

## Vegetation heterogeneity and diversity in flat and mountain landscapes of Patagonia (Argentina)

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**Abstract.** We studied floristic and diversity patterns and their environmental controls in two landscapes of contrasting topography in the Patagonian steppe. The analyses were focused on the effects of water availability gradients and landscape configuration on plant species distribution and coexistence.

Floristic variation was investigated using Correspondence Analysis. The relationship between floristic and environmental variation was analyzed using Canonical Correspondence Analysis and correlation tests. We explored diversity patterns by relating spatial distance to floristic dissimilarities. The floristic gradient was determined by shrub and grass species and was related to precipitation in the flat area, and to precipitation, elevation and potential radiation in the mountain area. Site species richness increased with water availability in both areas. Mean site species richness and species turnover in space was higher in the mountain than in the flat area. Landscape species richness and floristic gradients were more concentrated in the mountain than in the flat area. In contrast to shrubs and grasses, forb species distributions were uncoordinated and probably independent of any environmental gradient. Our results suggest (1) that landscape configuration affects species composition and diversity through its direct effect on abiotic environmental heterogeneity, and (2) that the environmental controls of the community composition vary depending on the plant functional type considered.

**Keywords:** Arid ecosystem; Floristic gradient; Landscape configuration; Mass effect; Multivariate analysis; Plant functional type; Topography.

**Nomenclature:** Correa (1969-1984).

### Introduction

Plant species composition and diversity patterns have been some of the earliest interests of ecologists. Early ecological work provided empirical evidence on the role of the environmental variation over plant species composition and diversity (e.g. Clements 1916; Gleason 1926; Bray & Curtis 1957; MacArthur 1965; Whittaker 1965). On the other hand, there is less empirical infor-

mation on the effects of the spatial configuration of environmental variation on plant species composition and diversity.

The environmental variation within landscapes may show different spatial configurations. Landscapes having a spatially continuous variation (or spatial dependence) can be considered homogeneous. In contrast, landscapes showing a discontinuous variation in space (or spatial independence) can be considered heterogeneous (Kolasa & Rollo 1991). The potential role of landscape heterogeneity over plant species diversity and distribution has been suggested by different authors using conceptual (Shmida & Wilson 1985; Auerbach & Shmida 1987) and mathematical (Palmer 1992) models. Species richness is expected to be higher in heterogeneous landscapes; because of the closer distance between dissimilar habitats, species may be present in unfavorable habitats supported by nearby populations in favorable habitats. It has been proposed that this phenomenon, named mass effect (Shmida & Wilson 1985), may be a determinant of the number of species per site.

In arid ecosystems structural and functional variation is primarily controlled by water availability (Noy Meir 1973). In flat landscapes spatial changes in water availability depend mainly on precipitation. Precipitation varies continuously in space generating homogeneous gradients of water availability in flat areas. In hilly or mountain landscapes water availability is also influenced by slope, aspect and elevation. At the landscape scale these topographic variables show a discontinuous variation. Consequently, water availability gradients in mountain landscapes are heterogeneous.

There is a strong relationship between water availability (or its main controls) and plant species distribution in arid and semiarid ecosystems (*i.a.* Whittaker & Niering 1975; Yeaton & Cody 1979; Burke et al. 1989; Dargie & El Demerdash 1991; Ward et al. 1993). The increase of plant species richness with precipitation within the range of arid and semiarid conditions has been documented (Aronson & Shmida 1992). However, the effects of changes in the spatial configuration of

water availability gradients on species composition or diversity remain poorly explored.

In this study we describe the floristic and diversity patterns of the Patagonian steppe, analyse their relation with water availability gradients, and explore effects of the spatial configuration of these gradients in landscapes of contrasting topography.

### Study areas

The Patagonian steppe is a cool semidesert ecosystem that occupies nearly 600 000 km<sup>2</sup> of the southern portion of Argentina (Soriano 1983). The climate is semiarid (Walter & Box 1983). Precipitation, concentrated in winter months, declines from west to east (Prohaska 1976; Paruelo et al. 1995). Along this gradient of decreasing precipitation, starting from the subantarctic forest border, grass steppes give way to shrub-grass steppes and those to semideserts in the east (Soriano 1956; Paruelo et al. 1991). León & Facelli (1981) described the floristic replacements that occur in a flat portion of the steppe along this precipitation gradient in Patagonia, using a direct gradient approach (ter Braak 1986). At a more detailed scale, vegetation variation has been described on a phytosociological basis for several areas of the region (Bertiller

et al. 1977; Golluscio et al. 1982; Movia et al. 1987). Hilly and mountain terrain comprise an important portion of the Patagonian steppe, however no attempts have yet been made to describe diversity pattern or vegetation-environment relationships at the landscape scale for these areas.

Our two study areas were located in central western Patagonia (Fig. 1). They share the same macroclimatic conditions and regional flora but show a highly contrasting topography. The flat area (Table 1, Fig. 1), surveyed by León & Facelli (1981), has a smooth elevation gradient decreasing eastward. The terrain is generally flat; slopes are always less than 3%. Consistent with all of western Patagonia, precipitation decreases eastward (Barros et al. 1979, Fig. 1). The mountain area is smaller than the flat one (Table 1, Fig. 1) and includes Andean ranges, 'sierras', and glaciation valleys. While western Andean ranges show the highest elevations of the area, high elevations also occur in the eastern sierras. Precipitation follows the typical west to east decrease in precipitation, but the gradient is steeper than in the flat area (Jobbágy et al. 1995). The study areas encompass a transition zone between western grasslands and eastern semideserts. There is a continuous change both in the structure (León & Facelli 1981) and in the function (Paruelo et al. 1993) of vegetation along this gradient.

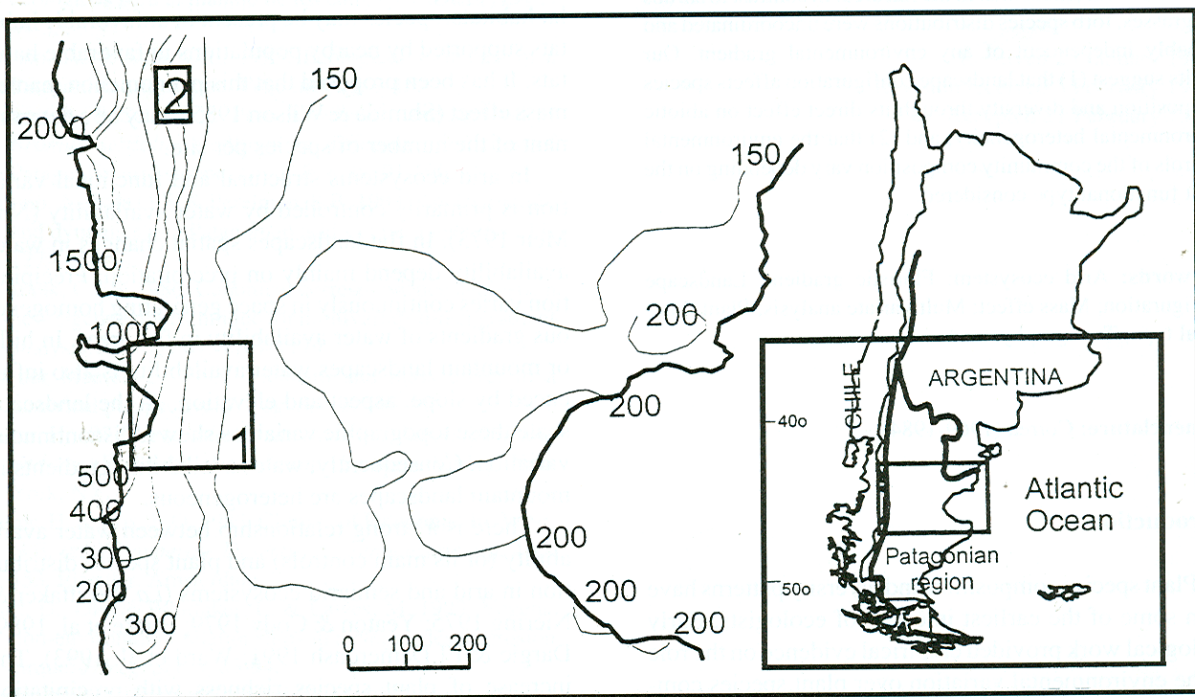


Fig. 1. Map of isohyets and location of the study areas. Square 1 indicates the flat area and square 2 the mountain area. Precipitation values are expressed in mm.

## Material and Methods

### Data collection

Data for the flat area (40 sites) were collected in the summer of 1980 (see León & Facelli 1981), whereas data for the mountain area (61 sites) were collected during the 1991 and 1992 summers. We preferentially placed sample sites in homogeneous stands (Orlóci 1976; Gauch 1982), avoiding meadows, riversides, water run-on areas and rock outcrops. Intra-site environmental heterogeneity can be assumed to be the same in both areas. Our goal was to cover the range of variation of the main environmental variables related to the water balance in each area: precipitation in the flat area, and precipitation, altitude, slope and aspect in the mountain area. We increased the number of sites in the mountain area because of the larger range of variation of topographic variables in this terrain. In each site, we listed all vascular plants within an area of 0.25 ha (50 m × 50 m) and estimated the abundance-cover values (Braun-Blanquet 1950) of each of the species recorded.

We estimated the main controls of water availability in both areas: slope, elevation, potential radiation and precipitation. Slope has a direct effect on water availability by controlling the amount of water lost through runoff (Williams 1991). The interaction between slope and aspect determines the potential radiation (Frank & Lee 1966) and consequently the potential evapotranspiration of the site. Temperatures decline with increasing elevation which also affects potential evapotranspiration. Precipitation, and thus water input, generally increases with altitude, especially at intermediate and high latitudes (Barry 1981). For each site, slope was visually estimated, aspect was recorded with a compass and elevation was measured with a barometric altimeter. Potential radiation was estimated from slope, aspect and latitude (Frank & Lee 1966; see also Hungerford et al. 1989). We obtained mean annual precipitation values for each flat area site from precipitation charts (1:1 500 000) (Barros et al. 1979). For the mountain area these values were calculated using a regression model that estimates precipitation values from the distance of the Andean range (Jobbágy et al. 1995).

**Table 1.** Physiographic features of the study areas. Potential radiation is taken as 100% in flat terrain.

	Flat area	Mountain area
Area	15 000 km <sup>2</sup>	1000 km <sup>2</sup>
Length from west to east	120 km	20 km
Altitudinal range	450 m - 950 m	700 m - 1300 m
Slope range	0 - 3%	0 - 12%
Potential radiation	100 %	45 % to 153 %
Precipitation range	100 - 550 mm	250 - 450 mm

### Data analysis

We classified all the species recorded into three functional types: shrubs, grasses and forbs. Those species having lignified structures were classified as shrubs. Herbaceous species were divided into grasses and forbs. Two cactus species were not included in this classification. Grasses, shrubs and forbs have contrasting water use strategies in the Patagonian steppe (Soriano & Sala 1983; Sala et al. 1989; Golluscio & Sala 1993). We calculated the total number of species and the number of species of each functional type both for the landscape and for each individual site.

We used two related multivariate techniques to analyse the variation of the vegetation structure and its relationship with the environmental variation. For these analyses species with a constancy value lower than 12 % were rejected. This was the highest rejection percentage that did not exclude the dominant species from any site. We investigated compositional gradients using Correspondence Analysis (Hill 1973). CA was performed for each area, first for all species, and then for two separated groups, one composed of grasses and shrubs and the other of forbs. We used the Spearman correlation coefficient to compare species ordination values between areas.

We explored the relationship between floristic composition and environmental variation using Canonical Correspondence Analysis (ter Braak 1986). The site ranks in the first CA and CCA axes were compared using the Spearman correlation test. We avoided axis detrending in our analyses (i.e. DCA analysis, Hill & Gauch 1980) because it may remove meaningful information from the ordination plane. For example, arch effects, considered artifacts by some authors (Hill & Gauch 1980; M.V. Wilson 1981), provide useful information revealing the dominance of the main floristic gradient of the matrix on further axes (Wartenberg et al. 1987). On the other hand, axis detrending may decrease the stability of the solution as it was previously demonstrated (Oksanen 1988; Knox 1989). One potential advantage of DCA is that it yields a better axis scaling than CA (Hill & Gauch 1980), however this advantage disappears when only ranks of samples are considered, as in this study.

We described site diversity (alpha diversity) using site species richness and the exponential form of the Shannon diversity index (Shannon & Weaver 1949):

$$\exp H' = \exp\left(-\sum p_i \log p_i\right) \quad (1)$$

where  $p_i$  is the proportion of plant cover belonging to the  $i$ th species. We tested the difference between the mean values species richness and the diversity index for each

study area using the Mann-Whitney *U*-test. To examine the relationship between diversity and water availability we analyzed the correlation between species richness and the diversity index, and precipitation for the flat area, and precipitation, elevation and potential radiation for the mountain area.

To assess plant species turnover in space (beta diversity) we analyzed the relationships between floristic variation and spatial distance. We calculated the dissimilarity between all possible pairs of sites within each study area using the complement of the Jaccard index:

$$\text{Dissimilarity} = 1 - c/(a + b - c) \quad (2)$$

where *c* = the number of co-occurring species and *a* and *b* are the numbers of species in the two sites. We chose an index based on presence-absence data to avoid dissimilarity values close to 1. This analysis was first performed considering all the species involved and then with the forbs separated from the grasses and shrubs. We analyzed the differences in beta diversity between areas by comparing the mean floristic dissimilarities for equal ranges of between-sites distances. We considered all pairs of sites falling into four distance intervals (0-10 km, 11-20 km, 21-30 km and 31-40 km) and tested differences using the Mann-Whitney *U*-test. We also calculated the rate of variation of environmental variables at increasing distances as the difference between every possible pair of sites for each of the distance intervals.

## Results

The two areas shared a large number of species (Table 2). As previously observed for the Patagonian steppe (Soriano 1956; Golluscio & Sala 1993), a small number of shrub and grass species accounted for a high proportion of the total plant cover, whereas the richest group (forbs) accounted for less than 6% of the cover. Three shrubs: *Senecio filaginoides*, *Mulinum spinosum*

**Table 2.** Species richness in flat and mountain areas and number of species shared in common between both areas. The difference between the number of all species, 98, and that of the functional types, 96, corresponds to the two cactus species, which were not considered.

	Flat area	Mountain area	Shared species
All species	98	112	72
Shrubs	27	25	18
Grasses	17	17	11
Forbs	52	69	43

and *Nassauvia glomerulosa*, and three tussock grasses: *Stipa speciosa*, *S. humilis* and *Festuca pallescens* were the dominant species in both areas (a complete species list is available upon request).

Main floristic gradients explained a larger proportion of the total variation in the flat area than in the mountain area for all the species groups considered (Table 3). In both areas indirect ordination analyses showed that the first and second CA axes eigenvalues increased when forbs were removed from the data set. Shrub and grass species displayed strong gradients, while forbs displayed weak ones. Considering only shrub and grass species, the first and second axes accounted for 51% of the total floristic variation in the flat area and for 35% of the variation in the mountain area.

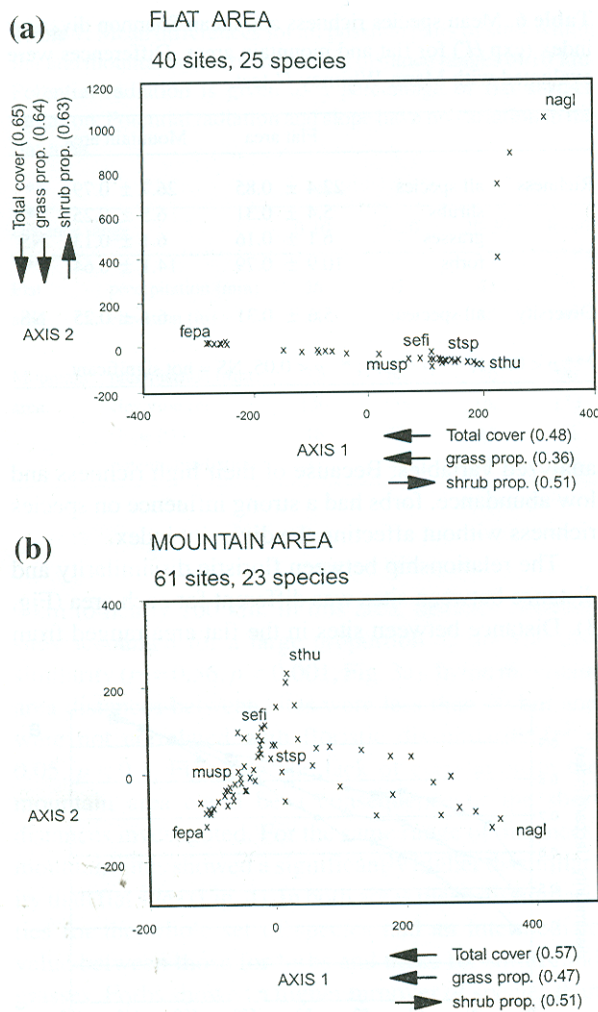
The first CA axes for flat and mountain areas showed similar floristic gradients when only shrubs or grasses were considered. Particularly for dominant species the ordination was the same. Species ranking in the first CA axis had a high correlation between the two areas (Spearman correlation coefficient:  $r = 0.78$ ,  $p < 0.001$ ).

At one end of the first CA axis sites had high cover values of *Festuca pallescens* (Fig. 2). This species is the characteristic dominant grass of the Subandean district of grass steppes (Paruelo et al. 1991). Sites with an intermediate position on this axis were characterized by shrubs and grasses typical of the Occidental district: *Mulinum spinosum*, *Senecio filaginoides*, *Stipa speciosa* and *S. humilis* (Paruelo et al. 1991). At the other end of the axis, sites had a large cover of *Nassauvia glomerulosa*, a dominant shrub of the Central district (Paruelo et al. 1991). There was a strong relationship between the first and second floristic gradients of the CA and total plant cover and shrub and grass proportions in both areas.

In the flat area, the second CA axis accounted for the differences at the high end of the first axis. The second axis is related to the variation in cover of *Nassauvia glomerulosa*, which was high at four sites to the right of the axis (Fig. 2a). In the mountain area the second axis

**Table 3.** Proportion of the total floristic variation accounted for by the first (Ax 1) and the second (Ax 2) axes of the Correspondence Analysis considering all the species, shrubs plus grasses, and forbs for the flat and the mountain areas. The number of species considered in each case is indicated (#sps).

	Flat area			Mountain area		
	Ax 1	Ax 2	#sps	Ax 1	Ax 2	#sps
All species	22%	18%	56	18%	11%	60
Shrubs and grasses	29%	22%	25	20%	15%	23
Forbs	12%	9%	31	9%	9%	37



**Fig. 2.** Diagram of first and second Correspondence Analysis axes for the flat (a) and the mountain areas (b). Each site is represented by a cross; dominant species position is shown by abbreviated names: fepa = *Festuca pallescens*; stsp = *Stipa speciosa*; sthu = *Stipa humilis*; musp = *Mulinum spinosum*; nagl = *Nassauvia glomerulosa*; sefi = *Senecio filaginoides*. The correlation coefficients for all the significant associations ( $p > 0.05$ ) between physiological variables and ordination axes is indicated on each axis. Site total cover and shrub and grass relative cover were considered.

showed a slight arch effect. This artifact usually reveals a strong influence of the first axis gradient on the second axis construction which result in an arch because of the method-imposed orthogonalization of the axes (Jongman et al. 1987) (Fig. 2b).

The first axes of the CA and CCA showed similar site ordination in both areas, and were significantly correlated (Table 4). The second axes of the CA and CCA had a low but significant correlation in the mountain area (Table 4). In the flat area the second CCA axis

**Table 4.** First and second axes eigenvalues of the Correspondence Analysis (CA) and Canonical Correspondence Analysis (CCA).  $r_s$  is the Spearman rank correlation coefficient of CA and CCA site scores. In both analyses only shrubs and grasses were considered.

		Eigenvalues		$r_s$
		CA	CCA	
Flat area	Ax 1	0.76	0.63	0.91 ***
	Ax 2	0.64	0.05	0.07 NS
Mountain area	Ax 1	0.56	0.37	0.72 ***
	Ax 2	0.37	0.12	0.25 *

\*\*\*  $p < 0.001$ ; \*\*  $p < 0.01$ ; \*  $p < 0.05$ , NS = not significant.

showed a very low eigenvalue and was not correlated with its corresponding CA axis (Table 4). The main floristic gradient was highly correlated with precipitation in the flat area (Table 5). Precipitation also showed a high correlation with the variation in vegetation in the mountain area. However, elevation and potential radiation were also important controls of the floristic gradient in this landscape (Table 5). Mesic species became more abundant on sites with high precipitation, greater elevation, or south-facing slopes.

The floristic analyses of both areas showed some common patterns. Shrubs and grasses were the functional types that accounted for the main floristic trends. The main floristic gradient was composed of the same species and was associated with water availability in both areas. Humid sites had higher plant cover and a larger proportion of grasses, while arid sites had less total cover and a higher proportion of shrubs. Correspondence Analysis considering only forb species did not show any significant floristic trend. The lack of gradients among forbs reveals that this species group had no coordinated response to any environmental

**Table 5.** Correlation coefficients between environmental and physiological variables and Canonical Correspondence Analysis axes (Ax 1 and Ax 2). In the flat area, slopes, and thus potential radiation, had a very low range of variation. For this analysis only shrubs and grasses were considered.

	Flat area		Mountain area	
	Ax 1	Ax 2	Ax 1	Ax 2
Precipitation	0.99 ***	—	0.81 ***	0.57 ***
Elevation	-0.14 NS	—	0.68 ***	0.02 NS
Pot. radiation	no variation	-0.50 ***	0.55 ***	
Slope	no variation	0.20 NS	0.58 ***	

\*\*\*  $p < 0.001$ ; \*\*  $p < 0.01$ ; \*  $p < 0.05$ , NS = not significant.

gradient at the scale of this study. All the floristic gradients in the mountain area were weaker than in the flat area, indicating a lower coordination of species distribution in the mountain terrain.

Site species richness showed a significant difference between areas, due to a higher number of forb and shrub species per site in the mountain landscape (Table 6). In the flat area site species richness ranged from 11 to 33 species per site, while in the mountain area it varied between 13 and 39 species per site. Shannon diversity index values were not significantly different between areas. Total species richness increased significantly with precipitation in both areas ( $r = 0.47$ ,  $p < 0.01$  for the flat area;  $r = 0.62$ ,  $p < 0.001$  for the mountain area). Forb species explained this trend ( $r = 0.62$ ,  $p < 0.01$  for the flat area;  $r = 0.61$ ,  $p < 0.001$  for the mountain area). The number of shrub and grass species did not show any significant association with the environmental factors that determine water availability. Shannon diversity index did not show any trend along the gradient of the

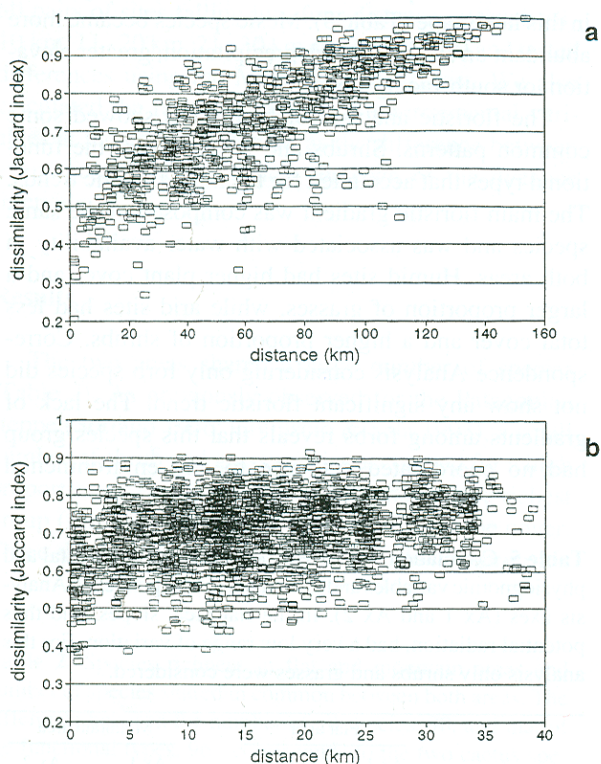
**Table 6.** Mean species richness and mean Shannon diversity index ( $\exp H'$ ) for flat and mountain areas. Differences were evaluated with Mann-Whitney  $U$ -test.

		Flat area	Mountain area	
Richness	all species	22.4 ± 0.85	26.7 ± 0.79	***
	shrubs	5.4 ± 0.31	6.5 ± 0.25	***
	grasses	6.1 ± 0.16	6.1 ± 0.13	NS
	forbs	10.9 ± 0.79	14.1 ± 0.64	***
Diversity	all species	5.6 ± 0.31	6.1 ± 0.25	NS

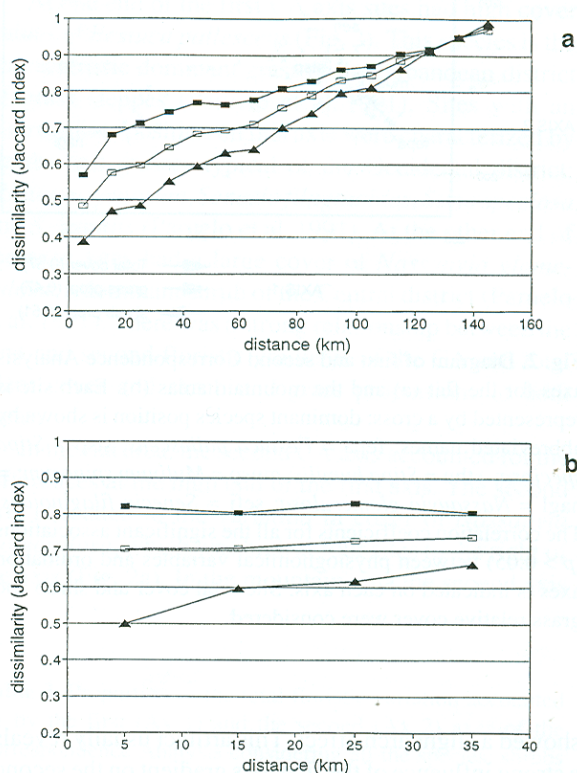
\*\*\*  $p < 0.001$ ; \*\*  $p < 0.01$ ; \*  $p < 0.05$ , NS = not significant.

analyzed variables. Because of their high richness and low abundance, forbs had a strong influence on species richness without affecting the diversity index.

The relationship between floristic dissimilarity and distance between sites was different for each area (Fig. 3). Distance between sites in the flat area ranged from



**Fig. 3.** Species dissimilarity (1 – Jaccard index) for all pairs of sites of each area in relation to the distance between sites. In the flat area (a) distances ranged from 0 – 160 km and explained a large proportion of species dissimilarity ( $r^2 = 0.56$  and  $p < 0.001$ ). In the mountain area (b), the longest distances reached were 40 km and were not correlated with species dissimilarity ( $r^2 = 0.05$  and  $p < 0.1$ ).



**Fig. 4.** Mean dissimilarity (1 – Jaccard index) for all possible pairs of sites within flat (a) and mountain (b) areas for increasing distance ranges of 10 km. Dissimilarities were calculated considering all the species (empty squares), forbs only (filled triangles) and shrubs and grasses (filled squares). Study areas were significantly different (Mann-Whitney  $p < 0.001$ ) for all tested ranges (0 – 10 km, 10 – 20 km, 20 – 30 km, 30 – 40 km) and all the considered species groups.

**Table 7.** Mean differences for all possible pairs of sites within flat and mountain area for increasing distance ranges of 10 km. Potential radiation is given as a percentage of flat surface radiation. Potential radiation and slope have no variation in the flat area.

Distance range		0-10	10-20	20-30	30-40
Flat area	precipitation (mm)	26	32	43	45
	elevation (m)	34	40	50	86
Mountain area	precipitation (mm)	31	68	70	96
	elevation (m)	130	134	162	173
	slope (%)	16	17	18	16
	potential radiation	31	29	29	32

0 km to nearly 160 km. In this area, distance between sites accounted for a large proportion of floristic dissimilarity ( $r^2 = 0.56$ ,  $p < 0.001$ , Fig. 3a). In the mountain area distances between sites were less than 40 km and were not correlated with floristic dissimilarity ( $r^2 = 0.05$ ,  $p < 0.1$ , Fig. 3b). The lack of correlation in the mountain area could be a consequence of the short distances investigated. For the same range of distances, mountain sites showed a significantly higher dissimilarity than flat sites (Fig. 4). In both areas mean dissimilarities for the whole set of species had an intermediate value between those for forbs and those for shrubs and grasses. Forbs showed a higher turnover of species than the other functional types. These differences were higher at shorter distances. In the flat area forb dissimilarities converged with those of shrubs and grasses at the longest distances. In the mountain area shrub and grass-based dissimilarities increased with distance, whereas forb-based dissimilarities did not change with distance (Fig. 4).

For the examined range of distances environmental variation was lower in the flat area (Table 7). Pairs of sites separated by the same distance had larger differences of precipitation and elevation in the mountain area than in the flat one. Precipitation and elevation were spatially dependent in both areas. In the mountain area slope and potential radiation appeared as spatially independent variables (Table 7).

## Discussion

Flat and mountain landscape displayed the same main floristic gradient and in both cases it was associated with factors that control water availability (Fig. 2, Table 5). Changes in landscape heterogeneity did not affect the main floristic trend of the steppe. The spatial scale at which this floristic variation occurred was different between the two areas (Table 1). Species ordination was consistent with previous physiognomical and phytosociological descriptions of Patagonian steppe (Soriano 1956; León & Facelli 1981; Golluscio et al. 1982; Paruelo et al. 1991). A physiognomical gradient determined by total cover and shrub-grass proportion coincided with floristic changes. In both landscapes, total cover and grass proportion were positively associated with water availability. The increase of grass proportion with water availability is typical within the range of arid and semiarid conditions analyzed (Walter 1973; West 1988).

In the two studied landscapes site species richness was positively associated with precipitation. No peaks of species number per site were found along the precipitation gradient. Our results fit with the generally observed increase of site species number from very poor environments to intermediate ones (Rosenzweig & Abramsky 1993), but they did not show the expected decay for the most productive environments. The species richness decay may take place outside the range of hydric conditions explored in this study. Aronson & Shmida (1992) described a uniform increase of site plant species richness from 40 mm to 500 mm of mean annual precipitation in natural communities in Israel. In contrast to species richness, site species diversity did not show any significant trend. Forbs may explain this difference because they determined a change in species number across the water availability gradient without affecting dominance.

In the mountain landscape site species richness and species spatial turnover were higher than in the flat area. These differences can be explained by at least two different mechanisms related to the contrasting environmental heterogeneity of the studied areas (Table 7). The influence of landscape heterogeneity on diversity can be directly determined by abiotic environmental heterogeneity or mediated by biotic mechanisms such as 'mass effect' (Shmida & Wilson 1985; Auerbach & Shmida 1987), also defined as vicinism (Zonneveld 1995; van der Maarel 1995). The consequences of these two types of effects of environmental heterogeneity on diversity components are contrasting. In a null model in which communities are in equilibrium and only abiotic heterogeneity is considered, an increase in heterogeneity at the landscape scale will lead to shorter distances

between different environments and thus to a higher turnover of species in space (beta diversity). Assuming that a higher landscape heterogeneity is not associated with an increase of within-site heterogeneity, site species richness (alpha diversity) will remain unchanged (see Crawley 1986 for an extended description of models). If mass effects are overimposed to the previous situation, the effect on diversity would be different. Mass effects imply the occurrence of species outside their favorable habitats. Propagule migration increases site species richness but, at the same time it reduces floristic differences between sites. Thus, mass effects will increase alpha diversity and decrease beta diversity. In a heterogeneous landscape, alpha and beta diversities will be the result of the balance between direct abiotic influence and mass effects. It is important to remark that we refer to beta diversity as species turnover per unit of distance and not to the classical concept of species turnover along a predefined environmental gradient (Whittaker 1977).

Simulations of species distribution in landscapes with different fractal dimensions supported the existence of mass effects in heterogeneous situations (Palmer 1992). Palmer (1992) proposed mass effects to be one of the major mechanisms mediating landscape heterogeneity influences on species distribution and coexistence at the site level. Our results showed a significant but low increase of site species richness in the mountain area, explained mainly by forbs (Table 6). On the other hand, floristic dissimilarities were higher in the mountain area (Fig. 3), indicating a higher beta diversity for all the groups of species. The higher alpha diversity can be the result of an increasing importance of mass effects in the mountain area. However, if present, mass effects were not strong enough to diminish beta diversity to the levels observed in the flat landscape.

Functional types had contrasting responses to environmental variation. Shrubs and grasses had coordinated distributions and determined floristic gradients, whereas forbs did not (Table 3). Even though forbs showed a high turnover among sites (Fig. 3), their replacements did not respond to any environmental gradient. We suggest that at the spatial scale of this study forbs distribution is independent of the considered abiotic factors, whereas shrubs and grasses distribution is mainly controlled by the hydric environment. At broader scales Paruelo & Lauenroth (in press) also found that forbs showed a weak relationship with environmental variables.

Forbs have a smaller size than shrubs and grasses and can explore local microhabitats (Golluscio & Sala 1993). The extent of microenvironmental variability within-sites, determined by the presence of large individuals of shrubs or grasses (Soriano & Sala 1986;

Soriano et al. 1994), can overshadow the effect of large scale water availability gradients on forb species distribution between sites. We propose that the high turnover of forb species in space is caused by a localized dispersal or nucleation (Zobel et al. 1993) or by local species-specific disturbances (as proposed by Palmer & van der Maarel 1995) such as sheep grazing, which is a common disturbance in the Patagonian steppe (León & Aguiar 1985; Soriano & Paruelo 1990).

Functional types in this work were established on the basis of resource use strategies (Soriano & Sala 1983; Sala et al. 1989; Golluscio & Sala 1993) and thus can be compared to the concept of guild (Simberloff & Dayan 1991). In previous studies guild discrimination aided the analysis of community structure on the basis of competition for resource (J.B. Wilson 1989; J.B. Wilson & Roxburgh 1994). In our study the use of plant functional types helped in the understanding of the determinants of community structure by recognizing the relative importance of the abiotic environment on different community components.

## Conclusions

Abiotic environmental variability determined the same floristic and physiognomic changes in flat and mountain landscapes of the Patagonian steppe. The higher environmental heterogeneity in the mountain landscape lead to spatial concentration of floristic variation and landscape species richness.

Site species richness varied within and between landscapes. Within landscapes, species number was positively associated with precipitation. Between landscapes a higher site species richness was found in the mountain area. Biotic mechanisms such as mass effects or abiotic mechanisms such as environmental heterogeneity could be the cause of the higher site species richness detected in the mountain area.

Species displayed contrasting distributions and relationships with the abiotic environment according to their functional types. While shrubs and grasses responded in a coordinated way to water availability gradients, forbs distributions were uncoordinated and independent of any abiotic gradient. These results highlight the importance of functional type recognition and discrimination for the analyses of the controls of community composition. Not all the community components respond to the same type of controls.



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