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Climatic and land-use drivers along a latitudinal gradient: species diversity in temperate grasslands on agricultural soils

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Agriculture; C_4 grasses; Grassland; Landscape fragmentation; Latitude; Pampa; Scales; Species diversity; Species turnover

Nomenclature
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Abstract

Questions: Do remaining mesophytic grasslands on soils with agricultural potential respond to a latitudinal gradient? Are climatic or land-use factors the principal drivers of regional and local diversity of these grasslands?

Location: Mesophytic grasslands, Argentine Pampas, Rio de la Plata grasslands.

Methods: The species presence and cover was recorded in each of 96 remnant grasslands on soils suitable for cropping, grouped into five sampling locations. In each region, CIs for γ-diversity and for the slope of species/area curves were estimated. Unconstrained ordination was applied to detect the principal gradients in floristic composition and correlation analysis to identify their main drivers. Mantel test was used to evaluate the correlation between floristic similarity and geographic distance, and with Euclidean distance in fragmentation and climatic variables. To rank the climatic and land-use factors that account for local species richness and percentge of exotics, we applied correlation analysis and regression models.

Results: Community composition (73% native species) was mainly related to climatic variables determined by latitude, with a slight influence of fragmentation variables. Regional species richness responded to latitude: γ-diversity decreased linearly with increasing distance from the Equator, as did the rate of species accumulation with expanding area. Alpha-diversity did not vary in a systematic way with latitude, being associated with landscape fragmentation and mean annual precipitation. Relative importance of C_4 grasses and mean percentage exotics showed opposite latitudinal tendencies, the former decreasing and the latter increasing towards the south.

Conclusions: Latitude was a strong determinant of regional diversity and community composition, but a partial driver for local species richness, mainly influenced by landscape fragmentation. While climatic and geographic drivers determined gradual latitudinal turnover in regional species pools, within regions land-use history, stochastic processes and biotic interactions were also important. All these patterns need to be considered together when delimiting grassland nature reserves for conservation of the most diverse ecosystems of this region, currently threatened by agricultural expansion and intensification.

Introduction

Faced with concerns about the possible effects of land-use and climatic change on biodiversity and ecosystem function (Foley et al. 2008), it is essential to provide information about the response of natural vegetation to climatic gradients (Hillebrand 2004; Thuiller 2007; Graae et al. 2012). Despite the fact that climate change has already caused alterations to the distribution of many plants and animals, leading to range contraction and species extinction, knowledge of how plant communities respond to climate may still allow us to avert species loss through

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rational conservation practices (Hoegh-Guldberg et al. 2008; Vitt et al. 2010). Grasslands are one of the most severely threatened ecosystems, as they are easily subjected to a variety of drastic perturbations, ranging from grazing by confined exotic cattle, introduction of exotic plant species, to complete replacement by either perennial or annual crops (Hoekstra et al. 2005; Gibson 2009). This last perturbation, replacement of the native grassland by an annual crop, is particularly severe as it determines reduction and fragmentation of the natural habitat of native species, with decreases in their frequency and eventually elimination from the landscape (Hodgson et al. 2005). The most severely threatened grassland communities are, therefore, those associated with deep, well-drained soils that can be readily incorporated into agriculture (Deák et al. 2016a,b). As agriculture expands, these grassland communities tend to occupy progressively smaller, isolated patches surrounded by vast extensions of cropland.

Studies along latitudinal gradients are a valuable and much needed complement to manipulation field experiments (Fukami & Wardle 2005; De Frenne et al. 2013) in order to design guidelines for sustainable management of remaining grasslands, to restore those replaced or to protect native populations from rapid environmental change. The detection of pattern in natural systems and the identification of its determinant factors depend critically on scale (Levin 1992; Gardner et al. 2001). Studies that search for species diversity pattern over large areas rarely discriminate components of landscape heterogeneity, as they are frequently based on regional floras (Willig et al. 2003; Stohlgren et al. 2005; Thuiller et al. 2005; Kreft & Jetz 2007; Qian et al. 2007; Mannion et al. 2014). Therefore, important processes of particular species specialization for aridity–humidity and topographic heterogeneity may be under-appreciated, generating a distorted perception of the gradient diversity patterns (Visser et al. 2014). To avoid this source of misinterpretation in the comparison among regions, research must focus on the same relative position in the landscape and/or the same community type. In this study we adopted this approach.

The South American Pampas are one of the main grassland biomes in the world largely replaced by crops following the intensification and expansion of agriculture (Soriano 1992; Gibson 2009; Viglizzo et al. 2011). The most replaced and fragmented community type is the zonal mesophytic grassland. In different areas within the region, sites of mesophytic grassland are surrounded with matrices of varying proportions of remnant grassland and crop fields. While the natural diversity in these zonal grasslands has been coupled with factors linked to biogeographic, evolutionary and dispersal history that shaped the regional flora (Ricklefs 2004), the current diversity in their remnants would exhibit association with the pattern and intensity of agricultural perturbation, which primarily affect the abundance and frequency of species within sites and across the landscape.

In this study, we assess the relative importance of climate and land fragmentation through agriculture as controls on the diversity and composition of the mesophytic grasslands of the Pampas. We hypothesize that the regional patterns of composition and diversity of these grasslands are still driven primarily by the climatic gradients that constrained the evolution and migration of plant species in the Pampas over the Holocene. Furthermore, we hypothesize that the local patterns of species composition and diversity of the remnant grasslands are nowadays accounted for to a large extent by varying degrees of landscape perturbation by agriculture. Relatively recent perturbation of grassland sites or their surroundings are likely to have affected such patterns of local diversity through both local extinctions and exotic species invasions. Test of these hypotheses using data from large vegetation surveys, remote sensing imagery and climate records may help understanding what might be the most severe impact of agriculture on the grassland biomes, and point to promising guidelines for the preservation of their natural biodiversity.

Methods

Study area

Within the Rio de la Plata grasslands (Soriano 1992), the present study covers around 160 000 km^2 (32°–38° S), a distance of 600 km in a straight line (57°–61° W). It encompasses three of the Pampean phytogeographic subdivisions: Mesopotamic, Rolling and Flooding Pampas (Fig. 1). The Pampas are included within the temperate sub-humid grasslands of South America (Gibson 2009), mean annual temperatures range from 18.5 °C in the north to 14 °C in the south, and mean annual precipitation of 1150 and 950 mm in the north and south, respectively. It is a vast and continuous plain formed by a deep mantle of loessic sediments of Pleistocene age deposited over a crystalline structure, which lies at a depth of 300–5000 m. To the north (Rolling and Mesopotamic Pampas) the relief is gently rolling with an extensive exoreic drainage network of rivers and valleys. To the south (Flooding Pampa), it is a large plain with low morphogenetic potential as a result of a very slight slope, with endorheic drainage leaving free water surfaces and extensive areas with lengthy flooding during winter (Chaneton et al. 2005).

All the area has been grazed with domestic cattle since the arrival of European settlers in the mid-1600s, and most arable land has been used for crops. Different plant communities associated with various habitat types are: mesophytic prairies, humid prairies, meadows and halophyte

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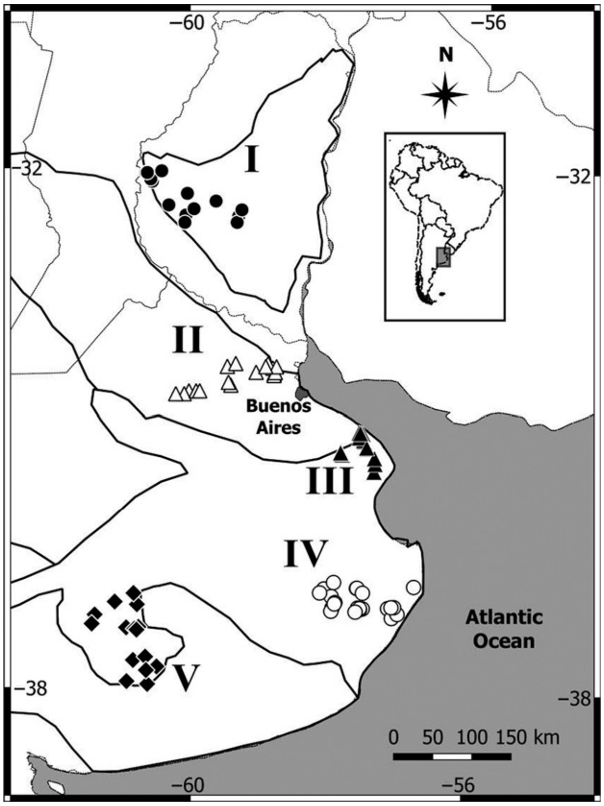

Fig. 1. Study area: roman numbers correspond to the five latitudinal regions; each point represents a sampling location. Region I: samples located in the Mesopotamic Pampa, region II in the Rolling Pampa, regions III, IV and V in the Flooding Pampa.

steppes (Perelman et al. 2001). In this study we focus on the mesophytic prairies on positive and convex terrain with deep well-drained soils suitable for agriculture, which are associated with Typic Hapludolls, Argiudolls and Vertic Argiudolls. Dominant genuses are *Stipa, Piptochaetium, Paspalum, Bothriochloa, Melica* and *Aristida* (Soriano 1992). These grasslands predominate in extensive areas of the Rolling and Mesopotamic Pampas, while in the Flooding Pampa they cover restricted areas in a matrix of azonal, halo-hydromorphic complexes strongly influenced by flooding (Perelman et al. 2001). In each of the Pampean subdivisions a different proportion of land surface has been modified by human activity, being converted mainly into croplands: 30% of the area remains as grasslands in the Rolling Pampa, 62% in the Mesopotamic Pampa and 89% in the Flooding Pampa (Viglizzo et al. 2011).

Sampling and data analysis

Ninety-six grasslands on deep soils without hydro-halomorphic limitations were surveyed, grouped into five regions located at different latitudes. Region I: mean latitude 33°25′ S, 19 samples; region II: 34°20′ S, 17 samples; region III: 35°40′ S, 20 samples; region IV: 36°50′ S, 20 samples and region V: 37°10′ S, 20 samples (Fig. 1). Each vegetation sample consisted of a complete list of vascular plants present in the site, and an estimate of species cover within an area of 25 m^2 (Mueller-Dombois & Ellenberg 1974). Sampling was carried out in late spring–early summer, when most species were present and easily identifiable through their reproductive organs. The floristic data belong to inventories carried out during a 15-yr period (1988–2003).

Precipitation records for the period 1998–2014 were obtained from the TRMM mission product 3b42, which provides daily precipitation at a spatial resolution of $0.25 \times 0.25°$ (https://trmm.gsfc.nasa.gov/3b42.html). Land surface temperature was used as a proxy for air temperature. Data for the 2000–2015 period was used, obtained from the MODIS/Terra LST/E 8-Day L3 Global 0.05Deg CMG (MOD11C2), at a spatial resolution of $0.05 \times 0.05°$. Grassland fragmentation was evaluated based on mean patch size (MPS) and number of patches (NumP) using a hexagonal grid of 6400 ha, as proposed in previous studies in this area (Baldi et al. 2006). Land cover was characterized at 30-m spatial resolution using four LANDSAT imagery dates of the 2003/2004 winter and summer seasons. The supervised classification was done using a maximum likelihood algorithm, with an overall accuracy of 89%. Agriculture (soybean, maize, sorghum, sunflower and winter cereals), water bodies, urban and miscellaneous classes were discarded in order to characterize only the grassland fragmentation.

The variability in floristic composition was evaluated through unconstrained ordination, CA applied to the presence/absence species matrix, excluding species present in <9% of sites (McGarigal et al. 2000). This method was used for identification of the main underlying patterns in floristic composition. Then we explored the association among site ordination scores in the first two axes with geographic location, climatic and fragmentation variables, through CA. Simultaneously we compared similarities in floristic composition with distances in climatic and fragmentation variables. We calculated the Jaccard similarity index for species presence/absence and the Euclidean distance for standardized fragmentation and climatic variables. Mantel test was applied to evaluate the correlation between floristic similarity with geographic distance, and then with distance in fragmentation and climatic variables.

Number of species in a region (γ-diversity) is represented by all species present in all sites of a region. As some species could have been missed during sampling, the first-order Jackknife index (Palmer 1990) was used to estimate the true number of species (1) and its variance (2)

$$\hat{\gamma} = \gamma_{\mathrm{obs}} + u\frac{n-1}{n} \tag{1}$$

$$\mathrm{Var}(\hat{\gamma}) = \frac{n-1}{n}\left(\sum_{s=1}^{\gamma_{\mathrm{obs}}} s^2 f_s - \frac{u^2}{n}\right) \tag{2}$$

where γ_{obs} is the observed species number in the n sites, u is the total number of unique species (recorded in only one site) and f_s is the number of sites containing s unique species.

Species–area curves were calculated through subsampling of a given size from all samples in each region (MjM Software Design, Gleneden Beach, OR, US). The slope of the relationship between the two-way transformed (ln) species–area curve and CIs for this slope were estimated through ordinary least squares (OLS).

For each sample we calculated the species richness per site (α-diversity), the percentage of exotics per site, and the number and cover of native grasses per site. For comparison among regions, simple ANOVA and Tukey tests were applied for data meeting all assumptions, and multiple response permutation procedure (MRPP; Biondini et al. 1985) for comparison in mean floristic composition similarity. The photosynthetic pathway (C_3 or C_4) was determined on the basis of published information (mainly Sánchez & Arriaga 1990; Waller & Lewis 1979). For identification of the main determinants of local richness and proportion of C_4 and exotic species, CA was applied to describe the direct and indirect associations among the set of variables, followed by OLS linear regression. Confounding variables too highly inter-correlated and variables with higher indirect than direct correlation with the response variables were not included in the regression model.

Results

From the total of 359 species recorded, of which 73% were native, 35 species had medium-high constancy values along the entire latitudinal gradient, which is 9.3% of all native species and 10.2% of all exotics, 14 of which are native perennial grasses (Table 1). Native grasses corresponded to 31.3% of site richness and 60.5% of site cover. Native species cover did not show differences among latitudes ($R^2 = 0.017$; mean = 76.3 ± 1.2%, $n = 96$).

Unconstrained site ordination based on presence/absence of all species present in eight or more sites (171 species) revealed the existence of species turnover among the mesophytic grasslands of different regions. The pattern of site distribution in the ordination graph resembled the geographic location of samples (Fig. 1); to emphasize this similarity, the first ordination axis was represented along the vertical (Fig. 2). The first two axes together explained only 23% of total inertia but clearly grouped the samples according to the region where they were collected. In concordance with the ordination, we also found significant differences in total floristic composition among grasslands of the different latitudes (MRPP, $P < 0.0001$).

The first axis ordered vegetation samples pole-ward from region I to V. Sample scores correlated significantly and positively with latitude ($r = 0.94$) and also with mean annual ($r = 0.90$) and winter (Jul) temperatures ($r = 0.96$). It correlated negatively with intra-annual monthly temperature variation ($r = -0.96$) and inter-annual variation in Jul temperature ($r = -0.75$) and positively with mean annual precipitation ($r = 0.83$). The second axis represented the contrast between regions I to V on the left and III to IV on the right and is related to longitude, a gradient of half the extent of the former in this study. The second axis sample scores correlated significantly and positively with longitude ($r = 0.94$) and mean grassland patch size ($r = 0.68$) and negatively with intra-annual variation in precipitation ($r = -0.63$) and number of patches ($r = -0.56$).

Mean Jaccard similarity index based on presence absence for each region (I: 39.9, II: 54.1, III: 58.3, IV: 61.5 and V: 55.5) showed a weak relation to latitude ($R^2 = 0.70$, $P = 0.08$), with higher species turnover among sites of the northern region. The Mantel correlation test showed significant association between Jaccard floristic similarity and geographic distance ($r = -0.73$, $P < 0.001$), largely explained by the significant association of this floristic similarity with Euclidean climatic distance ($r = -0.68$, $P < 0.001$). This association increased slightly with the addition of fragmentation distance ($r = -0.71$, $P < 0.001$). Decay in Jaccard floristic similarity with climatic distance fitted a second-order polynomial regression ($R^2 = 0.48$, $P < 0.001$; Fig. 3).

Regional species richness responded to latitude: the Jackknife estimate of γ-diversity decreased linearly ($R^2 = 0.96$, slope = −30.3 species/degree, $n = 5$, $P = 0.0031$) from 304 species in the north to 148 species in the south (Table 2, Fig. 4a). The slope of the two-way transformed (ln) species–area curve decreased significantly with latitude. Regions I and II presented the largest slope with high γ-diversity while III, IV and V had the lowest slope (Table 2).

Alpha-diversity did not vary in a systematic way with latitude. Region III presented the highest mean richness per site (Fig. 4a) in concordance with the higher mean patch size (Fig. 4c). In mean patch size also region IV differed significantly from regions I and II. Although local richness showed no latitudinal response, some components of diversity at this scale do so. Mean percentage exotic species (Fig. 4b) and mean percentage C_4 grasses (Fig. 4d) showed opposite latitudinal tendencies, the

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Table 1. Species with wide distribution along the gradient (species present in all regions and with constancy values >40% in at least three of them): percentage constancy within a region; species longevity (L: p = perennial, a = annual) and origin (O: n = natives, e = exotics). Nomenclature follows: http://www2.darwin.edu.ar/Proyectos/FloraArgentina/FA.asp.

	I	II	III	IV	V			
Mean latitude	32.36	34.44	35.23	37.03	37.45			
Species/number of sites	19	17	20	20	20	Family	L	O
Bothriochloa laguroides	78.9	94.1	90.0	85.0	55.0	Poaceae	p	n
Chascolytrum subaristatum	63.2	94.1	50.0	25.0	10.0	Poaceae	p	n
Bromus catharticus	73.7	64.7	45.0	40.0	95.0	Poaceae	p	n
Eragrostis lugens	78.9	88.2	25.0	10.0	30.0	Poaceae	p	n
Melica brasiliana	31.6	76.5	80.0	50.0	35.0	Poaceae	p	n
Piptochaetium bicolor	5.3	41.2	85.0	95.0	25.0	Poaceae	p	n
Piptochaetium montevidense	26.3	47.1	55.0	40.0	80.0	Poaceae	p	n
Setaria parviflora	42.1	52.9	100.0	85.0	25.0	Poaceae	p	n
Sporobolus indicus	42.1	47.1	45.0	95.0	70.0	Poaceae	p	n
Nasella neesiana	89.5	94.1	65.0	80.0	80.0	Poaceae	p	n
Jarava plumosa	84.2	100.0	75.0	65.0	45.0	Poaceae	p	n
Carex bonariensis	15.8	52.9	65.0	25.0	95.0	Cyperaceae	p	n
Cyperus reflexus	10.5	52.9	85.0	60.0	10.0	Cyperaceae	p	n
Juncus imbricatus	31.6	82.4	85.0	80.0	70.0	Juncaceae	p	n
Eryngium eburneum + horridum	78.9	58.8	70.0	65.0	10.0	Apiaceae	p	n
Cyclospermum leptophyllum	78.9	70.6	80.0	80.0	65.0	Apiaceae	a	n
Oxypetalum solanoides	63.2	76.5	80.0	65.0	25.0	Asclepiadaceae	p	n
Ambrosia tenuifolia	94.7	76.5	90.0	90.0	35.0	Asteraceae	p	n
Berroa gnaphalioides	26.3	64.7	65.0	75.0	75.0	Asteraceae	p	n
Acmella decumbens	15.8	47.1	70.0	45.0	55.0	Asteraceae	p	n
Conyza blackei	10.5	41.2	55.0	35.0	50.0	Asteraceae	a	n
Conyza bonariensis	52.6	58.8	90.0	65.0	90.0	Asteraceae	a	n
Dichondra microcalyx	57.9	41.2	60.0	45.0	40.0	Convolvulaceae	p	n
Adesmia bicolor	21.1	11.8	75.0	95.0	55.0	Fabaceae	p	n
Agalinis communis	26.3	76.5	60.0	75.0	10.0	Scrophulariaceae	a	n
Physalis viscosa	57.9	41.2	30.0	70.0	80.0	Solanaceae	p	n
Phyla nodiflora	26.3	70.6	95.0	80.0	85.0	Verbenaceae	p	n
Cirsium vulgare	73.7	70.6	90.0	70.0	60.0	Asteraceae	a	e
Medicago lupulina	84.2	76.5	75.0	85.0	50.0	Fabaceae	a	e
Ammi majus	31.6	41.2	45.0	65.0	85.0	Apiaceae	a	e
Centaurea calcitrapa	15.8	58.8	50.0	80.0	85.0	Asteraceae	a	e
Centaurium pulchellum	31.6	100.0	95.0	75.0	25.0	Gentianaceae	a	e
Lolium multiflorum	63.2	88.2	100.0	85.0	100.0	Poaceae	a	e
Cynodon dactylon	78.9	88.2	35.0	10.0	40.0	Poaceae	p	e
Hypochaeris radicata	5.3	88.2	90.0	100.0	55.0	Asteraceae	p	e

former increasing and the latter decreasing towards the south.

The main environmental factor that explained the variation in local richness was mean patch size, followed by mean annual precipitation (Table 3). On the other hand, two important components of local richness, percentage C_4 grasses and percentage exotics showed significant relationships with a factor associated with the latitudinal gradient: mean Jul temperature, the coldest month in the Southern Hemisphere. Percentage of C_4 grasses was also explained by inter-annual variability in precipitation, while percentage exotics was in turn influenced by number of C_4 grasses and by mean annual precipitation (Table 3).

Discussion

Severely threatened grassland communities, those on soils with agricultural potential, exhibited substantial latitudinal variation in correspondence with climatic and geographic gradients. While those drivers determined gradual turnover in regional species pools, within regions stochastic processes played an important role. Our results do not contradict the fact that habitat heterogeneity is the best predictor of species diversity (Perelman et al. 2001; Stohlgren et al. 2005; Moeslund et al. 2013), as we intentionally limited the extent of the internal heterogeneity explored within each region so as to focus our study on one community type.

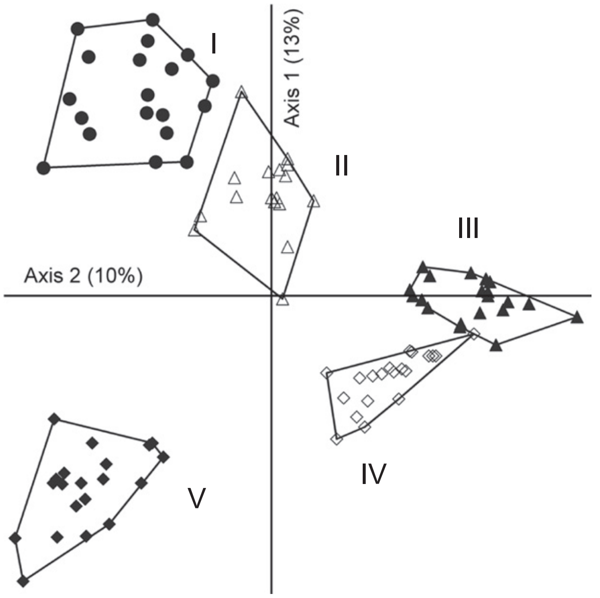

Fig. 2. Unconstrained site ordination obtained through CA applied to plant species presence/absence. Axes were interchanged to emphasize the similarity with geographic location of the different regions (Fig. 1). Closed polygons (convex hulls) enclose all sites of a region.

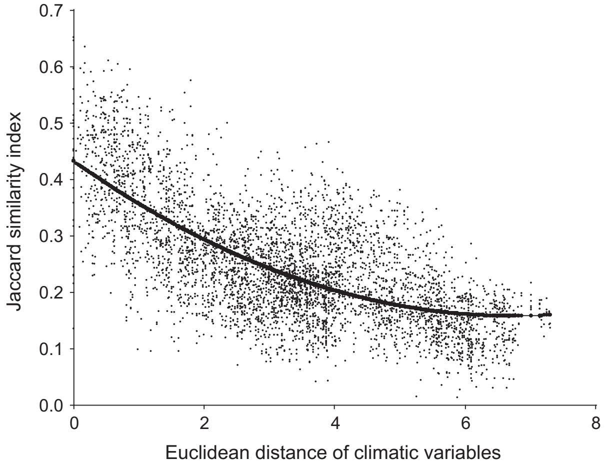

Fig. 3. Floristic similarity among sites plotted against their climatic distance. Solid line characterizes the ordinary least squares linear regression model ($R^2 = 0.48$, $P < 0.001$).

Unrestricted ordination revealed the response of plant communities to latitude, which is correlated with variables associated with the water–energy dynamics hypothesis (Kreft & Jetz 2007): mean annual precipitation, inter-annual variability and minimum temperature. Second, it showed association with landscape fragmentation and variability of intra-annual precipitation. As seasonal variation in precipitation increases with distance from the Atlantic Ocean, the variability of intra-annual precipitation may be a sign of continentality. This result complements the functional diversity response to water body proximity found from remote sensing at ecosystem level in South American temperate environments (Alcaraz-Segura et al. 2013). Floristic turnover with increasing geographic distance, mostly explained by climatic variables (Mantel correlation test), is consistent with predictions derived both from the neutral theory of spatially limited dispersal and from the hypothesis of environmental control of species distribution (Tuomisto et al. 2003).

Table 2. Regional diversity structure of the different regions of the Pampa grasslands: γ-diversity (first Jacknife estimate and SE in brackets). γ-diversity decreased linearly with latitude ($R^2 = 0.96$, slope = −30.3 species/degree, $P = 0.0031$). Slope of linearized species–area curve (point and CI estimations).

Region	Mean Latitude (°S)	γ-Diversity	Slope Species–Area Curve	CI 95% Slope
I	32.36	304 (10.5)	0.463	0.43–0.50
II	34.44	221 (8,7)	0.363	0.33–0.39
III	35.23	231 (9.4)	0.313	0.29–0.33
IV	37.03	155 (4.9)	0.287	0.26–0.31
V	37.45	148 (7.6)	0.285	0.25–0.32

Although the ordination explained a low fraction of the compositional variability, it was sufficient to differentiate the mesophytic grasslands between regions. Within each region, species composition variability among patches of the same community remains largely unexplained, probably due to stochastic factors, which have a strong influence on community assembly in other productive ecosystems (Chase 2010). In our study, we focused on the most productive grasslands of the region (Aragón & Oesterheld 2008), excluding the influence of soil salinity and flooding, the primary underlying cause of co-ordinated species turnover in these grasslands (Perelman et al. 2001).

The regional species pool of the mesophytic grasslands of the Pampas decreases in size with increasing distance from the Equator, as reported for other world ecosystems (Hillebrand 2004; Kreft & Jetz 2007). This relationship also holds for the Uruguayan grasslands, where 322 species were recorded in the Centro Sur region (Bresciano et al. 2014), located at lower latitude than region I in this paper. Yet, two regions deviated slightly from this general latitudinal trend. In region II, where grassland replacement by crop fields is highest, our target grasslands exhibited relatively depressed γ-diversity. In region III, where replacement is minimal, the mesophytic grasslands exhibited increased γ-diversity. These patterns could represent early signs of fragmentation impact on species pool size.

As reported by other authors (Qian et al. 2007; Drakare et al. 2006), the rate of species accumulation with increasing area decreased with latitude. Species–area curves for sites of the same community type can be

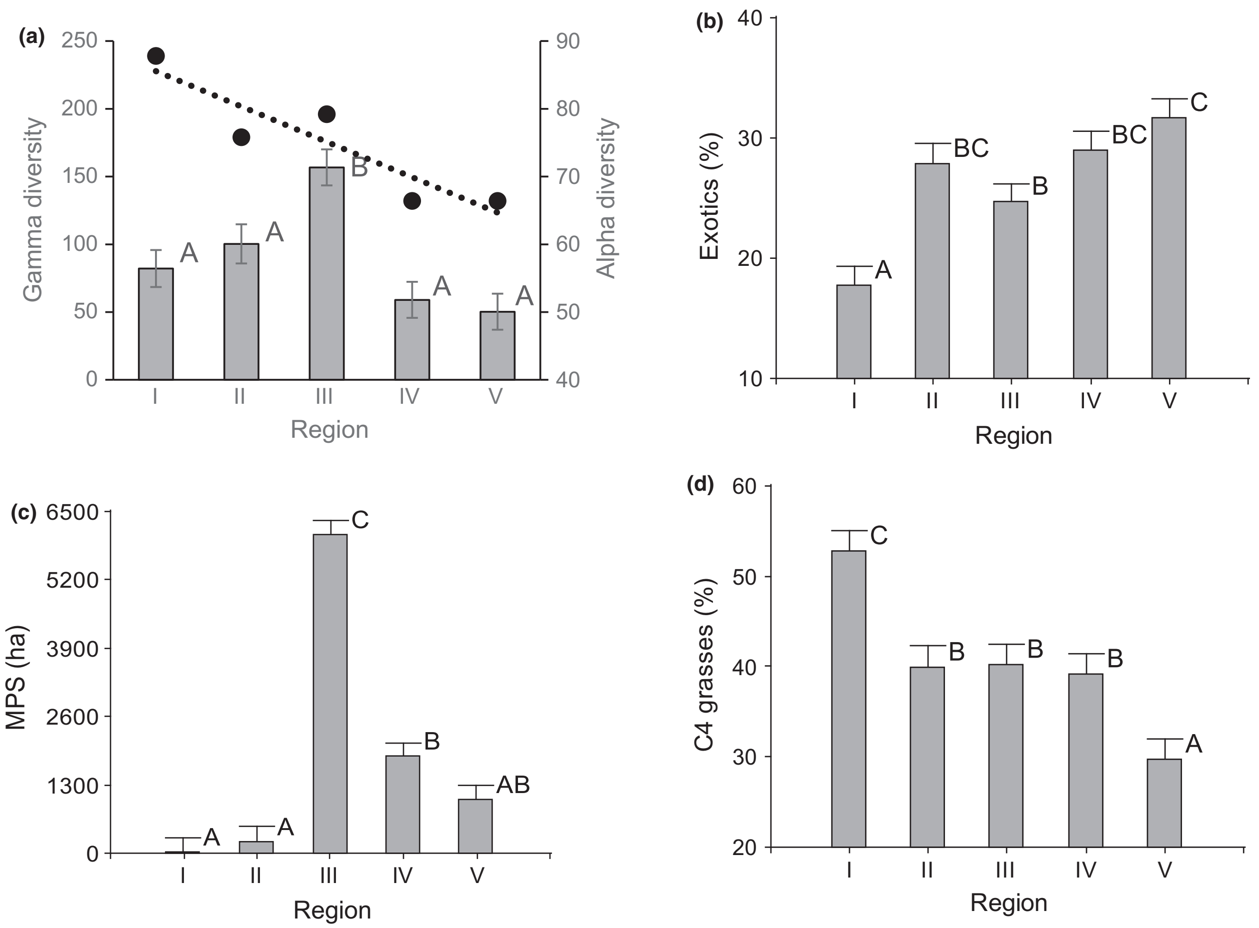

Fig. 4. Gamma-diversity (full circles and dotted line) and mean number of species per site (**a**), mean percentage number of exotic species (**b**), mean patch size (**c**) and mean percentage of C_4 grasses (**d**), for each latitudinal region. Vertical capped lines are SE. Means labelled with different letters differ at $P < 0.05$ (Tukey test after ANOVA).

Table 3. Regression models for local diversity variables. MPS = mean patch size, MAP = mean annual precipitation, MJT = mean July (Southern Hemisphere winter) temperature, PCV = intra-annual precipitation coefficient of variation.

Response Variable	Predictor Variables	R^2	AIC
Local Richness	Constant = 8.87 MPS (0.002) MAP (0.04)	0.32	749
% C_4 Grass Species	Constant = 30.42 MJT (4.61) PCV (−1.29)	0.39	713
% Exotics	Constant = 37.65 C_4 sp. number (−1.14) MJT (−3.12) MAP (0.02)	0.46	631

homologated to those arising from geographic units similar to islands (Dengler 2009), and thus are particularly appropriate for addressing the question of the latitudinal response of the relationship between area and species richness. At this scale, our study produces results suitable to disentangle the habitat heterogeneity effect on plant species richness from the area effect generated by dispersal factors (Steinmann et al. 2011).

Local species richness appeared to be poorly associated with the size of the corresponding regional pool. Therefore, association between local richness and the latitudinal gradient was weak at most. Species richness at this scale was explained by landscape fragmentation, as was also the second axis of the ordination based on floristic composition. Theoretical and empirical studies (Cerezo et al. 2010; Didham et al. 2012; Fahrig 2017) suggest that the effects of habitat loss are generally higher than those of habitat fragmentation *per se*. In our study, the level of landscape fragmentation is not only restricted to habitat configuration (Villard & Metzger 2014), but also involved large differences in remaining grassland cover among regions (Viglizzo et al. 2011). Our results add to the evidence that habitat loss is an important cause of diversity decline, which does not mean it supports responses to habitat fragmentation independent of habitat amount. The slight change in the response of γ-diversity to latitude for regions at both extremes of landscape fragmentation seems to indicate that land-use impact on biodiversity crosses from local to regional scales in the most severe conditions.

The small percentage of exotics found in regions with high γ-diversity, and the negative relationship with richness of C_4 warm-season grasses (mostly native perennials), provided some evidence of biotic resistance of the native community to invasion, as observed in the humid mesophytic prairies, a similar community of the Flooding Pampa (Perelman et al. 2007). This relationship holds also for the Uruguayan grasslands (Bresciano et al. 2014) that have 60% of C_4 grasses and 11% of exotic species vs 53% and 18%, respectively, in region I. Exotics also responded to climatic factors related to latitude, increasing with lower winter temperatures. The mainly Mediterranean origin of the species introduced into the Pampas since European colonization in the 16th century, most of them currently naturalized to these environments (Perelman et al. 2007; Poggio et al. 2015), is another possible explanation for the increase in exotics with latitude in these grasslands.

Urban (2015) assigned the highest world extinction risk to South American biomes. While the advance of agricultural expansion and intensification endangers one of the most diverse ecosystems of this region, conservation policy has prioritized “forest” over the “non-forest” ecosystems (Overbeck et al. 2015). From a conservation viewpoint, it is important to protect these grasslands where, as shown by our results, 31% of site richness and 60% of site cover corresponds to native grasses, which in addition have an important influence in preserving the bird community structure (Cerezo et al. 2011). Despite the observed latitudinal changes in the floristic composition of this community, there are more than 30 ubiquitous species that occur in all regions with noteworthy cover, which provide an interesting resource for research in latitudinal adaptations in life-history strategy traits associated to intraspecific variability (Davis et al. 2005; Woods et al. 2012; De Frenne et al. 2013).

Conclusions

Along this 5° latitudinal gradient, the predominant drivers of grassland diversity at a broad spatial scale were the climatic variables associated with latitude, while at local scale, land-use variables and biotic interactions prevailed.

Based on our analysis, we suggest the following broad guidelines for efforts directed to the preservation or restoration of temperate grasslands with agricultural potential: (1) because floristic differences are substantial among regions, efforts in one region do not compensate for lack of initiatives in another, at least from the standpoint of biodiversity preservation; (2) the region subjected to the highest intensity of agriculture is the most endangered, therefore preservation or restoration initiatives are urgently needed therein; (3) the ubiquitous species that occur in all regions might be the most successful candidates for the restoration of vegetation, at least maintaining the structure of the mesophytic grasslands.

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Graphical Abstract

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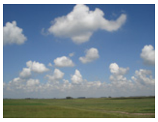

In remnant temperate grasslands on Argentine agricultural soils, latitudinal climatic gradients associated to the water-energy dynamics hypothesis were a strong determinant of regional diversity and community composition, but a partial driver for local species richness, mainly influenced by landscape fragmentation. While climate determined gradual latitudinal turnover in regional species pools, stochastic processes played an important role on community composition variation within regions. Our results provide promising guidelines for the preservation of the natural biodiversity of these ecosystems, severely threatened by agricultural expansion and intensification. Photo credit: P. M. Tognetti.