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PATCH STRUCTURE IN NATURAL GRASSLANDS OF CORDOBA MOUNTAINS (ARGENTINE) IN RELATION TO DIFFERENT ROCK SUBSTRATES

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Abstract. This paper focuses in the study of patch structure of natural grasslands of Córdoba mountains associated to the rock substrate variability (coarse-grained structure). Grasslands with a relatively homogeneous spatial distribution (conglomerate environments) are compared with grasslands where the patchwork was conspicuous (gneiss and granite environments). A stratified sampling design based on plant physiognomy was carried out. Presence of species was recorded and frequency values used as final expression of species abundance. The data were ordinated by detrended correspondence analysis (DCA) and classified by two-way indicator analysis (TWINSPAN). Shannon-Wiener diversity index was also calculated. Grasslands growing on a conglomerate bed rock showed as continuous tall-tussock cover, while on granite and gneiss substrates a complex mosaic of tall-grasslands (on well developed soils) and dry-grasslands (on excesively drained soils) is recognized. In granite environments, poorly drained patches, with summer waterlogged turfs are also described. When grasslands form a continuous tall tussock cover, diversity was low and increased with increasing spatial heterogeneity (patches). These patches are differentiated through structural, floristic composition and species diversity features. Diversity was high in dry-grasslands, decreased in tall-grasslands and the lowest values were found in turfs. Diversity models the results conform best are discussed.

Introduction

Although many speculations in community ecology assume an even distribution of organisms in a homogeneous environment, nature rarely satisfies this assumption. Instead, communities are irregular assemblages of plant and animals (Kareiva, 1985). "Patch" implies a relatively discrete spatial pattern, but does not establish any constraint on patch size, internal homogeneity or discretness (White and Pickett, 1985). Since landscapes vary in topography, soil nutrient and mineral content, it could be argued that patchiness begins at the level of physical environment. Moreover, even when the environment is continuous and homogeneous, communities are influenced by spatially varying demographic processes (Kershaw, 1973; Wiens *et al.*, 1976; Diamond, 1980). Besides, most disturbances produce heterogeneity and patchy effects (Denslow, 1985; Loucks *et al.*, 1985; Shorrocks and Rosewel, 1987; Diaz *et al.*, 1989).

Patchiness, also referred as spatial heterogeneity, community pattern or community mosaic, is a characteristic of most plant communities (Pielou, 1975; Greig-Smith, 1979). Grain is the scale of patch size within a community (Pielou, 1977) and may reflect the underlying biological and environmental causes of spatial pattern. An understanding of the factors that structure vegetation requires the knowledge of the processes that direct patch formation. Also, when a patchy structure is beared in mind, community variation is likely to be better described and interpreted.

Rock substrate and disturbances (grazing and burning) have been reported as apparent causes of patch structure in natural grasslands of Córdoba mountains (Cabido, 1985; Cabido and Acosta, 1986a; Cabido and Acosta, 1986b; Menghi, 1988; Cabido *et al.*, 1989; Acosta *et al.*, 1989). We seek now for the understanding of patch structure and its association with different rock substrates (coarse-grained structure). To this purpose, we compare grasslands with a relatively homogeneous spatial distribution by one side, with grasslands where the patchwork was evident by the other. In the first case, grassland developed on sedimentary substrate (conglomerates) were studied, and for the second case, communities occuring on igneous and crystalline substrate (granite and gneiss respectively) were considered.

In order to gain understanding of vegetational patterns associated with the underlying bedrock, this work pretends to answer the following questions:

- to what extent rock substrates determine the spatial distribution of the grasslands communities?

- to what extent changes in the spatial pattern of grasslands communities reflect changes in composition and species diversity?

Material and methods

Study area

Córdoba Mountains are located in the western region of Córdoba Province, between 29°S and 33° 30'S. Elevations range from 500 m up to almost 3000 m. The montane grassland belt (Luti *et al.*, 1979) is found from around 1000 m upwards, representing the highest vegetational belt in these mountains (Fig. 1).

Over most of the region, the parent material comprises pre-Cambric crystalline rocks (gneiss) intruded by granite batholits during the early Paleozoic. Rests of an eroded cretaceous sedimentary cover of conglomerates and sandstones can locally be found (Gordillo and Lencinas, 1979).

The sedimentary landscape is dominated by tussock grasslands where a main variation trend along the topographic gradient is detected. However, over gneiss substrate dry-grasslands could be also recognized (Menghi, 1988). In a study of granite grasslands, Acosta *et al.* (1989) identify discrete units associated to local edaphic discontinuities. A mosaic of tall tussock grasslands, alterning with dry-grasslands and wet turfs is described.

Study sites on granite, gneiss and tertiary conglomerates are located around 1400 m. Macroclimate in this region can be classified as humid, with short cool summers and long cold winters (Capitanelli, 1979). The average annual temperature is 11° C with an average annual precipitation around 800 mm, mainly concentrated in summer.

At present, grasslands are grazed mostly by cattle and sheep; burning is a traditional practice for management. Palatability of old shoots appears to be much lower and fire is used to promote resprouting and consumption.

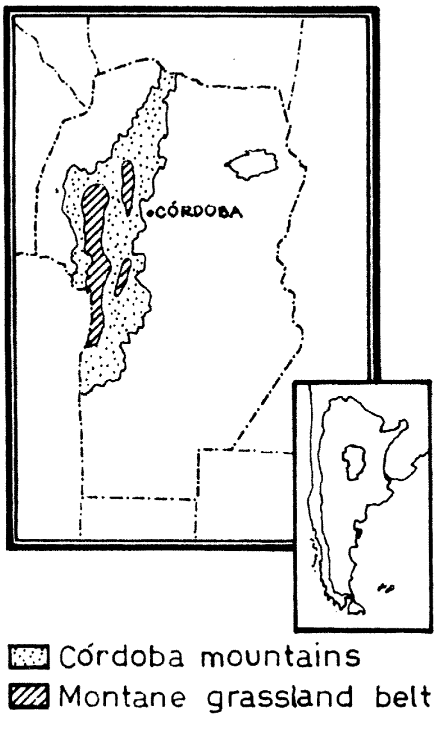

Fig. 1. Location of the study area.

Sampling design

Field data were collected through a stratified sampling based on vegetation appearance. Upper and lower slopes were taken into account to allow the expression of topographic gradients in composition and relative abundance of species. When a relatively continuous grassland cover was found (conglomerate environments), ten regularly separated sample plots from the upper to the slower part of slopes were placed. In areas where rocky outcrops predominate and discontinuities appeared (granite and gneiss environments), each patch was considered as a different strata. In this way, 3 types of patches were identified: tall-grasslands, dry-grasslands and turfs. Each strata was sampled twice, both on the upper and lower parts of the slopes. Within each 3×5 m sample plot, the presence of species was recorded in eight randomly located 20×20 cm squares. The final expression of species abundance was a frequency value, ranging from 1 to 8.

All the slopes were N facing with an inclination around 10 to 20%. Samples were taken in relatively undisturbed sites in order to avoid disturbance effects in spatial heterogeneity.

Data analysis

The 147 species ×80 samples data matrix (vegetational data from all sample plots) was ordinated by detrended correspondance analysis (DCA; Hill, 1979a) and also classified by two-way indicator analysis (TWINSPAN; Hill, 1979b).

For quantifying species diversity, the Shannon-Wiener index

$$H' = -\sum p_i (\log_2 p_i)$$

was calculated. Importance values (p_i) were measured as frequency of species per plot.

Results

Ordination and classification

The ordination of all sample plots on the first two DCA axes is showed in Fig. 2. Dry grasslands had the highest scores in axis I while mesic and wet samples had the lowest scores. Tall grasslands and turfs were separated along the second axis. In this way, the scatter plot of samples showed a definite separation of plots belonging to the patches considered. However, substrates were not so clearly defined. There was a complete separation between plots from granite grasslands and the rest of samples, but gneiss and conglomerate grasslands appeared to be mixed up.

The ordination of the DCA was consistent with TWINSPAN results (Fig. 3). The first TWINSPAN division differentiated the wet-mesic and dry extremes in vegetation patches. Thus, in the first major bifurcation, dry-grasslands were segregated from the rest of samples. In the second bifurcation, the dry-grassland group was classified accordin to the rock substrate (granite or gneiss). Within the second group turfs were separated from tall-grasslands, which were later differentiated in granite and gneiss plus conglomerate tall-grasslands.

Dry-grasslands (Fig. 4a, b)

Dry-grasslands typically occur in granite or gneiss landscapes, where soils are coarsed textured and excesively drained or with the parent material near the surface.

Plant cover ranges between 50 and 70% compared

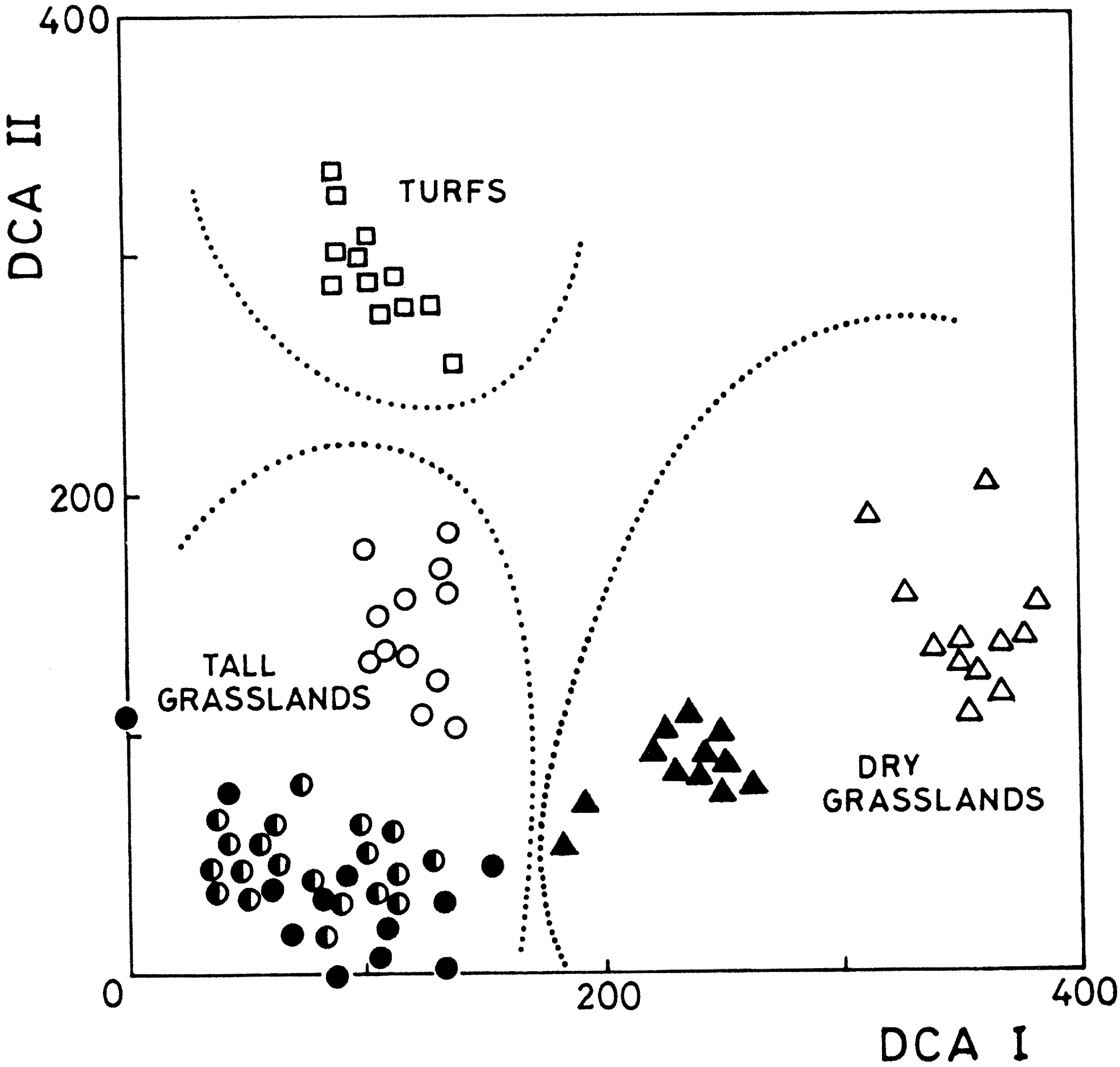

Fig. 2. Ordination of vegetation samples along the first two DCA axes. Open symbols = granite grasslands, solid symbols = gneiss grasslands, half solid symbols = conglomerate grasslands.

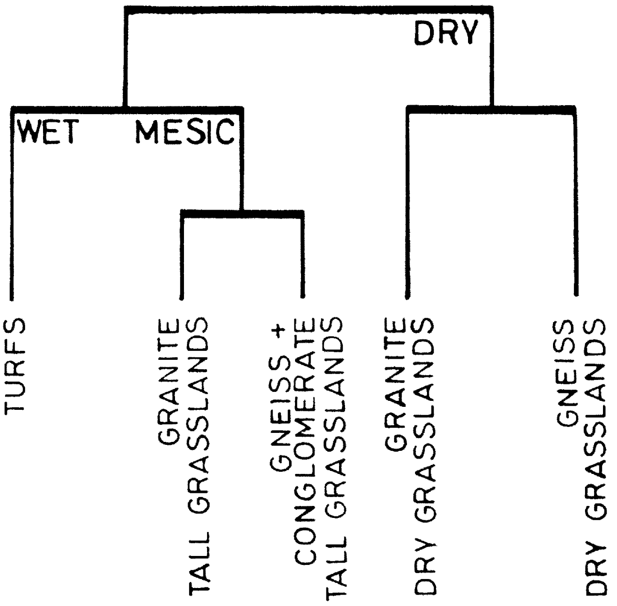

Fig. 3. A dendrogram illustrating the classification of samples by TWINSPAN.

to the 100% cover in tall-grasslands and turfs. Caespitose species, small grasses and species with storage organs are common. *Stipa flexibarbata* and *Aristida spegazzini* are the dominant grasses both in granite and gneiss environments. Conspicuous non-grass species are *Sisyrinchium unguiculatum* and *Noticastrum marginatum*. Most of the mentioned species are restricted to this patch.

Tall-grasslands (Fig. 4a, b, c)

Tall-grasslands occupy an intermediate position on the moisture gradient. This patch is found on well developed soils in granite or gneiss environments and

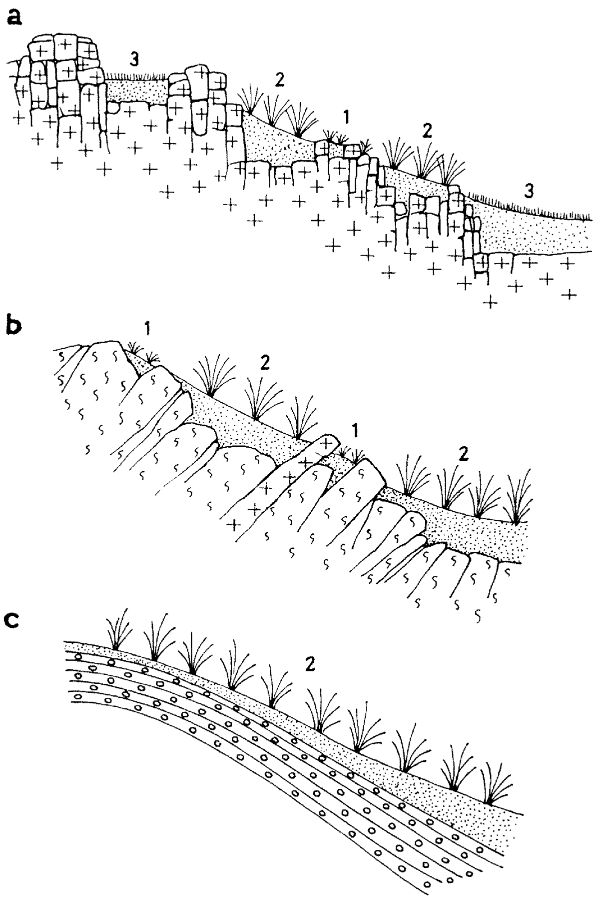

Fig. 4. Diagrammatic representation of the different patches found in granite grassland (A), gneiss grassland (B) and conglomerate grassland (C). 1 = dry-grasslands, 2 = tall-grasslands, 3 = turfs.

it is the current unit in conglomerates where no patches occur in undisturbed grasslands. Tussock grasses characterize tall-grasslands; generally they form dense

Table 1. Summarization of results.

	DRY-GRASSLANDS	TALL-GRASSLANDS	TURFS
Bioforms %			
hemicryptophytes (*)			
tussock grasses	low	high	–
short bunch grasses	high	low	interm.
tall grasses	low	high	low
short sward grasses	low	low	high
Geophytes	high	low	low
Herbs	interm.	high	low
Plant cover %	50-70%	100%	100%
Soils	coarse-grained texture	intermerdiate texture	fine-grained texture
Drainage	excesive	moderate	incomplete

(*) According to Box (1981).

Table 2. Main associated species in each patch.

DRY-GRASSLANDS	TALL-GRASSLANDS	TURFS
Alternanthera pumila	Stipa filiculmis	Axonopus fissifolius
Aristida spegazzini	Festuca hieronymi	Panicum milioides
Bulbostylis juncoides	Bromus auleticus	Eragrostis bahiensis
Sisyrinchium unguiculatum	Stipa neesiana	Panicum savulorum
Stipa flexibarbata	Setaria geniculata	Vulpia megalura
Noticastrum marginatum	Stipa tenuissima	Paspalum dilatatum
Stipa hunzikerii	Cologania ovalifolia	Chaptalia runcinata
Microchloa indica	Oxalis sexenata	Tagetes argentina
Facelis retusa	Taraxacum officinale	Hypoxis humilis

clumps with little open space in between. All samples are strongly dominated by the tussock grass *Stipa filiculmis*. The grasses *Festuca hieronymi. Bothriochloa saccharoides, Bromus auleticus, Stipa neesiana, Stipa tenuissima* and several herbs including *Cologania ovalifolia, Sida prostrata and Oxalis sexenata* are also common.

Turfs (Fig. 4a)

The third type of patch only occurs in granite landscapes. Turfs are found in poorly drained sites, in shallow depressions with the nonpermeable bedrock near the surface. Summer rains accumulate water with the consequent saturation of the whole soil profile (Cabido et al., 1987). This is a low, dense turf, 5 to 10 cm. tall. Turfs comprise mostly small grasses and some sedges. Dominant grasses include *Eragrostis bahiensis, Paspalum dilatatum. Axonopus fissifolius* and *Panicum milioides. Chaptalia runcinata* and *Tagetes argentina* could be also mentioned. Most of these species are confined to turfs.

A general summary of results is presented in Table 1. Table 2 shows major associated species for each patch (extracted from TWINSPAN arrangement).

Pattern diversity

Diversity index for granite and gneiss patches and for conglomerate tall-grasslands are showed in Table 3 (between-patch diversity). The comparison revealed that the highest values occured in the driest sites (dry-grasslands). The wet extreme (turfs) appeared with the lowest scores. It can also be mentioned that diversity in granite patches was considerably lower than in gneiss or conglomerates.

Diversity results for each substrate (without considering patches) can be seen from Table 4. The lowest value occured together with the highest spatial homogeneity and a relatively uniform vegetation cover (conglomerate grasslands), while exceeded 6 bits where spatial heterogeneity was conspicuous (granite and gneiss grasslands).

Discussion and conclusions

Vegetational patches analyzed in the present study are differentiated through structural and floristic features. However, when considering different substrates, the groups of sample plots are not so clearly defined. Coarse-grained variability in grassland communities associated with rock substrate can be summarized in the following way:

Tall-grasslands developed on sedimentary substrate (conglomerate). On igneous (granite) and crystalline rocks (gneiss), well developed soils with dominant tussock grasses are also found, but alternating with a mosaic of rock outcrops and dry-grasslands on excesively drained, sandy soils. In granite environments, poorly drained turfs, with summer waterlogging also occur.

According to the rock substrate, montane grasslands vary in species diversity. When grasslands appear to be

Table 3. Between-patch species diversity.

	TALL-GRASSLANDS	DRY-GRASSLANDS	TURFS
Conglomerate Grasslands	5.87		
Geniss Grasslands	5.86	6.11	
Granite Grasslands	5.35	5.57	5.03

Table 4. Total species diversity according to rock substrate.

CONGLOMERATE GRASSLANDS	GNEISS GRASSLANDS	GRANITE GRASSLANDS
5.871	6.283	6.122

uniform, diversity is lower and increases with increasing spatial heterogeneity (patches). In this way, patchiness would promote species coexistence. This is a generalized idea, discussed in detail by a number of authors (Levin, 1974; 1979; Yodzis, 1978; Dale, 1978; Goh, 1980; Hastings, 1980; Tilman, 1982; 1986). However, the highest spatial heterogeneity observed in granite grasslands does not reflect a maximum in species diversity. The low diversity values obtained for granite patches may be associated with resource availability and soil types derived from this rock. Rabinovitch-vin (1983) found for the upper Galilee considerable variation in plant composition corresponding closely with the original parent material from which the soils had originated. Similar correspondences have been reported in a variety of areas (Olson, 1958; Lindsey, 1961; Hole, 1976; Olsvig-Whittaker *et al.*, 1983).

Trends in species diversity between patches suggest that diversity scores are higher for dry-grasslands while they decrease in tall-grasslands besides the increase in water availability all through the year (Cabido *et al.*, 1987). The effect of dominance depends partly on the structure of the dominant species (tussock grasses). These clumps produce numerous overhanging leaves and much litter in the absence of disturbance. According to these characters, they might be considered as competitors sensu Grime (1979). One aspect of dominance is a heavy competitive effect on adult plants of subordinate species, and a number of them could be driven to competitive exclusion (fall in species diversity). Tussock grasses would avoid the developement of species by a combination of shade and below-ground interference and the physically constraining effects of accumulated litter. In the moist parts of the Northern Cool Temperate Zone, there are many examples of grasslands in which diverstity decreases and it is causally related to dense shading, below-ground interference and accumulation of litter (Wheeler and Gillier, 1982; Vermeer and Berendse, 1983; During and Willems, 1984). However, the decline in turfs diversity (with the lowest values) is a special case that cannot be explained with the models set so far. The comparatively few species that grow on these sites would be a consequence of waterlogging. In north american prairies, Dix and Smeins (1967) detected the lowest species diversity in poorly drained sites with high water retention. The reduction in species diversity at waterlogged sites has not only been reported for grasslands but also in european and american forests (Lang, 1973; Curtis, 1959), tropical forest (Witmore, 1984) and savannas (Eiten, 1978). According to Grubb (1987) it seems that for reasons not yet understood, that the chance of evolution of a tolerant genotype has not been equal for all potentially limiting environmental factors and persistent waterlogging apperars to be a prime example.

Finally, it can be concluded that the criteria chosen in this work are useful for the description and interpretation of grassland variability. In natural grassland of Córdoba mountains spatial patterns in plant distribution associated with the underlying bedrock are recognized. Conglomerate grasslands are relatively uniform but granite and gneiss grasslands could be described as a mosaic of patches varying either in structure, species composition and diversity. In each patch, however, floristic or diversity differences between substrates are not so clearly defined. For this case, the necessity of obtaining environmental information (specially soil mineral, and nutrient contents) should be stressed.

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