Small-scale spatial dynamics of vegetation in a grazed Uruguayan grassland

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Abstract   We explored the small-scale plant species mobility in a subhumid native grassland subjected to grazing by cattle in south-western Uruguay. We established four permanent plots of 40×40 cm, divided in 16×16 cells. In each cell, the presence of species was seasonally recorded for 2 years and annually recorded for 4 years. By nesting the cells, we studied the mobility at different scales, from 6.25 cm^2 to 400 cm^2. At each scale we measured species richness, cumulative richness and the turnover rates of the dominant species. We found that the cumulative species richness was an increasing power function, with higher accumulation rates with smaller spatial scale. Although species richness showed seasonal fluctuations, the mean species richness was constant during the study period. We detected significant spatio-temporal variability in mobility patterns among species. Certain species showed a high capacity to colonize new sites, whereas other species rotate among sites that they previously occupied. Grazed communities in Uruguayan Campos are structured as a dense matrix of perennials grasses and forbs, where vegetative propagation is the main form of growth of the species. The small-scale dynamics and the high variability in the mobility characteristics could be linked with the diversity of growth forms and spatial strategies of the species in this community. We believe that a high degree of small-scale spatial dynamics contribute to explain the species coexistence and the apparent stability of communities at local scales.

Key words: Río de la Plata grasslands, species mobility, turnover rates.

INTRODUCTION

Several authors proposed that different mechanisms would determine coexistence and plant richness (Qian & Ricklefs 2000; Chase & Leibold 2002). The relative importance of these different mechanisms varied according to the spatial scale considered (Shmida & Wilson 1985).

At regional scales, factors associated to resource availability (Tilman 1982; Crawley 1986) and the species pool (Taylor *et al.* 1990; Glenn & Collins 1992) seems to control plant richness.

At the local scale habitat heterogeneity, mass effects, species interactions and disturbances become the dominant factors (Terborgh 1977; Connell 1978; Shmida & Wilson 1985). Grazing is a key disturbance in grasslands (McNaughton 1983, 1985) that may either increase or decrease species richness. At even smaller scales, plant mobility would determine coexistence and richness (Bell 1984), and may also explain

richness patterns at higher scales (Palmer 1992). Grasslands are an ideal system to study the importance of mobility on coexistence and richness patterns.

Most of the studies that explored the small-scale dynamics of plant communities have been carried out in European dry grasslands. Such environments are characterized by a high proportion of annuals, and species turnover is associated with frequent and severe droughts (Herben *et al.* 1993a,b; van der Maarel & Sykes 1993, 1997; van der Maarel *et al.* 1995; Geißelbrecht-Taferner *et al.* 1997) and high rates of gap formation (van der Maarel & Sykes 1997; Palmer & Rusch 2001). Snow cover and severe winters would play also an important role in resetting the system every year.

In subhumid and humid grasslands with almost no winter dormancy (as the Río de la Plata grasslands in South America), experimental evidences showed that, at local scale, grazing increased species richness by reducing the dominance of superior competitors (Sala *et al.* 1986; Altesor *et al.* 1998, 2005, 2006; Chaneton *et al.* 2002; Rodríguez *et al.* 2003). Grazing leads to a dense matrix of perennial grasses with a second group of interstitial, less abundant species (subdominant grasses and forbs) (Rodríguez *et al.* 2003). Annuals are scarce and there are not real gaps.

The Rio de la Plata grasslands comprise one of the largest areas of natural temperate subhumid grasslands

in the world (Soriano 1991). They occupy more than 70 000 km², across eastern Argentina, Uruguay and southern Brazil (Soriano 1991) and represent one of the highest diversity grasslands with more than 400 species of grasses (Cabrera 1970; Sala *et al.* 1986). Regional studies have highlighted that the major determinants of species diversity are, aside the regional pool of species, water availability, flooding regime and soil sodicity (Faccelli *et al.* 1988; Perelman *et al.* 2001; Chaneton *et al.* 2002; Lezama *et al.* 2006). Because of the low thermal amplitude (Paruelo *et al.* 1995) of the region, there is not a clear dormancy period and the grassland canopy remains photosynthetically active year round (Guerschman & Paruelo 2005). What are the controls of species coexistence at small scales under a less seasonal climate, continuous grazing and an almost complete vegetation cover? Is space availability a limiting factor for species colonization? Do space utilization strategies vary with scale? These questions remain unanswered especially for communities as those in the Uruguayan Campos.

All the studies on the small-scale dynamics of grassland species have been carried out on permanent plots or transects, with a spatial resolution that ranges from 1 cm² (Thórhallsdóttir 1990) to 2.25 m² (Klimeš 1999). These studies developed or applied specific methods to describe small-spatial dynamics: cumulative species richness and cumulative species frequency (van der Maarel & Sykes 1993; van der Maarel *et al.* 1995; Geißelbrecht-Taferner *et al.* 1997; Klimeš 1999), species persistence (Herben *et al.* 1993b), seed establishment patterns and turnover rates (Rusch & van der Maarel 1992) and variability in the spatial association of the species (Thórhallsdóttir 1990; Herben *et al.* 1993a; Herben 1996). Palmer and Rusch (2001) compared the performance of these methods and direct mobility measures, derived from metapopulation theory.

In Uruguayan grasslands, the only study at small scales (Altesor *et al.* 1999) grouped dominant species in four types of spatial strategies: (i) persisting over the year in the same cell without showing any type of mobility; (ii) continuously growing because of the solid advancing front of ramets, persisting in the same cells; (iii) not persisting in the same cells; and (iv) multi-strategy with high persistence an both high short and long-distance spread.

In this paper, we report two aspects of the temporal dynamics of plant species mobility in continuously grazed grassland: (i) seasonal and annual changes in cumulative species numbers and frequencies in nested subplots; and (ii) a description of annual species turnover during 4 years. Our objectives were: (i) to describe the mobility patterns of the dominant species; (ii) to test the hypothesis by van der Maarel and Sykes (1997) that species accumulation rate and mobility increases with decreasing scale; and (iii) to compare the recorded species cumulative frequencies with two null models of extremely mobile types.

METHODS

Study area

The study area was located in Mal Abrigo, Departamento de San José, south-western Uruguay (34°21′S, 56°43′W). For the study period (between 1995 and 2000), the mean annual precipitation was 857 mm and mean annual temperature 16.4°C, with a mean of 10.7°C in July and 22.2°C in January. The soils are shallow, developed on loam-clay sediments deposited on the crystalline basement. Phytogeographically, the study site belongs to the Southern Campos of the Río de la Plata grasslands. In these communities, grazing usually leads to a two-strata system: a low and dense stratum, no more than 5 cm high, and a higher stratum of bunch grasses and small woody plants (Soriano 1991). The study area is under continuous cattle grazing at a density of 0.5 cows per hectare and it has not been cultivated during the last 25 years.

In 1995, a rectangular plot of 12 m × 15 m was established in a homogeneous area. Inside this plot, four permanent quadrats of 40 cm × 40 cm were randomly established. At each sampling date, an aluminium frame with a grid of 16 × 16 cells, 2.5 cm × 2.5 cm each, was placed on each quadrat. The presence of species that were rooted in each cell was recorded seasonally (February, May, August and November) during 1996 and 1997, and in May 1998 and May 1999. For rosettes, we recorded the presence in a cell if the plant covered more than 50%. Nesting the smallest cells allowed us to study successively greater scales:

1/256 scale: 2.5 cm × 2.5 cm cells (0.000625 m²).
1/64 scale: 5 cm × 5 cm subquadrats (0.0025 m²).
1/16 scale: 10 cm × 10 cm subquadrats (0.01 m²).
1/4 scale: 20 cm × 20 cm subquadrats (0.04 m²).
Quadrat scale (not nested): each of the quadrats (0.16 m²).

A month before each sampling date, the rectangular plot was fenced to prevent defoliation and dunging by cattle.

Species richness

To estimate the mobility for the whole community, we calculated the average richness and average cumulative richness for all nested scales, considering all species and the four quadrats as replicates. The seasonal samples (those from May 1996 to November 1997) were used for this analysis. For this dataset, we calculated the number of frequent species (appearing at

least in 80% of the cells) and the cumulative number of species with this frequency value.

Temporal trends in average species richness were analysed using linear regression models. The relationship between average cumulative richness and time was analysed using a power function regression model. The hypothesis that the species accumulation rate (an indirect measure of mobility) increases with decreasing scale (van der Maarel & Sykes 1997) was tested by a slope homogeneity test (Zar 1996) on the slopes of the log–log transformed cumulative richness regression curves.

Species frequency

Frequency was analysed annually (each May from 1996 to 1999), considering only those species with a spatio-temporal frequency higher than 5% for each pair of adjacent years. This spatio-temporal frequency was calculated as:

$$F = ((N_{t,t-1} + N_t + N_{t-1})/256) \times 100$$

Where, $N_{t,t-1}$ represents the number of quadrats in which the species was present in the year t and year t-1 (one year persistence), N_t, is the number of quadrats in which the species appeared only in year t, and N_{t-1} is the number of quadrats in which the species appeared only in the previous year. The species that fit this criterion are listed in Table 1. For these species, we calculated the frequency as the number of cells or subquadrats in which the species occurred each year. The cumulative frequency was also calculated as the number of cells or subquadrats in which the species was observed since the beginning of the study. The observed cumulative frequencies for all the scales

in each plot were compared with the cumulative frequency predicted by two null models (van der Maarel & Sykes 1997; Klimeš 1999):

- Random mobility: In this model, the distribution of each species in the plot is randomly generated, taking into account the observed frequency each year. This model considers all species as annuals with random dispersal over the cells.
- Restricted mobility: In this model, species are allocated to the same cell where they occurred earlier. When the frequency in the following year was higher, the occurrences in the previous year were used, and the remaining new occurrences were distributed randomly over the cells. When the frequency in the following year was lower, the cells occupied in the previous year were randomly freed until they reached the actual frequency.

For each species in each quadrat, we generated 20 000 randomizations (Manly 1991) of the observed frequency each year in order to generate the expected distribution of cumulative frequency for that year. These distributions were used to compare the observed cumulative frequency each year by means of one-tailed tests. These models were implemented in language C.

Turnover rates

We calculated turnover rates of the species selected according to the spatio-temporal frequency criterion, for the 1/256 and 1/16 scales, in order to determine the specific mobility capabilities of the species:

$$T = I + D$$

Where, 'T' represents turnover, 'I' represents increments (immigration events, the number of cells where

Table 1. List of dominant species (with spatio-temporal frequency >5%), families, species code, life-cycle, growth habit, growth period, type of vegetative spread and Spatial strategy exhibited (according to Altesor *et al.* 1999): 1, high persistence without mobility, 2, high persistence and short distance mobility, 3, low persistence and high short distance mobility, 4. multi-strategy species with high persistence, short distance and long distance mobility. En dashes (–) mean that information was not available for the trait. Nomenclature is according to Lombardo (1984)

Species	Family	Code	Persistence	Habit	Growth period	Veg. spread	Spatial strategy
Andropogon ternatus	Poaceae	Ant	Perennial	Erect	Warm-season	Short rhizomes	4
Aristida uruguayensis	Poaceae	Aru	Perennial	Erect	Warm-season	Short rhizomes	4
Axonopus affinis	Poaceae	Axa	Perennial	Prostrate	Warm-season	Stolons	–
Botriochloa laguroides	Poaceae	Bol	Perennial	Erect	Warm-season	Short rhizomes	–
Bulbostylis juncoides	Cyperaceae	Buj	Perennial	Erect	Warm-season	Short rhizomes	3
Carex phalaroides	Cyperaceae	Cap	Perennial	Erect	Cool-season	Short rhizomes	4
Chaptalia exscapa	Asteraceae	Che	Perennial	Rosette	Cool-season	Bulb	1
Chaptalia pilloseloides	Asteraceae	Chp	Perennial	Rosette	Cool-season	–	1
Chevreulia sarmentosa	Asteraceae	Chs	Perennial	Rosette	Cool-season	–	2
Oxalis macachin	Oxalidaceae	Oxm	Perennial	Rosette	Cool-season	Bulb	1
Paspalum notatum	Poaceae	Pat	Perennial	Prostrate	Warm-season	Long rhizomes	2
Richardia humistrata	Rubiaceae	Rih	Perennial	Rosette	Warm-season	–	2
Schiyzachirium tenerum	Poaceae	Sct	Perennial	Erect	Warm-season	Short rhizomes	4

the species appeared for the first time), and 'D' represents decrements (extinction events, the number of cells where the species disappeared, relative to the previous year). With 4 years we have three periods with four replicates each. Because these turnover rates are dependent upon the frequency of the particular species, we standardized them as follow: after fitting the quadratic regression model to the turnover values and the mean frequency between 2 years (for all species, quadrats and years together), we considered the residuals of the regression as measures of the standardized turnover. Turnover values below or above those expected based on the species mean frequencies were identified by a Box and Whisker plot of the residuals (Wilkinson 1990). We identified outlier and far outside values. Outliers are turnover values outside the boundaries defined as:

Lower boundary = 25% percentile − 1.5 × (75% percentile − 25% percentile)

Upper boundary = 75% percentile + 1.5 × (75% percentile − 25% percentile)

Far outside values are turnover values outside the outer boundaries:

Lower boundary = 25% percentile − 3.0 × (75% percentile − 25% percentile)

Upper boundary = 75% percentile + 3.0 × (75% percentile − 25% percentile)

We applied a non-parametric ANOVA (Kruskal–Wallis test, Zar 1996) to the turnover values and turnover *versus* mean frequency regression residuals, considering the species as grouping variables. When the Kruskal–Wallis test was significant, we applied a non-parametric multiple comparison test (Nemenyi joint-rank test, Zar 1996) to identify the most and least mobile species.

The ability of different species to move to new sites was estimated by means of the proportion of new appearances respect to the annual frequency in two scales (1/256 and 1/16). To detect differences among species, we applied a Kruskal–Wallis test. We then applied the non-parametric version of the Dunn test for tied ranks (Zar 1996).

RESULTS

Species richness

During the study, 90 species were recorded. The percentage of grasses was 36%; forbs represented 62% and shrubs 2%. Among grasses the most frequent were native C_4 species (68% of the grass species).

Species richness did not show trends during the period considered (Fig. 1a, Table 2a), as expected for a non-successional system. However, there was a clear
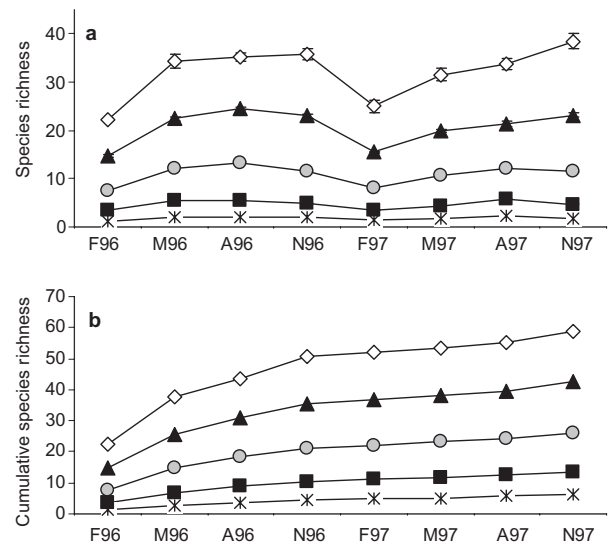
Fig. 1. (a) Species richness (±1 standard error) *versus* time and (b) Cumulative species richness (±1 standard error) *versus* time for each spatial scale considered. ◇ quadrat scale, ▲ 1/4 scale, ● 1/16 scale, ■ 1/64 scale, ✴ 1/256 scale. F96, M96, A96 and N96 stands for February, May, August and November 1996 respectively, whereas, F97, M97, A97 and N97 stands for the same months but from 1997.

seasonality in the species richness pattern with greater number of species in the cool season. For 1/256, 1/64, 1/16, 1/4 and quadrat scales, the mean richness values (±SE) were 1.757 (±0.010), 4.696 (±0.056), 10.876 (±0.259), 20.541 (±0.918) and 32.032 (±2.798) respectively.

The cumulative richness increased according to a power function (Fig. 1b). The cumulative richness slopes showed significant differences among different scales ($F_{4,30} = 36.7$, $P < 0.01$). The species accumulation rate (represented by the slope 'b' in Table 2b) increased with decreasing scale.

Species frequency

During the 2-year period, only eight species were present on 80% of the smallest cells (Fig. 2): the cool season forbs *Chaptalia exscapa*, *Chaptalia pilloseloides*, *Oxalis macachin*, *Oxalis perdicaria* (this species reach this frequency only in 1 year, and thus was not considered further in the analysis), the warm-season grasses *Andropogon ternatus*, *Aristida uruguayensis* and *Schyzachirium tenerum*, and the cool-season cyperaceae, *Carex phalaroides*.

Null models

At the smallest scale, 135 observed cumulative frequency values were significantly smaller than the mean

Table 2. Regression models parameters: (a) Richness linear regression model (Richness = a + b.*time*) parameters, R^2 adjusted, $F_{(d.f.)}$ statistic and probability, (b) Cumulative richness power regression model (Cumulative richness = $a_x(t)^b$)

Scale	a	b	R_{adj}^2	$F_{(1,6)}$	P	
a						
1/256	1.627	0.029	0.054	0.377	0.562	NS
1/64	4.368	0.073	0.040	0.247	0.637	NS
1/16	10.040	0.186	0.048	0.303	0.602	NS
1/4	18.768	0.393	0.069	0.444	0.53	NS
Quadrat	27.25	1.063	0.216	1.655	0.246	NS
b						
1/256	1.664	0.646	0.981	437.22	8×10^{-7}	$\star$
1/64	4.623	0.530	0.952	168.01	1×10^{-5}	$\star$
1/16	10.363	0.456	0.916	94.15	7×10^{-5}	$\star$
1/4	18.470	0.413	0.923	103.72	5×10^{-5}	$\star$
Quadrat	27.623	0.376	0.912	89.60	8×10^{-5}	$\star$

$\star$Significant regression at $P = 0.001$. NS, no significant regression.
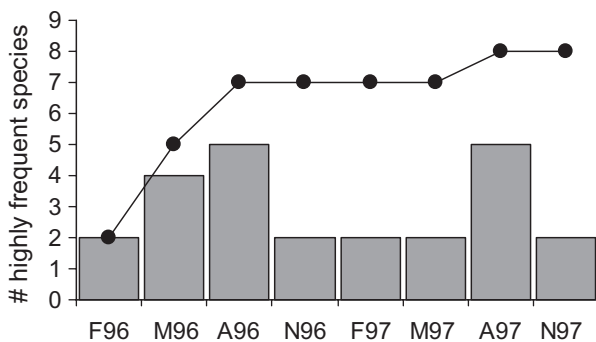

Fig. 2. The Number of highly frequent species (bars) and the cumulative number of highly frequent species (lines with dots). Abbreviations on X axis are the same as in Figure 1.

of the resampled random mobility distribution of cumulative frequency, and 141 were significantly greater than the mean of the resampled minimum mobility distribution. In the 1/16 scale, 40 observed cumulative distribution values were significantly smaller according to the resampled random mobility distribution and 45 cases were significantly greater according to the resampled minimum mobility distribution. Most of the statistically significant values were tailed: when we rejected the random mobility in a species in a quadrat, we also rejected the minimum mobility. On the other side, the 'indeterminate' cases (those where we could not reject any of extreme mobility models) where more frequent in the scale 1/16 (because of a smaller n): seven pairs cases out of 144 pairs in scale 1/256, and 73 pairs out of 144 pairs. These cases involved very frequent or rare species. These indirect mobility measures (Palmer & Rusch 2001) have the same shortcomings as the turnover method; it cannot detect any pattern in very common or very rare species.

Turnover rates

Turnover rates did not show a clear pattern. *Andropogon ternatus*, *S. tenerum* and *C. phalaroides* showed the highest turnover rates at the smallest scale but not at largest (Fig. 3a). At the largest scale, the warm-season cyperaceae *Bulbostilys juncoides*, was the most mobile species (Fig. 3a). The results of the Kruskal–Wallis test showed highly significant differences among species in turnover rates at both scales ($H_{scale1/256} = 90.432, 12$ d.f., $P < 0.001$; $H_{scale1/16} = 45\ 910, 12$ d.f., $P < 0.001$). The Nemenyi test did not detect clear groupings of species according to their turnover rates (Fig. 4a,b). At the 1/16 scale, the standardized turnover rates of *C. phalaroides*, *Ch. pilloseloides* and *S. tenerum* suggest that they move more than expected according to their frequencies (Fig. 5a). The opposite occurred with *Chevreulia sarmentosa* that moved less than expected. At the 1/256 scale, *A. ternatus* moved more than expected whereas *A. uruguayensis* and *C. exscapa* moved less than expected (Fig. 5b). At both scales *Richardia humistrata* exhibited an indeterminate turnover pattern.

The proportion of new appearances showed significant differences at both scales ($H_{scale\ 1/256} = 4244$ with 12 d.f., $P < 0.001$, $H_{scale\ 1/16} = 30, 36$ with 12 d.f., $P < 0.01$). At the 1/256 scale, the species that more actively occupied new sites respect to their frequencies were *A. uruguayensis*, *Botriochloa laguroides* and *C. phalaroides*. On the other side, *O. macachin*, *Ch. pilloseloides* and *Ch. exscapa* were the species that colonized new sites less than expected. In the 1/16 scale, the species that occupied more new sites were *Axonopus affinis*, *R. humistrata* and *A. uruguayensis*, and the species that occupied less new sites were *C. exscapa*, *Ch. pilloseloides* and *A. ternatus* (Fig. 6).
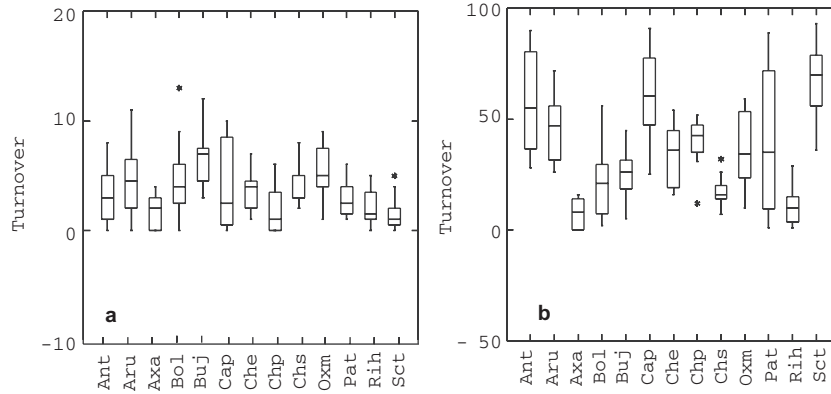
Fig. 3. Turnover values for each species in scale 1/16 (a) and scale 1/256 (b). The vertical lines are the ranges, the horizontal lines are the medians, the boxes represent the inner fences (see *Methods*), and the asterisks are values far outside the outer fences. For species abbreviations see Table 1.
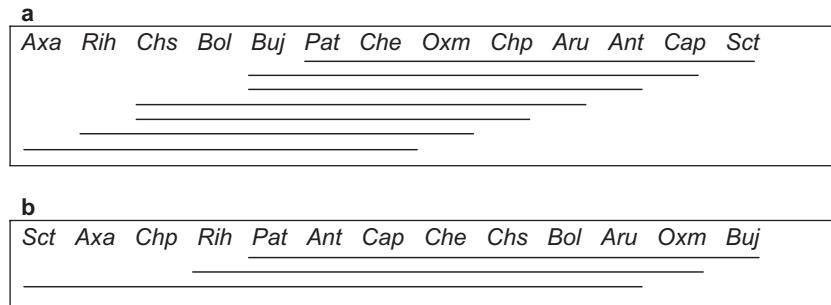

Fig. 4. Nemenyi test results for the turnover values, with $\alpha = 0.05$, $k = 13$. (a) Scale 1/16, (b) scale 1/256. Horizontal lines represent groups of species that showed significant differences. For species abbreviations see Table 1.
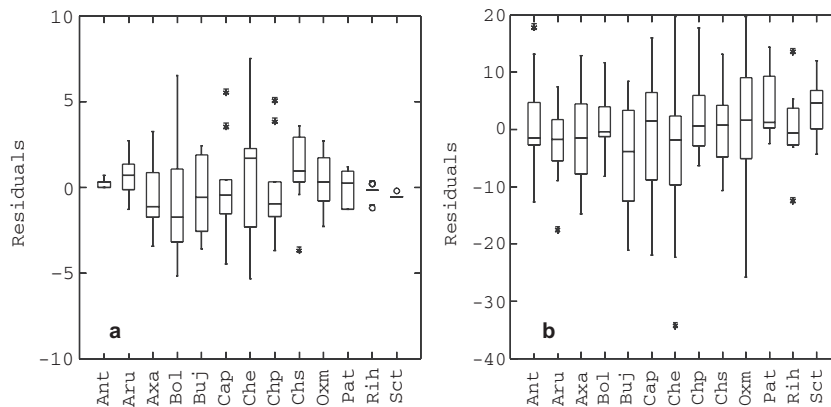

Fig. 5. Standardized turnover values for each species in scale 1/16 (a) and scale 1/256 (b). The vertical lines are the ranges, the horizontal lines are the medians and the boxes represent the inner fences (see *Methods*). The dots represent outside values and the asterisks are far outside values.

DISCUSSION

We found that the rate of species accumulation increased as the scale decreased, providing indirect support to the hypothesis supported by van der Maarel and Sykes (1997) that species mobility increases with decreasing scale. The mobility characteristics at different scales differed among species and depended on their spatial strategies.

On an annual scale, species richness did not show any trend over the whole period, whereas the cumulative species richness increased through time. This
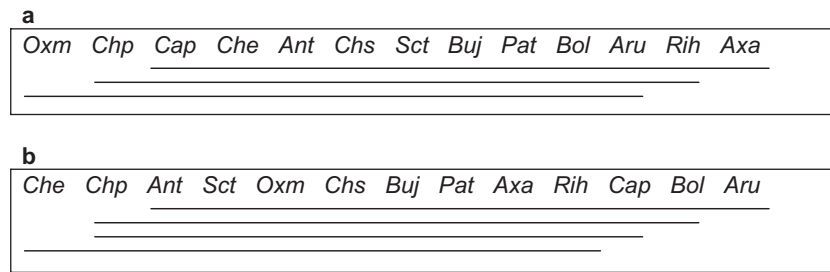
a

| Oxm | Chp | Cap | Che | Ant | Chs | Sct | Buj | Pat | Bol | Aru | Rih | Axa |

b

| Che | Chp | Ant | Sct | Oxm | Chs | Buj | Pat | Axa | Rih | Cap | Bol | Aru |

Fig. 6. Dunn tests results for the proportion of new appearances, with α = 0.05, k = 13. (a) Scale 1/16, (b) scale 1/256. Horizontal lines represent groups of species that showed significant differences. For species abbreviations see Table 1.

implies that the species identity was changing in each subquadrat, that is, the species changed positions constantly. The seasonality observed in species richness is explained by a group of species composed mostly by forbs that were present only in winter and spring. Forbs represented 70% of the total number of species in this group in both years. Grasses represented 20%, and the rest was composed by lichens, mosses and ferns. Most of these species were native and perennial plants. Previous findings in Uruguayan Campos reported an increase in the number of perennial and native forbs in grazed communities (Altesor *et al.* 1998; Rodríguez *et al.* 2003). All of them were cool-season species. In the case of the Flooding Pampa grasslands in Argentina, many authors have reported that the increase in species richness in grazed plots is due to an increase in exotic cool-season species (Faccelli *et al.* 1988; Rusch & Oesterheld 1997).

Turnover rates allowed us to detect differences in mobility among species, but when we removed the effect of the species frequency, the differences in turnover rates vanished. This implies that specific differences in turnover could be explained mostly by differences in species frequencies. Turnover values, as well as species frequency, varied greatly among both quadrats and years. This spatio-temporal variability has been found in other small-scale studies (Herben *et al.* 1990, 1993a; Thórhallsdóttir 1990; Rusch & van der Maarel 1992).

At the smallest scale (1/256), most of the species exhibited a spatial behaviour between the extremes represented by the null models. Because the null models results are sensitive to extreme values of species frequency, they must be considered with caution for species with very high or very low frequency. In these situations, differences respect to the null models cannot be detected. At the largest scale considered by the null models (1/16), the clear 'between-extremes-mobility' pattern of the smallest scale disappeared, that is, in some years and quadrats they moved randomly, whereas in others they almost did not move or moved within the results of the extreme mobility models. An example of a species that

showed one of the most consistent patterns at this scale was *B. juncoides*, which moved randomly in almost every year and quadrat (see Appendix S1).

The calculated turnover rates may overestimate mobility because some 'increments' may result from underground persistence of vegetative organs (i.e. *Oxalis sp.*, *C. exscapa*). To circumvent this potential problem, we calculated the proportion of new appearances. This was derived from turnover measurements and allowed us to estimate the species abilities to move to new sites. When we analysed it, we found that certain species showed high values in a scale and low values in another scale. This highlights that species differ in scales at which they move to new sites. Such scales depend on their spatial strategies (Altesor *et al.* 1999). For example, species that showed short-range colonization capabilities (spatial strategies 2 and 4 in Table 1) had a greater proportion of new appearances in the scale 1/256 and relatively low values in the scale 1/16. On the other hand, species that showed long-range colonization capabilities (spatial strategy 4 in Table 1) had a greater proportion of new appearances values at the scale 1/16 (e.g. *R. humistrata*, *A. uruguayensis* and *A. affinis*).

When we analysed the standardized turnover values and new appearances, we saw that certain species with high turnover values showed the lowest new appearances values: *C. phalaroides*, *C. exscapa* and *Ch. pilloseloides* at scale 1/16, and *Schizachyrium tenerum* at scale 1/256. This implies that these species were not colonizing new sites but they were moving around the previously occupied sites, a pattern related to the 'carousel model' (van der Maarel & Sykes 1993). Other species showed the opposite behaviour, low turnover values and high new appearances values (e.g. *A. uruguayensis* and *R. humistrata* at scale 1/256). This implies that these species moved very little, but when they did, they truly colonized new sites (i.e. previously unoccupied sites). The simultaneous application of different spatial mobility measures allowed us to improve our previous analyses (Altesor *et al.* 1999) and discriminate between release and occupation of previously occupied space and colonization of new cells.

Grazed communities in Uruguayan Campos are structured as a dense matrix of perennials grasses and forbs (Altesor *et al.* 1999). As in other grasslands, vegetative propagation is the main form of growth of the species in these communities (Abrahamson 1980; Schmid 1985; Rodríguez *et al.* 2003). These two main factors, vegetation structure and reproduction mode, determine the very scarce opportunities for seedling recruitment. Our field observations support these assertions. In a similar study in Swedish alvar grasslands, Rusch and van der Maarel (1992) reported high turnover rates associated with seedling recruitment variability and vegetative propagation. The differences with this system could be attributed mostly to climate severity. The lack of real gaps, given the absence of severe climate conditions, precludes the success of seedling recruitment, but promotes vegetative propagation. Moreover, grazing promoted the proliferation of species with prostrated growth forms or underground and superficial reserve organs that allow them to persist and colonize new sites. In this kind of community, where space availability may be a limiting factor for species colonization, the differences among species in the use of space would be the main mechanism promoting species richness. Wildová *et al.* (2007) explained the above-ground replacement patterns by species differences in dynamics of rhizome growth. This mechanism is likely to operate in our system because the diversity of below-ground structures.

Our results highlight the advantages of a multiple (micro)scales study. The application of multiple indirect measures of mobility (cumulative richness, cumulative frequency) and more direct measures (turnover and new appearances), allowed us to obtain a thorough description of the small-scale spatial dynamics. The high small-scale dynamics and the variability in the mobility characteristics of species could be linked with the diversity of growth forms and spatial strategies exhibited by plants in this type of community. Many authors have reported the high species coexistence in grazed sites in the Rio de la Plata grasslands (Sala *et al.* 1986; Altesor *et al.* 1998; Chaneton *et al.* 2002; Rodríguez *et al.* 2003; Altesor *et al.* 2005, 2006). Our results allowed us to connect lower-level mechanisms, like the species mobility patterns, with higher-level patterns. The high small-scale dynamics may contribute to explain the apparent stability in floristic composition at local scales.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Frequency (F), observed cumulative frequency (CF), predicted cumulative frequency by the random mobility model (CFR) and predicted cumulative frequency by the minimum mobility model (CFM), for each species in each quadrat and year: (**a**) 1/16 scale and (**b**) 1/256 scale. (★) significant lower (CFR) or greater (CFM) at p = 0.05, (★★) at p = 0.01 and (★★★) at p = 0.001

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