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EVALUATION OF THE RELATIONSHIPS BETWEEN FLORISTIC HETEROGENEITY OF *Panicum prionitis* Ness TALL GRASSLANDS AND THE FIRE HISTORY, HYDROLOGICAL REGIME AND SOIL TEXTURE IN THE PARANÁ RIVER FLOODPLAIN, ARGENTINA

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SUMMARY

Tall grassland landscapes in the Paraná River floodplain are associated with a particular natural fluctuation, and to anthropic disturbances that determine their floristic assemblages. This paper addresses tall-grasslands of Panicum prionitis and evaluates the relationship between its floristic composition and the occurrence of fire, hydrological pulses and soil texture. Fifty-eight plots of tall grasslands of 25m² each were analyzed in eight patches; abundance-cover of each species was recorded. Of the plots, 15 were distributed in three of the eight patches. The three patches had different fire histories: 7 months, 4 years and 14 years from the last fire event. In the eight patches, sediment samples of 0-20cm depth were collected and 20 topographic readings were performed. Vegetation was analyzed by applying classification and indirect ordination multivariate techniques. One hundred and eighteen species distributed in four floristic groups were found. No statistically significant differences in diversity and floristic composition were identified among tall grasslands with different fire history. Differentiation in floristic groups was mainly associated with hydrological pulses and soil texture. Fire does not generate significant changes in species richness, diversity or structure in Panicum prionitis tall grasslands. From the conservation perspective, we believe it is appropriate to suggest that to maintain the permanence of the Panicum prionitis tall grasslands the fire events should not be avoided.

Introduction

Worldwide, both disturbances (events caused by humans) and perturbations (events occurring naturally without human intervention) have been recognized as important processes in ecosystem functioning (Neiff, 2001), since they constitute a source of environmental variability and, at intermediate intensities, generally result in increased species diversity (Denslow, 1985).

Fires, either as disturbances or perturbations, are men-

tioned as a main agent of environmental variability, having been documented in geological records early after the rise of terrestrial plants. Fire influences ecosystem distribution patterns and processes, including vegetation distribution and structure, carbon cycle and climate (Bowman *et al.*, 2009).

With regard to vegetation, fire (natural or anthropogenic), has been assigned diverse roles which range, among others, from the regulation of the proportion of herb to woody species (Bran *et al.*, 2007) to

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EVALUACIÓN DE LAS RELACIONES ENTRE HETEROGENEIDAD FLORÍSTICA DE PAJONALES DE *Panicum prionitis* Ness, HISTORIA DE FUEGO, RÉGIMEN HIDROLÓGICO Y TEXTURA DE SUELOS EN LA PLANICIE INUNDABLE DEL RÍO PARANÁ, ARGENTINA

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RESUMEN

Los paisajes de pajonales en la planicie inundable del Río Paraná se encuentran asociados a fluctuaciones naturales particulares y a disturbios antrópicos que determinan sus ensambles florísticos. En este trabajo se estudia el pajonal de Panicum prionitis y se evalúa la relación entre su composición florística y la ocurrencia de incendios, los pulsos hidrológicos y la textura del suelo. Se analizaron 58 censos de pajonales de 25m² cada uno, distribuidos en ocho parches y la abundanciacobertura de cada una de las especies ha sido registrada. Del total de censos, 15 fueron distribuidos en tres de los ocho parches. Los tres parches tuvieron diferentes historias de fuego: 7 meses, 4 años y 14 años desde el último evento de fuego. En los ocho parches se colectaron muestras de sedimentos hasta 20cm de profundidad y se realizaron 20 lecturas topográficas. La vegetación fue analizada aplicando técnicas multivariadas de clasificación y ordenación indirecta. Se identificaron 118 especies pertenecientes a cuatro grupos florísticos. No hubo diferencias estadísticamente significativas en la diversidad y composición específica de los pajonales con diferentes historias de incendios. La diferenciación de grupos florísticos estuvo asociada principalmente a los pulsos hidrológicos y a la textura de los suelos. Los incendios no generaron cambios significativos en la riqueza, diversidad y estructura de los pajonales de Panicum prionitis. Desde una perspectiva de conservación, creemos que es apropiado sugerir que para mantener la permanencia de los pajonales de Panicum prionitis los eventos de fuego no deberían ser evitados.

EVACUAÇÃO DAS RELAÇÕES ENTRE A HETEROGENEIDADE FLORÍSTICA DE PASTAGENS DE *Panicum prionitis* Ness, HISTORIA DO FOGO, REGÍMEN HIDROLÓGICO E TEXTURA DO SOLO NA PLANÍCIE DE INUNDAÇÃO DO RIO PARANÁ, ARGENTINA

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RESUMO

As paisagens de pastagens na planície de inundação do Rio Paraná, encontrarem-se, associados às flutuações naturais particulares e a distúrbios antropogênicos que determinam suas assableas florísticas. Este trabalho estuda as pastagens de Panicum prionitis e avalia a relação entre sua composição florística e a ocorrência de incêndios os pulsos hidrológicos e textura do solo. Foram anualizados 58 censos de pastagens de 25m² cada um distribuídos em oito patches onde foi regestrada a abundância-cobertura de cada uma das espécies. Do total dos censos, 15 foram distribuidos em 3 dos 8 patches. Os tres patches amostrarom diferentes historias de fogo; Sete meses, quatro e 14 anos desde o último evento de incendio. Nos 8 patches coletaram-se amostras de sedimento ate 20cm e fizeram 20 leituras topográficas. A vegetação foi anualizada aplicando técnicas multivariadas de calcificação e ordenarão indiretas. Foram identificadas 118 espécies pertencentes a quatro grupos florísticos. Não houve diferenças estatisticamente significativas entre a diversidade e a composição específica das pastagens com diferentes historias de incêndios. A diferenciação dos grupos florísticos esteve associada principalmente aos pulsos hidrológicos e a textura dos solos. Os incêndios não geraram câmbios significativos na riqueza, diversidade e estrutura das pastagens de Panicum prionitis. Desde uma perspectiva da conservação, cremos que é apropriado sugerir que para manter a permanência das pastagens de Panicum prionitis os eventos de fogo não deveriam ser evitados.

the creation of plant and animal habitat variability (Safaian *et al.*, 2005) and, in some cases, to the control of exotic species invasion (Vermeire and Rinella, 2009). In natural grasslands, fire events have been proposed as a key management factor in the maintenance and enhancement of structure, diversity and vigor (Morgan, 1999).

In spite of this, some authors consider that fire is not the major factor in shaping ecosystems because, in the long term and under recurrent fire events, plant communities would tend to evolve mechanisms to adapt their structure and functioning to the fire disturbance regime (Li *et al*, 2007).

Another factor that generates environmental variability are the hydro-sedimentological pulses, since they affect the characteristics and distribution of vegetation (Lewis *et al.*, 1987; Neiff, 1990, 1996; Franceschi *et al.*, 2000; Neiff, 2001; Ishida *et al.*, 2008).

The floodplain of the Lower Paraná River (Argentina) covers 13063km² up to the delta, and it is conditioned by the hydro-sedimentological regime (Junk et al., 1989; Neiff, 1990). The floodplain dynamics is characterized by successive phases of rise (ordinary and extraordinary floods) and fall of the water level, occurring in annual, biannual or multi-annual cycles (Neiff et al., 1994; Neiff, 1996, 1997). In addition to the direct effect of floods on vegetation (Casco, 2003), floods cause differential sediment deposition, thus proving edaphic heterogeneity in a

floodplain landscape (Neiff and Orellana, 1972; Lewis *et al.*, 1987).

Among the typical vegetation communities of the floodplain of the Paraná River, *Panicum prionitis* tall grasslands constitute the richest and most diverse herbaceous vegetation units (Aceñolaza, 2004, 2005, 2008; Marchetti y Aceñolaza, 2005) which, together with forests, are the most widespread communities in the floodplain.

Tall grasslands serve diverse productive uses, livestock grazing being one of the most common. Grazing is accompanied by prescribed fires as a tool to eliminate dry matter that accumulates on the soil (Zamboni and Aceñolaza, 2005).

Due either to its use for grazing, which constitutes an anthropic disturbance, or to environmental heterogeneity at the landscape level, P. prionitis tall grasslands are associated with different agents of environmental variability (Franceschi et al., 2000), such as fire caused by humans and floods. Lewis et al. (1987) and Franceschi et al. (2000) have studied P. prionitis tall grasslands in relation to the impact of extraordinary floods on community structure and diversity. However, the effect of the anthropic fires on tall grasslands is still poorly understood.

In this context, the two main objectives of this study were: 1) to investigate floristic variability of *P. prionitis* grasslands, and 2) to evaluate the relationship among floristic variability, fire history, hydro-sedimentological pulses (related to mirco-topography) and soil texture.

Study Area

The study was carried out in a portion of the alluvial plain of the Lower Paraná river, located at 31°32'29.5"; 31°38'56.18"S and 60°19'35.3"; 60°30'9.36"W (Figure 1).

The study area is under the influence of the hydro-sedimentological pulses of the Paraná River. These pulses bring matter and energy during the increasing phase of the river, which return to the main channel during the low water phase. The pulse regime (Casco, 2003) generates an array of environmental conditions that are reflected by the matrix of different vegetation units along the topographic gradient (Marchetti and Aceñolaza, 2005; Casco et al., 2010). The soils in the study area correspond to an overlay of sediments of alluvial origin with textures



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Ν

loodplain

Figure 1. Study area in the floodplain of the Paraná River.

Santa Fe

Province

Parana

River

Entre Rios

10km

Plots with different fire histories

Sampling localization

Water flow direction

Provincial boundary

Province

Methods

Vegetation: data collection and analysis

Landsat TM 7 satellite images (scale 1:250000), aerial photographs and terrestrial surveys, were used to identify and select the tall grasslands of Panicum prionitis. Eight areas of 1-2ha were selected in two private properties where livestock farming is the main activity. Some places in one of the two properties are used as wildlife refuge. The time elapsed since the last fire event was known in only three of the eight areas selected, where it was 7 months, 4 years and 14 years.

The information about time since the last fire event was provided by the property owner. In the study zone, fires are anthropic events because people use them as a strategy for management of tall grasslands.

Fifty eight plots of tall grasslands of 25m² each were analyzed and compared; 15 plots were established in the three areas with known time since the last fire (5 replicates in each because they were the smallest areas) and 43 plots were established in the following 5 areas (with 8, 8, 9, 9 and 9 replicates, respectively). For each plot, all species present were recorded and abundance-cover and sociability values were assigned according to Muller-Dombois and Ellenberg criteria (1974).

All of the eight areas selected are under the pulse regime and they are used for livestock farming, the main difference among them being related to micro-topography and fire events. Three areas are protected as a wildlife refuge.

Based on the abundancecover values of species, vegetation plots were classified in floristic groups by cluster analysis, using Euclidean distance as a dissimilarity measure and the Ward method as a linking criterion (McCune and Mefford, 1999). For each floristic group the species richness was calculated. The Shannon-Weaver diversity index was calculated in plots with different fire events.

All plants were classified according to life form (woody, herbaceous) and life cycle (annual, perennial) according to Zuloaga *et al.* (1994) and Zuloaga and Morrone (1999 a, b).

Statistical significance of analyses was tested by oneway ANOVA; variables met homocedasticity and normality assumptions. Whenever statistically significant differences were found, contrasts of Tukey test were used.

Environmental heterogeneity: data collection and analysis

The relationship between floristic composition and environmental variables (fire. hydro-sedimentological pulse and soil) were assessed by detrended correspondence analyses (DCA; McCune and Mefford, 1999). This multivariate technique, through the simultaneous ordination of plots and species, allows the inference of environmental gradients. Two DCA were made; they used all vegetation plots and two secondary classification matrices, fire history and number of floristic group (defined previously by the cluster analysis), respectively. Multivariate analyses were performed with the PC Ord 4.1 statistical package (Mc-Cune and Mefford, 1999).

Three soil samples from the first 20cm depth were collected in each floristic group of tall grasslands and the fractions of loam, sand and clay were analyzed by gravimetry (Bowles, 1978).

Also, 20 topographic positions were registered and re-

ferred to the hydrometric level of the Parana river recorded in the port of the city of Paraná, Entre Ríos. The final topographic position added 1125m according to the regional slope $(0.45 \text{m} \cdot \text{km}^{-1})$ and it was referred to as 0 (zero) hydrometric level at the mentioned port, in order to obtain the height above sea level. From the 20 topographic levels, mean values were obtained for each floristic group.

The regime of the hydro-sedimentological pulses was studied from a 39-year hydrological series (1970-2009), given that it corresponds to a uniform period in the variability of the river flow for the last century (Amsler et al., 2005). Hvdrometrical levels used to study the river dynamics correspond to the daily records made by Prefectura Naval Argentina in the city of Entre Ríos. From the hydrological series, frequency, amplitude, mean intensity of the floods and potamophase/limnophase days, were obtained with the PULSO Software (Neiff y Neiff, 2003).

The PULSE software studies phenomena that are repeated according to a sinusoidal function over time, and considers flood and drought, two complementary phases of pulse hydro-sedimentology (Casco *et al.*, 2005). From the average topographic distribution of each floristic group, PULSE allows to know the relationship of the floristic group with the hydro-sedimentological pulses through the mentioned attributes.

Such attributes are defined in the software *fFITRAS* function, which stands for frequency, intensity, tension, regularity, amplitude, seasonality (Neiff, 1990).

The selected attributes that were calculated by the soft-





ware were: 1) frequency, defined as the number hydrosedimentological pulses recorded over a given time period; 2) intensity, defined by a magnitude phase of flood or drought; 3) amplitude, also expressed as duration, the time slot that the river remains at high or low water stage; 4) potamophase days, the number of days with surface water over a period of time; and 5) lymnophase days, the number of days without surface water.

The differences among floristic groups for sediments and topographic positions were tested by one-way ANOVA which followed the same procedure applied to vegetation data. The relationship between each floristic group and hydro-sedimentological pulse are summarized in its main parameters.

Results

Floristic characterization of Panicum prionitis *tall grasslands*

One hundred and eighteen species of vascular plants were collected and identified in the 58 plots analyzed. The classification of sample units (plots) allowed the definition of four floristic groups (Figure 2) representing tall grassland heterogeneity. Their distinctive features are:

Group 1. It is composed of 10 plots and 53 species, including the oldest tall grassland patches without fire (14 years after fire). Some of its exclusive species, not found in the other groups, are *Lycium vimineum*, *Nicotiana*

longiflora and Eryngium coronatum.

Group 2. It comprises 15 sample units and 60 species. Neither the time elapsed since the last fire nor the fire regime could be determined. Among its exclusive species are Baccharis pingraea, Dichondra sericea, Hymenachne amplexicaulis, Paspalum laxum and Vigna adenantha.

Group 3: It comprises 18 plots grouping tall grasslands with recent and intermediate time since fire periods (7 months and 4 years since the last fire event). This group includes 55 species and among the exclusive ones are Acalypha communis, Byttneria scabra, Hybanthus parviflorus, Ipomoea cairica, Paspalum inaequivalve and Vernonia incana.

Group 4: It is the group with highest species richness; its 15 sample units including 73 species. Neither the time elapsed since the last fire nor the fire regime could be determined.

Eclipta prostrata, Echinochloa crusgalli, Poa annua, Poa lanigera, Polygonum punctatum and *Paspalum dilatatum* are some of the exclusive species of this group.

Floristic heterogeneity associated to the environmental variability

Given the environmental heterogeneity found in *P. prionitis* tall grasslands, time elapsed since the last fire event, hydro-sedimentological pulses (related to micro-topography) and soil texture were evaluated as agents causing environmental variability in the floristic richness of these tall grasslands.

Fire history. Sample units of tall grasslands with different fire history were distributed

in two of the four floristic groups defined in Figure 2. Sample units in patches with no recent fire (14 years since the last fire event) are clustered in Group 1, while those units with recent and intermediate time since fire periods (7 months and 4 years) are part of Group 3.

Life form

Woody species

Annual species

Perennial species

Herbaceous species

Diversity (Shannon-Weaver) Floristic differences that allow group-Richness ing are displayed in Table I. Mean richness recorded in each life form (woody, herbaceous, annual, perennial) shows a different trend depending on the different fire histories. Woody, herbaceous and perennial species increase at the intermediate time but, while the first one does not change at the longest time from the last fire, the herbs and perennial species decrease. On the other hand, annual species decrease from the recent to the distant fire event. The percentage of each life form within total species (in brackets in Table I), shows a different pattern: woody and perennial species are more abundant at the longest time from the last fire event, while herbaceous and annual species are more abundant

at the shorter time since the last fire event. Finally, the highest diversity and richness values were recorded at the intermediate time since the last fire event.

Despite the differences found in each life form with different fire histories, these differences were statistically significant only within the woody species category (Table I). This difference was significant between the recent and intermediate time

FOR EACH FLORISTIC CATEGORY ACCORDING TO TIME ELAPSED

SINCE LAST FIRE EVENT

Intermediate

 5 ± 0.70 b

(15.4)

24.4 ±3.78

(84.6)

 5 ± 2.54

(21.5)

 23.8 ± 3.27

(78.5)

 1.34 ± 0.08

29.4 ±4.39

Late

5 ±0.70 b

(17.5)

 19.6 ± 5.02

(82.5)

 4.8 ± 0.83

(20)

 20.4 ± 4.15

(80)

 1.30 ± 0.08

 24.4 ± 4.66

F value

7.53

2.21

0.06

1.47

2.21

1.87

P value

0.007 *

0.151 NS

0.938 NS

0.268 NS

0.151 NS

0.196 NS

Recent

3.6 ±0.54 a

(10.6)

 23.8 ± 2.58

(89.4)

52 + 148

(23.4)

 21.6 ± 1.58

(76.6)

 1.32 ± 0.03

 27.2 ± 2.28

for the floristic heterogeneity observed.

Other agents of environmental variability: hydrological pulse and soil texture

The scarce influence of time elapsed since the last fire in the floristic differentiation of *Panicum prionitis* community encourages the consideration of other agents that may account for environmental variability. In this sense, Figure 4 together with data in

Data represent $125m^2$ in each fire category (5 plots of $25m^2$ used for each fire category). Recent: 7 months since last fire, Intermediate: 4 years since last fire, Late: 14 years since last fire. Percentage coverage represented by each category is given in brackets. F values for one-way ANOVA with n= 5 for each fire category. Different letters indicate significant differences in contrasts for p<0.05 in posthoc Tukey comparison.



Figure 3 Detrended correspondence analysis (DCA) performed on 58 sample units. Fire history is denoted as 1: no data, 2: recent (7 months since last fire), 3: intermediate (4 years since last fire) and 4: late (14 years since last fire). Sample units with different fire histories are clustered in the lower left quadrant, indicating the scarce importance of fire as an agent of floristic variation.

> since fire categories and between the recent and late time since-fire categories. No statistically significant difference was found between the intermediate and late time since fire categories. Other floristic categories did not show any differences with respect to the fire history.

> Fire history as an indirect environmental gradient is shown in Figure 3. Axis 1 explains 14% of total vari-

Figure 4. Detrended correspondence analysis (DCA) performed on 58 sample units. Groups correspond to the classification of sample units performed in Figure 2.

ability and separates plots in two quadrants, with the

units influenced by different fire histories located in the left quadrant. Alternatively, axis 2 explains 12% of total variability and also does not separate the plots mentioned earlier. While the percentage of total variability explained is low, all plots subject to different fire histories form a single group in the left lower quadrant. This distribution does not indicate that fire history is an environmental variable responsible Tables II and III point to micro-topography and the pulse regime associated as one of the main agents causing environmental variability in tall grasslands.

Group 4 was significantly different from the other groups with regard to its topographic location (Table II). On the other hand, no statistically significant difference was found between Groups 1, 2 and 3. Such differences account for the spatial distribution of floristic groups along axis 1 in Figure 4. While Group 4 is located at the right end, Groups 2, 3 and 1 are located at the opposite end of the axis. In Table II it can be observed that the mean elevation values indicate a strong difference between Group 4, which is at the highest topographic position, and the rest, at lower elevations and with minimal differences among them. MAIN HYDROLOGICAL PARAMETERS OBTAINED WITH THE PULSO

The differences in topographic position of each floristic group in the landscape, determine the relationships between floristic groups and hydro-sedimentological pulses. According to this, it can be seen in Ta-

ble III that Group 4 had the least number of floods (37) and it was flooding less than 25% of the period considered. On the contrary, Group 2 had the largest number of flooding events (47) and it had water on the surface during 65% of time studied. Both Groups 4 and 2 are at opposite extremes on axis 1 of Figure 4 indicating that the hydro-sedimentological pulse is the most important variable in the floristic differentiation of these groups of tall grassland.

In addition, the presence of species such as Caperomia castaneifolia, Cleome hassleriana, Aeschynomene denticulada, Cyperus odoratus, Cyperus giganteus and Hymenachne amplexicaulis, characteristic of flooding areas, have been exclusively recorded in groups 1, 2 and 3. It can be observed that Groups 1, 2 and 3 are distributed at the lowest positions and, according to Table III and Figure 5, they are the Groups most frequently flooded.

On the other hand, the spatial distribution of Groups 1, 2 and 3 in axis 2 could be explained from the soil texture of each group (Table IV). Groups 3 and 4 have sandy soils, while Group 2 is characterized by the presence of

TABLE II MEAN TOPOGRAPHIC DISTRIBUTION FOR EACH FLORISTIC GROUP DEFINED IN FIGURE 2

Grou	ıps	Mean msnm ±SE	Group 1	Group 2	Group 3	Group 4
Grou	p 1	14.20 ±0.40		0.149565	0.724492	0.000151
Grou	p 2	14.50 ± 0.67			0.690089	0.000152
Grou	p 3	14.35 ±0.27				0.000151
Grou	p 4	15.31 ± 0.13				

Values on the upper diagonal correspond to p value obtained from one-way ANOVA, n= 18. Contrasts were performed with Tukey test.

TABLE III

SOFTWARE* FOR THE 39 YEAR PERIOD							
Groups / Hydrological	Frequency	Amplitude	Mean intensity	Potamophase		Limnophase	
atributte	N° floods	N° days	Hydrometric level	N° days	%	N° days	%
1	41	346	2.07	9479	65	5101	35
2	47	308	2.12	7389	51	7191	49
3	41	308	2.08	8605	59	5975	41
4	37	392	2.36	3409	23	11171	77

* Neiff and Neiff (2003).



Figure 5 Variation of hydrometric level in a 39 year period and its relationship with the topographic level of each floristic group.

clay-loam soils and Group 1 displays an intermediate condition

group were statistically significant between Groups 2 and 3, located at opposite ends along axis 2 (Figure 4), and between Groups 4 and 2,

Differences in fractions of sand, loam and clay for each

TABLE IV MEAN AND STANDARD DEVIATION FOR SAND. CLAY AND LOAM FOR EACH GROUP

	Group 1	Group 2	Group 3	Group 4
	ab	а	b	b
Texture/Type of soil	Sandy clay loam	Silty clay	Sandy loam	Sandy loam
Sand (%)	39.06 ±21.5	11.83 ±6.66	58.28 ±4.01	49.44 ±4.12
Clay (%)	37.27 ± 40.2	46.77 ±9.25	5.12 ± 4.37	2.29 ± 0.54
Silt (%)	13.72 ±21.5	40.22 ± 5.24	31.14 ± 3.97	45.29 ± 7.46

Different letters indicate significant differences in contrasts for p<0.05 in post-hoc Tukey comparison.

also located at opposed ends along axis 1.

Discussion and Conclusions

There are no specific studies on the relationship between fire and floristic composition of Panicum prionitis tall grasslands for the study area. However, similar results

have been obtained in different latitudes. For subtropical grasslands in SE Brazil, Overbeck et al. (2005) point out that the number of species and species turnover rate was highest one vear after the fire and that both parameters declined after a peri-

od of 3-4 years since the fire. The highest richness and diversity values were recorded in sites that had not suffered fire events in the last 4 years although, in that case, a decline in richness was only recorded for areas that had not suffered fire for a long period. Despite of this temporal difference (probably explained by differences in species composition, climate and environmental conditions between both study sites) the explanation may be that fire suppression of open areas for the establishment of new seedlings of the dominant tall grass P. prionitis also allows the recovery of already established plants. Thus, the colonization and dominance of P. prionitis following a period of fire suppression would explain the long term decrease in community richness and diversity.

The results indicate that fires, as events caused by human intervention as a management practice, would not have highly negative impact on richness, diversity or structure of *P. prionitis* tall grasslands, at least under the present study conditions. In accordance, Neiff (2001) mentioned experiments carried out in tropical peatland swamps (Chaco, Argentina) with controlled fire on a 5ha area. After 40min of flames 2m high and a maximum temperature of 580°C, roots, rhizomes and rosette leaves of plants were not affected.

On the contrary, long fire suppression periods (14 years) could cause some changes in the community structure. Not only the lowest richness and diversity values were found in places without fires for a long time, but also the first indicators of changes in tall grassland structure, the increase in woody species, were observed.

Areas at the intermediate time since last fire event (4 years) showed the highest richness and diversity values; therefore, as long as fires are regular events, tall grassland physiognomy would persist and richness and diversity would be high. In the long term, fire suppression would imply changes in the structure of vegetation units. Similar results have been reported by Borghesio (2009) in a study of the effect of fire on vegetation in northern Italy. This author concluded that after 7 years since fire, grasslands were replaced by shrublands, thus suggesting that the conservation of highly rich and diverse grasslands would require a fire frequency of one fire every 3-6 years.

Floristic heterogeneity in P. prionitis tall grasslands can be more soundly explained on the basis of hydro sedimentological pulses (in relation to the micro-topography) and soil texture. Chacón-Moreno et al. (2004) showed, in grasslands of flooding savannas of the Orinoco River, that the hydrological dynamics and the capacity to accumulate water in the soil given by micro-topography are the key factors for species distribution in that ecosystem. The authors also recognized the significant relationship between the surface portion of clay, loam and vegetation distribution. The amount of clay and loam horizon can affect some soil properties. First, it reduces the capacity to accumulate

water during flood events; second, it determines evaporation rates. Dry soil shrinks and damages the roots of herbaceous plants. Both conditions would generate microhabitats with different moisture levels that would induce floristic differentiation in these tall grasslands.

In the upper portion of the present study area, Lewis *et al.* (1987) identified five floristic groups or communities. Although those groups have dissimilar species composition to the groups identified herein, the authors also found different soil textures in the sites inhabited by these floristic groups.

In relation to micro-topography and its relationship with floods, while Neiff (1986) found P. prionitis tall grasslands in concave zones frequently flooded, Franceschi et al. (1979) found these tall grasslands in higher topographic zones, less affected by floods. According to the present results, there is evidence that P. prionitis tall grasslands colonize topographically different environments, which makes them differentially exposed to Paraná River floods. In this sense, in the 39 year period studied, all groups had between 37 and 47 floods and the flooded time was different among groups. Even when Groups 1 and 3 had the same number of floods, the potamophase days were different between them. This hydrological variable, more than the number of floods, could explain the richness pattern found among groups. The richness decreased when the potamophase days increased.

Besides the direct effects of floods, they ultimately determine differential sedimentation processes, which are evident from textural composition of soils and floristic groups. Different hydro-sedimentological pulses and soil textures, together with scarce separation in floristic composition among tall grasslands with different fire history, suggest that the floristic heterogeneity observed herein could be attributed to the hydro-sedimentological pulse, which, moreover, causes differences in soil texture and its capacity to accumulate water.

From the conservation perspective, we believe that it is appropriate to suggest that in order to maintain Panicum prionitis tall grasslands the anthropic disturbances by fire should not be avoided. It would be necessary to consider that a four year fire interval yielded the highest richness and diversity values, while at 14 years since fire the first indicators of structural changes in vegetation units can be observed, along with a decrease in richness and diversity. It is desirable to program burnings to avoid damage through the loss of some functions performed by birds and others animals in these habitats.

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