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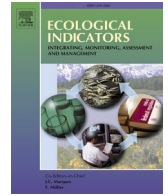
Original Articles

Bryophyte, lichen, and vascular plant communities of badland grasslands show weak cross-taxon congruence but high local uniqueness in biancana pediments

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ABSTRACT

Cross-taxon congruence, i.e., using certain taxonomic groups as surrogates for others, is receiving growing interest since it may allow decreasing efforts in biodiversity studies. In this work, we investigated the patterns of cross-taxon congruence in species richness and composition between communities of bryophytes, lichens, and vascular plants in different biancana grasslands of a Special Area of Conservation (SAC) of central Italy. We recorded species presence and abundance in 16 plots of 1×1 m size and analyzed the data using Procrustes correlation, co-correspondence analysis, and indicator species analysis. We did not highlight any correlation in species richness and composition between the three taxonomic groups. Conversely, the species composition of bryophyte communities was predictive of the species composition of lichen communities. Moreover, lichen richness was negatively correlated with the total cover of vascular plants. Indicator species analysis evidenced the presence of species from the three biotic communities being particularly related, at least at the local scale, to biancana pediments, like the bryophytes *Didymodon acutus* and *Trichostomum crispulum*, the lichens *Enchylium tenax*, *Cladonia foliacea,* and *Psora decipiens*, and the vascular plants *Brachypodium distachyon*, *Parapholis strigosa*, and *Artemisia caerulescens* subsp. *cretacea*. In the biancana pediments, acrocarp mosses, squamulose lichens, therophyte plants and chamaephyte plants coexisted. In spite of the weak cross-taxon congruence between the three taxonomic groups, this study could highlight a locally unique diversity of bryophytes, lichens, and vascular

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plants related to the extreme environment of biancana pediments, selected by high soil salinity and deposition from the upper eroded slope. Soil erosion and deposition in biancana badlands supports the increase of local multi-taxonomic plant diversity by creating unique ecosystems. Such biodiversity should be considered locally at risk of disappearance, due to the ongoing vanishing of biancana badlands in central Italy.

1. Introduction

In the past two decades, there has been growing interest in the exploration of cross-taxon congruence of biological communities, meaning the use of surrogate taxa or biodiversity correlates as a means to optimize resources and sampling efforts in biodiversity studies. This approach assumes that selected organisms can serve as potential indicators of the overall biodiversity or specific taxonomic groups (Chiarucci et al., 2005; Rodrigues and Brooks, 2007; Brunbjerg et al., 2020). The main aim of investigating cross-taxon congruence is to understand if and how taxonomically different biotic communities co-vary in response to changing conditions, either spatially or temporally. This can finally lead to identifying surrogate organisms that effectively indicate such variations (Duan et al., 2016). In this context, well-known taxonomic groups can be used as surrogates of less-known or difficult-to-study taxonomic groups, with a potential reduction of sampling efforts and an improvement in efficacy of conservation strategies (Sabatini et al., 2016; Brunbjerg et al., 2020; Burrascano et al., 2023). Several factors drive the co-variation among distinct taxonomic communities, including a shared biogeographical history, similar responses to specific environmental gradients, or biotic interactions between different organisms (Rooney and Azeria, 2015; Bonari et al., 2017; Barbato et al., 2019; Bazzato et al., 2023). The effectiveness of cross-taxon surrogates can vary depending on spatial scales and taxonomic groups, being the greatest at large spatial scales and within the same realm (terrestrial, marine − Rodrigues and Brooks, 2007; Qian and Kissling, 2010).

However, compared to surrogates like environmental features, cross-taxon surrogates have proved to perform better in specific habitats (Rodrigues and Brooks, 2007; Sabatini et al., 2016).

Badlands are peculiar geomorphological elements resulting from the severe erosion of Pliocene or Pleistocene marine clays (Torri et al., 2000). As unproductive land, they have been often reclaimed in the past, left undisturbed to natural succession, or used for livestock grazing. By contrast, the recognition of their importance for biodiversity conservation has led to their protection in various parts of the world, through the establishment of national parks (Stoffer, 2003). The decline of badland ecosystems due to land-use changes and to the decrease of erosion/deposition rates is causing biodiversity loss in some areas (Fanfarillo et al., 2023).

Italian badlands on Plio-Pleistocene marine clays are classified into two categories: "calanchi", represented by knife-edge, rill-gully erosion spots on hillslopes, and the less common "biancane", which are small dome-shaped remnants of intensely digitated, gully, and pipe erosion spots, resembling miniature clay hills (Calzolari and Ungaro, 1998; Phillips, 1998). Such landforms are characterized by a dome top with high vegetation cover and a highly eroded slope (usually the southern one) almost without vegetation. Gently sloping areas characterized by the deposition of the clay eroded from the upper slope, known as basal pediments, are present at the lower margin of each biancana (Calzolari and Ungaro, 1998). Biancana Badlands are exclusive to Italy and can be found only in Tuscany, Basilicata, and Calabria regions (Bazzoffi et al., 1997). In southern Tuscany, in particular, biancana badlands are
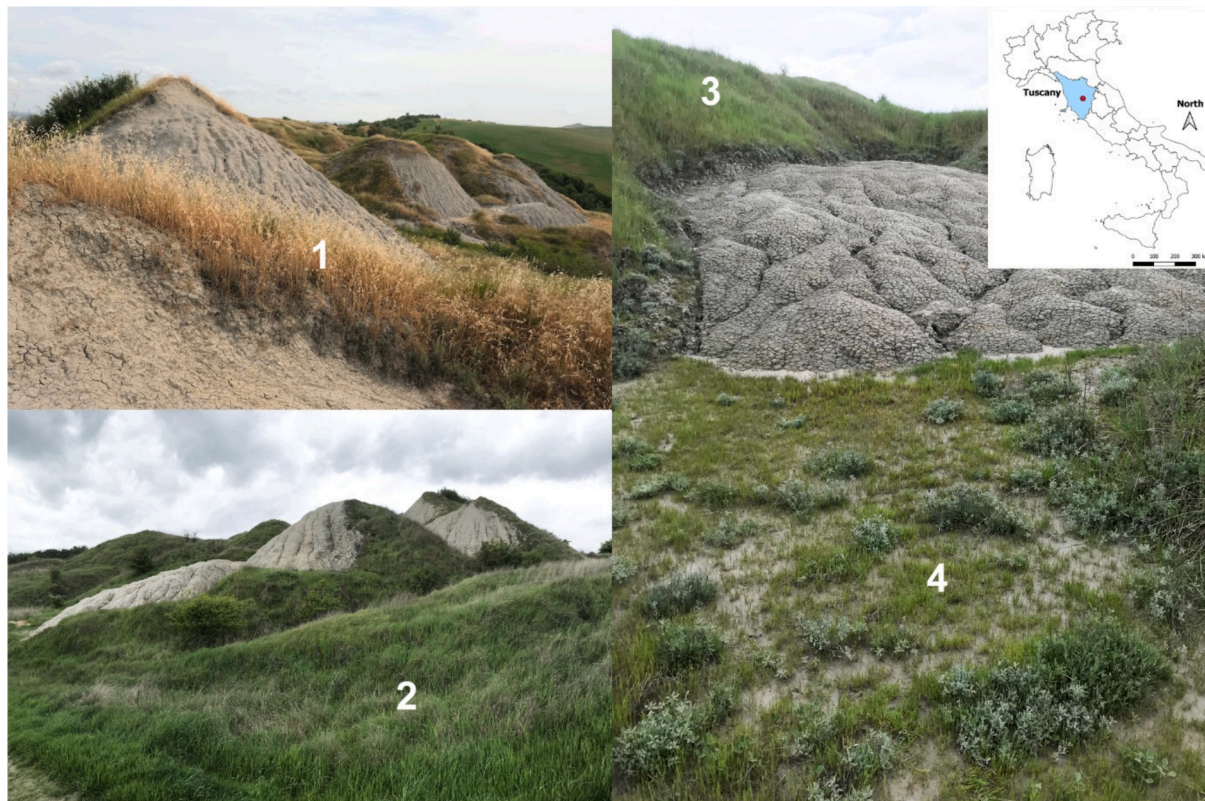
Fig. 1. Biancane at Leonina, with different grassland types developing on differently eroded soils (photos: G. Bonari, L. de Simone) and location of the study area (red dot) in Tuscany and Italy. 1 = *Avena sterilis* grassland; 2 = *Elymus repens* grassland; 3 = *Bromopsis erecta* grassland; 4 = *Artemisia caerulescens* subsp. *creatacea* −*Parapholis* spp. grassland.
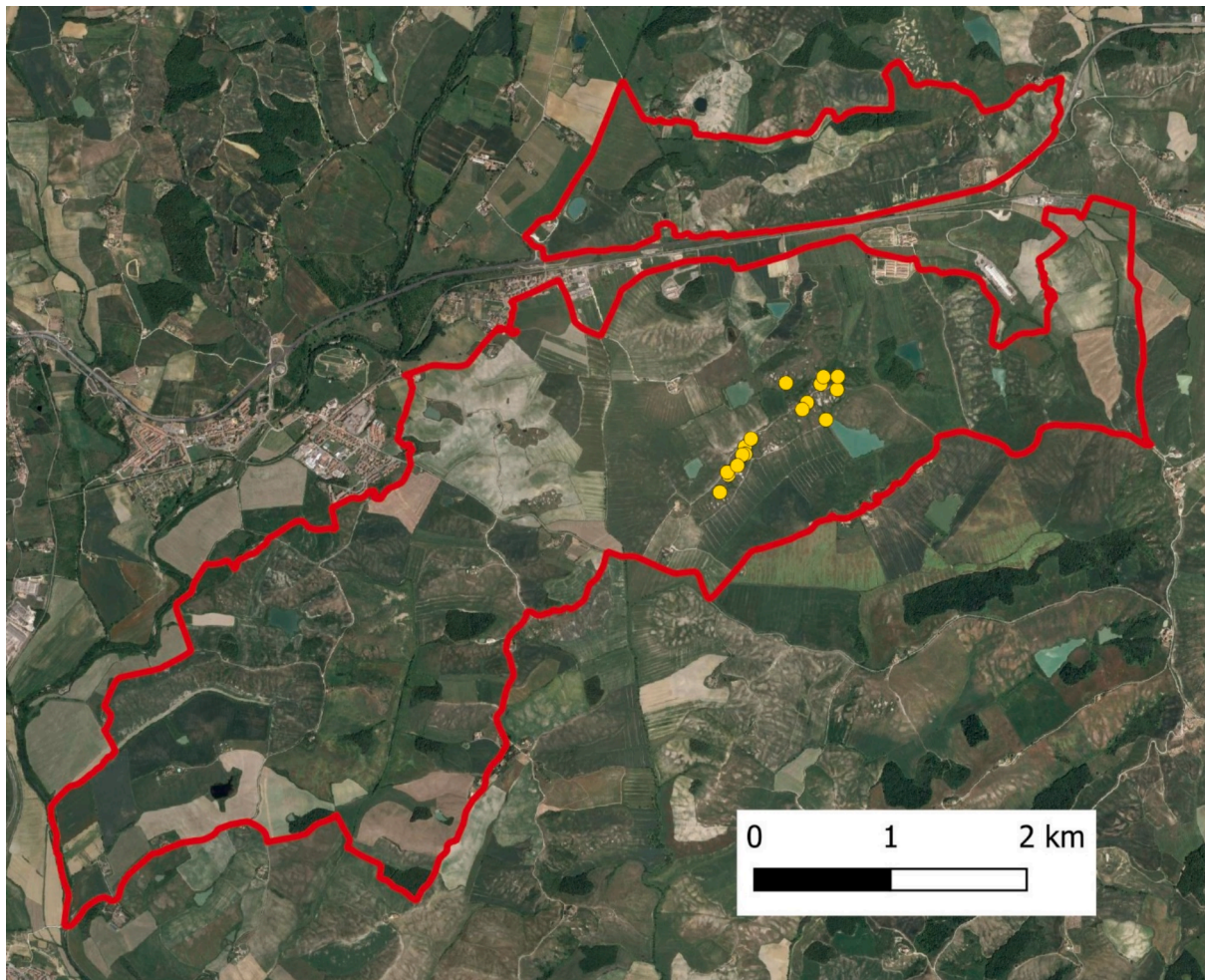
Fig. 2. Location of the sampled plots (yellow dots) within the Special Area of Conservation of Leonina (red lines).

distinctive elements of the cultural landscapes of "Crete Senesi" and "Val d'Orcia", the latter being listed among UNESCO World Heritage sites (Fresta, 2011). In these areas, the diversity of ecosystems generated by erosion/deposition patterns in biancana badlands supports distinct fungi, lichen, and vascular plant communities (Chiarucci et al., 1995; Maccherini et al., 2000; Loppi et al., 2004; Mazza et al., 2022). Conversely, there is still no knowledge of bryophyte diversity in Tuscan badlands. Lichen and vascular plant diversity is mainly driven by the gradient of soil electrical conductivity and sedimentation rates (Maccherini et al., 2011; Torri et al., 2018). Some biancana badland plant communities, like orchid-rich *Bromopsis erecta* grasslands, are protected under the European Habitats Directive (European Commission, 1992), and others were recently proposed to be included, like pioneer grasslands with the Italian endemic *Artemisia caerulescens* subsp. *cretacea* (Casavecchia et al., 2021). For these reasons, some biancana badland sites were protected by the Natura 2000 network in the last decades. However, active management like shrub cutting, prescribed burning, or grazing is needed for their effective conservation (Marignani et al., 2007; Marignani et al., 2008a,b). In lack of such management and due to rural abandonment, the badlands of southern Tuscany and badland-specialist species are disappearing (Torri et al., 2013; Fanfarillo et al., 2023).

So far, very few studies simultaneously assessed cross-taxon congruence between bryophytes, lichens, and vascular plants. For example, in forest and shrubland ecosystems of a southern Tuscan small nature reserve, these three taxonomic groups showed no cross-taxon congruence either in species richness or composition (Santi et al.,

2010). However, further analyses on the same dataset detected some predictive power of vascular plant communities towards bryophytes and lichens, but with varying magnitude depending on the spatial scale considered and the type of predictors used (Santi et al., 2016). Other studies testing congruence only between vascular plants and lichens or between vascular plants and bryophytes showed different results depending on the studied ecosystem (Chiarucci et al., 2007; Maccherini et al., 2013; Bacaro et al., 2019).

Lichen and vascular plant communities are known to respond significantly to environmental gradients across the different grassland ecosystems of biancana badlands (Loppi et al., 2004; Fanfarillo et al., 2023). However, their patterns of covariation were never tested. Moreover, there is no knowledge on biancana badland bryophyte communities, which could supposedly have similar responses to lichens and vascular plants to the gradient of salinity and erosion/deposition. Thus, in this work, we tested if bryophyte, lichen, and vascular plant communities have congruent variations in species richness and composition along such gradient in a biancana badland site of southern Tuscany, central Italy. We hypothesized that the communities of the three studied taxonomic groups had consistent patterns of change in response to changing soil salinity and erosion/deposition rates. We finally aimed at verifying the possibility to use one or more of these communities as a surrogate of the others, to improve the efficacy of sampling efforts in biodiversity knowledge and conservation prioritization. Moreover, we aimed to achieve a thorough taxonomic and ecological characterization of the bryophyte, lichen, and vascular plant communities of biancana pediments, whose previous knowledge has highlighted a relevant local
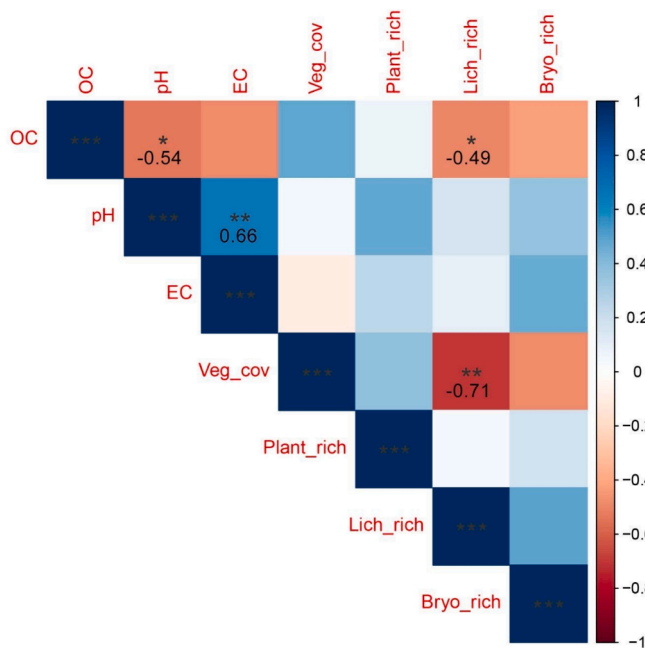
Fig. 3. Pearson correlation heatmap of the species richness of the three taxonomic groups and environmental variables. OC = Soil organic carbon content; EC = Soil electrical conductivity; Veg_cov = total percentage cover of vascular plants; Plant_rich = Vascular plant species richness; Lich_rich = Lichen species richness; Bryo_rich = Bryophyte species richness. Significance codes: *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$.

Table 1
Procrustes correlations in species composition between the three taxonomic groups. No value was statistically significant.

	Bryophytes	Lichens	Vascular plants
Bryophytes	1		
Lichens	0.39	1	
Vascular plants	0.37	0.49	1

uniqueness as regards lichens and vascular plants.

2. Materials and methods

2.1. Study area

The research site is situated within the Municipality of Asciano and it is part of the cultural landscape known as the "Crete Senesi," located to the southeast of Siena, in Tuscany, central Italy (Fig. 1). This area has been included into the Natura 2000 network through the establishment of the Special Area of Conservation (SAC) IT5190004 – "Crete di Camposodo e Crete di Leonina" (Italian Ministry for the protection of land and sea, 2016).

The elevation of the study area ranges between 200 and 250 m a.s.l. The badland site is characterized by hills primarily composed of Pliocene marine sediments in the elevated areas, while more recent fluvial deposits occur in the valleys. The climate exhibits a transition between a sub-humid and sub-arid type, featuring an average annual temperature of ca. 13 °C and an annual rainfall averaging between 700 and 800 mm. Precipitations follow the typical Mediterranean pattern, with the lowest rainfall occurring during the summer months (Tuscany Region, 2022).

The biancana badlands found within the "Crete Senesi" area are distinguished by the presence of cascading small domes and hummocks, with base diameters ranging from 2 to over 20 m, typically protruding 3 to 10 m (rarely up to 20–30 m) above gently sloping pediments. Such pediments may sometimes be absent, or in other cases they can extend up to 10–15 m from the slopes of the eroded hummocks (Calzolari and Ungaro, 1998).

The biancana soils in the study area have different development stages, characterized by different rates of erosion/deposition, and are spatially distributed in distinct patches. Distinct vegetation types develop on such differently developed and eroded soils (Fig. 1). On the pediments of the biancana badlands, pioneer vegetation is found. This is characterized by halotolerant species, including *Artemisia caerulescens* subsp. *cretacea*, *Hordeum marinum*, *Parapholis incurva*, *Parapholis strigosa*, and *Scorzonera laciniata*. Such vegetation type is at risk of disappearance due to the decrease of erosion/deposition rates (Fanfarillo et al., 2023). The biancana pediment habitat was recently proposed to be included in the Annex I of the Habitats Directive under the name "Habitat 15XX – Pioneer halophilous and subhalophilous communities of "Calanchi" and "Biancane" badlands" (Casavecchia et al., 2021). Perennial grasslands develop in areas with lower salinity and reduced erosion (Natura 2000 habitat 6210* – Semi-natural dry grasslands and scrubland facies on calcareous substrates – *Festuco-Brometalia* – *important orchid sites) (European Commission, 1992). They are characterised by species like *Galatella linosyris* subsp. *linosyris*, *Bromopsis erecta*, *Dactylis glomerata*, *Phleum nodosum*, and *Plantago lanceolata*. The biancana tops and east-southeast-facing slopes support dry grasslands dominated by *Bromopsis erecta*, *Galatella linosyris* subsp. *linosyris*, and *Linum corymbulosum*. As soil stability and water availability increase, *Bromopsis erecta* becomes more abundant, often accompanied by shrubs. Sites with higher moisture and cooler conditions host dense *Thinopyrum acutum* grasslands. Shrublands are dominated by *Crataegus monogyna*, *Prunus spinosa* subsp. *spinosa*, *Pyrus spinosa*, *Spartium junceum*, and *Ulmus minor* subsp. *minor*. Finally, mixed deciduous oak woodlands featuring *Quercus cerris* and *Q. pubescens* are present (Torri et al., 2018).

Like vascular plant communities, the lichen communities of southern Tuscan badlands are highly influenced by the intensity of soil erosion/deposition and the presence of bare soil, since herbaceous vascular plants outcompete lichens. Pediment and erosion front morphologies are colonized by *Placidium squamulosum*, *Enchylium tenax*, *Gyalolechia fulgens*, *Squamarina cartilaginea*, and *Thalloidima sedifolium*, with *Psora decipiens, Lathagrium cristatum*, and *Xanthocarpia lactea* being exclusive to such habitats (Loppi et al., 2004). As erosion stops and *Bromopsis erecta* grasslands stabilize the soil, lichen vegetation becomes scarcer and mainly represented by *Cladonia* spp. assemblages (Loppi et al., 2004).

Contrary to lichen and vascular plant communities, bryophyte communities of Tuscan biancana badlands are completely unknown so far.

2.2. Field sampling

In late May 2022, we surveyed the bryophyte, lichen, and vascular plant communities of biancana badlands in Leonina using 16 square plots of 1 m^2 (Fig. 2). Such plot size resulted to be adequate to discriminate plant communities in badlands (Marignani et al., 2008b). Moreover, it is the best trade-off to simultaneously catch the highest possible variability of bryophyte, lichen, and vascular plant communities for cross-taxon analyses (Santi et al., 2016). To capture the variability of grassland vegetation across the gradients of soil salinity and erosion/deposition rates, being the most important in shaping plant communities in badlands (Chiarucci et al., 1995), the sampling was stratified on four different grassland types (*Artemisia caerulescens* subsp. *cretacea-Parapholis* spp. grasslands; *Avena sterilis* grasslands; *Elymus repens* grasslands; *Bromopsis erecta/Brachypodium rupestre* grasslands) in each biancana, according to a stratified random sampling based on Maccherini et al. (2011). We sampled four plots per grassland type. For each plot, we recorded species presence and abundance. Vascular plant abundance was visually estimated as the percentage cover of each species. Lichen and bryophyte abundances were measured as species frequencies on a scale from 0 to 16, dividing the plot in 16 sub-quadrats of
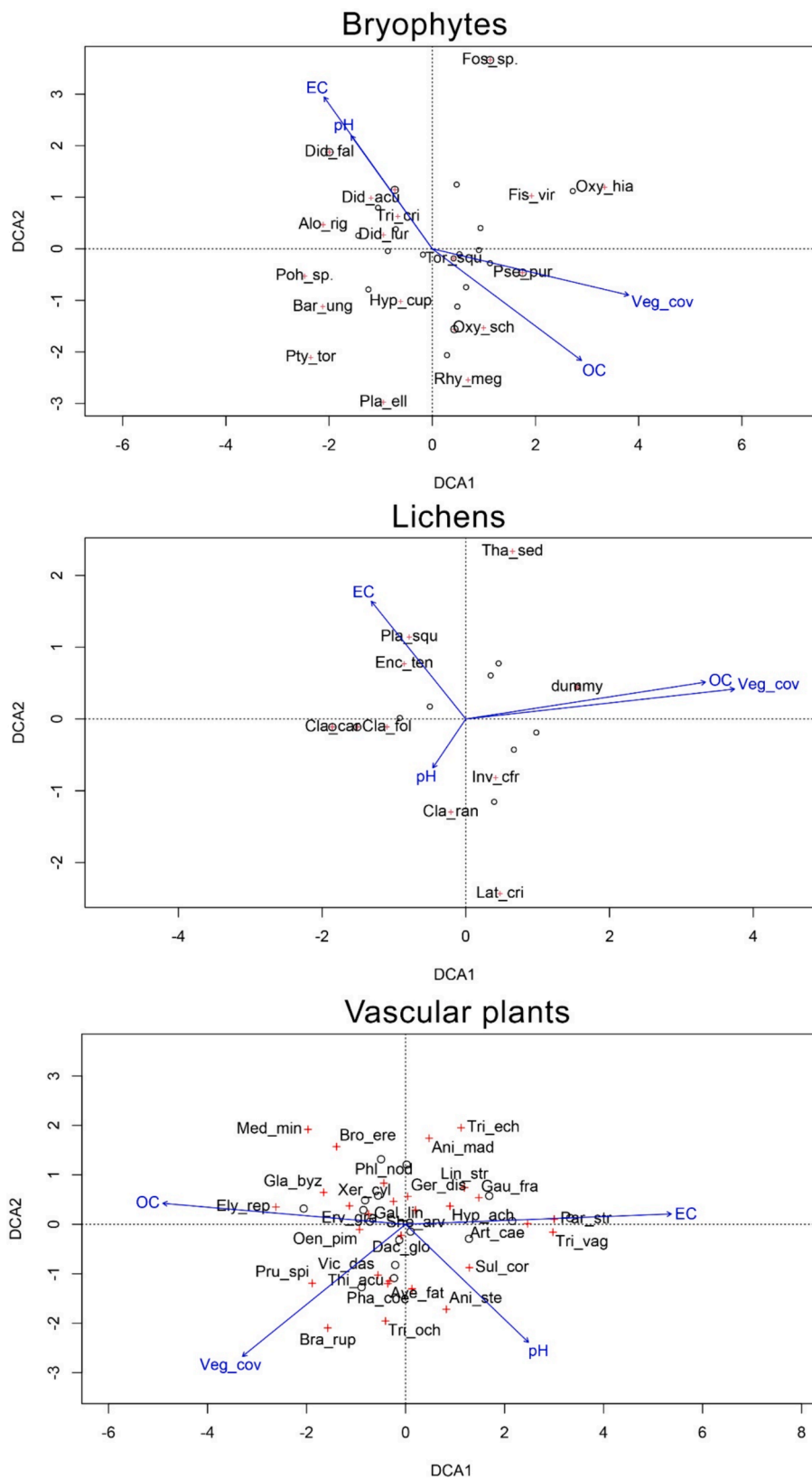
Fig. 4. Detrended Correspondence Analysis triplots of bryophyte (variance explained: DCA1 = 17.6 %; DCA2 = 13.6 %), lichen (variance explained: DCA1 = 35.2 %; DCA2 = 20.5 %), and vascular plant (variance explained: DCA1 = 15.3 %; DCA2 = 9.2 %) communities. Environmental variables are passively transposed on the plot. Veg_cov = Total percentage cover of vascular plants; OC = Soil organic carbon content; EC = Soil electrical conductivity. Species names abbreviations: see Appendix A.

Table 2
Summary of the co-correspondence analyses carried out on abundance data.

	Inertia	Cross-validatory % fit
Vascular plants *vs* lichens		
Axis 1	1.695	19.245
Axis 2	1.369	13.565
Vascular plants *vs* bryophytes		
Axis 1	3.087	9.303
Axis 2	2.800	11.943
Lichens *vs* vascular plants		
Axis 1	3.908	3.168
Axis 2	3.784	8.512
Lichens *vs* bryophytes		
Axis 1	3.087	6.963
Axis 2	2.872	8.518
Bryophytes *vs* vascular plants		
Axis 1	3.908	6.914
Axis 2	3.638	8.718
Bryophytes*vs* lichens		
Axis 1	1.695	23.099*
Axis 2	1.303	16.771
—		
Significance codes: * = p < 0.05.		

25 × 25 cm size.

Bryophytes were identified according to Cortini Pedrotti (2001-2005) and their nomenclature was then updated according to Aleffi et al. (2020). For the identification of the lichen species several keys were used, mainly Smith et al. (2009) and online identification keys on ITALIC 7.0 (Nimis and Martellos, 2020). Their nomenclature was then updated according to Nimis (2023). Vascular plants were identified according to Pignatti et al. (2017–2019) and their nomenclature was then updated according to the Portal to the Flora of Italy (2023).

We collected one soil sample from the center of each plot to measure soil pH, organic carbon content (%), and electrical conductivity (μS/cm at 20 °C). The soil samples were dried at 40 °C in a ventilated oven. Subsequently, they were sieved through a 2 mm mesh, homogenized through quartering, and mechanically pulverized before the analyses. The determination of pH and conductivity was conducted on soil samples (particle size < 2 mm) using a 1:2.5 (w/v) soil-to-water suspension, following the methods defined in the US Epa (United States Environmental Protection Agency) (2004). The method adopted to assess the content of organic carbon was that proposed by Walkley and Black (1934).

2.3. Data analysis

We assessed correlations in species richness between the three taxonomic groups through two-sided Pearson's tests (function *cor.test* in the package *vegan* of R – Oksanen et al., 2022; R Core Team, 2023). Similarly, we checked for correlations between environmental variables and species richness and between the total cover of vascular plants and the species richness of bryophytes and lichens.

For further analyses, the abundance values of vascular plants were rescaled at the same scale that was used for bryophyte and lichen abundances (1–16) to make them comparable. Then, abundance data of all communities were transformed into relative abundances (range: 0–1). Correlations in species composition were assessed through Procrustes tests based on Detrended Correspondence Analysis (DCA) using the function *protest* in the package *vegan*. DCAs were carried out through the function *decorana* in the package *vegan*. The predictive power of the species composition of each community against the others was tested by means of predictive Co-Correspondence analysis (hereafter Co-CA) using the function *coca* in the package *cocorresp* (Simpson, 2009). Both DCAs and Co-CAs were carried out on square root-transformed relative abundance data. Biancana pediments are the most locally unique geomorphological types in terms of lichen and plant communities, and the most threatened of disappearance (Loppi et al., 2004;

Fanfarillo et al., 2023). Thus, to check for the presence of unique bryophyte, lichen, and vascular plant species in biancana pediments, we carried out indicator species analysis for the two groups: i) pediment grasslands (*Artemisia caerulescens* subsp. *cretacea-Parapholis* spp. grasslands) and ii) the rest of grasslands (*Avena sterilis* grasslands, *Elymus repens* grasslands, *Bromopsis erecta/Brachypodium rupestre* grasslands), using the function *multipatt* in the package *indicspecies* (De Cáceres and Legendre, 2009). Since life/growth forms give ecological information on bryophytes, lichens, and vascular plants (Lavorel et al., 1997; Kürschner, 2004; Nimis, 2023), we visualized the patterns of variation of life/growth forms (bryophytes: acrocarp, pleurocarp, thalloid; lichens: crustose, foliose, fruticose, squamulose; vascular plants: chamaephyte, geophyte, hemicryptophyte, therophyte) along environmental gradients by carrying out three PCAs on life/growth forms and their abundance (sum of relative abundances) per each plot, and then passively plotting environmental variables on them. PCAs were carried out using the function *rda* in the package *vegan*. For these analyses, we selected PCA instead of DCA since the gradient of variation of the communities on the first ordination axis based on life/growth forms was much shorter than their gradient of variation based on species composition. We retrieved bryophyte, lichen, and vascular plant life/growth forms from Cortini Pedrotti (2001-2005), Nimis (2023), and Pignatti et al. (2017–2019), respectively. For all analyses, we set α at 0.05.

3. Results

3.1. Detected biodiversity

We detected the presence of 22 taxa of bryophytes (1 to 8 per plot), 11 of lichens (0 to 8 per plot), and 96 of vascular plants (7 to 28 per plot). The most frequent bryophyte species was *Tortella squarrosa* (12 plots), followed by *Didymodon luridus, Trichostomum crispulum, Oxyrrhynchium schleicheri, Dicranella howei*, and *Fissidens viridulus* (6 plots). As regards lichens, the most frequent species were *Involucropyrenium* cfr. *pusillum* (4 plots), *Cladonia rangiformis, Enchylium tenax*, and *Placidium squamulosum* (3 plots). The most frequent vascular plant species were *Hypochaeris achyrophorus* (14 plots), *Ervum gracile, Sherardia arvensis* (13 plots), *Linum strictum*, and *Xeranthemum cylindraceum* (12 plots).

In terms of mean frequency within plots (bryophytes and lichens) or mean cover (vascular plants), *Tortella squarrosa, Fissidens viridulus, Oxyrrhynchium schleicheri*, and *Didymodon acutus* were the most abundant bryophytes; *Cladonia rangiformis, Enchylium tenax*, and *Placidium squamulosum* were the most abundant lichens; *Bromopsis erecta, Elymus repens* subsp. *repens*, and *Brachypodium rupestre* were the most abundant vascular plants.

3.2. Correlation in species richness and relationships with environmental variables

We detected no significant correlations in species richness between any of the three taxonomic groups. Lichen species richness was negatively correlated with the soil content in organic carbon (r = -0.49; *p* < 0.05) and with the total cover of vascular plants (r = -0.70; *p* < 0.01) (Fig. 3). We also found a decreasing trend of bryophyte species richness with increasing cover of vascular plants, though not statistically significant.

3.3. Congruence in species composition

We did not highlight any Procrustes correlations in species composition between the three taxonomic groups (Table 1).

The DCA triplots highlighted the presence of some species of all the three groups related to high soil electrical conductivity/salinity (pediment morphologies), such as *Didymodon* spp. and *Trichostomum crispulum* for bryophytes, *Cladonia cariosa, Enchylium tenax*, and *Placidium squamulosum* for lichens, and *Artemisia caerulescens* subsp. *cretacea* and
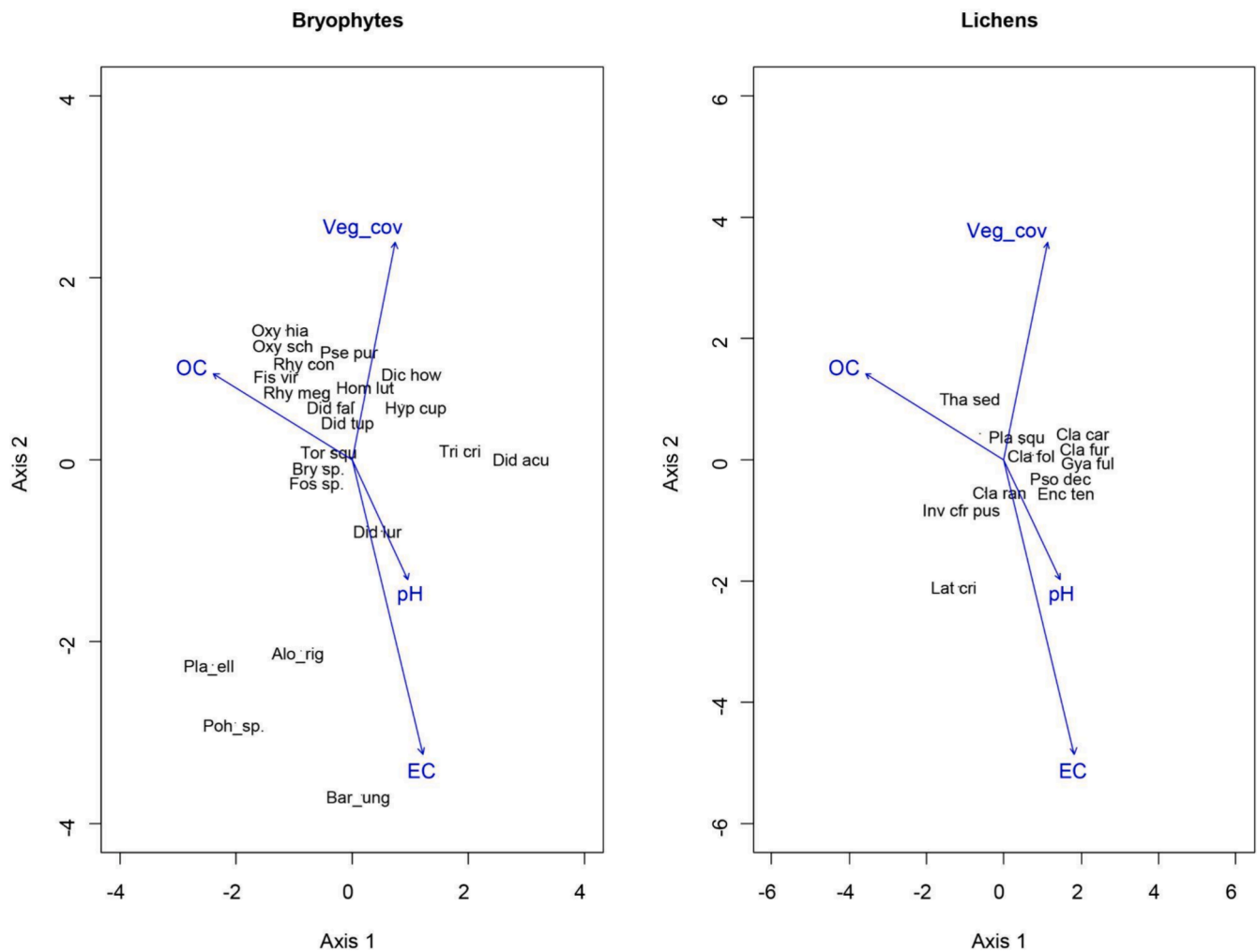
Fig. 5. Predictive Co-CA biplot of bryophyte community composition *vs* lichen community composition, based on abundance data (square-root transformed). Veg_cov = Total percentage cover of vascular plants; OC = Soil organic carbon content; EC = Soil electrical conductivity. Bryophyte names abbreviations: Alo rig = *Aloina rigida*; Bar ung = *Barbula unguiculata*; Bry sp. = *Bryum* sp.; Dic how = *Dicranella howei*; Did acu = *Didymodon acutus*; Did fal = *Didymodon fallax*; Did lur = *Didymodon luridus*; Did top = *Didymodon tophaceus*; Fis vir = *Fissidens viridulus*; Fos sp. = *Fossombronia* sp.; Hom lut = *Homalothecium lutescens*; Hyp cup = *Hypnum cupressiforme*; Oxy hia = *Oxyrrhynchium hians*; Oxy sch = *Oxyrrhynchium schleicheri*; Pla ell = *Plagiomnium ellipticum*; Poh sp. = *Pohlia* sp.; Pse pur = *Pseudoscleropodium purum*; Rhy con = *Rhynchostegium confertum*; Rhy meg = *Rhynchostegium megapolitanum*; Tor squ = *Tortella squarrosa*; Tri cri = *Trichostomum crispulum*. Lichen names abbreviations: Cla car = *Cladonia cariosa*; Cla fol = *Cladonia foliacea*; Cla fur = *Cladonia furcata*; Cla ran = *Cladonia rangiformis*; Enc ten = *Enchylium tenax*; Gya ful = *Gyalolechia fulgens*; Inv cfr pus = *Involucropyrenium* cfr. *pusillum*; Lat cri = *Lathagrium cristatum*; Pla squ = *Placidium squamulosum*; Pso dec = *Psora decipiens*; Tha sed = *Thalloidima sedifolium*.

Parapholis strigosa for vascular plants (Fig. 4).

The Co-CA analysis revealed a significant predictive power of bryophyte communities species composition towards lichen communities species composition (Table 2, Fig. 5).

3.4. Indicator species analysis

There were two bryophyte, three lichen, and seven vascular plant species that were associated with pediment morphologies. Two plant species, but no bryophytes and lichens, were associated with the grasslands located in other geomorphological types (Table 3).

3.5. Patterns of variation of life forms

Acrocarp mosses were related to high pH and electrical conductivity and to low cover of vascular plants (pediment), whereas pleurocarp mosses followed an opposite trend (perennial grasslands). All lichen life forms, and especially squamulose lichens, were related to low cover of vascular plants and high values of soil pH and electrical conductivity

(pediment). Vascular plants were mainly represented by therophytes and chamaephytes in sites with high values of soil pH and electrical conductivity (pediment), while hemicryptophytes had an opposite pattern (perennial grasslands – Fig. 6).

4. Discussion

4.1. General outlines

Our results highlighted a weak cross-taxon congruence between bryophyte, lichen, and vascular plant communities in the studied biancana badland grasslands. This is at some variance with previous evidence that the species composition of both lichen and vascular plant communities changes along the gradient of salinity and erosion/deposition rates (Chiarucci et al., 1995; Loppi et al., 2004; Maccherini et al., 2011). This could suggest that a similar response to environmental features may result in consistent compositional shifts at least for these two biotic communities. Possibly, considering the ecological requirements of the studied organisms in further analyses could help

Table 3

Results of the indicator species analysis for bryophyte, lichen, and vascular plant communities of pediment grasslands *vs* other grasslands.

Bryophytes		
Pediment grasslands	IndVal	Growth form
Didymodon acutus	0.844**	Acrocarp
Trichostomum crispulum	0.808*	Acrocarp
Lichens		
Pediment grasslands	IndVal	Growth form
Enchylium tenax	0.866**	Foliose
Cladonia foliacea	0.707*	Fruticose
Psora decipiens	0.707*	Squamulose
Vascular plants		
Other grasslands	IndVal	Life form
Ervum gracile	0.907*	Therophyte
Galatella linosyris subsp. *linosyris*	0.866*	Hemicryptophyte
Pediment grasslands	IndVal	Life form
Brachypodium distachyon	1.000***	Therophyte
Parapholis strigosa	1.000***	Therophyte
Artemisia caerulescens subsp. *cretacea*	0.998***	Chamaephyte
Triticum vagans	0.866**	Therophyte
Polygala monspeliaca	0.862*	Therophyte
Festuca danthonii subsp. *danthonii*	0.707*	Therophyte
Poa bulbosa subsp. *bulbosa*	0.707*	Hemicryptophyte
—		

Significance codes: *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$.

detecting stronger relationships between the three taxonomic groups (Brunbjerg et al., 2018).

While the lichen and vascular plant communities of Tuscan badlands were already well-known (Chiarucci et al., 1995; Loppi et al., 2004; Maccherini et al., 2011; Fanfarillo et al., 2023), these are the first data regarding the bryophyte communities of badlands in the study area. Species composition of bryophyte communities was consistent with the results from previous studies in clay or gypsum badlands of southern Italy and Sicily, where the bryophyte vegetation of eroded sites is characterized by terricolous species like *Thrichostomum crispulum, Tortella squarrosa,* and *Didymodon* spp. (Privitera and Puglisi; Puglisi et al., 2022).

4.2. Congruence in species richness and composition

Previous evidence suggests that lichen and vascular plant species richness are correlated only in some ecosystems. Vascular plant richness was positively correlated with epiphytic lichen richness in old-growth forests (Blasi et al., 2010) and shrublands (Bacaro et al., 2019). Conversely, it was negatively correlated with lichen richness in swamps (Bacaro et al., 2019). Particularly in forests, open patches where more sunlight reaches the forest-floor are more likely to host a higher species richness of both herb-layer plants and lichens (Sabatini et al., 2016). The detected negative correlation between lichen richness and the cover of vascular plants was already highlighted before in the badlands of southern Tuscany. A dense cover of herbaceous vascular plants (e.g., *Bromopsis erecta*) outcompetes terricolous lichens that need open spaces and an adequate amount of bare ground to survive (Loppi et al., 2004). In grasslands, both lichen and bryophyte species richness is known to decrease with increasing cover of vascular plants, consistently with our results (Löbel et al., 2006; Gheza et al., 2020). However, the decrease of bryophyte species richness with increasing cover of vascular plants was not statistically significant.

We did not highlight congruences in either species richness or composition between bryophyte and vascular plant communities. Previous studies showed contrasting results. In most cases, no congruences were highlighted regarding species richness (Santi et al., 2010). On the contrary, congruence in species composition was detected in several works (Chiarucci et al., 2007; Maccherini et al., 2013; Burrascano et al., 2018; Bacaro et al., 2019; Marignani et al., 2020).

The only significant cross-taxon congruence highlighted in this study was the predictive power of the species composition of bryophyte communities towards the species composition of lichen communities. Based on this evidence, we can speculate about the existence of positive biotic interactions between the two taxonomic groups. Bryophytes can be a growth substratum for some lichen species, also acting as facilitators along the vegetation succession, prolonging their assimilation time during dry days (Colesie et al., 2012). In addition to the pioneer species (such as *Enchylium tenax* and *Thalloidima sedifolium*), some biancana badland lichens, like *Cladonia* spp., are mesophytic and often associated with moss carpets of *Hypnum cupressiforme* and *Homalothecium lutescens* (Loppi et al., 2004), forming more mature communities.

4.3. Indicator species analysis

The indicator bryophyte species of pediments *Didymodon acutus* and *Trichostomum crispulum* are both typical species of dry loamy soils, frequently found in badland habitats (Privitera and Puglisi, 1999; Puglisi et al., 2022). Moreover, they grow in salt-rich ecosystems, like coastal dunes and cliffs (Dierssen, 2001; Atherton et al., 2010; Blockeel et al., 2014). The lichen species related to pediment morphology were previously found in other biancana badlands of southern Tuscany, in particular *Enchylium tenax* and *Psora decipiens*, both of which only occur, at least at the local scale, in such habitats (Loppi et al., 2004). As regards vascular plants, pediment grasslands confirmed its uniqueness with respect to grasslands located in other geomorphological types, with the presence of both locally (*Parapholis* spp., *Brachypodium distachyon*) or globally (*Artemisia caerulescens* subsp. *cretacea*) unique taxa (Fanfarillo et al., 2023).

The presence of species of all three groups being exclusively linked to pediment morphologies, with its high levels of clay deposition and salinity, confirms the uniqueness and conservation value of this vanishing habitat. As regards plants and lichens, positive associations between specialist species of pediments were already found in other Tuscan badlands (Loppi et al., 2004). Such results suggest that, despite the low consistency in co-variation of the communities across the main environmental gradient, there was some congruence between the three taxonomic groups limited to the co-existence of species adapted to high salinity and erosion/deposition in pediment grasslands.

4.4. Patterns of variation of life/growth forms

We found that acrocarp mosses (*Barbula unguiculata, Didymodon acutus*) were related to pediment morphologies, where soils have higher salinity and pH. Conversely, pleurocarp mosses (*Homalothecium lutescens, Oxyrrhynchium schleicheri*), were related to more stable soils with lower salinity and a higher content of organic carbon. This is in line with previous evidence, since acrocarpous mosses dominate in sunny and dry habitats, while pleurocarpous mosses are more related to shady and mesic habitats (Kürschner, 2004). Consistently, acrocarp mosses in our dataset were all colonialist species, except for the competitive/perennial *Tortella squarrosa*. Conversely, pleurocarp mosses were all perennial species, competitive or stress-tolerant (Dierssen, 2001). Lichens tended to occur in open vegetation with all of their life forms, having overall affinity for basic to subneutral/subacid substrata, with the exception of the more acidophilic *Cladonia cariosa*. In general, squamulose lichens (*Placidium squamulosum, Psora decipiens*, and *Thalloidima sedifolium*) were particularly related to pediments while fruticose ones (*Cladonia* spp., with the exception of *Cladonia furcata*) were more able to compete under high covers of vascular plants. This is consistent with previous evidence from Tuscan badlands (Loppi et al., 2004). The patterns of vascular plant life forms were consistent with the literature, with therophytes (*Parapholis* spp.) and chamaephytes (*Artemisia caerulescens* subsp. *cretacea*) being related to the pediment and hemicryptophytes (*Bromopsis erecta, Brachypodium rupestre*) being related to other
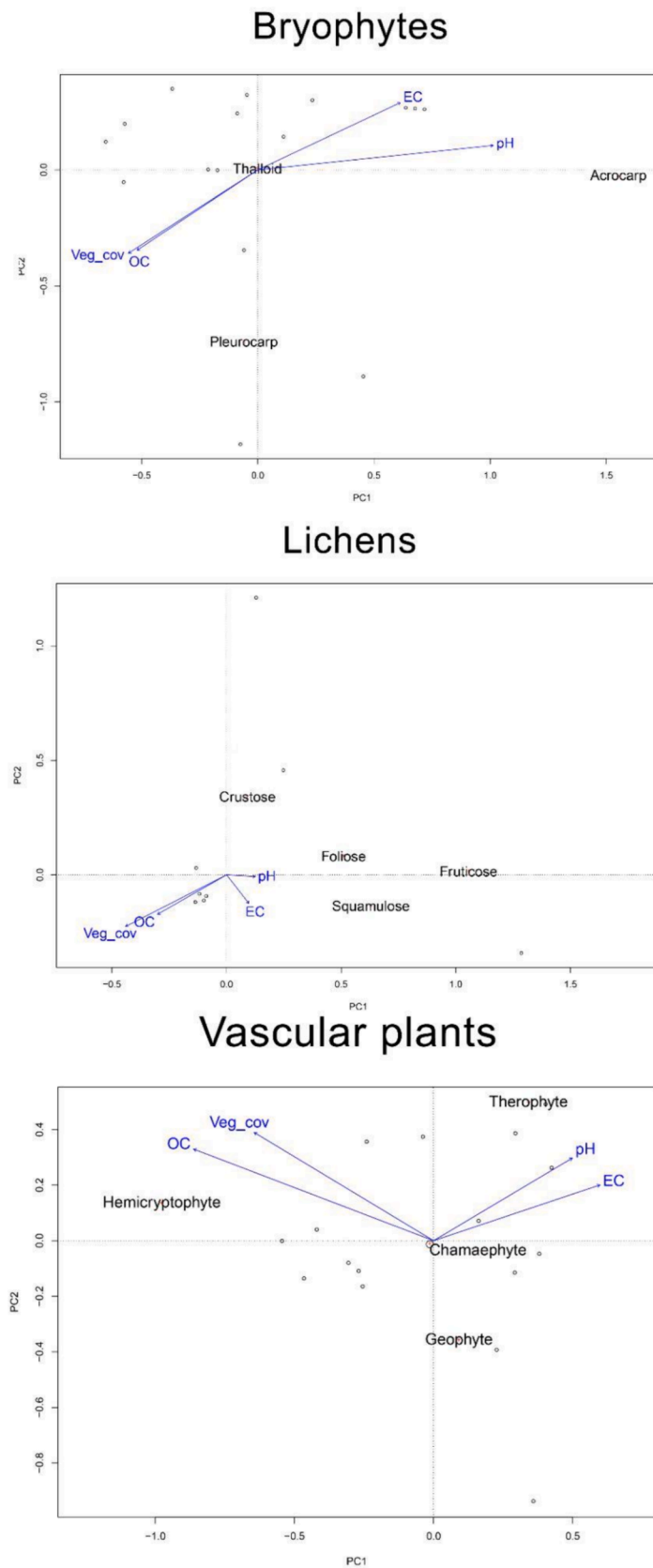
Fig. 6. PCA plots showing the variation in occurrence and abundance of life/growth forms of bryophyte (variance explained: PC1 = 81.1 %; PC2 = 18.7 %), lichen (variance explained: PC1 = 91.4 %; PC2 = 7.3 %), and vascular plant (variance explained: PC1 = 59.8 %; PC2 = 21.3 %) communities. Veg_cov = Total percentage cover of vascular plants; OC = Soil organic carbon content; EC = Soil electrical conductivity.

geomorphological types (Chiarucci et al., 1995). According to the variance explained in the ordination analyses, life/growth forms were more effective than species composition in explaining community variation across the gradients of EC, OC, pH, and cover of vascular plants. This suggests how, even when there is a species turnover, species adaptations in terms of life/growth forms stay similar in similar ecological conditions (Pescador et al., 2015).

5. Conclusion

With this study, we highlighted the existence of a locally unique diversity of bryophytes, lichens, and vascular plants related to the extreme environment of biancana pediments, characterized by a strong species filtering. Despite this, we found a weak cross-taxon congruence between the three taxonomic groups. However, we also highlighted that bryophyte community composition is a good indicator of lichen community composition, to be used to reduce efforts in biodiversity survey and monitoring in the area. Our work increased the understanding of how soil erosion in biancana badlands contributes to increase local multi-taxonomic plant diversity by creating unique environmental facets. Biodiversity hosted in biancana grasslands is at risk of disappearance, at least at the local scale, due to the ongoing vanishing of biancana badlands in central Italy. Future conservation efforts should be focused on active management of badland areas, to maintain soil erosion and the associated biodiversity through prescribed cutting and burning and the reintroduction of grazing. Further efforts will be useful to assess cross-taxon congruence between the studied taxonomic groups at wider spatial scales, or including more taxonomic groups, such as fungi, animals, or microbiota.

CRediT authorship contribution statement

Emanuele Fanfarillo: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Stefano Loppi:** Writing – review & editing, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Claudia Angiolini:** Writing – review & editing, Investigation, Data curation. **Giovanni Bacaro:** Writing – review & editing, Formal analysis, Data curation. **Elisabetta Bianchi:** Writing – review & editing, Investigation, Data curation. **Gianmaria Bonari:** Writing – review & editing, Investigation. **Ilaria Bonini:** Writing – review & editing, Investigation, Data curation. **Giulia Canali:** Writing – review & editing, Investigation, Data curation. **Giacomo Cangelmi:** Writing – review & editing, Investigation, Data curation. **Silvia Cannucci:** Writing – review & editing, Investigation, Data curation. **Annalena Cogoni:** Writing – review & editing, Investigation, Data curation. **Paola De Giorgi:** Writing – review & editing, Investigation, Data curation. **Luca Di Nuzzo:** Writing – review & editing, Investigation, Data curation. **Leopoldo de Simone:** Writing – review & editing, Investigation, Data curation. **Tiberio Fiaschi:** Writing – review & editing, Investigation, Data curation. **Daniel Fontana:** Writing – review & editing, Investigation, Data curation. **Jacopo Franzoni:** Writing – review & editing, Investigation, Data curation. **Antonio Giacò:** Writing – review & editing, Investigation, Data curation. **Paolo Giordani:** Writing – review & editing, Investigation, Data curation. **Martina Grattacaso:** Writing – review & editing, Investigation, Data curation. **Lorenzo Lazzaro:** Writing – review & editing, Investigation, Data curation. **Stefano Martellos:** Writing – review & editing, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Irene Mazza:** Writing – review & editing, Investigation. **Michele Mugnai:** Writing – review & editing, Investigation, Data curation. **Giulio Pandeli:** Writing – review & editing, Investigation, Data curation. **Claudia Perini:** Writing – review & editing, Investigation, Data curation. **Lorenzo Pinzani:** Writing – review & editing, Investigation, Data curation. **Silvia Poponessi:** Writing – review & editing, Investigation, Data curation. **Sonia Ravera:** Writing – review &

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Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Stefano Loppi reports financial support was provided by Italian Botanical Society. Emanuele Fanfarillo, Stefano Loppi, Claudia Angiolini, Gianmaria Bonari, Ilaria Bonini, Silvia Cannucci, Michele Mugnai, Claudia Perini, Lorenzo Pinzani, Sonia Ravera, Simona Maccherini reports was provided by Italian Ministry of University and Research. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgments

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2024.112171.

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