

Cross-scale vegetation patterns of Flooding Pampa grasslands

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Summary

1 The spatial pattern of vegetation heterogeneity across different scales may indicate the major environmental controls on vegetation structure, and thus guide strategies for the conservation of biodiversity.

2 We analysed cross-scale vegetation patterns in a 90 000-km² area of natural grasslands in the Flooding Pampa, Argentina. We assessed the contribution of regional (latitudinal) and landscape (topographic) patterns of species turnover to overall heterogeneity using data from 749 censuses.

3 A large proportion of the variation in species composition across the entire region was observed at very fine spatial scales (0.1–10 km²), associated with subtle topographic features and soil salinity gradients. Latitudinal variation played a secondary role.

4 Species turnover among stands occupying different landscape positions at the same latitude was 50% greater than among inventories encompassing two degrees of latitude. The fine-grain heterogeneity determined that an area of 10 km² was often sufficient to include 50% of all vascular plant species of the region.

5 Although a large proportion (nearly 70%) of the vascular flora was composed of rare (satellite) species that occurred in less than 10% of the samples, few core species (i.e. those occurring in more than 90% of the samples) were seen at any scale of analysis.

6 Latitude contributed most clearly to variation in species composition among the zonal communities located in well-drained soils where differences in relative cover of C₃ and C₄ grasses were seen. However, photosynthetic pathways still varied more along salinity or topographic gradients than across regions. A latitudinal pattern in abundance of the different *Poaceae* tribes was also consistent with their climatic classification.

7 Alpha diversity showed a threefold variation among different stands within a landscape: it increased from low topographic positions and high soil salinity to high topographic positions and low salinity. However, it was constant among surveys within the region.

8 Nearly 25% of the species were exotic, mostly European, whose invasion was promoted by livestock grazing. Compared with the native species, exotics were consistently enriched in annuals, particularly forbs, across latitude, and were less tightly associated with landscape heterogeneity than native species.

Key-words: alpha and beta diversity, core-satellite hypothesis, C₃ and C₄ grasses, exotics, heterogeneity, species–area relationship.

Journal of Ecology (2001) **89**, 562–577

Introduction

Vegetation spatial patterns are closely linked to the concept of scale, which is a function of both the ‘grain’

and the ‘extent’ of variation. The former refers to the size of the individual units of variation, while the latter refers to the size of the system (Allen & Hoekstra 1991; Turner & Gardner 1991). Holding the grain constant, an increase in extent may increase spatial variation because new patch types are included (Wiens 1989). In this broader scale, regional patterns may become stronger than local patterns. Alternatively, environmental constraints operating at fine scales may determine patterns

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of vegetation so strong that they propagate across broader scales, as particular small-scale vegetation–environment relations are repeated over larger spatial extents. Discriminating between these two forms of scale-dependency increases our ability to perform cross-scale extrapolations, to develop conceptual models of vegetation variation along environmental gradients, to understand the organization of plant communities and to implement conservation or restoration policies (Collins *et al.* 1993; Reed *et al.* 1993; Chaneton *et al.* 1996; Hoagland & Collins 1997; Palik *et al.* 2000).

In this paper we investigate vegetation patterns at landscape and regional scales in the Flooding Pampa, a 90000-km² area in southern South America (Soriano *et al.* 1992). Most of the area (80%) is still covered by natural grasslands because the soil quality and flooding regime have limited land use to extensive range-land (León *et al.* 1984), although grazing and regional drainage projects currently threaten its biodiversity. Four similar phytosociological studies have been carried out at different latitudes (range 35°20' S to 37°20' S, Fig. 1) and describe vegetation heterogeneity at the landscape scale (León *et al.* 1979; Batista *et al.* 1988; Burkart *et al.* 1990; Burkart *et al.* 1998). In this study, we have undertaken a synthesis of vegetation heterogeneity over the entire region and explore the relative importance of species turnover associated with latitudinal gradients and with landscape-scale variation.

First, we analysed how heterogeneity in species composition was associated with particular spatial scales. Our approach was to generate an overall classification of all vegetation samples from the four inventories and thus define plant community types and larger vegetation units for the whole region. If vegetation heterogeneity

were mainly determined by regional-scale gradients, community types or vegetation units would correspond with latitudinal ranges more than with landscape features, and species turnover would be smaller within than between vegetation inventories. McNaughton (1983, 1994) decomposed the heterogeneity of the Serengeti ecosystem, which covers an area a quarter of the size of the Flooding Pampa. He found that the diversity among community types located along habitat-gradients in the landscape was about twice the variation among landscapes of the region. The North American tall grass prairie has a climate that more closely resembles our study region, and there, species turnover across topographic or disturbance gradients within the Konza Prairie site (Gibson & Hulbert 1987) was between one-half and one-fourth the turnover among sites located along gradients of 3–8 degrees of latitude (Diamond & Smeins 1988).

Secondly, we investigated whether the Flooding Pampa grassland communities are organized according to either of the two currently accepted models of hierarchical structure of species composition (Collins & Glenn 1991). The niche-based model (Brown 1984) states that across an entire, environmentally heterogeneous region, most species will be restricted to a relatively reduced number of sites and only a few or none will be found in all samples. In contrast, the core-satellite model (Hanski 1982) incorporates plant demography and stochastic environmental variation to predict that at any time there is a group of core species that are found in nearly all sites (90–100%) within a region, and a group of satellite species found in only a few sites. The first model may apply to large regions, whereas the second model is consistent with data from smaller areas such as the 30-km² Konza Prairie (Collins & Glenn 1991). We explored the frequency distributions of species among sites at different scales to search for bimodalities that identify core species.

Thirdly, we constructed a regional species-area curve (Rosenzweig 1995) to show how species diversity was spatially distributed. This type of analysis results in a graphical representation of the scale-dependency of biodiversity, and helps define the area that must be conserved to protect a desirable amount of the regional diversity (Palmer & White 1994; Rosenzweig 1995).

Fourthly, we explored the regional and landscape-level variations of major species groups or plant functional types that may be indicators of ecosystem processes, such as biological invasions or seasonality production. Exclosure studies at a single site have shown that grazing promotes dominance of short-lived species and facilitates the invasion and persistence of exotic plantophiles, mostly annuals (Sala *et al.* 1986; Rusch & Oesterheld 1997). We therefore evaluated the relative contribution of exotic species across the region and studied the proportion of growth forms or plant functional groups in the native and exotic flora. Previous studies have suggested that both regional climatic factors and local environmental variations are of primary importance in determining the contribution of species

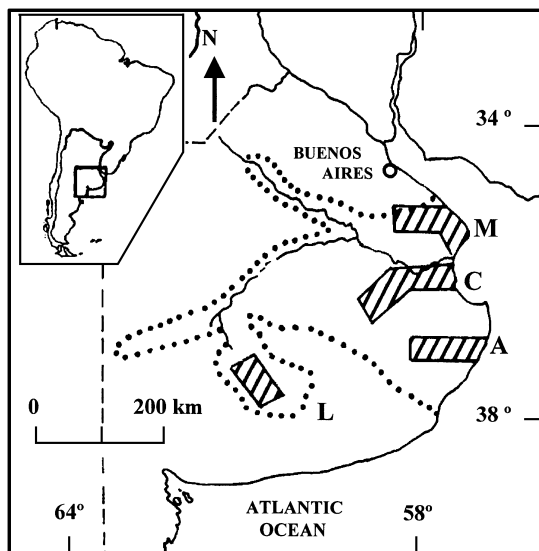


Fig. 1 Location of the Flooding Pampa and the four vegetation inventories. The dotted line indicates the limit of the Flooding Pampa *sensu* León *et al.* (1984). M = Magdalena-Brandesen counties (León *et al.* 1979); C = Castelli-Pila-Rauch counties (Burkart *et al.* 1990); A = Gral. Madariaga-Ayacucho counties (Burkart *et al.* 1998); L = Laprida region (Batista *et al.* 1988).

with different photosynthetic pathways or taxonomic relations in both temperate and tropical regions. Several studies at a continental scale have shown a close association between relative abundance of C₃ and C₄ species and latitude or temperature (Hattersley 1983; Diamond & Smeins 1988; Paruelo & Lauenroth 1996; Epstein *et al.* 1997). Similarly, some tribes within the *Poaceae*, like *Panicaceae* and *Andropogoneae*, occupy areas with higher mean temperature than others, like *Stipeae* and *Eragrosteae* (Burkart 1975). At landscape-level scales, a greater proportion of C₄ grass species is found in microsites characterized by lower levels of shade and drier soils (Terri & Stowe 1976), while C₃ species are more abundant on fine-textured soils with relatively high moisture levels (Barnes & Harrison 1982). We compared the relative cover of C₃ and C₄ grasses along environmental gradients operating at landscape and regional scales in the Flooding Pampa, which is located between the C₄-dominated subtropical Campos grasslands to the north and the C₃-dominated Pampa Austral and Patagonia to the south (Soriano *et al.* 1992).

Methods

STUDY AREA

The Flooding Pampa is a large subregion at the centre of the Pampas in Argentina (Fig. 1). Its climate is temperate-humid, with mean annual temperatures ranging from 13.8 °C in the South to 15.9 °C in the North. Mean annual precipitation ranges from 850 to 900 mm. The minimal general slopes in the region have prevented the development of a hydrologic network and, under the present humid conditions, groundwater remains near the soil surface for long periods in winter and spring (Paruelo & Sala 1990; Sierra & Montecinos 1990). Such flooding is heterogeneously distributed in space, according to subtle topographic variations of a few centimetres (Chaneton 1995). In summer, however, soil water content decreases and water deficits frequently occur, also with a strong spatial pattern (Sala *et al.* 1981; Lavado & Taboada 1987). As a result of this topographic heterogeneity, more than 60% of the soils of the Flooding Pampa are azonal, halo-hydromorphic complexes and associations strongly influenced by flooding (Natraquolls, Natraqualfs, Natralbolls, and Argialbolls) with zonal, well-drained soils (Hapludols and Argiudolls) restricted to the highest areas.

Vegetation is arranged as a complex mosaic of herbaceous plant communities (Burkart *et al.* 1990). Species composition responds to local variations in topography and soil salinity, but it has also been shaped by a century of livestock grazing (León *et al.* 1984; Sala *et al.* 1986) which has not only modified native species composition, but has also favoured the introduction of a number of exotic species. Scattered vegetated ponds dominated by species of *Typha*, *Zizaniopsis*, or *Scirpus* and cultivated areas (which occur only on well drained soils) do not form part of our study.

Table 1 Mean latitude and climatic characteristics for each inventory (see Fig. 1). Climate data correspond to 20-year records (1961–80) provided by Servicio Meteorológico Nacional weather stations (M = Punta Indio, C = Dolores, Las Flores, A = Pinamar, Azul, L = Tandil, Laprida)

Inventory	M	C	A	L
Mean latitude	35°40'	36°10'	36°50'	37°10'
Annual precipitation (mm)	885	891	895	856
Average annual temperature (°C)	15.9	14.8	14.3	13.8
Average minimum temperature in July (winter) (°C)	6	4.3	3.8	1.8

DATA ANALYSIS

We compiled a single database from four inventories that encompass the entire region (León *et al.* 1979; Batista *et al.* 1988; Burkart *et al.* 1990; Burkart *et al.* 1998; Fig. 1). They extend over two degrees of latitude and have similar mean annual precipitation but differ in mean annual temperature and seasonality (Table 1). Each inventory was preceded by a detailed analysis of aerial photographs (scale = 1 : 20 000), to identify the major landscape elements and physiographic units. Vegetation samples were taken in the field from the identified physiographic units, excluding situations with current or recent agricultural use (< 5–10 years). Each vegetation sample consisted of a complete list of the vascular plants present in the whole stand (*c.* 0.25 ha) and an estimation of species cover within an area of 25 m², together with a record of its physiographic landscape position. Sampling was in early summer, when most species are present and easily identifiable through their reproductive organs.

In order to determine and describe the variation in species composition across different spatial scales, we used three complementary approaches. First, we estimated beta diversity (Magurran 1988) among observations within 40 random samples in each inventory and among the four inventories (i.e. the total number of species divided by the average number of species per observation or per inventory) to assess species turnover at landscape and regional scales, respectively. Because beta diversity may be influenced by the sample size, which determines their maximum value, the two estimates were based on similarly small samples (*n* = 4).

The second approach was the classification of all the observations into community types and vegetation units. Community types were derived using the unweighted pair-group average method (UPGMA) (Kaufman & Rousseeuw 1990) with Sorensen's similarity coefficient (Goodall 1973) calculated from presence-absence data in the 749 vegetation censuses. Only those species which presented high values of Jancey's (1979) discriminant coefficient (> 3.0), were classified, to obtain floristic groups, using the complete linkage algorithm with Pearson's correlation coefficient. Community types

and the floristic groups were ordered simultaneously through concentration analysis (Feoli & Orlóci 1979) using frequency data of species groups in the communities, to obtain a partial ordered constancy table (Mueller-Dombois & Ellenberg 1974). We classified community types into vegetation units using the same fusion algorithm and distance measure used to classify observations, but calculated on the basis of the frequency of each species in each community type (constancy). Association of community types or vegetation units with particular inventories would indicate that species composition had a strong regional variation, whereas inclusion of samples from several inventories would suggest that landscape-scale variation was stronger.

Finally, correspondence analysis (Greenacre 1984) of presence-absence data of species in each sample unit was carried out in order to identify and describe the principal gradients in species composition. The centroids of community types separated for each inventory were plotted on the three principal axes and inspected to determine whether the major sources of variation were regional or local.

In order to test Brown's and Hanski's models, we calculated frequency distributions of species presence at different scales and in relation to different amounts of habitat heterogeneity. We compared patterns at the scales of the entire area, within an inventory, and within a 10-km² area inside the same inventory. We also compared distributions for different amount of habitat heterogeneity: the entire region, within a vegetation unit, within a community type in the same vegetation unit, and within stands in the same community type that shared a single dominant species. For each frequency distribution, we tested bimodality by the method proposed by Tokeshi (1992) and recently used by Collins & Glenn (1997) and Guo *et al.* (2000). Under the null hypothesis of a uniform distribution over frequency classes, we calculated the probability of the presence of as large or larger numbers of species in the two observed extreme classes (P_c). If P_c was below 0.05, we calculated, under the same null hypothesis, the probability of the observed frequency for either the left- or right-most class (P_l and P_r , respectively). If both P_l and P_r were below 0.05, the distribution was considered bimodal (supporting Hanski's model), whereas if only P_l was below 0.05, the distribution was considered unimodal (supporting Brown's model) (Collins & Glenn 1997).

We built a species-area curve by calculating the cumulative number of species as area increased. We worked with a group of pilot areas, whose vegetation had been mapped at a scale of 1 : 20000 (Burkart *et al.* 1990). We gradually increased the size of an observation window, starting from a single stand, and registered the expected number of cumulative species based on the community types that were included in the window, their average species diversity at the stand level, and the average beta diversity among community types and among stands of the same community type. We repeated the same procedure using four different starting points

corresponding to distinct community types and/or inventories. This approach is a combination of nested and non-nested procedures for building species-area curves (Palmer & White 1994; Rosenzweig 1995): the increase of area was nested and reflected the actual grain of habitat diversity, but the species diversity corresponding to that increase in area was based on average alpha and beta diversity values of the entire inventory. As the pilot areas had originally been mapped because they best represented the normal within-landscape heterogeneity, we are confident that our species-area curves did not start from spots that were unusually heterogeneous. Once the area covered by the observation window exceeded the mapped pilot area, we added a single extra point for the area of the entire inventory and its cumulative species richness. We estimated the z -value of the species-area curve as the slope of the log-species vs. log-area relationship.

We compared the proportional contribution of different plant functional groups (annual grasses, perennial grasses, annual forbs, perennial forbs and shrubs) with the exotic and native flora between inventories, testing the hypothesis of homogeneity between inventories using chi-square tests (5 guilds \times 4 inventories for native species, and 4 guilds \times 4 inventories for exotics, because there are no exotic shrubs). For tribes in the *Poaceae* we compared the mean relative cover among inventories separately for each tribe (Kruskall Wallis one way ANOVA), with P -values corrected according to the Bonferroni method for multiple comparisons. Regression curves were fitted to explore the response of floristic richness and relative cover of C_3 and C_4 species from the *Poaceae* family to landscape and regional gradients. The photosynthetic pathway (C_3 or C_4) was determined on the basis of published information (mainly Sánchez & Arriaga 1990) and relative cover was averaged for each vegetation unit and for each inventory. Soil properties at the level of vegetation units were represented by average pH values at 15-cm depth. Data were taken from studies with explicit descriptions of vegetation units (see Results). Most of them were carried out in the Flooding Pampa and report community types that correspond with those in our inventories. Only the data from Ragonese & Covas (1947) represent a different region, but their vegetation coincides remarkably with one of our vegetation units. For each vegetation unit we averaged soil reaction data from several studies to represent a scale similar to that of the present analysis. Relative topographic position for each community type was represented by the relative coordinates of its centroid in the first ordination axis of the correspondence analysis, with which, for community units in the central part of this region, it is closely correlated (León *et al.* 1975; Movia 1975).

Results

Species turnover among stands occupying different landscape positions within an inventory was 50% greater than species turnover among inventories (beta diversity

Table 2 Different indices of diversity for each latitude and the entire region. Alpha diversity is the average number of species per sample, beta diversity within inventories = total number of species in four sites/average number of species per site (averaged for 40 random samples of four sites in each inventory), and beta diversity between inventories (total set) = total number of species in the entire set/average total number of species per inventory

Inventory	M	C	A	L	Total set
Alpha diversity	29.9	33.1	35.8	32.7	32.6
(95% confidence interval)	(28.6–31.2)	(31.9–34.3)	(34.1–37.5)	(30.7–34.6)	
Total number of species	271	254	234	202	430
Beta diversity	2.9	2.8	2.8	2.6	1.79
(Standard errors)	(0.14)	(0.11)	(0.13)	(0.13)	

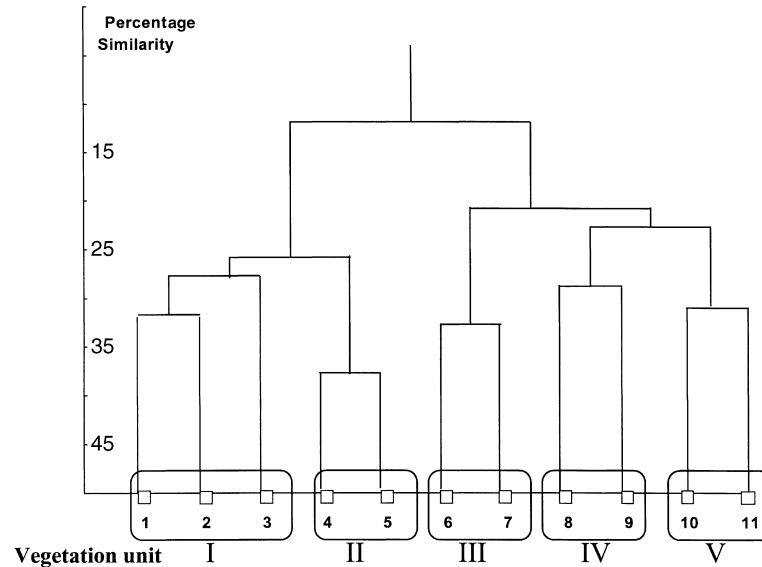


Fig. 2 Classification of the 11 community types and their fusion into five vegetation steps at 27% similarity. I = mesophytic meadows; II = humid mesophytic meadows; III = humid prairies; IV = halophytic steppes; V = humid halophytic steppes.

Table 3 Percentage representation in each latitude, alpha diversity and internal similarity of the 11 community types. Alpha diversity = average number of species per observation in each community. Min–max values = extreme averages of alpha diversity for communities represented in distinct inventories. Percentage similarity = Sorensen's similarity coefficient calculated with presence-absence data and averaged between all pairs of observations within each community type

Community type	Percent representation in each inventory				Alpha diversity	Min–max values	Percentage similarity
	M	C	A	L			
1	100%				42.2		49.2
2		60%	40%		44.4	44.1–44.8	47.7
3				100%	38.6		44.1
4	30%	40%	30%		39.1	38.8–39.5	40.5
5	29%	49%	22%		32.7	31.5–35.4	41.3
6	40%	26%	18%	16%	28.2	27.7–29.1	35.8
7	44%	28%	28%		17.7	13.8–19.6	31.1
8		29%	39%	32%	26.1	25.9–26.5	38.4
9	100%				19.9		39.0
10	42%		30%	28%	17.3	16.8–17.6	30.0
11	52%	48%			12.6	12.2–12.9	33.1

values Table 2). This indicates a stronger heterogeneity at the landscape than at the regional level. Each inventory included 46–60% of the flora and there was therefore a large overlap of species among inventories.

The complete set of vegetation samples was classified into 11 community types and five vegetation units (Fig. 2).

Most community types were found in at least three inventories, confirming that there was more heterogeneity at the landscape than at the regional level (Table 3, Appendix I). Only three communities were exclusive to a single inventory (1 and 9 to the most northern, and 3 to the most southern inventory). The association of

Table 4 Landscape and soil characteristics of the vegetation units derived from the dendrogram in Fig. 2. Superscripts indicate bibliographic sources for soil information

Vegetation unit	Position in the landscape and soil description	Predominant soil types
I: Mesophytic meadows	Positive and convex terrains, highest areas. Deep, well drained soils, acidic, non-saline, poligenetic soils ⁽¹⁾⁽²⁾⁽³⁾	Typic Argiudolls and Poligenetic Thaptoargic Hapludolls
II: Humid mesophytic meadows	Flat areas. Intermediate topographic position. Acidic, non-saline A1 horizon and saline, highly alkaline B2 horizon ⁽²⁾⁽³⁾⁽⁴⁾⁽⁵⁾⁽⁶⁾⁽⁷⁾⁽¹¹⁾	Typic Natraquolls with natric B _{2t} horizon Natrahbolls
III: Humid prairies	Extended lowlands, with groundwater near the surface, subject to flooding. Soils range from acidic throughout the profile to acidic in the upper and alkaline in the deeper layer ⁽¹⁾⁽²⁾⁽³⁾⁽⁸⁾	Argiacuic Argialbolls Argiacuolls
IV: Halophytic steppes	Small depressions in flat areas, or rings surrounding humid areas. Very shallow, alkaline soils with very high salt content in the upper layer ⁽¹⁾⁽²⁾⁽³⁾⁽⁸⁾⁽⁹⁾⁽¹⁰⁾	Mollic Natraqualfs
V: Humid halophytic steppes	Negative positions on fluvial valleys, tidal areas poorly drained. Alluvial, saline sodic soils ⁽¹¹⁾⁽¹²⁾	Typic Natraqualfs

(1) Taboada & Panuska (1985); (2) Batista & León (1992); (3) Berasategui & Barberis (1982); (4) Lavado & Taboada (1985); (5) Alconada *et al.* (1993); (6) Lavado & Taboada (1988); (7) Taboada and Lavado (1988); (8) Batista (1991); (9) Lavado *et al.* (1992); (10) Taboada *et al.* (1998); (11) Ragonese & Covas (1947); (12) Sánchez *et al.* (1976).

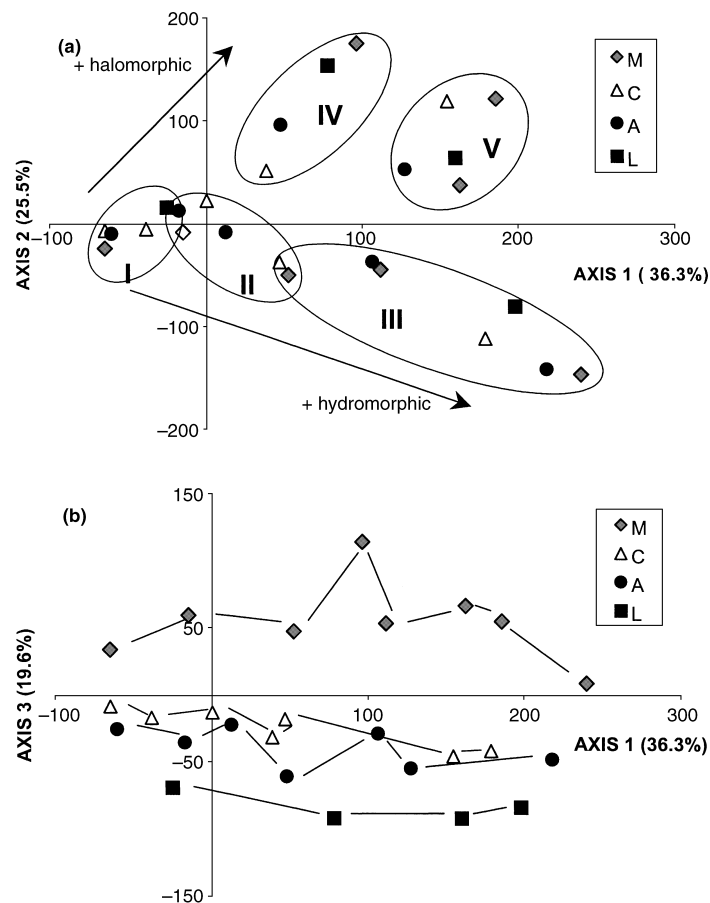


Fig. 3 Centroids of community types of each inventory in the CA ordination based on presence-absence of species in the samples. (a) First and second axes. Ellipsoids represent vegetation units derived from dendrogram in Fig. 2. Arrows indicate principal subjacent environmental gradients (see text). (b) First and third axes.

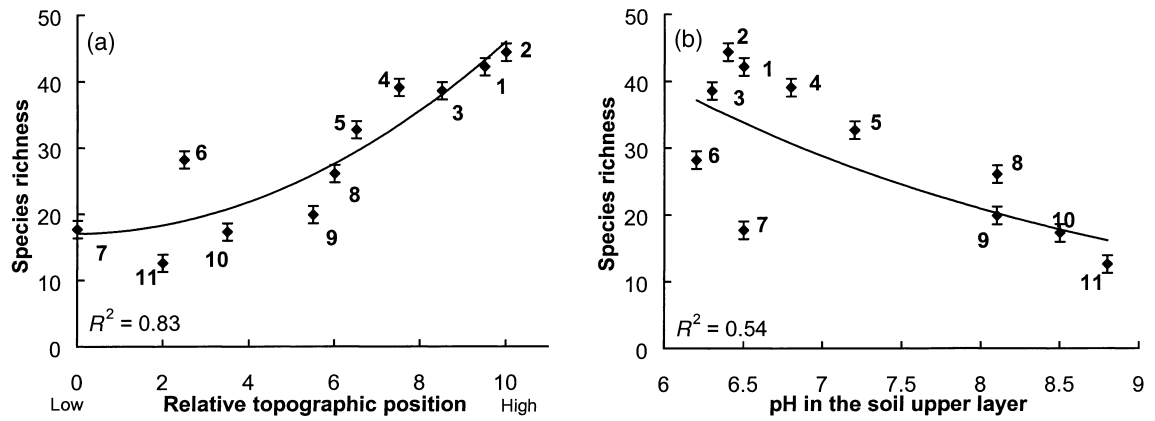


Fig. 4 Average species richness for each community type in relation to (a) relative topographic position and (b) pH in the soil upper layer. Vertical lines are 95% confidence intervals, sample sizes for community types are reported in Appendix I.

community type 11 with the two northern inventories is not due to latitude, but rather to the presence of coastal salt marshes and fluvial valleys. The five vegetation units, defined at a 27% similarity fusion level, were: I: mesophytic meadows, II: humid mesophytic meadows, III: humid prairies, IV: halophytic steppes, and V: humid halophytic steppes (Fig. 2). Each was clearly associated with particular landscape and soil attributes (Table 4). The low fusion level (13% similarity) at which vegetation units I and II (which correspond to highest and intermediate topographic position) combined with vegetation units III, IV and V (located in lowlands and depressions), indicates the strong composition differences associated with position in the landscape.

The first two axes of correspondence analysis, which together accounted for 61.8% of the total variance, showed two principal gradients of species composition (Fig. 3a). The first reflected the topographic gradient from uplands to lowlands and hence different flooding regimes in units I, II and III (Table 4). The second gradient represented by the transition from I to IV is clearly associated with increasing soil salinity and pH (Table 4). Vegetation unit V, which is associated with salt marshes in both tidal areas and fluvial valleys and thus combines both halomorphic and hydromorphic conditions, lay between the more rigorous extremes of the two gradients. On the third axis, which explained 19.6% of variance, the species composition was ordered according to latitude (Fig. 3b).

Alpha diversity also suffered a greater variation at the landscape than at the regional scale. The three community types within the mesophytic meadows (1, 2 and 3), were found in distinct inventories but showed minimal differences (5.8 species between 2 and 3) and no trend with latitude. Community types that occurred in more than one inventory also had minimal differences in alpha diversity among inventories (see min–max values in Table 3). In contrast, alpha diversity varied by a factor of 3.5 between community types (Table 3), decreasing sharply from upland landscapes (unit I) to the lowest topographic positions (unit III) and soils with highest levels of pH and salinity (unit V). Species-

richness increased significantly as relative topographic position increased (Fig. 4a) and soil pH in the upper layer decreased (Fig. 4b).

The shape of frequency distributions of species was a right-skewed exponential, with no signs of the bi-modality predicted by the core-satellite model of species distribution (Fig. 5). The distributions were significantly unimodal, P_c -values ranged from 10^{-23} to 10^{-10} , P_r -values ranged from 0.96 to 0.99 and P_f -values ranged from 10^{-11} to 10^{-15} in all cases (we tested 25 sets of samples within the 11 community types, the four inventories and within sites dominated by different dominant species). The pattern was similar for areas of very different sizes (Fig. 5a–c). At the regional level, approximately 70% of the species were rare, occurring in less than 10% of the sites. The absence of a distinct group of core species (those occurring in more than 90% of the sites) may have been due to the strong habitat heterogeneity of this region. However, frequency distributions within particular vegetation units or community types showed the same unimodal pattern (Fig. 5d,e). Even when we deliberately searched for groups of samples with maximum percentage similarity in species composition or groups of samples that shared the same dominant species (as in Fig. 5f), we did not find significant bi-modality in species distributions.

Although the high number of rare species suggested that diversity might be widely scattered, species-area curves showed high concentrations of species within comparatively small areas (Fig. 6). Nearly 50% of the regional flora should be found within areas of just 10 km² as the fine-grained heterogeneity of the landscape meant that such areas often contained stands of four or five community types and that these belong to several different vegetation units. The estimated z -value was 0.14 (SD = 0.0054).

The regional flora of exotic and native species showed different life-form composition and these differences were maintained across inventories (Fig. 7, natives: chi-square = 5.84, d.f. = 12, $P = 0.9$; exotics: chi-square = 4.69, d.f. = 9, $P = 0.8$): 85% of the native species were perennials, with similar contribution of grasses and

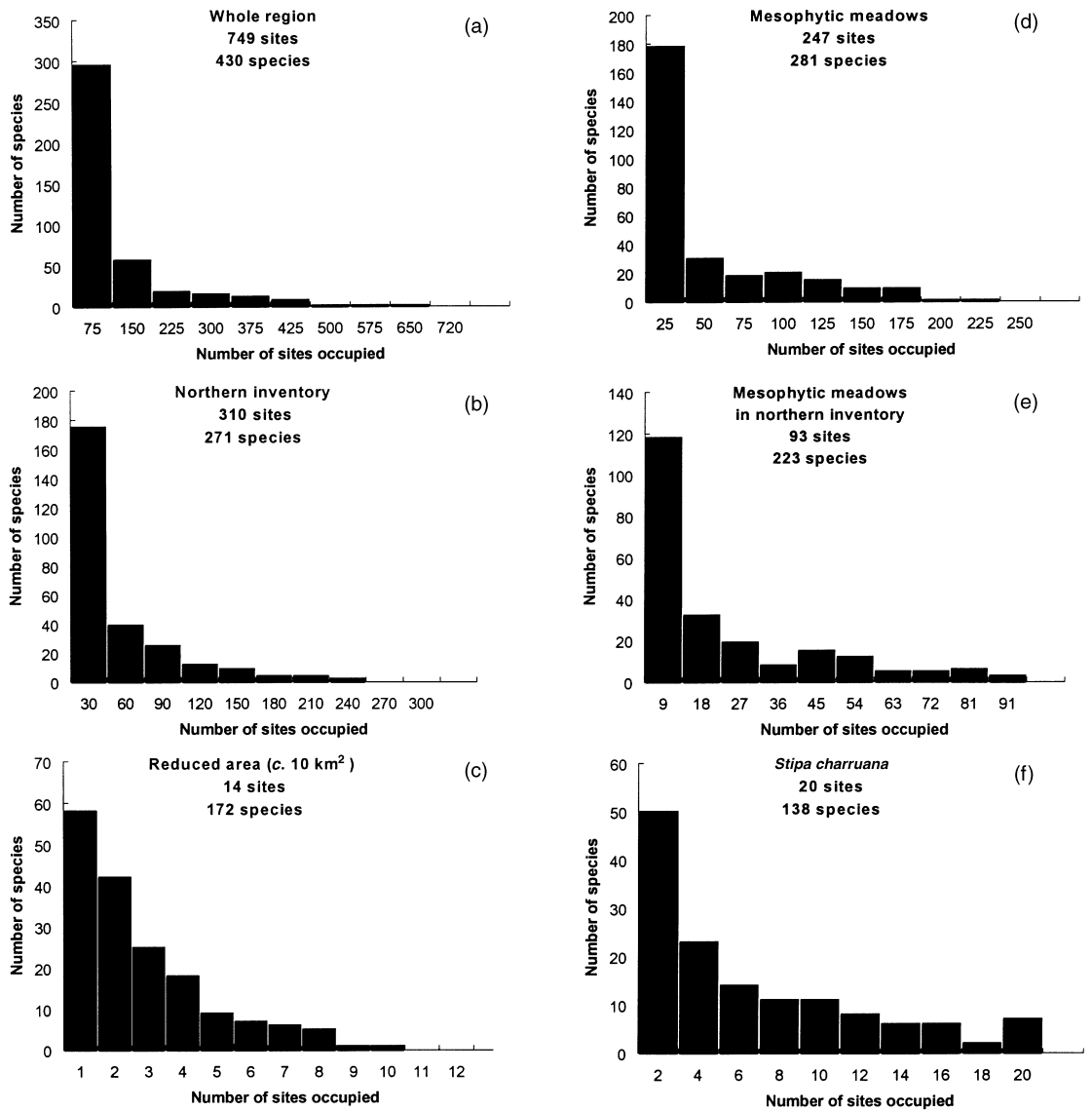


Fig. 5 Frequency distributions of species for (a) whole region and areas of different sizes, (b) inventory, (c) 10 km², and for different habitat heterogeneity: (d) within a particular vegetation unit, (e) within a particular community type, (f) within a group of sites that shared the same dominant species.

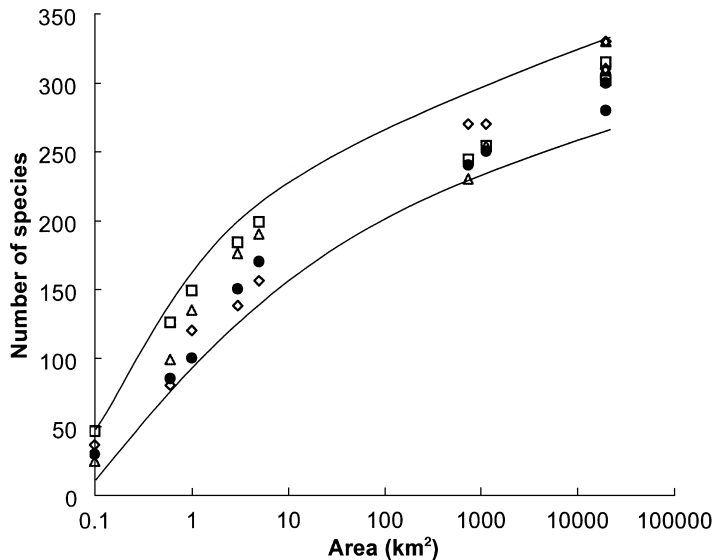


Fig. 6 Species-area curves: cumulative number of species in relation to increased area, starting from a single stand, in four different pilot areas (represented by distinct symbols). Boundary lines were drawn through the highest and lowest richness for a given area.

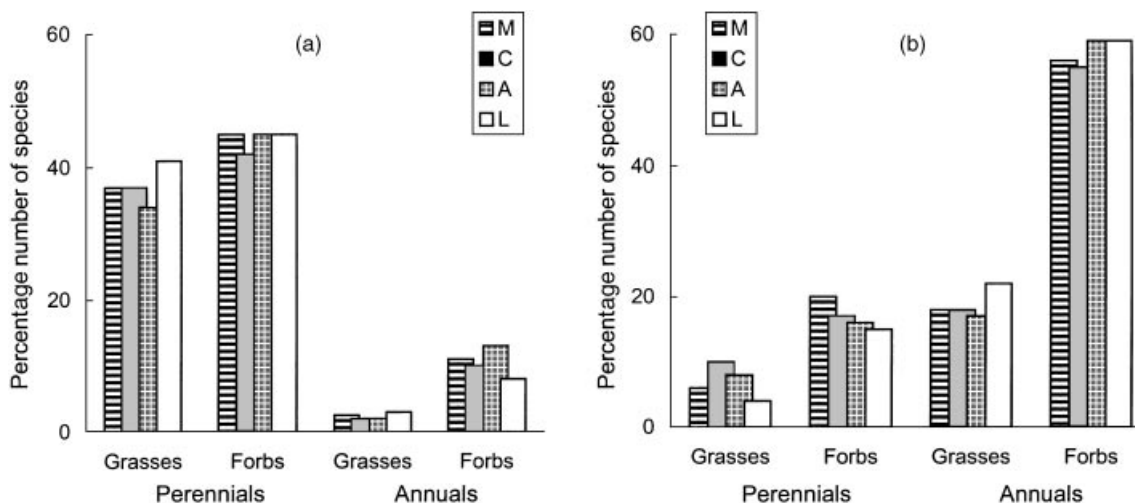


Fig. 7 Proportional contribution (percentage number of species) of different guilds (perennial grasses, perennial forbs, annual grasses and annual forbs) to the (a) native and (b) exotic flora in each inventory. Acronyms for inventories as in Fig. 1.

Table 5 Percentage of exotic species in different vegetation units and percentage of indicator species within the native and exotic components of those units (listed in Appendix I). Units I and II were pooled due to the lack of exclusive species groups

	Units I–II	Unit III	Unit IV	Unit V
Percentage of exotics (95% confidence interval)	27.1% (21.8–33.4) <i>n</i> = 225	20.6% (15.3–27.6) <i>n</i> = 165	23.7% (17.6–31.7) <i>n</i> = 139	29.2% (21.5–38.9) <i>n</i> = 106
Percentage of indicators within natives (95% confidence interval)	26.2% (20.2–33.6) <i>n</i> = 164	14.5% (9.6–21.7) <i>n</i> = 131	12.3% (7.4–19.9) <i>n</i> = 106	16% (9.6–26.3) <i>n</i> = 75
Percentage of indicators within exotics (95% confidence interval)	26.2% (17.1–39.1) <i>n</i> = 61	2.9% (0.8–7.3) <i>n</i> = 34	6.1% (1.9–15.2) <i>n</i> = 33	0% (0–11.2) <i>n</i> = 31
Indicator species groups (Appendix I)	I–VIII	X–XII	XVI–XVIII	XIX–XXI

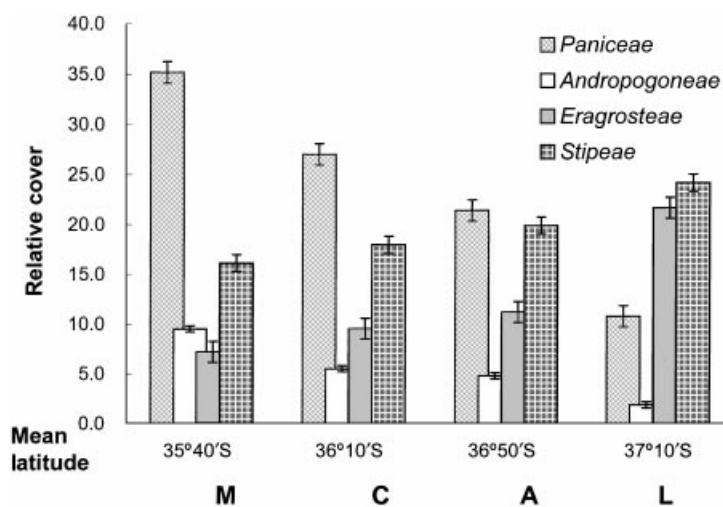


Fig. 8 Relative cover of *Poaceae* tribes along latitudes, averaged for each inventory. Vertical lines are standard errors for the means. Kruskal Wallis one-way ANOVA for *Paniceae*, *Andropogoneae* and *Eragrosteae* $P < 0.00001$, while for *Stipeae* $P = 0.0179$.

forbs, whereas 74% of the exotic species were annuals, 75% of them being forbs. All shrubs were native and constitute 6% of the native flora (not represented in Fig. 7). At the landscape level, exotics were found in all vegetation units at approximately similar proportions.

However, they were less tightly associated with particular vegetation units than native species (Table 5).

Within the *Poaceae*, the average relative cover of *Paniceae* and *Andropogoneae* decreased with latitude, while that of *Stipeae* and *Eragrosteae* increased (Fig. 8).

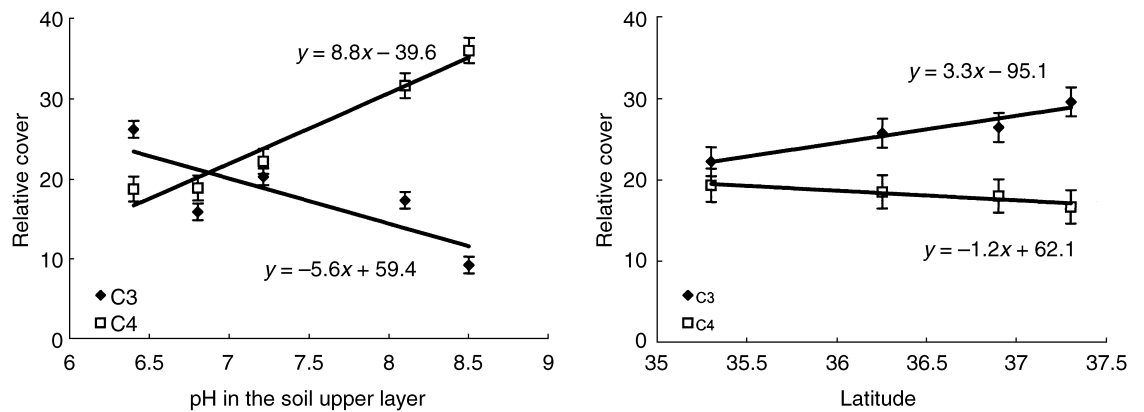


Fig. 9 Relative cover of C_3 and C_4 grasses, as proportion of total cover, of each vegetation unit, in relation to (a) averaged values of soil pH in the upper layer for each vegetation unit, and (b) latitude, considering only the mesophytic meadow communities, which showed the largest segregation among inventories and correspond to $\text{pH} = 6.4$ in (a). Vertical lines are 95% confidence interval.

The slight increase of relative cover of *Stipeae* with latitude was underlain by a stronger turnover of some species: *Stipa hyalina* and *S. charruana*, exclusive to the northern inventory, and *S. ambigua*, exclusive to the southern inventory (Appendix II).

C_3 grass cover decreased and C_4 grass cover increased, both by a factor close to 2, along a soil pH gradient of the upper layers from 6.5 to 8.5 (Fig. 9a). C_3 cover increased and C_4 cover decreased, both by a factor of about 25–30%, as latitude increased (Fig. 9b). Thus, the relative importance of these functional groups was more affected by landscape-level soil conditions than by latitude.

Discussion

The combination of quantitative approaches used in this study consistently indicated that edaphic factors associated with subtle topographic features were the principal environmental constraint for the observed variation in vegetation structure of the Flooding Pampa grasslands. Latitude played a secondary role in determining vegetation spatial heterogeneity. Thus, strong local variations in vegetation survived the transition from the landscape to the broader regional scale.

Plant species richness in this region is due to small-scale patterns rather than to regional or alpha diversity. The regional pool of species is smaller than similarly sized areas of comparable latitude around the world (Rapoport 1996), and the number of species per stand of the richest community type of the Flooding Pampa (42.2, Table 3) is lower than average stand-level species richness in the tall grass prairie (50–60, Diamond & Smeins 1988). In contrast, beta diversity across topographic and salinity gradients in the Flooding Pampa is 3–5 times larger than beta diversity across topographic or disturbance gradients in the tall grass prairie (Gibson & Hulbert 1987).

Topography is not strictly an environmental variable, but it acts as a surrogate for a complex array of factors that can greatly influence plant distribution (Whittaker 1960; Austin *et al.* 1984). In the Flooding Pampa, an extremely flat plain with a relatively small height range

(< 4 m), elevation relates to depth of A1 horizon and soil organic matter content (Batista 1991), and controls the timing and duration of flooding events (Paruelo & Sala 1990), which are known to be important filters for plant composition in this and other systems (van der Valk 1981; Chaneton *et al.* 1988; Hill & Keddy 1992; Weiher & Keddy 1995; Insausti *et al.* 1999).

In contrast to other grassland regions (Collins & Glenn 1991), the Flooding Pampa lacks a distinct group of core species that tend to be present in most sites, and is particularly rich in satellites (i.e. those species that are present in just a small proportion of sites). Across topographic gradients in the Konza Prairie Natural Research Area, about 15–20% of the species pool is found in more than 90% of sites, and 30–40% of the species pool is found in less than 10% of sites (Collins & Glenn 1991). No species occurred in more than 90% of the sites in our inventories, whereas more than 50% of the species were found in less than 10% of the sites. When smaller areas or smaller amount of habitat heterogeneity were considered, the proportion of species occurring in more than 90% of the sites slightly increased, but never reached the high values expected for a bimodal distribution. Thus, vegetation heterogeneity of the Flooding Pampa follows predictions of the niche-base model of species distribution, even at the small-scale level in which the core-satellite species model is more likely to apply (Collins & Glenn 1991; Brown 1995). Guo *et al.* (2000) found bimodal distributions at the same scale as this study (0.25-ha plots) but using subsamples representing 0.16% of the total area of each plot. They suggested that bimodality may have arisen as a consequence of incomplete sampling of the plot, missing many of the rare species whose inclusion would make the distribution much more unimodal. Our results support their suggestion because we worked with complete lists of species, obtained after an exhaustive study of the entire stand, with minor possibility of loss of rare species.

The combination of low richness at the stand level, the lack of common thread of core species across habitats, and the high proportion of rare species, would suggest that the area needed to enclose most of the

species pool of the Flooding Pampa should be large. However, the spatial arrangement of habitats is so fine-grained, and beta diversity is so large, that nearly 50% of the species may be found in any portion of about 10 km². We also estimate that an area of 10 km² in the central subregion plus two similar areas including a few stands of mesophytic meadows in the northern and southern subregions will enclose approximately 70% of all species.

The impact of regional processes on community composition was only evident among the mesophytic meadows (vegetation unit I) that occupy well-drained, acidic soils. Within this vegetation unit, the relative cover of C₃ and C₄ grasses and overall species composition changed with latitude. Species turnover across a three degree latitude gradient in the tall grass prairie was about twice that among inventories in the Flooding Pampa (Diamond & Smeins 1988). Thus, both greater landscape diversity and smaller regional diversity contributed to the importance of landscape-level effects in our study. The Flooding Pampa, being oceanic, shows much lower temperature variation than the continental tall-grass prairie and this will reduce the effect of latitude.

However, despite the effect of latitude, the relative cover of C₃ and C₄ grasses is more influenced by soil pH. While relations between functional-type cover and latitude can be attributed to different optimum temperatures for photosynthesis (Black 1973; Ehleringer 1978), the mechanisms underlying the relations with soil pH are not clear. However, high salt concentration causes osmotic retention of water (Larcher 1995) and C₄ grasses, which we observed in a major proportion in halomorphic environments, have a higher water-use efficiency than C₃ species (Black 1973) and therefore are expected to be more abundant in drier environments (Brown & Simmons 1979; Pearcy & Ehleringer 1984). Sites of the Flooding Pampa grasslands reached the highest mean percentage error in the prediction of regional distribution of C₃ and C₄ grasses by correlative models based on climatic controls (Paruelo *et al.* 1998). It is therefore necessary to include the landscape-scale constraints which translate across scales. In this case, the understanding of scale dependency in community pattern can also greatly improve predictions of vegetation structure and function.

Latitude was also reflected in taxonomy with a latitudinal pattern in the abundance of *Poaceae* tribes correlating with climatic classifications of these grasses. The *Panicaceae* and *Andropogoneae*, whose relative cover decreased with latitude, belong to the mega-mesothermic groups (Hartley 1950) and are the dominant tribes in the region of the Campos Cerrados in central Brazil (Burkart 1975), located between 10° and 20° S. The *Stipeae*, which increased with latitude, are major components of South American meso- and microthermic grasslands, dominate Patagonian steppes and are absent in the megathermic zones (Burkart 1975).

The native and exotic flora showed contrasting composition of life-forms and a different breadth of habitat

distribution. Previous exclusion studies carried out in a single location showed that grazing promoted the invasion of exotic plant species, largely annuals, introduced after the European colonization (Sala 1988). Our results indicate that at any latitude the exotic flora is mainly composed of groups favoured by grazing: 74% of exotic species are annuals, with 75% of these being forbs, while 85% of native species are perennials, and 79% of the grasses are native perennials. Exotic species have therefore invaded these grasslands at a regional scale as a consequence of grazing by domestic animals, as in other regions of the world (Mack & Thompson 1982; Milchunas *et al.* 1988). The homogeneous pattern of exotic plant invasion recorded across latitudes would suggest that grazing history acted as a large-scale process that, together with other factors that are nearly constant throughout the region (such as amount and distribution of annual precipitation), generated the context for the expression of smaller-scale processes (Allen & Hoekstra 1991). Exotic species were important at all positions in the landscape (from 21% to 29%) but they extended over more than one vegetation unit, whereas particular groups of native species had a narrower distribution. Thus, although grazing has increased plant diversity at the stand level by favouring the introduction of exotics and the coexistence of a greater number of native species, it has decreased it at the landscape level because the introduced exotics tend to be less tightly associated with particular positions along topographic or salinity gradients (Sala *et al.* 1986; Sala 1988). This evidence suggests that a Flooding Pampa without livestock would have fewer species but, perhaps, more community types.

The close association between vegetation and landscape suggests that artificial drainage systems that are aimed at altering flooding and salinity regimes will cause strong modifications of regional diversity. The fine-grained packaging of species diversity suggests that most of the heterogeneity at the species level could be conserved by establishing relatively small protected areas, although the minimum area needed to include a given amount of diversity may not necessarily be sufficient for its persistence. Furthermore, our results indicate that the major conservation challenge for this region is not at the species, but at the landscape, level. The spatial arrangement of habitats is much more diverse than the flora.

Our results also have theoretical implications. The core-satellite species model that applies so consistently in the climatically similar tall grass prairie does not apply here, even when observations are restricted to small areas or to more homogeneous sets of samples. This would suggest that the Flooding Pampa grasslands have either a particularly high habitat heterogeneity or species with particularly narrow niches. The species with such narrow distributions, closely matching the subtle topographic or soil features of the landscape, are largely native species, suggesting that evolutionary adaptation has taken place. In contrast, although the more recently arrived invaders are narrow in the sense that they quickly

disappear in the absence of grazing, they are generalist in terms of tolerance to drought, flooding or salinity. Finally, the increasing proportion of cool-season and C_3 species as latitude increases must be superimposed on a stronger local pattern associated with topography. These changes in the proportion of functional types suggest that there would be two seasonal waves of primary production: a regional wave, produced by the variation of latitude, and a superimposed local wave from the early spring production in the uplands to a mid-summer peak in the lowlands or in the saline habitats.

Acknowledgements

This research was supported by Consejo Nacional de Investigaciones Científicas y Técnicas (Argentina) and Facultad de Agronomía, Universidad de Buenos Aires, Argentina. We wish to thank William Batista, Silvia Burkart and Enrique Chaneton for their input and/or improvements to the manuscript.

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Received 15 June 2000

revision accepted 30 November 2000

Appendix I

Partial ordered table for community types named with numbers from 1 to 11. Values are constancy (% frequency) of species in the community types. Dots represent constancy values < 10. Only species clustered in floristic groups are presented. The partial ordered table synthesizes the main gradients of floristic composition. At the common extreme of both gradients are the floristic groups I, II, III, IV and V, whose species are associated with deep, non-saline and well-drained soils (Batista 1991; Burkart *et al.* 1998). Floristic group XII, with species adapted to long periods of flooding, and floristic groups XVIII to XXI, associated with saline-alkaline soils and high surface saline concentration (Batista 1991; Burkart *et al.* 1998), represent the more rigorous extremes of both gradients. Generalist species, listed at the bottom of the table, respond to a coarser environmental grain (Kolasa 1989), represented by the entire region sampled. Nomenclature follows Cabrera (1963–70).

Floristic group	Community type	1	2	3	4	5	6	7	8	9	10	11
	Number of samples	93	74	80	102	82	90	47	67	59	35	20
I	<i>Wahlenbergia linarioides</i>	29
	<i>Tragia geraniifolia</i>	18
	<i>Vernonia rubricaulis</i>	18
	<i>Eryngium nudicaule</i>	17
	<i>Glandularia peruviana</i>	17
	<i>Baccharis spicata</i>	16
	<i>Briza brizoides</i>	14
	<i>Baccharis coridifolia</i>	11
II	<i>Diodia dasycephala</i>	71	31
	<i>Sida rhombifolia</i>	58	43
	<i>Aster montevidensis</i>	22	43
	<i>Solidago chilensis</i>	16	11
	<i>Echium plantagineum</i>	14	34
III	<i>Eryngium elegans</i>	.	30
	<i>Carduus microcephalus</i>	.	27
	<i>Facelis retusa</i>	.	16
	<i>Soliva pterosperma</i>	.	16
	<i>Silybum marianum</i>	.	15
	<i>Cyperus eragrostis</i>	.	12
	<i>Chrysanthemum leucanthemum</i>	.	12
IV	<i>Bromus unioloides</i>	20	43	56
	<i>Eleusine tristachya</i>	20	24	56	12	.
	<i>Turnera pinnatifida</i>	12	.	29
	<i>Jaborosa integrifolia</i>	23	.	33
V	<i>Crepis setosa</i>	.	.	51
	<i>Stipa caudata</i>	.	.	49
	<i>Spergula laevis</i>	.	.	33
	<i>Digitaria sanguinalis</i>	.	.	24
	<i>Geranium mölle</i>	.	.	16
	<i>Geranium dissectum</i>	.	.	16
VI	<i>Cynara cardunculus</i>	84	26	16	14
	<i>Ammi majus</i>	70	30	45	15
	<i>Centaurea calcitrapa</i>	48	62	50	28
	<i>Piptochaetium stipoides</i>	44	.	34	16
	<i>Carthamus lanatus</i>	43	54	.	28
	<i>Margyricarpus pinnatus</i>	42	54	.	28
	<i>Conyza chilensis</i>	41	11	.	19
	<i>Convolvulus hermanniae</i>	41	58	18	19
	<i>Chevreulia sarmentosa</i>	40	35	19	23
	<i>Eragrostis lugens</i>	36	26	19	23
	<i>Oxypetalum solanoides</i>	31	38	11	11
	<i>Physalis viscosa</i>	28	50	43	17
	<i>Melica brasiliana</i>	27	61	16	24
	<i>Briza subaristata</i>	12	38	.	12
VII	<i>Stipa trichotoma</i>	.	39	66	19
	<i>Hybanthus parviflorus</i>	.	30	25	19
	<i>Micropsis spathulata</i>	.	16	.	18
	<i>Trifolium dubium</i>	.	14	.	14
VIII	<i>Carduus acanthoides</i>	76	76	60	34	13
	<i>Piptochaetium bicolor</i>	74	76	15	55	23

Appendix I Continued

Floristic group	Community type	1	2	3	4	5	6	7	8	9	10	11
	Number of samples	93	74	80	102	82	90	47	67	59	35	20
	<i>Piptochaetium montevidense</i>	53	43	53	45	17
	<i>Asclepias mellodora</i>	27	.	50	30	34
	<i>Hypochoeris radicata</i>	28	69	39	28	16
	<i>Silene gallica</i>	20	64	.	35	20
	<i>Verbena montevidensis</i>	63	30	.	21	17
	<i>Juncus capillaceus</i>	45	22	.	17	12
	<i>Cuphea glutinosa</i>	37	30	.	23	11
	<i>Oxalis sp</i>	.	43	74	20	15
	<i>Glandularia dissecta</i>	.	39	10	27	18
IX	<i>Paspalum dilatatum</i>	98	92	.	64	60	20	.	.	.	23	.
	<i>Vulpia sp</i>	54	72	48	62	61	19
	<i>Cyperus reflexus</i>	50	55	39	19	13	27	.	.	22	.	.
	<i>Adesmia bicolor</i>	47	54	49	54	50	11
	<i>Danthonia montevidensis</i>	15	.	.	36	38	18
	<i>Stipa formicarum</i>	.	.	54	.	11	42
X	<i>Solanum glaucophyllum</i>	.	.	30	.	11	41	72
	<i>Pamphalea bupleurifolia</i>	.	.	.	11	24	47	26
	<i>Alternanthera philoxeroides</i>	17	50	79
	<i>Paspalidium paludivagum</i>	11	41	40
	<i>Leersia hexandra</i>	13	31	60
	<i>Agrostis jurgensii</i>	17	29	15
	<i>Eleocharis viridans</i>	15	.	21
XI	<i>Eleocharis macrostachya</i>	18
	<i>Gratiola peruviana</i>	21	21
	<i>Agrostis avenacea</i>	18	11
	<i>Echinochloa helodes</i>	11	40
	<i>Marsilea concinna</i>	16	28
XII	<i>Glyceria multiflora</i>	53
	<i>Ludwigia peploides</i>	51
	<i>Polygonum punctatum</i>	36
	<i>Echinodorus grandiflorus</i>	19
	<i>Lilaeopsis sp</i>	17
	<i>Scirpus californicus</i>	17
	<i>Paspalum lividum</i>	17
	<i>Luziola peruviana</i>	15
XIII	<i>Stipa papposa</i>	61	81	15	64	44	.	.	55	46	.	.
	<i>Stipa neesiana</i>	37	87	50	53	33	.	.	21	20	.	.
	<i>Bothriochloa laguroides</i>	86	81	43	70	56	.	.	12	14	.	.
XIV	<i>Eleocharis haumaniana</i>	20	21	19	.	.	17	15
	<i>Panicum gouinii</i>	20	42	26	.	.	23	.
XV	<i>Hydrocotyle sp</i>	28	28	18	.	49	.
	<i>Polyogon monspeliensis</i>	19	32	16	.	46	45
	<i>Apium sellowianum</i>	11	13	21	.	37	40
XVI	<i>Lepidium bonariense</i>	.	11	18	.	.	.
	<i>Parapholis incurva</i>	16	.	.	.
XVII	<i>Monerma cylindrica</i>	40	29	11	15
	<i>Hordeum stenostachys</i>	.	.	30	11	.	.	.	13	92	11	25
	<i>Nostoc sp</i>	.	.	14	.	.	.	17	34	70	.	.
	<i>Lepidium parodii</i>	28	31	.	.
	<i>Sporobolus pyramidatus</i>	28	80	.	.
	<i>Puccinellia glaucescens</i>	18	20	11	.
XVIII	<i>Pappophorum mucronulatum</i>	20	.	.
	<i>Acicarpa procumbens</i>	44	.	15
	<i>Chloris berroi</i>	37	.	.
	<i>Petunia parviflora</i>	25	.	.
	<i>Spergula villosa</i>	20	.	.
	<i>Senecio pinnatus</i>	22	.	.
	<i>Diplachne uninervia</i>	41	.	.

Appendix I *Continued*

Floristic group	Community type Number of samples	1	2	3	4	5	6	7	8	9	10	11
		93	74	80	102	82	90	47	67	59	35	20
XIX	<i>Picrosia longifolia</i>				29	.
	<i>Scirpus olneyi</i>					.		.	.		46	.
	<i>Bacopa monnieri</i>							.			17	
	<i>Triglochin striata</i>						57	.
	<i>Pluchea sagittalis</i>						.	.			17	
XX	<i>Spartina densiflora</i>		.	.					.		20	35
	<i>Sesuvium portulacastrum</i>								.		14	40
	<i>Salicornia ambigua</i>		.				.	.	19		14	95
XXI	<i>Hymenoxys anthemoides</i>					20
	<i>Heliotropium curassavicum</i>				19	.	40
	<i>Limonium multiflorum</i>							.			.	15
	<i>Cressa truxillensis</i>					50
Generalist species												
	<i>Lolium multiflorum</i>	84	69	86	79	88	74	21	72	49	54	25
	<i>Phyla canescens</i>	89	69	91	74	96	83	49	42	29	51	30
	<i>Aster squamatus</i>	51	12	38	35	54	77	51	39	29	69	50
	<i>Eryngium echinatum</i>	57	30	48	68	74	78	15	31	41	31	.
	<i>Spilanthes stolonifera</i>	44	42	68	72	72	67	17	25	41	23	.
	<i>Centaurium pulchellum</i>	69	64	34	69	78	39	.	82	24	11	35

Appendix II

Distribution of species from genus *Stipa* across inventories. X represents presence of the species at the correspondent inventory. Acronyms for inventories as in Fig. 1.

Species	M	C	A	L
<i>S. hyalina</i> (*)	X			
<i>S. charruana</i> (*)	X			
<i>S. philippii</i> (*)	X	X	X	X
<i>S. formicarum</i> (*)	X	X	X	X
<i>S. papposa</i>	X	X	X	X
<i>S. neesiana</i> (*)	X	X	X	X
<i>S. trichotoma</i> (*)		X	X	X
<i>S. brachychaeta</i>		X		X
<i>S. clarazii</i> (*)	X		X	
<i>S. caudata</i>			X	X
<i>S. melanosperma</i> (*)			X	
<i>S. ambigua</i>				X

(*) Species changed recently to genus *Nassella* (Barkworth 1990).