DR. ANDREA LAURA MAGNANO (Orcid ID : 0000-0001-7477-041X)

Article type : Research article

Norbert Hölzel

Changes in vegetation composition and structure following livestock exclusion in a temperate fluvial wetland.

Running tittle: Wetland vegetation changes by cattle exclusion

Full author names and institutional affiliations

Andrea L. Magnano, Pamela Krug, Valeria Casa, Rubén D. Quintana

Instituto de Investigación e Ingeniería Ambiental (IIIA), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) - Universidad Nacional de San Martín (UNSAM), Buenos Aires, Argentina.

Correspondence:

1. Andrea. L. Magnano. Present adress: Instituto Argentino de Investigaciones de las Zonas Áridas (IADIZA), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Universidad Nacional de Cuyo, Gobierno de Mendoza. Av. Ruiz Leal s/n, Parque General San Martín (C.P. 5500), Mendoza, Argentina. Email: andrea.magnano@gmail.com

Funding Information: Agencia Nacional de Promoción Científica y Tecnológica (PICT Bicentenario 2227 and PICT-2017-2982) and Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET, PIP 092 and PIP 571/15).

Conflict of Interest: The authors declare no conflict of interest

Abstract

Questions: Responses of wetland systems to grazing can be highly variable with both positive or negative responses. However, the sustainable use of wetlands for grazing will depend on the management implemented and the resilience of each type of them. In this context, we addressed to the question: will the vegetation in the studied wetland be able to recover its structural and functional parameters after livestock exclusion in the short-term?

Location: Temperate fluvial wetlands in the Middle Delta of the Paraná River, Argentina, South America.

Methods: We evaluated the effect of cattle ranching on vegetation composition and diversity by determining changes in species richness and evenness, biomass (green and dry vegetative, and reproductive biomass) and litter content. We also analyzed the changes in biomass of weeds and of species according to their forage quality, toxicity and growth form. We applied a randomized block design (by topographic position) with repeated measures over time, using livestock exclusion as treatment.

Results: After 16 months, livestock exclusion affected vegetation species richness, but did not have a significant effect on diversity due to a slightly compensatory effect of evenness. Species composition differed markedly among treatments over time. There was an increase in dry and green vegetative biomass and litter content after 8 months of exclusion, while changes in reproductive biomass occurred later. The increase in these variables was closely related to changes in biomass of species with erect habit and good forage quality.

Conclusions: Livestock exclusion increased the forage value for the studied wetland by the development of natural palatable species typical of these environments. This shift in species composition promoted a higher production in biomass in the ungrazed areas. This suggest a remarkable recovery of the structural and functional parameters of the vegetation communities in the short-term (2 years).

Keywords: Wetland plants, vegetation diversity, biomass, temperate wetland, recovery, livestock exclusion, Paraná River Delta, Argentina.

Introduction

Wetlands are among the most important ecosystems because of the economic, social and environmental services they provide (Brander et al. 2006; Mitsch & Gosselink 2007). However, currently they are severely threatened by land-use change (Mitsch & Gosselink 2000; Sica et al. 2016) and highly vulnerable to climate change (Junk et al. 2013) due to their close dependence on thermal and hydric regimes. Freshwater withdrawals, changes in land use and inappropriate management decisions have led to habitat loss for many species, which is a primary driver of global biodiversity decline (Musters et al. 2000; Sala et al. 2000; Polasky et al. 2011). Although wetlands are considered to be resilient ecosystems (Ripken 2009), they have shown a surface area decrease of 64 - 71% in the 20th century (Gardner et al. 2015).

In South America, the delta of the Paraná River in Argentina, together with the deltas of the Amazonas and Orinoco Rivers, are large macrosystem wetlands of major socio-economic and biodiversity importance (Junk et al. 2013). At present, they are undergoing dramatic changes resulting from anthropogenic activities such as cattle ranching, rice cultivation and plantations of commercial species, which often modify hydrological regimes (Bó et al. 2010).

In the region of the Paraná River Delta, ranching is a traditional productive activity since colonial times, which has been intensified in the last decades, with head of cattle increasing from 160 000 in 1997 to 1 500 000 in 2007 (Quintana et al. 2014). The main causes for this scenario are the expansion of the agricultural frontier in central Argentina (Paruelo et al. 2006) and the replacement of pastures by croplands (Aizen et al. 2009). The region of the Paraná River Delta has a high potential for livestock production and native grazers because it comprises extensive areas characterized by good quantity and quality forage and the availability of safe drinking water (Quintana et al. 2014). This region included native herbivores such us marsh deer (*Blastocerus dichotomus*), capybara (*Hydrochoerus hydrochaeris*) and coypu (*Myocastor coypus*). The former became extinct in some parts of the Paraná River Delta, so nowadays it is considered as endangered in this region (Fracassi et al. 2013). Regarding the other species, they are heavily hunted because of their relevance for the local communities as an additional source of proteins and for selling their furs and hides (Quintana et al. 1992), with the consequent impact on their populations (Quintana et al. 2014).

Many studies have been carried out worldwide concerning the effect of wild and domestic herbivores on different ecosystems (e.g. McNaughton 1985; Milchunas & Lauenroth 1993; Lezama et al. 2014; Hempson et al. 2015; Pizzio et al. 2016). However, the effect of cattle ranching on the structure and functioning of wetlands has been scarcely investigated (Grace & Jutila 1999; Crosslé & Brock 2002; Reeves & Champion 2004; Wu et al. 2009; Jones et al. 2011; Morris & Reich 2013). Overall, the impact of livestock trampling and grazing on vegetation and soil in wetlands is similar to that described for other ecosystems and the net result depends on the resilience of each type of wetland and management implemented (Taboada & Lavado 1993; Jansen & Robertson 2001; Middleton 2002; Lunt et al. 2007; Miller et al. 2010). In this context, our goal was to investigate the structural and functional responses of vegetation to cattle exclusion in a wetland of the Middle Paraná River Delta. To our knowledge, this is the first study addressing this issue and intends to contribute with useful information for sustainable management of cattle ranching in the fluvial wetlands of the region. Specifically, we aimed to analyze: (i) change on the species diversity and composition in relation to time after livestock exclusion; (ii) the variation in green, dry and reproductive biomass and litter content of vegetation communities; and (iii) changes in biomass of weeds and of species according to their forage quality, toxicity and growth form.

Methods

Study area

The Delta of the Paraná River (*ca* 17 500 km^2) constitutes a complex floodplain located strategically at the lower end of the Paraná River Basin and the beginning of the de La Plata River estuary, between 32°5'S 58°30'W south of Diamante City in Entre Ríos province and 34°29'S 60°48'W near Buenos Aires City (Fig. 1). This region has been described as a vast wetland macromosaic based on its distinctive climate and hydrological regimes, and a wide diversity of landscapes shaped through geomorphological processes (Brinson & Malvárez 2002). In turn, such remarkable landscape heterogeneity determines unique ecological features (Quintana & Bó 2011) providing a variety of valuable goods and services (Kandus et al. 2010).

The present study was conducted in a cattle ranch placed on the Lechiguanas Islands, in the Middle Delta of the Paraná River, Entre Ríos province, Argentina (33°27'S 59°55'W, Fig. 1). The cattle ranch has a mean stocking density of about 0.7 livestock units.ha^{-1}. This livestock density was representative for the typical grazing intensity in this part of the region, and it was considered as a moderate stocking rate (Quintana et al. 2014). According to local people, this field has a grazing history at least 100 years ago. In the studied period, animals were free-ranging throughout the year. Considering this, the studied topographic gradient was subject to the same stocking rate and remained constant during the two years of the study. In addition, this ranch is placed in a 1455-ha landscape subunit defined by a geomorphological pattern and a characteristic flooding regime (Ramonell et al. 2012; Borro et al. 2014). The landscape pattern comprises levees, mid-slopes and lowlands along a micro-topographical gradient with different levels of flooding (Malvárez 1999). The climate is temperate humid with a mean annual temperature of 17.4 °C; the coldest month is July (10.5 °C) and the warmest one is January (24.4 °C). The mean annual precipitation is 1015.9 mm, ranging from 26.4 mm in August to 1544 mm in February (2004-2014; Instituto Nacional de Tecnología Agropecuaria -INTA- San Pedro Agrometeorological Station, 33º44'S 59º41'W). The hydrological regime of the Paraná River is characterized by flooding pulses (Junk et al. 1989; Neiff 1996), with the highest levels in the delta region being reached in April-May (Barros et al. 2006). The study area is also influenced by the hydrological regime of the southeastern portion of the Paraná Pavón River (Zoffoli et al. 2008) (Fig. 1).

Experimental design

To analyze the influence of livestock on vegetation structure and function, we applied a randomized block design (by topographic position) with repeated measures over time, using livestock exclusion as treatment. The study was performed along a topographic gradient across three exclosure areas (ungrazed areas) of 2500 m^2 each, and three adjacent areas where livestock had unrestricted access to grazing (grazed areas). The ungrazed areas was excluded from large herbivores through the use of fences. Three topographic positions with different flooding levels were identified: 1- relative upland with unflooded or occasionally flooded sites; 2- high mid-slope with temporary flooding; and 3- low mid-slope with temporary to semi-permanent flooding. Division into zones was determined *in situ* by topographic profiles recorded with a laser theodolite Spectra Precision Laser plane 500-C and a laser distance meter. Field samplings for data collecting of species composition and biomass were carried out during 2 yr between July 2012 and April 2014; samples were collected every 30 d in summer and spring (increased vegetation growth) and every 45 d in autumn and winter. In July 2013 and May 2014 the floodplain of the Paraná River was completely inundated.

Field surveys

To characterize the vegetation communities and evaluate the successional process resulting from livestock exclusion, 2 x 2 m-permanent plots were established at each topographic position; five plots were located in the ungrazed areas and five in the grazed areas. On each sampling date, the abundance and cover of all vegetation species within the plots were estimated using a modified Braun-Blanquet's scale (Westhoff & Van Der Maarel 1978). Local bibliography was used for the taxonomic assignment of plant species (Burkart 1974, 1979, 1987; Cabrera & Zardini 1993) and their nomenclature was based on Zuloaga et al. (2009). The identification of some species was carried out by an expert taxonomist at the Laboratory of Vascular Plants (Departamento de Biodiversidad y Biología Experimental, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires).

On each sampling date, the aerial biomass was estimated by harvesting ten 0.120 m^2-quadrats for each treatment (livestock exclusion and grazing) and topographic position. The litter within these quadrats was also collected. Harvest sites were selected at random, excluding those already used. Once in the laboratory, collected material was separated per species into green and dry vegetative and reproductive biomass. Then, these were oven-dried at 60 ºC to constant weight and the dry biomass was recorded. This same procedure was conducted for litter.

Data analysis

Data from vegetation plots were used to estimated species diversity with the Shannon-Wiener index (Magurran 2013) and its two components: richness (species number) and evenness (Pielou's index; Moreno 2001). The values of these indices were compared between ungrazed and grazed areas using general linear mixed models. Treatment, time (sampling dates) and their interaction were fixed factors, while the topographic position (considered as block) and the plots surveyed in subsequent sampling periods were random factors. In addition, plot was nested in topographic position as random factor. Variance structure was modeled by the interaction between treatment and time using the varIdent function and subsequent multiple comparisons were performed with the DGC test (Di Rienzo et al. 2011). The Akaike's information and parsimony criteria were used to select the final models (Crawley 2009). Principal Component Analysis (PCA) of species abundance data was used to evaluate the variation of plant communities between treatments within each topographic position over time. Rare species (found in a single plot) were excluded from the analysis and the Hellinger distance was applied to the matrix of sites per species (Borcard et al. 2011). The plots corresponding each treatment and survey were represented by centroids to summarize their variability into a single point.

Significant differences between the values of the different fractions of biomass (green, dry and reproductive) and litter content were assessed using generalized linear models. The models were explored using plot as random factor, but it showed no significant contribution; therefore, we used the average from the ten measurements and seasons as time variable. Likewise, the block represented by the topographic gradient explained only a small proportion of total variability. On this basis, and according to the parsimony criterion (Crawley 2009), the type of biomass/litter content was selected as response variable, and treatment, time and their interaction as fixed factors. For all biomass types, errors followed a

Poisson distribution, while litter content showed a negative binomial distribution. In all cases, multiple comparisons were made using DGC (Di Rienzo et al. 2011).

Biomass values were used to classify species according the following categories: weeds, good forage quality, toxicity and growth form (erect and prostrate species), as proposed by Rossi et al. (2014) for the plant species of the Paraná Delta (Appendix S1). Seasonal changes in total biomass of species with good forage quality, toxic and erect habit were determined by significant differences in the mean values between treatments with a generalized linear model like the one described for litter. For weeds and prostrate species, a general linear model with treatment, seasons and their interaction as fixed factors was used. The variance structure was modeled using the varIdent function for the interaction between treatment and season.

The statistical analyses were performed with the softwares Infostat (Di Rienzo et al. 2011) and R (R Core Team 2014) and the packages lme4 (Bates et al. 2014) and vegan (Oksanen et al. 2013).

Results

Changes in vegetation structure

A total of 80 plant species were recorded during the study period, which belonged to 27 families, from which the most numerous were Asteraceae (16 species), Poaceae (16 species), Polygonaceae (7 species), Cyperaceae (6 species) and Fabaceae (4 species).

The analysis of vegetation diversity showed maximum values during the summer months (December-February) and during the first sampling year in both the grazed and ungrazed areas (Fig. 2a). The difference between treatments (F = 2.67; P = 0.11) and the interaction between treatment and time (F = 1.06, P = 0.39) were not significant. Species richness showed a pattern similar to that of diversity, but the interaction between treatment and time was significant (F = 2.69; P = 0.0006), with the number of species being lower in ungrazed than in grazed areas after 16 months of livestock exclusion (i.e. from summer 2014 onward; Fig. 2b). Evenness showed a significant interaction between treatment and time (F = 2.70; P = 0.0006). The highest differences in evenness values were found between ungrazed and grazed areas during the last sampling months (Fig. 2c).

For the upland, the first two PCA axes explain 53.7% of the total variance (Fig.3a). For the first axis, the grazed plots show a high cover of *Cynodon dactylon* and are located at positive values, while ungrazed plots have a high cover of *Echinochloa helodes* and *Mikania micrantha*, and are at negative values (Fig. 3a). The second axis separates grazed and ungrazed plots showing a high cover of *Baccharis salicifolia* during the first sampling months from those showing a high cover of *Setaria parviflora* in the second sampling year (Fig. 3a). For the high mid-slope, the first axis explains 21.0% of the total variance (Fig. 2b) and allows to separate grazed plots associated with *C. dactylon* and *Eleocharis* aff. v*iridans* from ungrazed plots associated with *Hymenachne pernambucense*, *Vigna luteola* and *M. micrantha* (Fig. 3b). The second axis explains 16.6% of the variance and allows distinguishing between plots sampled in the first and second years. There is no clear pattern for grazed plots over time. For the ungrazed area, the first axis separates between the plots corresponding to the first spring and the first summer (centroids 3, 4, 5 and 6), while the second axis distinguishes between samplings made in autumn and winter (centroids 1, 2, 8, 9 and 10) and those made during the second study year (Fig. 3b). For the low mid-slope, the first two axis explain 47.1% of the total variance (Fig. 3c). *Alternanthera philoxeroides* and *Stellaria parva* are negatively correlated with the first axis, while *Symphyotrichum squamatum* and *Phalaris angusta* were positively and negatively correlated with the second axis, respectively. For the ungrazed areas, the first axis shows vegetation changes over time (Fig. 3c), separating between the plots sampled in the first and the second years (Fig. 3c). The second axis discriminates between ungrazed and grazed plots, except for those with centroids 2, 3 and 11 corresponding to grazed areas.

Functional vegetation changes

The litter content and values of green and dry biomass were significantly higher ($P < 0.05$) for ungrazed than for grazed areas (Fig. 4a, b and d). For the three models, there was a significant interaction between treatment and season (green biomass: $P < 0001$; dry biomass: $P = 0.0057$; litter: $P < 0.001$). The combined effect between these variables had significantly higher differences in green and dry biomass and in litter production from the first summer onward ($P < 0.05$ for all three cases), corresponding to a livestock exclusion period of 7-8 months. From that moment on, the ungrazed areas showed significantly increased values ($P < 0.05$) and differences between treatments became more pronounced (Fig. 4a, b and d). In regard to reproductive biomass, the interaction between treatment and time was also significant ($P = 0.0049$); however, in contrast to the other variables, it was not until summer 2014 that the ungrazed areas showed significantly higher biomass (Fig. 4c).

The biomass of erect and forage species was significantly higher in ungrazed areas and increased with increasing time of livestock exclusion. No simple effects were found for the proposed models because the interaction between treatment and time was significant ($F_{\mathrm{Forage}} = 2.46$, $P_{\mathrm{Forage}} = 0.03$; $F_{\mathrm{Erect}} = 48.88$, $P_{\mathrm{Erect}} < 0.0001$). In this sense, there was an increase in the biomass of the forage species and, to a larger extent, of the erect species during the first year of the treatment (Fig. 5a and b). The increase in the biomass of both erect and forage species was significantly higher for the ungrazed areas from the first spring onward ($P < 0.05$), with these differences being maintained until the end of the experiment. Toxic plants biomass was also higher in the ungrazed areas ($F = 25.14$, $P < 0.0001$) but differences between treatments decrease as time of exclusion increases (Fig. 5a). In contrast, the grazed areas presented values significantly higher of weeds and prostrate species biomass ($P < 0.05$; Fig. 5a and b). For both models interaction between treatments and season was not significant (weeds: $F = 0.98$, $P = 0.46$; prostrate: $F = 2.06$, $P = 0.07$).

Discussion

Facing the livestock intensification which is occurring in many fluvial wetlands of both Argentina and other South American countries, the main novelty of this study was to analyze for the first time how the cattle grazing and trampling affect the structure and function of plant communities taking into account the lack of information about these processes in the region. The results show that livestock exclusion had a remarkable effect on structural traits of the vegetation along the analyzed environmental gradient. This exclusion resulted in a significant decline in the number of species and changes in their composition. In addition, the differences found in species richness between ungrazed and grazed areas would be related to the natural dominance of palatable species in these environments, which are selected by livestock (Quintana et al. 2014). In this sense, livestock removal induces an increase in the cover of these species, which in turn results in a decrease in total species richness. A tendency toward a decrease in species number has also been reported for other wetlands worldwide (Bullock & Pakeman 1997; Jutila 1999; Ausden et al. 2005; Keddy 2010; Marion et al. 2010). Besides, the recovery of palatable species not only for livestock but also for native herbivore mammals like capybara (*Hydrochoerus hydrochaeris*) (Corriale et al. 2011) could be seen as a positive effect from the point of view of the conservation of wild herbivores.

On the other hand, livestock had no significant influence on vegetation diversity due to the effect of evenness. In productive wetlands dominated by palatable species available for livestock, grazing may promote the maintenance of species diversity by avoiding competitive exclusion that they exert (Lunt et al. 2007).

The vegetation communities present in the ungrazed areas were similar to those previously described as typical of the different topographic positions in areas of the Paraná River Delta without ranching (Morandeira 2014). These results emphasize the high recovery of these wetlands, considering the short time elapsed since livestock exclusion. The first changes in these communities were observed between 3 and 5 months after livestock exclusion, which could be the result of the lack of cattle trampling, as was observed in other wetlands (Reeves & Champion 2004; Marion et al. 2010; Morris & Reich 2013). Particularly, at the beginning of the experiment, ungrazed areas showed an increase in the number of toxic and low forage quality species such as *Polygonum* spp. and *Baccharis salicifolia* in the upland and high mid-slope or *Bidens laevis* in the low mid-slope. However, high-quality forage species increased in number over time in free-grazing areas because of their higher competition capacity (Jutila 1999; Rebergen 2002), and finally outcompeted species that had shown high cover values at the beginning of the study.

Livestock grazing may favor the development of prostrate-growth or grazing-avoider species, as reported for other pasture types (McNaughton 1979, 1985; Pucheta et al. 1998; Dalle Tussie 2004; Díaz et al. 2007; Pizzio et al. 2016). Among these, we recorded a high abundance of *Cynodon dactylon* and *Mimosa pigra*. The former is a non-native graminoid species with prostrate growth habit, which is often associated with highly disturbed environments subjected to overgrazing (Dalle Tussie 2004; Godó et al. 2017). On the other hand, livestock exclusion promoted an increase in the cover of palatable species from upland and high mid-slope communities, such as *Echinochloa helodes*, *Alternanthera philoxeroides*, *Echinochloa polystachya* var *polystachya* and *Hymenachne pernambucense*. It is worthy to mention that the habit of *A. philoxeroides* varies depending on the environmental conditions

(Pan et al. 2006). Hence, *A. philoxeroides*, which was dominant in the low mid-slope, showed prostrate growth in grazed areas and an erect habit and increased development in ungrazed ones.

In regard to biomass, herbivory protection led to a significant increase in it when compared to initial levels, as reported for other wetlands (Ford & Grace 1998; Grace & Jutila 1999; Clary & Kinney 2002; Crosslé & Brock 2002; Ausden et al. 2005).

The dominance of erect species increased the accumulation of dry standing biomass and litter, as has also been observed for terrestrial grasslands (McNaughton 1979; Coppock et al. 1983; Rusch & Oesterheld 1997; Pucheta et al. 1998; Rodríguez et al. 2003), and for a native forage plant from the same study region (Magnano et al. 2018). Likewise, livestock exclusion promoted a higher production of green biomass, probably because the removal of valuable forage species by grazing favored the development of less productive species. In addition, the strong increment in the biomass of good forage quality species during the last months of exclusion would be related to the rise in the coverage of them. Considering this and according to Rusch and Oesterheld (1997), the species identity, than species number *per se*, has a higher influence on ecosystem functional processes.

The significant increase in dry biomass and litter content in ungrazed areas may affect wetland ecosystem services, such as accumulation of organic matter in soils (Reeves & Champion 2004; Morris & Reich 2013). The lower production of dry biomass in grazed than in ungrazed areas was probably due to a larger proportion of seedlings resulting from continuous grazing on resprouts (Casasús et al. 2007), thus reducing organic matter accumulation in soils.

Crosslé and Brock (2002), who simulated cattle grazing in fluvial wetlands, found that biomass and reproductive output depended on species identity. In ungrazed areas we observed a significant increase in reproductive biomass after species replacement. In this context, the effect of livestock on reproduction of plants has the potential to alter the dynamics of the populations, and consequently, the dynamics of the community itself (Morris & Reich 2013). In this sense, livestock may affect the recovery of this wetland by the removal of key species from the seed bank.

Vegetation communities showed changes in composition along the study period, with an increase in forage and erect species, and a reduction in weeds and toxic species, following livestock exclusion. Moreover, these species showed greater changes in biomass during the second study year, which was possibly related to their cover, and therefore to functional parameters. Erect species invest a large amount of resources in aerial biomass production, making them good competitors for light but more vulnerable to grazing (Milchunas & Lauenroth 1993). In addition, our results indicate that grazing induces profound changes in species composition and forage quality by loss of palatable species, which in turn may affect global system productivity (Rusch & Oesterheld 1997).

Conclusions

The landscape of the study area shows a diverse composition of plant species differing in the type of cover and adaptations to flooding conditions along the elevation gradient. The livestock management system implemented in the Middle Delta of the Paraná River appears as a shaping factor for community structure. However, the studied wetland showed a remarkable recovery of the structural and functional parameters of the vegetation communities in the short-term (2 yr). Nevertheless, this recovery capacity will be affected if these wetlands continue to be subjected to overgrazing or heavy stocking rates.

Finally, the wide range of valuable benefits that wetlands provide to society highlights the importance of their conservation and sustainable use (Maltby & Dugan 1994). In the case of the studied wetland, a starting point to reverse the effects of continued grazing would be the implementation of management actions that maximize the vegetation biomass production like a grazing rotation or a return to the traditional livestock model which was characterized by an extensive cattle raising and low stocking rates. In this context, our study contributes with baseline information for evaluating the effect of livestock activity on the structure and functioning of fluvial wetlands, which are currently strongly threatened by human pressure.

Acknowledgements

We thank Juan Nazar for allowing us to work in his ranch, and Argentino Bello, Emiliano Sánchez and Azul Sosa for field assistance.

Data Accessibility Statement

The primary data and datasets are available after contact with the corresponding author.

References

Aizen, M.A., Garibaldi, L.A. & Dondo, M. (2009). Expansión de la soja y diversidad de la agricultura argentina. *Ecología austral*, 19, 45-54.

Ausden, M., Hall, M., Pearson, P. & Strudwick, T. (2005). The effects of cattle grazing on tall-herb fen vegetation and molluscs. *Biological conservation*, 122, 317-326. https://doi.org/10.1016/j.biocon.2004.07.021

Barros, V., Clarke, R. & Silva Dias, P. (Eds.) (2006). *El cambio climático en la Cuenca del Plata*. CIMA/CONICET-UBA, Argentina.

Bates, D., Maechler, M., Bolker, B. & Walker, S. (2014). Fitting linear mixed-effects models using lme4. https://arxiv.org/abs/1406.5823.

Bó, R.F., Quintana, R.D., Courtalón, P., Astrada, E., Bolkovic, M.L., Coco, G.L. & Magnano, A. (2010). Efectos de los cambios en el régimen hidrológico por las actividades humanas sobre la vegetación y la fauna silvestre del Delta del Río Paraná. In: Blanco, D.E. & Méndez, F.M. (eds.) *Endicamientos y terraplenes en el Delta del*

Paraná. Situación, efectos ambientales y marco jurídico, pp. 33-63. Fundación Humedales/Wetlands International, Buenos Aires, Argentina.

Borcard, D., Gillet, F. & Legendre, P. (Eds.) (2011). *Numerical Ecology with R*. Springer New York.

Borro, M., Morandeira, N., Salvia, M., Minotti, P., Perna, P. & Kandus, P. (2014). Mapping shallow lakes in a large South American floodplain: A frequency approach on multitemporal Landsat TM/ETM data. *Journal of hydrology*, 512, 39-52.

Brander, L.M., Florax, R.J. & Vermaat, J.E. (2006). The empirics of wetland valuation: a comprehensive summary and a meta-analysis of the literature. *Environmental and Resource economics*, 33, 223-250. http://dx.doi.org/10.1007/s10640-005-3104-4

Brinson, M.M. & Malvárez, A.I. (2002). Temperate freshwater wetlands: types, status, and threats. *Environmental conservation*, 29, 115-133. https://doi.org/10.1017/S0376892902000085

Bullock, J.M. & Pakeman, R.J. (1997). Grazing of lowland heath in England: management methods and their effects on healthland vegetation. *Biological conservation*, 79, 1-13. https://doi.org/10.1016/S0006-3207(96)00117-6

Burkart, A.E. (Eds.) (1987). *Flora ilustrada de Entre Ríos (Argentina). Tomo VI, Parte III. Dicotiledóneas Arquiclamídeas. A: Salicales a Rosales (incluso Leguminosas).* Colección Científica del INTA, Buenos Aires, Argentina.

Burkart, A.E. (Eds.) (1979). *Flora ilustrada de Entre Ríos (Argentina). Tomo VI, Parte V. Dicotiledóneas Metaclamídeas (Gamopétalas). A: Primulales, Plumbaginales, Ebenales, Contortales, Tubiflorales, Callitrichales, Plantaginales.* . Colección Científica del INTA, BUenos Aires, Argentina.

Burkart, A.E. (Eds.) (1974). *Flora ilustrada de entre ríos (Argentina). Tomo VI, Parte VI. Dicotiledóneas Metaclamídeas (Gamopétalas) B: Rubiales, Cucurbitales,* *Campanulales (incluso Compuestas)*. Colección Científica del INTA, Buenos Aires, Argentina.

Cabrera, A.L. & Zardini, E.M. (Eds.) (1993). *Manual de la flora de los alrededores de Buenos Aires*. Acme, Buenos Aires, Argentina.

Casasús, I., Bernués, A., Sanz, A., Villalba, D., Riedel, J. & Revilla, R. (2007). Vegetation dynamics in Mediterranean forest pastures as affected by beef cattle grazing. *Agriculture, ecosystems & environment*, 121, 365-370. https://doi.org/10.1016/j.agee.2006.11.012

Clary, W.P. & Kinney, J.W. (2002). Streambank and vegetation response to simulated cattle grazing. *Wetlands*, 22, 139-148. https://doi.org/10.1672/0277-5212(2002)022[0139:SAVRTS]2.0.CO;2

Coppock, D.L., Detling, J., Ellis, J. & Dyer, M. (1983). Plant-herbivore interactions in a North American mixed-grass prairie. *Oecologia*, 56, 1-9.

Corriale, M. J., Arias, S.M. & Quintana, R.D. (2011). Forage quality of plant species consumed by capybaras (*Hydrochoerus hydrochaeris*) in the Paraná River Delta, Argentina. *Rangelands Ecology and Management*, 64, 257-263.

Crawley, M.J. (Eds.) (2009). *The R book*. John Wiley & Sons, London.

Crosslé, K. & Brock, M.A. (2002). How do water regime and clipping influence wetland plant establishment from seed banks and subsequent reproduction? *Aquatic Botany*, 74, 43-56. https://doi.org/10.1016/S0304-3770(02)00034-7

Dalle Tussie, G. (2004). *Vegetation ecology, rangeland condition and forage resources evaluation in the Borana lowlands, southern Oromia, Ethiopia.* PhD Thesis, Georg-August-Universität Göttingen.

Di Rienzo, J., Casanoves, F., Balzarini, M., Gonzalez, L., Tablada, M. & Robledo, y.C. (2011). InfoStat versión 2011. http://www.infostat.com.ar.

Díaz, S., Lavorel, S., McIntyre, S., Falczuk, V., Casanoves, F., Milchunas, D.G., Skarpe, C., Rusch, G., Sternberg, M. & NOY‐ MEIR, I. (2007). Plant trait responses to grazing–a global synthesis. *Global Change Biology*, 13, 313-341. https://doi.org/10.1111/j.1365-2486.2006.01288.x

Ford, M.A. & Grace, J.B. (1998). Effects of vertebrate herbivores on soil processes, plant biomass, litter accumulation and soil elevation changes in a coastal marsh. *Journal of Ecology*, 86, 974-982. https://doi.org/10.1046/j.1365-2745.1998.00314.x

Fracassi, N., Quintana, R.D., Pereira, J., Mujca, G. & Landó, R. (2013). *Estrategias de conservación de la biodiversidad en bosques plantados de Sálicaceas del Bajo Delta del Paraná*. Ediciones INTA, Argentina.

Gardner, R.C., Barchiesi, S., Beltrame, C., Finlayson, C., Galewski, T., Harrison, I., Paganini, M., Perennou, C., Pritchard, D. & Rosenqvist, A. (2015). State of the world's wetlands and their services to people: a compilation of recent analyses. Ramsar Briefing Note 7. In, Punta del Este, Uruguay.

Godó L., Valkó O., Tóthmérész B., Török P., Kelemen A., Deák B. (2017): Scale-dependent effects of grazing on the species richness of alkaline and sand grasslands. *Tuexenia*, 37, 229–246.

Grace, J.B. & Jutila, H. (1999). The relationship between species density and community biomass in grazed and ungrazed coastal meadows. *Oikos*, 398-408. DOI: 10.2307/3546689

Hempson, G.P., Archibald, S., Bond, W.J., Ellis, R.P., Grant, C.C., Kruger, F.J., Kruger, L.M., Moxley, C., Owen‐ Smith, N. & Peel, M.J. (2015). Ecology of grazing lawns in Africa. *Biological Reviews*, 90, 979-994. https://doi.org/10.1111/brv.12145

Jansen, A. & Robertson, A.I. (2001). Relationships between livestock management and the ecological condition of riparian habitats along an Australian floodplain river. *Journal of applied ecology*, 38, 63-75. https://doi.org/10.1046/j.1365-2664.2001.00557.x

Jones, W.M., Fraser, L.H. & Curtis, P.J. (2011). Plant community functional shifts in response to livestock grazing in intermountain depressional wetlands in British Columbia, Canada. *Biological conservation*, 144, 511-517. https://doi.org/10.1016/j.biocon.2010.10.005

Junk, W.J., An, S., Finlayson, C., Gopal, B., Květ, J., Mitchell, S.A., Mitsch, W.J. & Robarts, R.D. (2013). Current state of knowledge regarding the world's wetlands and their future under global climate change: a synthesis. *Aquatic sciences*, 75, 151-167. doi: 10.1007/s00027-012-0278-z

Junk, W.J., Bayley, P.B. & Sparks, R.E. (1989). The flood pulse concept in river-floodplain systems. *Canadian special publication of fisheries and aquatic sciences*, 106, 110-127.

Jutila, H. (1999). Effect of grazing on the vegetation of shore meadows along the Bothnian Sea, Finland. *Plant Ecology*, 140, 77-88.

Kandus, P., Morandeira, N. & Schivo, F. (Eds.) (2010). *Bienes y servicios ecosistémicos de los humedales del Delta del Paraná*. Fundación Humedales/Wetlands International, Buenos Aires, Argentina.

Keddy, P.A. (Eds.) (2010). *Wetland ecology: principles and conservation*. Cambridge University Press, England.

Lezama, F., Baeza, S., Altesor, A., Cesa, A., Chaneton, E.J. & Paruelo, J.M. (2014). Variation of grazing- induced vegetation changes across a large- scale productivity gradient. *Journal of Vegetation Science*, 25, 8-21. https://doi.org/10.1111/jvs.12053

Lunt, I.D., Eldridge, D.J., Morgan, J.W. & Witt, G.B. (2007). A framework to predict the effects of livestock grazing and grazing exclusion on conservation values in natural ecosystems in Australia. *Australian Journal of Botany*, 55, 401-415. https://doi.org/10.1071/BT06178

Magnano, A.L., Nanni, A.S., Krug, P., Astrada, E., Vicari, R. & Quintana, R.D. (2018). Effects of livestock exclusion on density, survival and biomass of the perennial sagebrush grass Hymenachne pernambucense (Poaceae) from a temperate fluvial wetland. *Acta Oecologica*, 86, 72-78. https://doi.org/10.1016/j.actao.2017.12.006

Magurran, A.E. (Eds.) (2013). *Measuring biological diversity*. Blackwell Publishing, Malden, USA.

Maltby, E. & Dugan, P.J. (1994). Wetland ecosystem protection, management, and restoration: an international perspective. In: Davis, S.M. & Ogden, J.C. (eds.) *Everglades: The ecosystem and its restoration*, pp. 29-46. St. Lucie Press, Boca Ratón, Florida.

Malvárez, A.I. (1999). El Delta del río Paraná como mosaico de Humedales. In: Malvárez, A.I. (ed.) *Tópicos sobre humedales subtropicales y templados de Sudamérica*, pp. 33-51. ORCYT-UNESCO, Montevideo, Uruguay.

Marion, B., Bonis, A. & Bouzillé, J.-B. (2010). How much does grazing-induced heterogeneity impact plant diversity in wet grasslands? *Ecoscience*, 17, 229-239. https://doi.org/10.2980/17-3-3315

McNaughton, S. (1985). Ecology of a grazing ecosystem: the Serengeti. *Ecological monographs*, 55, 259-294. http://doi/10.2307/1942578

McNaughton, S. (1979). Grazing as an optimization process: grass-ungulate relationships in the Serengeti. *The American Naturalist*, 113, 691-703. https://doi.org/10.1086/283426

Middleton, B. (2002). Nonequilibrium dynamics of sedge meadows grazed by cattle in southern Wisconsin. *Plant Ecology*, 161, 89-110. https://doi.org/10.1023/A:1020361021072

Milchunas, D.G. & Lauenroth, W.K. (1993). Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecological monographs*, 63, 327-366. https://doi.org/10.2307/2937150

Miller, J., Chanasyk, D., Curtis, T., Entz, T. & Willms, W. (2010). Influence of streambank fencing with a cattle crossing on riparian health and water quality of the Lower Little Bow River in Southern Alberta, Canada. *Agricultural water management*, 97, 247-258. https://doi.org/10.1016/j.agwat.2009.09.016

Mitsch, W.J. & Gosselink, J.G. (2000). The value of wetlands: importance of scale and landscape setting. *Ecological economics*, 35, 25-33. https://doi.org/10.1016/S0921-8009(00)00165-8

Mitsch, W.J. & Gosselink, J.G. (Eds.) (2007). *Wetlands*. John Wiley & Sons.

Morandeira, N.S. (2014). *Tipos funcionales de plantas en humedales de la planicie de inundación del Bajo Río Paraná (Entre Ríos, Argentina) y su observación con datos polarimétricos de radar*. PhD Thesis, Universidad de Buenos Aires.

Moreno, C. (Eds.) (2001). *Métodos para medir la biodiversidad*. M&T-Manuales y Tesis SEA, Zaragoza.

Morris, K. & Reich, P. (2013). Understanding the relationship between livestock grazing and wetland condition. In. Arthur Rylah Institute for Environmental Technical Report Series No 252, Heidelberg, Victoria.

Musters, C., De Graaf, H. & Ter Keurs, W. (2000). Can protected areas be expanded in Africa? *science*, 287, 1759-1760. https://doi.org/10.1126/science.287.5459.1759

Neiff, J.J. (1996). Large rivers of South America: toward the new approach. *Verhandlungen des Internationalen Verein Limnologie*, 26, 167-180. https://doi.org/10.1080/03680770.1995.11900701

Oksanen, J., Guillaume Blachet, F., Kindt, R., Legendre, P., Minchin, P.R., O'hara, R.B., Simpson, G.L., Solymos, P., Henry, M., Stevens, H. & Wagner, H. (2013). Vegan: Community ecology Package. R package version 2.0-7. http://cran.r-project.org/package=vegan.

Pan, X., Geng, Y., Zhang, W., Li, B. & Chen, J. (2006). The influence of abiotic stress and phenotypic plasticity on the distribution of invasive Alternanthera philoxeroides along a riparian zone. *Acta Oecologica*, 30, 333-341. https://doi.org/10.1016/j.actao.2006.03.003

Paruelo, J.M., Guerschman, J.P., Piñeiro, G., Jobbagy, E.G., Verón, S.R., Baldi, G. & Baeza, S. (2006). Cambios en el uso de la tierra en Argentina y Uruguay: marcos conceptuales para su análisis. *Agrociencia*, 10, 47-61.

Pizzio, R., Herrero- Jáuregui, C., Pizzio, M. & Oesterheld, M. (2016). Impact of stocking rate on species diversity and composition of a subtropical grassland in Argentina. *Applied Vegetation Science*, 19, 454-461. https://doi.org/10.1111/avsc.12229

Polasky, S., Nelson, E., Pennington, D. & Johnson, K.A. (2011). The impact of land-use change on ecosystem services, biodiversity and returns to landowners: A case study in the State of Minnesota. *Environmental and Resource economics*, 48, 219-242. http://dx.doi.org/10.1007/s10640-010-9407-0

Pucheta, E., Cabido, M., Díaz, S. & Funes, G. (1998). Floristic composition, biomass, and aboveground net plant production in grazed and protected sites in a mountain grassland of central Argentina. *Acta Oecologica*, 19, 97-105. https://doi.org/10.1016/S1146-609X(98)80013-1

Quintana, R. D., Bó, R. F., Merler, J. A., Minotti, P. G. & Malvárez, A. I. (1992). Situación y uso de la fauna silvestre en la región del Bajo Delta del río Paraná, Argentina. *Iheringia, Serie Zoologica*, 73, 13-33.

Quintana, R.D. & Bó, R.F. (2011). Por qué el Delta del Paraná es una región única dentro del territorio de la Argentina? In: Quintana, R.D., Villar, V., Astrada, E., Saccone, P. & Malzof, S. (eds.) *El Patrimonio Natural y Cultural del Bajo Delta Insular del Río Paraná. Bases Para su Conservación y uso Sostenible*, pp. 43-53. Fundación Humedales/Wetlands International, Argentina.

Quintana, R.D., Bó, R.F., Astrada, E. & Reeves, C. (Eds.) (2014). *Lineamientos para una ganadería ambientalmente sustentable en el Delta del Paraná*. Fundación Humedales/Wetland International, Argentina.

R Core Team, R. (2014). R: A language and environment for statistical computing. http://www.R-project.org/.

Ramonell, C.G., Kandus, P., Minotti, P.G., Borro, M.M. & Morandeira, N.S. (2012). Nueva interpretación geomorfológica del Complejo Fluviolitoral del Río Paraná en su desembocadura. In: *V Congreso Argentino de Cuaternario y Geomorfología*, Córdoba, Argentina.

Rebergen, A. (2002). Survey, monitoring and management of the native grass Amphibromus fluitans, especially in relation to the exotic grass *Paspalum distichum* (Mercer grass) at Lake Wairarapa wetlands. In. Department of Conservation, Wairarapa.

Reeves, P. & Champion, P.D. (2004). Effects of livestock grazing on wetlands: literature review. In. National Institute of Water & Atmospheric Research Ltd. Client report HAM2004-059, Hamilton, New Zealand.

Ripken, C. (2009). *Resilience and Vulnerability of Wetlands.* MSc Thesis, Rheinische Friedrich–Wilhems–Universität zu Bonn.

Rodríguez, C., Leoni, E., Lezama, F. & Altesor, A. (2003). Temporal trends in species composition and plant traits in natural grasslands of Uruguay. *Journal of Vegetation Science*, 14, 433-440.

Rossi, C., De Magistris, A., González, G.L., Carou, N. & De Loof, E. (Eds.) (2014). *Plantas de interés ganadero de la región del Bajo Delta del Paraná (Argentina)*. Universidad Nacional de Lomas de Zamora, Argentina.

Rusch, G.M. & Oesterheld, M. (1997). Relationship between productivity, and species and functional group diversity in grazed and non-grazed Pampas grassland. *Oikos*, 519-526. https://doi.org/10.2307/3545613

Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B. & Kinzig, A. (2000). Global biodiversity scenarios for the year 2100. *science*, 287, 1770-1774. http://dx.doi.org/10.1126/science.287.5459.1770

Sica, Y., Quintana, R., Radeloff, V. & Gavier-Pizarro, G. (2016). Wetland loss due to land use change in the Lower Paraná River Delta, Argentina. *Science of the Total Environment*, 568, 967-978. https://doi.org/10.1016/j.scitotenv.2016.04.200

Taboada, M. & Lavado, R. (1993). Influence of cattle trampling on soil porosity under alternate dry and ponded conditions. *Soil use and management*, 9, 139-143. https://doi.org/10.1111/j.1475-2743.1993.tb00943.x

Westhoff, V. & Van Der Maarel, E. (1978). The braun-blanquet approach. In: Whittaker, R. (ed.) *Classification of plant communities*, pp. 287-399. Springer Netherlands.

Wu, G.-L., Du, G.-Z., Liu, Z.-H. & Thirgood, S. (2009). Effect of fencing and grazing on a Kobresia-dominated meadow in the Qinghai-Tibetan Plateau. *Plant and Soil*, 319, 115-126. https://doi.org/10.1007/s11104-008-9854-3

Zoffoli, M.L., Kandus, P., Madanes, N. & Calvo, D.H. (2008). Seasonal and interannual analysis of wetlands in South America using NOAA-AVHRR NDVI time series: the case of the Parana Delta Region. *Landscape ecology*, 23, 833-848. https://doi.org/10.1007/s10980-008-9240-9

Zuloaga, F., Morrone, O. & Belgrano, M.J. (2009). Catálogo de las plantas vasculares del Cono Sur. In. Missouri Botanical Garden - Instituto Darwinion. http://darwin.edu.ar

Supporting Information

Appendix S1. Plant species recorded in grazed and ungrazed areas from a fluvial wetland in the Middle Delta of the Paraná River, Argentina.

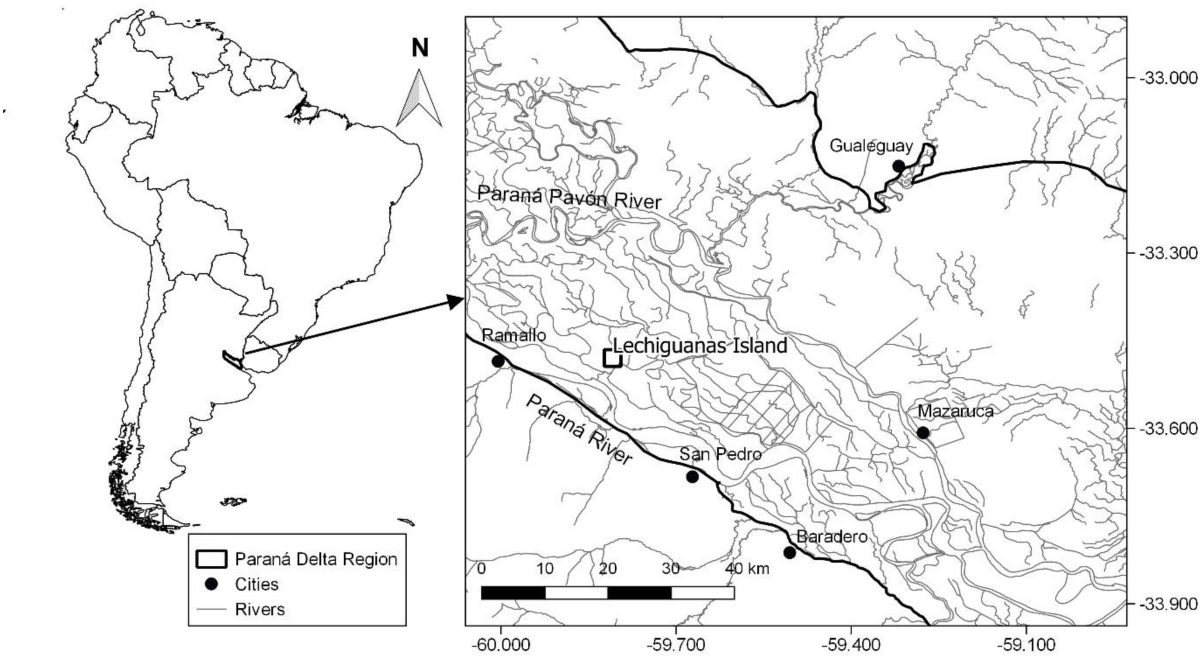

Figure 1: Location of the study area in the Delta of the Paraná River, Argentina.

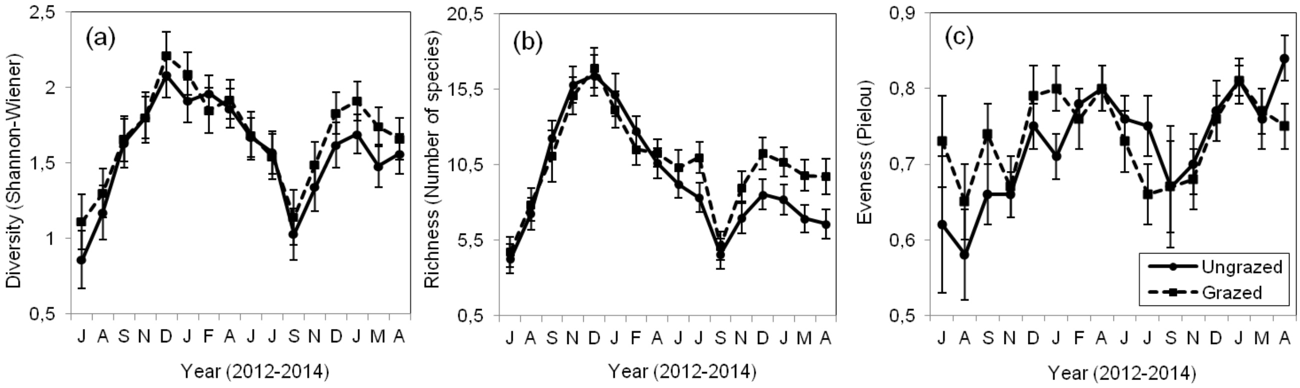

Figure 2: Community parameters (mean ± SE) estimated for ungrazed and grazed areas from a fluvial wetland in the Middle Delta of the Paraná River (Argentina). (a) Diversity (Shannon-Wiener index), (b) richness (number of species) and (c) evenness (Pielou).

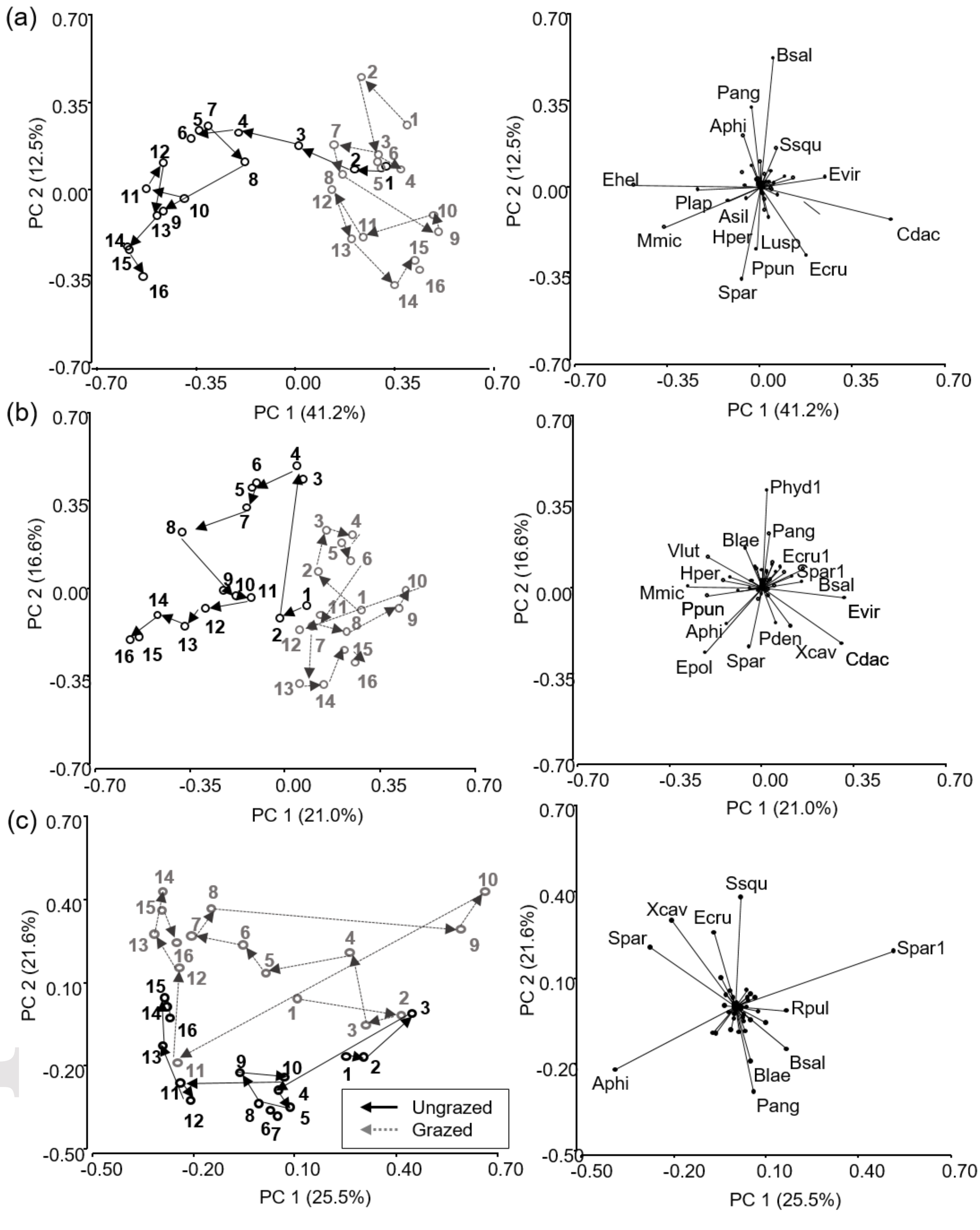

Figure 3: Principal Component Analysis (PCA) of plots (n= 5) clustered into centroids in function of the abundance of plant species on a topographic gradient from a fluvial wetland in the Middle Delta of the Paraná River (Argentina). The arrows show the temporal progression for ungrazed and grazed areas from July 2012 to April 2014. For acronyms see Appendix S1. (a) Upland, (b) High mid-slope, and (c) Low-mid-slope.

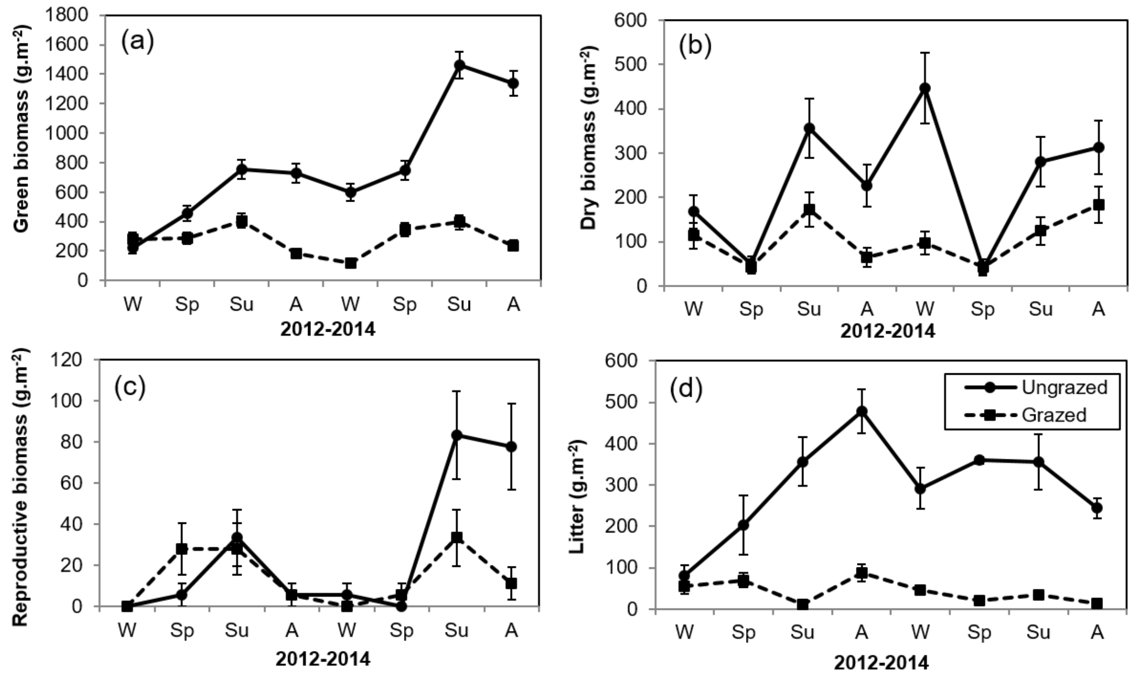

Figure 4: Aerial green biomass (a), dry (c) and reproductive (c); and litter content (d) for ungrazed and grazed areas from a fluvial wetland in the Middle Delta of the Paraná River (Argentina). Results (mean ± SE) were obtained for the four seasons of the two studied years.

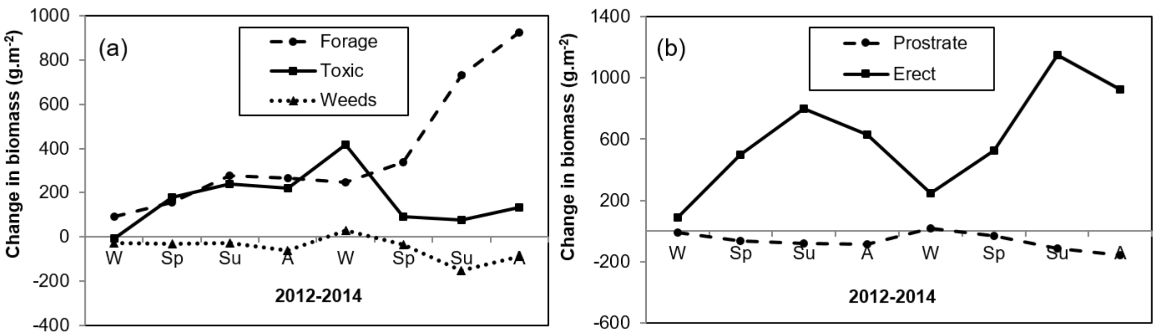

Figure 5: Changes in the total biomass of weeds, toxic and good forage quality species (a) and growth form (erect and prostrate species) (b) from a fluvial wetland in the Middle Delta of the Paraná River (Argentina) due to livestock exclusion. Results (mean ± SE) were obtained for the four seasons of the two studied years.