, S., Allegrezza, M., Angiolini, C., Biondi, E., Bonini, F., Del Vico, E., Fanfarillo, E., Foggi, B., Gigante, D., Gianguzzi, L., Lasen, C., Maccherini, S., Mariotti, M., Pesaresi, S., Pirone, G., Poldini, L., Selvi, F., Venanzoni, R., Viciani, D., Vidali, M., Ciaschetti, G., 2021. Proposals for improvement of Annex I of Directive 92/43/EEC: Central Italy. Plant Sociol. 58 (2), 99–118. https://doi.org/10.3897/pls2021582/08.

Chiarucci, A., De Dominicis, V., Ristori, J., Calzolari, C., 1995. Biancana badland vegetation in relation to soil and morphology in Orcia Valley, central Italy. Phytocoenologia 25, 69–87. https://doi.org/10.1127/phyto/25/1995/69.

Core Team, R., 2022. R: A language and environment for statistical computing. R. Found. Stat. Comput., Vienna. ⟨https://www.R-project.org/⟩.

Crain, C.M., Bertness, M.D., 2006. Ecosystem engineering across environmental gradients: implications for conservation and management. Bioscience 56 (3), 211–218. https://doi.org/10.1641/0006-3568(2006)056[0211:EEAEGI]2.0.CO;2.

De Baets, S., Torri, D., Poesen, J., Salvador, M.P., Meersmans, J., 2008. Modelling increased soil cohesion due to roots with EUROSEM. Earth Surf. Process Land. 33, 1948–1963. https://doi.org/10.1002/esp.1647.

de Bello, F., Valencia, E., Ward, D., Hallett, L., 2020. Why we still need permanent plots for vegetation science. J. Veg. Sci. 31, 679–685. https://doi.org/10.1111/jvs.12928.

De Martonne, E., 1926. Aerisme, et índices d'aridité. Compte De L'Academie Des Sci. 182, 1395–1398.

EEA, 2016. Mapping and assessing the condition of Europe's ecosystems: progress and challenges. European Environmental Agency Report No 3/2016. https://www.eea.europa.eu/publications/mapping-europes-ecosystems. Accessed 20 Dec 2022.

European Commission, 1992. Council Directive 92/43/EEC of May 1992 on the Conservation of Natural Habitats and of Wild Fauna and Flora. Commission of the European Communities, Brussels. http://ec.europa.eu/environment/nature/legislation/habitatsdirective/index_en.htm. Accessed 20 Dec 2022.

Fanfarillo, E., Kasperski, A., Giuliani, A., Abbate, G., 2019. Shifts of arable plant communities after agricultural intensification: a floristic and ecological diachronic analysis in maize fields of Latium (central Italy). Bot. Lett. 166 (3), 356–365. https://doi.org/10.1080/23818107.2019.1638829.

Frate, L., Carranza, M.L., Evangelista, A., Stinca, A., Schaminée, J.H., Stanisci, A., 2018. Climate and land use change impacts on Mediterranean high-mountain vegetation in the Apennines since the 1950s. Plant Ecol. Divers. 11 (1), 85–96. https://doi.org/10.1080/17550874.2018.1473521.

Fresta, M., 2011. La Val d'Orcia: ovvero l'invenzione di un paesaggio tipico toscano. Lares 77 (2), 205–218.

Galasso, G., Conti, F., Peruzzi, L., Ardenghi, N.M.G., Banfi, E., Celesti-Grapow, L., et al., 2018. An updated checklist of the vascular flora alien to Italy. Plant Biosyst. 152 (3), 556–592. https://doi.org/10.1080/11263504.2018.1441197.

Gallart, F., Marignani, M., Pérez-Gallego, N., Santi, E., Maccherini, S., 2013. Thirty years of studies on badlands, from physical to vegetational approaches. A succinct review. Catena 106, 4–11. https://doi.org/10.1016/j.catena.2012.02.008.

García-Ruiz, J.M., Nadal-Romero, E., Lana-Renault, N., Beguería, S., 2013. Erosion in Mediterranean landscapes: changes and future challenges. Geomorphology 198, 20–36. https://doi.org/10.1016/j.geomorph.2013.05.023.

Halada, L., Evans, D., Romão, C., Petersen, J.E., 2011. Which habitats of European importance depend on agricultural practices? Biodivers. Conserv 20 (11), 2365–2378. https://doi.org/10.1007/s10531-011-9989-z.

Herzon, I., Raatikainen, K.J., Helm, A., Rūsiņa, S., Wehn, S., Eriksson, O., 2022. Semi-natural habitats in the European boreal region: Caught in the socio-ecological extinction vortex? Ambio 51, 1753–1763. https://doi.org/10.1007/s13280-022-01705-3.

Huisman, J., Weissing, F.J., 2001. Biological conditions for oscillations and chaos generated by multispecies competition. Ecology 82 (10), 2682–2695. https://doi.org/10.1890/0012-9658(2001)082[2682:BCFOAC]2.0.CO;2.

Italian Ministry for the protection of land and sea DM 24/05/2016. Decree of the Italian Ministry for the protection of land and sea. Designazione di 17 zone speciali di conservazione (ZSC) della regione biogeografica continentale e di 72 ZSC della regione biogeografica mediterranea insistenti nel territorio della Regione Toscana, ai sensi dell'articolo 3, comma 2 del decreto del Presidente della Repubblica 8 settembre 1997, n 357 2016.

Kapfer, J., Hédl, R., Jurasinski, G., Kopecký, M., Schei, F.H., Grytnes, J.-A., 2017. Resurveying historical vegetation data – opportunities and challenges. Appl. Veg. Sci. 20, 164–171. https://doi.org/10.1111/avsc.12269.

Kent, M., 2011. Vegetation description and data analysis: a practical approach, 2nd edition. John Wiley & Sons, Hoboken.

Kettermann, M., Poniatowski, D., Fartmann, T., 2022. Active management fosters species richness of wild bees in limestone quarries. Ecol. Eng. 182, 106733 https://doi.org/10.1016/j.ecoleng.2022.106733.

Kopecký, M., Macek, M., 2015. Vegetation resurvey is robust to plot location uncertainty. Divers Distrib. 21 (3), 322–330. https://doi.org/10.1111/ddi.12299.

Lelli, C., Nascimbene, J., Alberti, D., Agostini, N., Zoccola, A., Piovesan, G., Chiarucci, A., 2021. Long-term changes in Italian mountain forests detected by resurvey of historical vegetation data. J. Veg. Sci. 32 (1), e12939 https://doi.org/10.1111/jvs.12939.

Lelli, C., Chiarucci, A., Tomaselli, M., Di Musciano, M., Lasen, C., Poloniato, G., Nascimbene, J., 2022. Temporal beta diversity patterns reveal global change impacts in closed mountain grasslands. Plant Biosyst. https://doi.org/10.1080/11263504.2022.2100498.

Lepš, J., 1987. Vegetation dynamics in early old field succession: a quantitative approach. Vegetatio 72, 95–102.

Loeb, R.E., 1990. Measurement of vegetation changes through time by resampling. Bull. Torre Bot. Club 117 (2), 173–175. https://doi.org/10.2307/2997057.

Ma, X., Zhao, C., Zhu, J., 2021. Aggravated risk of soil erosion with global warming–A global meta-analysis. Catena 200, 105129. https://doi.org/10.1016/j.catena.2020.105129.

Maccherini, S., Santi, E., 2012. Long-term experimental restoration in a calcareous grassland: Identifying the most effective restoration strategies. Biol. Conserv. 146 (1), 123–135. https://doi.org/10.1016/j.biocon.2011.11.032.

Maccherini, S., Chiarucci, A., De Dominicis, V., 2000. Structure and species diversity of *Bromopsis erecta* grasslands of Biancana badlands. Belg. J. Bot. 133, 3–14.

Maccherini, S., Marignani, M., Gioria, M., Renzi, M., Rocchini, D., Santi, E., Torri, D., Tundo, J., Honnay, O., 2011. Determinants of plant community composition of remnant biancane badlands: a hierarchical approach to quantify species-environment relationships. Appl. Veg. Sci. 14, 378–387. https://doi.org/10.1111/j.1654-109X.2011.01131.x.

Maccherini, S., Bacaro, G., Marignani, M., 2018. Beneficial effects of restoration practices can be thwarted by climate extremes. Sci. Total Environ. 626, 851–859. https://doi.org/10.1016/j.scitotenv.2018.01.117.

Maccherini, S., Santi, E., Torri, D., 2019. Germinable soil seed bank in Biancana badlands. Diversity 11 (12), 223. https://doi.org/10.3390/d11120223.

Marignani, M., Del Vico, E., Maccherini, S., 2007. Spatial scale and sampling size affect the concordance between remotely sensed information and plant community discrimination in restoration monitoring. Biodivers. Conserv. 16, 3851–3861. https://doi.org/10.1007/s10531-007-9184-4.

Marignani, M., Del Vico, E., Maccherini, S., 2008a. Performance of indicators and the effect of grain size in the discrimination of plant communities for restoration purposes. Community Ecol. 9, 201–206. https://doi.org/10.1556/ComEc.9.2008.2.9.

Marignani, M., Rocchini, D., Torri, D., Chiarucci, A., Maccherini, S., 2008b. Planning restoration in a cultural landscape in Italy using an object-based approach and historical analysis. Land. Urban Plan. 84, 28–37. https://doi.org/10.1016/j.landurbplan.2007.06.005.

Meyer, S., Wesche, K., Krause, B., Leuschner, C., 2013. Dramatic losses of specialist arable plants in Central Germany since the 1950s/60s–a cross-regional analysis. Divers. Distrib. 19 (9), 1175–1187. https://doi.org/10.1111/ddi.12102.

Moore, P.D., Chapman, S.B., 1986. Methods in plant ecology. Blackwell Scientific Publications, Oxford.

Norman, M.A., Koch, J.M., Grant, C.D., Morald, T.K., Ward, S.C., 2006. Vegetation succession after bauxite mining in Western Australia. Restor. Ecol. 14 (2), 278–288. https://doi.org/10.1111/j.1526-100X.2006.00130.x.

Oksanen J., Blanchet F.G., Friendly M., Kindt R., Legendre P., McGlinn D., Minchin P.R., O.'Hara R.B., Simpson G.L., Solymos P., Stevens MHH, Szoecs E., Wagner H., 2022. vegan: Community Ecology Package. R package version 2.6–4. https://CRAN.R-project.org/package=vegan.

Pedrotti, E., Rydin, H., Ingmar, T., Hytteborn, H., Turunen, P., Granath, G., 2014. Fine-scale dynamics and community stability in boreal peatlands: revisiting a fen and a bog in Sweden after 50 years. Ecosphere 5 (10), 1–24. https://doi.org/10.1890/ES14-00202.1.

Phillips, C.P., 1998. The badlands of Italy: a vanishing landscape? Appl. Geogr. 18 (3), 243–257. https://doi.org/10.1016/S0143-6228(98)00005-8.

Pignatti, S., 1982. Flora d'Italia. Edagricole, Bologna.

Pignatti, S., Guarino, R., La Rosa, M., 2017-2019. Flora d'Italia, 2nd edition. Edagricole di New Business Media, Bologna.

Poniatowski, D., Hertenstein, F., Raude, N., Gottbehüt, K., Nickel, H., Fartmann, T., 2018. The invasion of *Bromus erectus* alters species diversity of vascular plants and leafhoppers in calcareous grasslands. Insect Conserv. Divers. 11, 578–586. https://doi.org/10.1111/icad.12302.

QGIS Development Team, 2021. QGIS v. 3.20. QGIS Geographic Information System. QGIS Association. http://www.qgis.org. Accessed 20 Dec 2022.

Roveri, M., Flecker, R., Krijgsman, W., Lofi, J., Lugli, S., Manzi, V., Sierro, F.J., Bertini, A., Camerlenghi, A., De Lange, G., Govers, R., Hilgen, F.J., Hübscher, C., Meijer, P.T., Stoica, M., 2014. The Messinian Salinity Crisis: past and future of a great challenge for marine sciences. Mar. Geol. 352, 25–58. https://doi.org/10.1016/j.margeo.2014.02.002.

Sádlo, J., Chytrý, M., Pergl, J., Pyšek, P., 2018. Plant dispersal strategies: a new classification based on the multiple dispersal modes of individual species. Preslia 90 (1), 1–22. https://doi.org/10.23855/preslia.2018.001.

Schüle, M., Heinken, T., Fartmann, T., 2023. Long-term effects of environmental alterations in protected grasslands - Land-use history determines changes in plant species composition. Ecol. Eng. 188, 106878 https://doi.org/10.1016/j.ecoleng.2022.106878.

SPSS Inc, 2004. PASW Statistics for Windows, Version 13.0. SPSS Inc,, Chicago.

Taverna, K., Peet, R.K., Phillips, L.C., 2005. Long-term change in ground-layer vegetation of deciduous forests of the North Carolina Piedmont, USA. J. Ecol. 93 (1), 202–213. https://doi.org/10.1111/j.0022-0477.2004.00965.x.

CJF Ter Braak P. Smilauer Canoco 5, Windows release (5.00). Software for mutivariate data exploration, testing, and summarization Biometris, Plant Research International, Wageningen 2012.

Thiam, S., Villamor, G.B., Faye, L.C., Sène, J.H.B., Diwediga, B., Kyei-Baffour, N., 2021. Monitoring land use and soil salinity changes in coastal landscape: a case study from Senegal. Environ. Monit. Assess. 193 (5), 259 https://doi.org/10.1007/s10661-021-08958-7.

Torralba, M., Fagerholm, N., Hartel, T., Moreno, G., Plieninger, T., 2018. A social-ecological analysis of ecosystem services supply and trade-offs in European wood-pastures. Sci. Adv. 4, eaar2176 https://doi.org/10.1126/sciadv.aar2176.

Torri, D., Calzolari, C., Rodolfi, G., 2000. Badlands in changing environments: an introduction. Catena 40 (2), 119–125. https://doi.org/10.1016/S0341-8162(00)00119-3.

Torri, D., Borselli, L., Calzolari, C., Yañez MS, Salvador Sanchis, M.P., 2002. Soil erosion, land use, soil qualities and soil functions: effect of erosion. In: Rubio, J.L., Morgan, R.P.C., Asins, S., Andreu, V. (Eds.), Man and Soil at the Third Millennium, vol I. Geoforma Ediciones S.L, Logroño.

Torri, D., Santi, E., Marignani, M., Rossi, M., Borselli, L., Maccherini, S., 2013. The recurring cycles of Biancana badlands: erosion, vegetation and human impact. Catena 106, 22–30. https://doi.org/10.1016/j.catena.2012.07.001.

Torri, D., Rossi, M., Brogi, F., Marignani, M., Bacaro, G., Santi, E., Tordoni, E., Amici, V., Maccherini, S., 2018. Badlands and the dynamics of human history, land use, and vegetation through centuries. In: Nadal-Romero, E., Martínez-Murillo, J.F., Kuhn, N.J. (Eds.), Badlands Dynamics in a Context of Global Change. Elsevier, Amsterdam. https://doi.org/10.1016/B978-0-12-813054-4.00004-6.

Tuscany Region (2022a) Territory and landscape, Territorial Information: Geoscopio. https://www.regione.toscana.it/-/geoscopio. Accessed 24 Nov 2022.

Tuscany Region (2022b) SIR - Sistema Informativo Regionale. Settore Idrologico e Geologico Regionale - DATI / Archivio storico. http://www.sir.toscana.it/consistenza-rete. Accessed 19 Dec 2022 http://www.sir.toscana.it/consistenza-rete. Accessed 19 Dec 2022.

Verheyen, K., Bažány, M., Chećko, E., et al., 2018. Observer and relocation errors matter in resurveys of historical vegetation plots. J. Veg. Sci. 29, 812–823. https://doi.org/10.1111/jvs.12673.

Zhang, J.T., 2005. Succession analysis of plant communities in abandoned croplands in the eastern Loess Plateau of China. J. Arid Environ. 63 (2), 458–474. https://doi.org/10.1016/j.jaridenv.2005.03.027.

Zhang, X., Alexander, L., Hegerl, G.C., Jones, P., Tank, A.K., Peterson, T.C., Trewin, B., Zwiers, F.W., 2011. Indices for monitoring changes in extremes based on daily temperature and precipitation data. Wiley Interdiscip. Rev.: Clim. Change 2 (6), 851–870. https://doi.org/10.1002/wcc.147.