



Determinants of plant community composition of remnant biancane badlands: a hierarchical approach to quantify species-environment relationships

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Keywords

Bromus erectus grasslands; Conservation; Cultural landscape; Habitat degradation; Multi-scale approach; Remnant vegetation; Variation partitioning

Abbreviations

DEM = Digital Elevation Model; NDVI = Normalized Difference Vegetation Index; NIR = Near-infrared; RDA = Redundancy Analysis.

Nomenclature

Pignatti (1982) and Conti et al. (2005) for *Artemisia caerulescens* subsp. *cretacea*

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Abstract

Question: Which environmental variables best explain patterns in the vegetation of biancane badlands? What is the role of spatial scales in structuring the vegetation of biancane badlands within the agricultural matrix?

Location: Five biancane badlands in Central Italy (Tuscany).

Methods: An object-oriented approach on high-resolution multispectral images was used to classify physiognomic vegetation types in five biancane badlands. Within each badland, data on vascular plant species abundance were collected using a stratified random design. Variation partitioning based on partial redundancy analysis was used to evaluate the contribution of three sets of environmental predictors, recorded at the spatial scales of plot, patch and biancane badland in explaining patterns in plant community composition.

Results: Environmental variables included in the final model – electrical conductivity and carbon/nitrogen ratio (plot scale), shape index (patch scale) and area (biancane badland scale) – accounted for 15.5% of the total variation in plant community composition. Soil characteristics measured at the plot level explained the majority of variation. In the smallest badlands, *Bromus erectus* perennial grasslands were absent, while annual grasslands, linked with harsh soil conditions (i.e. high soil salinity), were not affected by either the surface area of biancane badlands or by the soil nitrogen availability.

Conclusions: The identification of the major predictors of patterns in remnant vegetation requires conducting investigations at multiple spatial scale. Management strategies should operate at different spatial scale, preventing any further reduction in the size of existing badlands and relying on habitat- instead of area-focused conservation practices.

Introduction

Modern agriculture represents a major threat to global biodiversity (McIntyre & Hobbs 1999; Mazzoleni et al. 2004) because of the interaction of two main processes: (1) loss of natural and semi-natural habitats to agriculture and subsequent habitat fragmentation (2) habitat degradation (Firbank et al. 2008). These processes operate at different spatial scales and have led to a general decrease in habitat heterogeneity within the agricultural landscape (Tscharntke et al. 2005). At the landscape/regional level,

larger farm units have resulted in larger areas under similar management systems (Firbank et al. 2008). At the level of farm/fields, there has been a general decrease in crop diversity, a removal of non-farmed areas such as ponds and non-farmed field margins, as well as an increase in field size and subsequent loss of field margins. Within fields, practices such as increases in nutrient and pesticides input have resulted in habitat degradation and eutrophication (Tscharntke et al. 2005; Firbank et al. 2008).

Changes within the agricultural matrix, at the landscape level, as well as within and between fields, have had detrimental effects on remnant vegetation, which has often become confined to small, fragmented patches, provoking loss of biodiversity (Benton 2001; Berendse et al. 2004; Cousins et al. 2007; Fisher & Lindenmayer 2007). A considerable number of studies have characterized the effects of habitat fragmentation on animal populations (see Fisher & Lindenmayer 2007 for a review) and temperate forest plant species (Honnay et al. 1999; Godfroid & Koedam 2003; Hobbs & Yates 2003; Kolb & Diekmann 2005; Rosati et al. 2010), although these investigations mainly focused on relatively homogeneous habitat patches and not on complex remnant patches with more than one vegetation type. In grassland ecosystems, the impact of changes in local environmental variables and management practices, including increases in soil nutrient levels and destruction of natural and semi-natural landscape features appear to be the major determinants of plant community patterns in remnant grassland communities, while the role of factors such as patch shape and dimension, that tend to operate at level of landscape, appear to be only secondary (Wright et al. 2003; Helm et al. 2006; Rocchini et al. 2006; Klimek et al. 2007, 2008; Marini et al. 2007, 2008).

Biancane badlands are listed on the UNESCO World Heritage list as valuable cultural landscape supporting several plant communities of high conservation interest, a number of endemic species (Chiarucci et al. 1995), as well as *Bromus erectus* grasslands, habitats considered of European concern (*Festuco-Brometalia* priority habitats, European Commission 1992). The major threats to the biodiversity of biancane badlands are natural vegetation succession and intensification of agricultural practices. Over the past 50 ys, agricultural activities have progressively transformed this cultural landscape through land reclamation for arable cultivation and field enlargement. These changes have led to a general homogenization of these landscapes, with a strong contraction of the remaining badlands, which became confined to small, sometimes protected, areas scattered within an intensively farmed landscape. Disruptions of these intensely-dissected landscapes have in turn resulted in changes in plant community

composition because of the spread of generalist plant species that occupy broad environmental ranges, leading to a general decline in plant diversity (Marignani et al. 2008). Recent studies on the invertebrate fauna in these landscapes have shown that the extent of the fields of biancane badlands is the primary determinant of orthopteran species richness, together with habitat diversity (Marini et al. 2010).

In this study, we aimed to identify the local and regional environmental variables and processes that are most important in determining patterns in the vegetation of biancane badlands. As the species–environment relationships are known to vary with scale of observation and because of the high heterogeneity of biancane landscape, we used a range of environmental predictors that were classified at three spatial scales (plot, patch and badland). Specifically, remote sensing techniques were employed to optimize our vegetation sampling design, and partitioning of variation was used to evaluate the contribution of spatial scale in determining vegetation patterns in such landscapes. This information is central to the development of sound management and conservation strategies aimed at protecting the diversity of the biancane badlands.

Methods

Study area

The study area is located in the district of Asciano (centroid coordinates: longitude 11°31'03" E, latitude 43°15'03" N, datum ED50), a 215 km² area situated in Crete Senesi, near Siena, central Italy (Fig. 1). The overall area of the Crete Senesi includes the basins of the Asso, Ombrone and Arbia rivers, north of Montalcino and Pienza and south of Siena covering an area of 320 km². The hilly parts of this landscape are characterized by outcrops that are mainly composed of Pliocene marine sediments, while valleys are typically formed by recent fluvial deposits (Guasparri 1978). The typical morphology of this landscape originates from the erosion of claystone, which results in particular forms of erosion and includes biancane badlands, balze, vertical facies, calanchi, eroded claystone hill sides and domes (Phillips 1998; Marignani et al. 2008). Badlands represent unique geomorphological features that often develop on unconsolidated or poorly cemented materials, usually present in arid and semi-arid areas, with alternating wet and dry periods (Bryan & Yair 1982). Biancane are badlands that are found specifically in central and south of Italy and consist of dome-shaped forms, generally less than 20 m high, which can often be found grouped into fields (Fig. 1, Guasparri 1978; Raglione et al. 1980; Alexander 1982). In biancane badlands, erosion has cut through a single substratum of Pliocene marine clays causing its differentiation into a

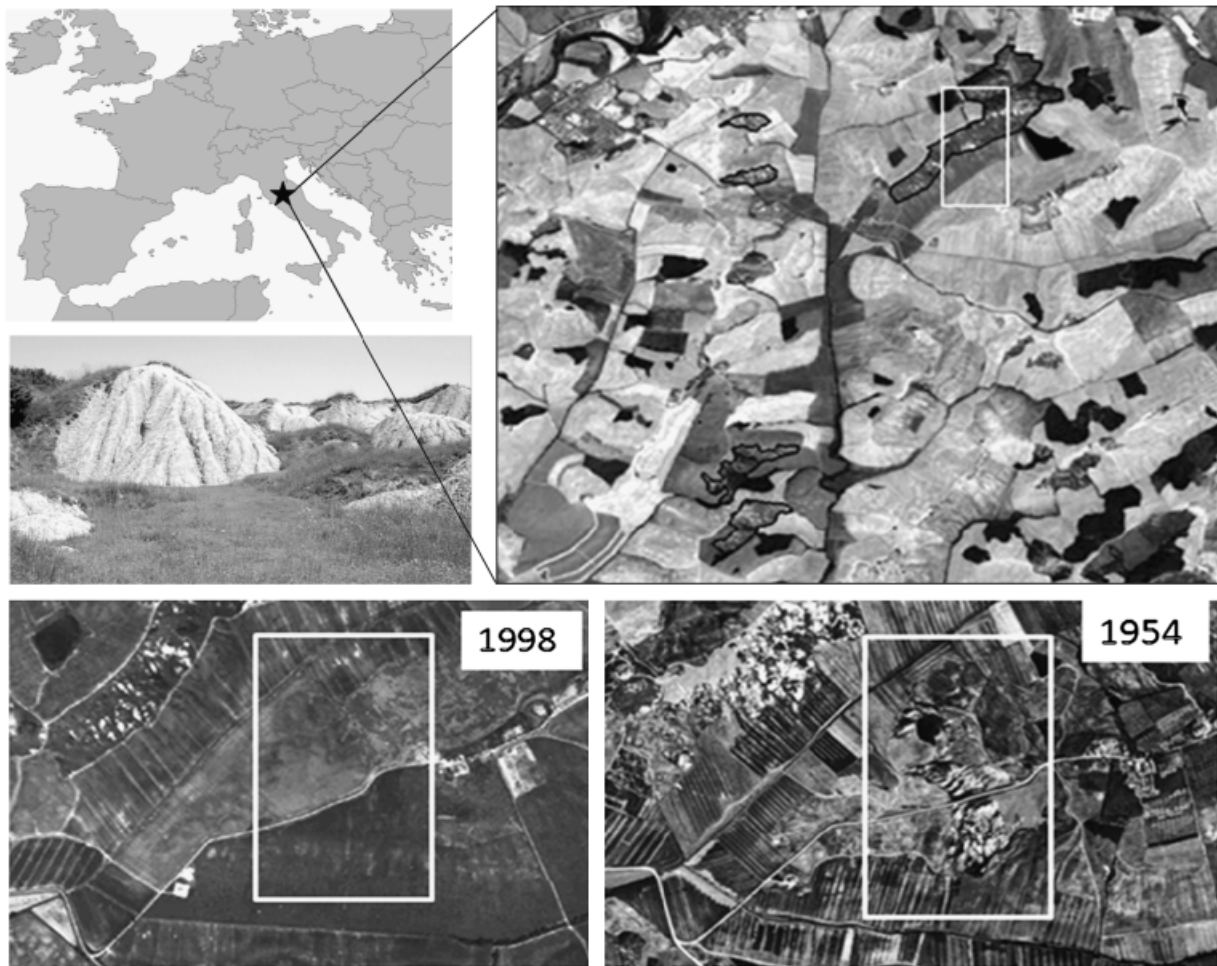


Fig. 1. Biancane are peculiar erosion forms, generated on Plio-Pleistocene marine clay outcrops, produced by the joint effects of retreating gullies and pipes, usually grouped together in fields. They are interspersed within an agricultural landscape matrix: the abandonment of traditional activities and the intensification of agriculture are quickly reducing traditional cultural landscapes (time-frame shown 1954–1998).

mosaic of habitats that range from bare ground with scarce or no vegetation to grassland communities with or without shrubs (Chiarucci et al. 1995; see Clarke & Rendell 2010). The southern slope of biancane, with marked soil erosion and mass movement, is colonized by scanty vegetation, while pioneer annual vegetation occurs on pediments near the feet of the biancane, representing the equilibrium area between plant colonization and soil sedimentation (Chiarucci et al. 1995; Marignani et al. 2008). Within the agricultural landscape, biancane badlands support uncommon species and plant communities of high conservation value (Chiarucci et al. 1995; Marignani et al. 2008; Marini et al. 2010).

Sampling design

We produced a land-cover map of the biancane badlands in the study area by using an object-oriented approach on

a QuickBird multispectral image (acquisition date 19 July 2004, spatial resolution 2.44 m in the multispectral channels), corrected both geometrically and radiometrically. Segments were automatically generated based on a technique that aggregates neighbor pixels according to their spectral similarity, using an agglomerative iteration process (Marignani et al. 2008; Blaschke 2010). Segmentation was performed using the eCognition software. Finally, we manually attributed classes to each segment (polygon) according to the physiognomic characteristics of the vegetation.

We identified five biancane badlands, which were then divided into two to four zones, depending on their surface area (Marignani et al. 2007). Within each zone, we established randomly three 1 m × 1 m plots representative of each of four land-cover class C, so that up to 12 plots were identified in those zones where all four land-cover classes were present (Fig. 2). The number of plots within

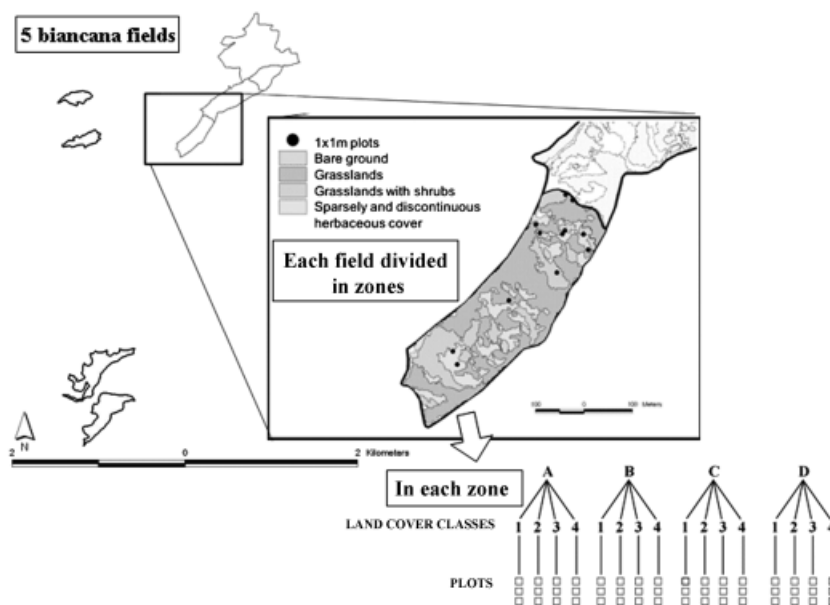


Fig. 2. Sampling design: each of the five biancane badlands was divided into inner zones. In this zoomed example, the biancane badland is divided into four zones. Within each zone (A, B, C and D), three plots of 1 m × 1 m per land cover class were randomly selected.

Table 1. Environmental variables recorded for each subset. NDVI = normalized difference vegetation index.

Description and unit	Specification of variables	Subset	Range
Slope	Degree	Plot	0–38.4
Total nitrogen	% Dry weight	Plot	0.01–0.97
Total carbon	% Dry weight	Plot	0.36–7.01
pH (H ₂ O)	–	Plot	7.36–8.87
Carbon/nitrogen ratio	Ratio	Plot	1.5– > 30
Electrical conductivity	dS m ⁻¹	Plot	0.19–8.62
Patch area	m ²	Patch	87.07–45 828.5
Patch shape index	–	Patch	1.18–7.53
Badland area	m ²	Biancane badland	34 440–553 770
Badland shape index	–	Biancane badland	0.96–1.55
Badland Shannon index	–	Biancane badland	1.82–2.64
Badland number of patches	–	Biancane badland	27–994
Badland mean NDVI	–	Biancane badland	0.25–0.41

each badland was thus proportional to its surface area and heterogeneity, which was expressed by the land cover class. The four land cover classes were: (1) bare ground with little or no vegetation (< 15%); (2) sparsely and discontinuous herbaceous cover (< 30%); (3) grasslands; and (4) grasslands with shrubs (shrub cover < 20%). Shrublands with shrub cover > 20% were excluded from this study. To classify the four land-cover classes, we adopted the CORINE land-cover legend (European Environment Agency 2000) with some revisions. In small biancane badlands, with two zones and three land-cover classes per zone ($Z=2$, $C=3$), we sampled $3 \times 3 \times 2$ plots. The number of plots per badland varied between 18 and 48, for a total of 132 plots. In June 2006,

the percentage cover of vascular plants in each 1 m × 1 m plot was estimated using a point-quadrant method (Moore & Chapman 1986), with a density of 100 pins m⁻². To account for the effects of spatial heterogeneity, the environmental predictors were grouped into three classes: plot, patch or badland (Table 1).

Plot-scale predictors

At the scale of plot, we used six variables (Table 1) recording both topographic and edaphic variables. Local topography was evaluated by measuring the slope in a 5 m × 5 m neighborhood starting from a 5 m DEM (Digital Elevation Model) derived from the local administration

topographic map of the area (scale of 1:5000). In each plot, we took one soil sample, which was then sieved using a 2-mm diameter mesh sieve and oven-dried at 105 °C for 2 days (Benton 2001). Dried sediments were analysed in triplicate by direct total flash combustion using a CHNS (carbon, hydrogen, nitrogen and sulphur) analyser with a thermo-conductivity detector TCD (mod. CHN/O 200; Perkin Elmer Inc., Waltham, MA, USA), to determine average total organic carbon (TOC) and total nitrogen (TN). When N was undetectable, an arbitrary value of 0.01 was assigned. We then calculated the C/N ratio as well as indices of soil N availability (Schroth & Sinclair 2003), while pH levels and electrical conductivity (EC, dS m^{-1}) were measured in leached water using two pre-calibrated electronic probes (WTW I 430 and WTW I 340 multimeter, respectively; WTW[®], Weilheim, DE).

Patch-scale predictors

At patch scale we used two variables (Table 1). The patch shape index was calculated as an indicator of habitat fragmentation, expressed at the level of patch i , as follows:

$$SI = P_i / (2\sqrt{\pi A_i}), \quad (1)$$

where P_i and A_i represent the perimeter and area of the patch i , respectively. SI directly estimates the complexity of the shape, also called compactness, of individual patches (see McGarigal & Marks 1995). The more the patches are elongated and complex, the higher the shape index.

Badland scale predictors

At the biancane badland scale we used five variables (Table 1). Plant biomass was estimated using the mean normalized difference vegetation index (NDVI), a normalized ratio of NIR (near infrared) and red bands. This vegetation index is based on (i) the high reflectance by vegetation in the NIR that is linked to scattering processes at the leaf scale (leaf shape and size), water content of the vegetation, overall plant architecture, and density of vegetation cover, as well as on (ii) the low reflectance in the Red due to the absorption by chloroplasts for photosynthesis (Lillesand et al. 2004). The NDVI varies theoretically from -1 (low biomass) and 1 (high biomass). The mean NDVI was derived from the QuickBird image.

The diversity of the vegetation at the level of badland was measured using the Shannon diversity index (Shannon & Weaver 1962; Boltzmann 1872), which was calculated as follows:

$$H' = - \sum_{c=1}^M (P_c \ln P_c), \quad (2)$$

where M , number of land cover classes (c); P_c , the proportion of the area occupied by each land cover class.

Data analysis

Three-way nested ANOVA was carried out to test if soil characteristics measured at the plot level differed among biancane badland (fixed factor), zone (fixed factor nested within biancane badland) and land-cover classes (fixed factor crossed with zone and biancane badland).

We used variation partitioning to decompose the variation in plant species composition of biancane badlands plant communities into a number of independent components reflecting the relative importance of multiple sets of predictors, measured at different spatial scales, and their joint effects (Borcard et al. 1992). This method is useful to analyse hierarchically structured landscape data, by explicitly evaluating the contribution of sets of factors that had been measured at different spatial scale to the structure of biotic communities (Cushman & McGarigal 2002). To date, hierarchical partitioning has been used sporadically to assess plant–environmental relationships in grassland ecosystems (Marini et al. 2008).

The variation in plant species composition was decomposed into the three sets of explanatory variables, one for each spatial scale (i.e. plot, patch and biancane badland). Partial regression analyses for each set of explanatory variables were performed using redundancy analysis (RDA; ter Braak 1988, see Borcard et al. 1992) and partitioning was based on an adjusted R^2 statistic (R^2_{adj} , see Peres-Neto et al. 2006). The significance of the first ordination axis and that of all the axes was tested using 499 Monte Carlo permutations.

Before data analyses, each set of explanatory variables was analysed separately using multiple regression analysis to obtain a subset of significative variables that may explain the residual variation in each model (for complete results see the Supporting Information, Appendix S1). Regression analyses were performed using a permutational forward procedure of model selection proposed by Blanchet et al. (2008). This procedure was used because it overcomes two major problems: (1) an inflated Type I error rate and (2) the overestimation of the overall variance explained by the model, by applying a permutation of residuals under a reduced model. The forward selection procedure used in this study is based on two stopping criteria: (1) the alpha significance level (here set at 0.05), and (2) the adjusted coefficient of multiple determination (R^2_{adj}) calculated using all explanatory variables. Only significant variables ($P < 0.05$) were included in the final models. Unconstrained ordination (principal component analysis) was performed to understand how much of the plant species composition data can be explained by the selected set of environmental variables (Lepš & Šmilauer 2003). For a list of selected explanatory variables used in the final model, see Table 3.

Table 2. ANOVA calculated on pH, electrical conductivity and carbon/nitrogen (C/N) ratio.

Source of variation	df	pH (H ₂ O)			Electrical conductivity (dS m ⁻¹)			C/N		
		MS	F	P	MS	F	P	MS	F	P
Biancane badland	4	0.202	1.944	0.204	2.198	2.933	0.091	76537.8	0.783	0.57
Zone (biancane badland)	7	0.108	2.553	0.018	0.743	0.877	0.527	103029.6	9.097	< 0.001
Land-cover classes	3	2.432	57.697	< 0.001	58.344	68.808	< 0.001	30800.5	2.719	0.047
Residual	117	0.040			0.848			11 326		

Partial redundancy analyses were performed with the subset of selected environmental variables to estimate the fraction of variation of dependent variable (plant species composition) that can be attributed to each environmental variables by treating the explanatory environmental variables as covariables. This method of variation partitioning allowed determining the following eight different components: (1) conditional effect of plot predictors (Pl); (2) conditional effect of patch predictors (Pa); (3) conditional effect badland predictors (B); (4) variation explained by plot and patch predictors ($Pl \cap Pa$); (5) variation explained by plot and badland predictors ($Pl \cap B$); (6) variation explained by patch and badland predictors ($Pa \cap B$); (7) variation explained by the three components ($Pl \cap Pa \cap B$); and (8) variation not explained by the explanatory variables included in the analysis. The shared variation components were obtained by subtraction within the variation partitioning approach. Before multivariate analyses, species abundance data were $\log(x+1)$ transformed and electrical conductivity values was log-transformed. Statistical analyses were performed using the software CANOCO for Windows (v. 4.5, ter Braak & Šmilauer 2002) and R for Windows (v. 2.9.2 R Development Core Team 2009). Multiple regression analysis based on the forward procedure proposed by Blanchet et al. (2008) was conducted using the “forward.sel” function available in the R “packfor” library (Dray 2004); variation partitioning analysis was performed using the “varpart” function in the “vegan” library (Oksanen et al. 2011).

Results

A total of 117 species were collected from 111 plots within five biancane badlands. Overall, we identified 21 empty plots, represented by bare ground with no vegetation, particularly on the southern slopes, and sparse vegetation characterized by substantial soil erosion and mass movement (typical clayey Xerorthents, Chiarucci et al. 1995). While the annual grassland type supporting the endemic species *Artemisia caerulescens* subsp. *cretacea* (Fiori) Br.-Catt. & Gubell and empty plots were present in all five

Table 3. Plot, patch, and badland variables selected for inclusion in the analysis using forward selection.

Subset	Variable name	F	P
Plot	Electrical conductivity	14.28	0.001
Plot	Carbon/nitrogen (C/N) ratio	1.65	0.023
Patch	Shape index	4.64	0.001
Biancane badland	Area	4.84	0.001

badlands, grasslands with scrubs were absent from the smaller biancane badlands.

Results of the three-way nested ANOVA (main effects) performed on soil variables measured at plot level showed that the factor biancane badland was not significant for any dependent variables while land-cover classes was significant for all variables (Table 2).

The amount of explained variation in species composition using variation partitioning was low (15.5%, $P < 0.05$). However, the first axis of unconstrained analysis (principal component analysis, PCA, Hotelling 1933) explained 17.6% of total variability in plant species data set (Appendix S2) hence, compared with this result, the explained variation of environmental predictors was not negligible. All conditional effects were statistically significant. Conditional plot level effects included two significant explanatory variables, electrical conductivity and C/N ratio (Table 3), which accounted for 8.5% of the variation in species composition (Fig. 3). The patch shape index accounted for 1% of variation at the level of patch (Table 3, Fig. 3). Badland surface area was the only significant variable at the conditional badland level, and accounted for 3.3% of the variation (Table 3, Fig. 3). Shared variation components explained by plot and patch accounted 2.4%, respectively, of totally explained variation, while the contribution of the other components was negligible (Fig. 3). The RDA biplot shows the effects of plot, patch and biancane badland components on species composition (Fig. 4).

Open and encroached *B. erectus* grassland were negatively associated with nitrogen availability and positively associated with badland surface area and with predictors at the level of patch. Empty plots and annual grasslands with *A. caerulescens* subsp. *cretacea* were positively associated with

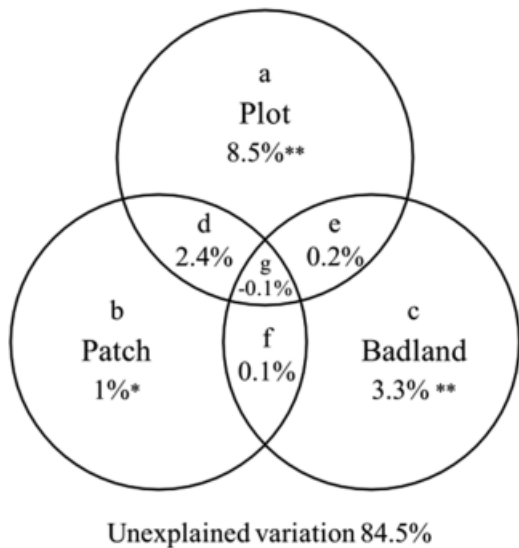


Fig. 3. Venn diagram showing the components of the variance decomposition. Significance levels according to Monte Carlo permutation tests: ** $P < 0.01$, * $P < 0.05$. The total variance explained by the three sets of explanatory variables is 15.5*. Letters a, b and c indicate the independent effects of plot, patch and Biancane badland variables; d, e, f and g indicate the joint effects.

electrical conductivity and negatively associated with the patch shape index (Fig. 4) Perennial grassland communities composed of ruderal species were negatively correlated with C/N ratio, soil electrical conductivity, and biancane badland surface area.

Discussion

Environmental predictors measured at different spatial scales and analysed with variation partitioning revealed plant community patterns and determinants otherwise undetectable if the study had been conducted at a single spatial scale (see also Grand & Mello 2004).

At plot level, soil variables played a major role in determining patterns of plant species composition, consistent with previous findings (Wright et al. 2003; Hérault & Honnay 2005; Klimek et al. 2007; Marini et al. 2008). In particular, high soil electrical conductivity was an important determinant of the persistence of annual grassland communities that supports the endemic species *A. caerulea* subsp. *cretacea*. Their persistence depended upon their higher competitive ability in shallow soils with high salinity content, generated by intense erosion and

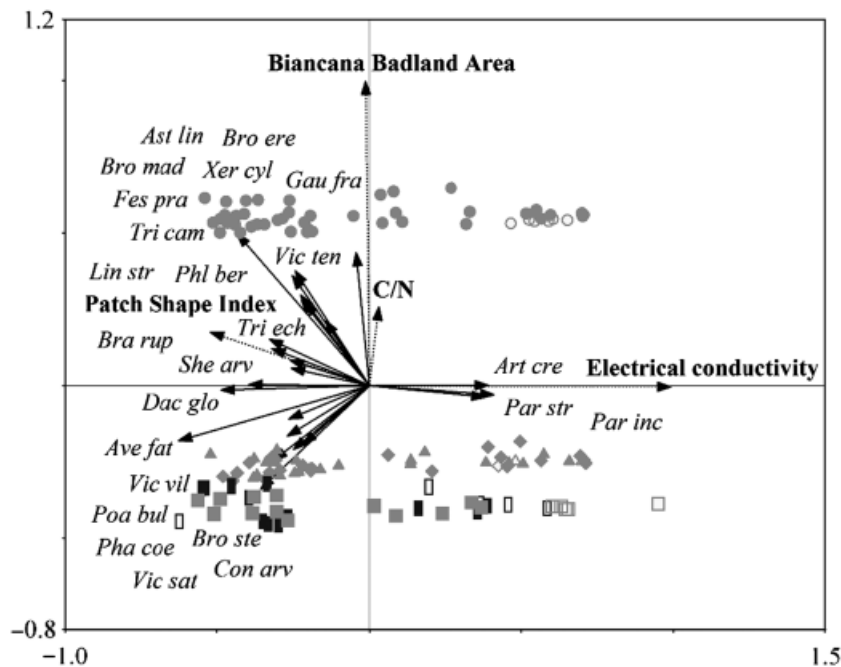


Fig. 4. Ordination biplot based on partial redundancy analysis (RDA axis 1 and 2) of the species composition data sampled in 132 plots with explanatory variables obtained by forward selection. Only species with scores > 0.20 are shown for clarity. Plots are labeled as follows: circles = biancane badland 1; diamond = biancane badland 2; triangles = biancane badland 3; rectangles = biancane badland 4; squares = biancane badland 5; empty symbols are empty samples. Species codes: ; Art cre = *Artemisia caerulea* subsp. *cretacea*; Ast lin = *Aster linosyris*; Ave fat = *Avena fatua*; Bra rup = *Brachypodium rupestre*; Bro ere = *Bromus erectus*; Bro mad = *Bromus madritensis*; Bro ste = *Bromus sterilis*; Con arv = *Convolvulus arvensis*; Dac glo = *Dactylis glomerata*; Fes pra = *Festuca pratensis*; Gau fra = *Gaudinia fragilis*; Lin str = *Linum strictum*; Par inc = *Parapholis incurva*; Par str = *Parapholis strigosa*; Pha coe = *Phalaris coerulea*; Phl ber = *Pheum bertolonii*; Poa bul = *Poa bulbosa*; She arv = *Sherardia arvensis*; Tri ech = *Trifolium echinatum*; Tri cam = *Trifolium campestre*; Vic sat = *Vicia sativa*; Vic ten = *Vicia tenuissima*; Vic vil = *Vicia villosa*; Xer cyl = *Xeranthemum cylindraceum*.

deposition processes, where they can outcompete species with a broader range of environmental requirements, as previously shown (Chiarucci et al. 1995; Maccherini et al. 1996). These highly specialized communities were not affected by nitrogen availability, patch shape or biancane badland area.

On less saline soils, two perennial grassland community types, characterized by wider ecological amplitude (*B. erectus* grasslands and grasslands supporting ruderal species), differed in their response to increases in nitrogen availability. The former and most valuable grassland communities (*B. erectus* grasslands and *B. erectus* grasslands with shrubs) were positively associated with C/N ratio. Conversely, grassland communities dominated by ruderal species, such as *Bromus sterilis*, *Convolvulus arvensis* and *Phalaris caerulea* were mainly found in soils characterized by high soil N availability. It is known that fragmentation may affect water fluxes resulting in the deposition of nutrient-rich material in lower areas and in the invasion by ruderal species (Hobbs & Atkins 1988). It is likely that area-related changes in nutrient conditions have resulted in the displacement of *B. erectus* grasslands and in a transition to perennial grassland with lower species richness dominated by ruderal and generalist species (see Maccherini 2006a, b). In addition, *B. erectus* grasslands on unstable morphologies characterized by frequent mass movements, such as creeping, mudflows and small landslides show a more abundant cover of grassland species and a greater number of species, compared with *B. erectus* grasslands on more stable morphologies (Maccherini et al. 2000). Hence, the existence of those communities could also be linked to the presence of disturbance determined by active geomorphological processes. Soil characteristics at plot level showed significance differences only among land-cover classes or zones (ANOVA), suggesting that morphology, determined by erosive processes, has a great influence on plant community distribution pattern at local scale.

Patch shape index, the only predictor at patch scale, confirmed that in biancane badlands ecosystems erosion and deposition processes are key determinants of vegetation patterns. Biancane pediments, characterized by a roundish shape (low shape index), supported annual grasslands that were clearly distinct from grassland communities recorded in complex, elongated and irregular-shaped patches (Chiarucci et al. 1995; Marignani et al. 2008).

The contribution of biancane badlands area in determining the composition of the vegetation was lower compared than that of local environmental variables measured at the spatial scale of plot. This is consistent with previous investigations, which have shown that remnant surface area has contrasting effects on species richness of grassland (Adriaens et al. 2006; Cousins & Aggemyr 2008). Nevertheless, our results showed that

smaller badlands are unsuitable for *B. erectus* grasslands, thus indicating that a minimum area is necessary to maintain the overall diversity of species and habitats hosted in biancane badlands. The importance of conducting a hierarchical approach to quantify the species–environment relationship was substantiated by the finding that even if plot scale predictors are the main drivers determining plant community composition, they are indirectly influenced by the size of the badlands. Accordingly, any manipulations of variables operating at the local scale, such as soil reclamation aimed at reducing the level of nutrients in the soil, would only have a marginal effect in restoring *B. erectus* grasslands in small biancane badlands. Conversely, the persistence of highly specialized annual grassland communities even in smaller biancane badlands suggested that conservation of every badland contributes to the maintenance of these peculiar plant community types. It appears that generalizations on conservation management of biancane badland landscapes are difficult: to maintain biodiversity the multiple spatial scale supports the idea of relying on habitat- instead of area-focused conservation practices (see also Marini et al. 2010).

Successful restoration and conservation of endangered communities depend on the knowledge of the conditions necessary for the survival and persistence of these communities (Van Diggelen & Marrs 2003). Based on our results, we propose to operate at different spatial scale to (1) conserve the few remaining large badlands and halt any further reduction in size of the remnants and (2) create a protective buffer strip of uncultivated vegetation around the smaller biancane badlands to reduce the input of chemical fertilizers used in agriculture. These findings have major implications to develop sound strategies aimed at conserving the biodiversity value of these unique landscapes, whose reclamation for agricultural purposes and the current abandonment of the traditional grazing regimes have irreversibly transformed biancane badlands, which are now considered as a vanishing landscape (Phillips 1998; Maccherini et al. 2000; Antrop 2005; Marignani et al. 2008; Marini et al. 2010).

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Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1. Results of the forward selection for plot, patch, and badland variables.

Appendix S2. Results of the ordination analysis, including principal component analysis (PCA), RDA, and the Monte Carlo permutation test.

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