Applied Vegetation Science **19** (2016) 391–400

Shrub encroachment influences herbaceous communities in flooded grasslands of a neotropical savanna wetland

Fernando Henrique Barbosa da Silva, Julia Arieira, Pia Parolin, Cátia Nunes da Cunha &
Wolfgang Johannes Junk

Keywords
Habitat heterogeneity; Herbaceous community; Invasion; Natural pastures; Plant cover; Plant diversity; Rangeland management; Wetland ecosystem

Abbreviations
AIC = Akaike information criterion; ANOSIM = Analysis of similarity; NMDS = Non-metric multidimensional scaling.

Nomenclature
The Missouri Botanical Garden website (http://www.tropicos.org/; accessed 18 Sep 2015)

Received 8 May 2015
Revised 9 December 2015
Accepted 18 December 2015
Co-ordinating Editor: Rob Marrs

Barbosa da Silva, F.H. (corresponding author, fernandon18@gmail.com)[1,2],
Arieira, J. (juarieira@gmail.com)[1,3],
Parolin, P. (pparolin@botanik.uni-hamburg.de)[4,5],
Nunes da Cunha, C. (nunesdacunhac@gmail.com)[1,2],
Junk, W.J. (wjj@evolbio.mpg.de)[1,2]

[1]Núcleo de Estudos Ecológicos do Pantanal, Instituto de Biociências, Universidade Federal de Mato Grosso (NEPA/IB/UFMT), Cuiabá, Mato Grosso 78060900, Brazil;
[2]Instituto Nacional de Ciência e Tecnologia em Áreas Úmidas (INCT-INAU), Cuiabá, Mato Grosso 78068410, Brazil;
[3]Programa de Pós-graduação em Ciências Ambientais, Universidade de Cuiabá, Cuiabá, Mato Grosso 78065900, Brazil;
[4]Biocentre Klein Flottbek, Dept. Plant Diversity, University of Hamburg, Ohnhorststr. 18, 22609 Hamburg, Germany;
[5]French National Institute for Agricultural Research (INRA), ISA– TEAPEA 1355, BP 167, 06903 Sophia Antipolis, France

Abstract

Question: The encroachment of woody species has been globally reported over much of arid and semi-arid biomes, and has been associated with a decrease in cover and number of herbaceous species. How does the encroachment of a woody shrub affect herbaceous community structure and species composition in grasslands of a wetland ecosystem?

Location: Seasonally flooded grasslands in a Neotropical Hyperseasonal Savanna, the Pantanal wetland, Brazil.

Methods: We investigated the effect of the encroaching plant *Combretum laxum* on a herbaceous community from seasonally flooded grasslands in the Pantanal wetland using 29 vegetation samples representing encroachment at different spatio-temporal stages. The point quadrat method was used to acquire vegetation data, as plant cover, species richness (S) and Shannon-Wiener diversity index (H′). We evaluated the existence of stages of encroachment related to differences in vegetation structure and species composition using non-metric multidimensional scaling ordination and analysis of similarity. The response of the herbaceous community to shrub advance was analysed using linear and quadratic polynomial regression models. Model fitness was tested using the ACI.

Results: The advance of the woody encroaching plant *C. laxum* over the seasonally flooded grassland occurs in three stages: *grassland stage*, *shrub islands stage* and *shrubland stage*. The initial advance of *C. laxum* over the grassland, represented by the *shrub islands stage* was correlated to an increase in species richness and a decrease in important native forage grasses. Critical changes in the herbaceous community were observed when the encroaching plant covered >30% of the periodically flooded grassland, when the richness of herbaceous species dropped from 22 to four.

Conclusions: Woody encroachment causes impoverishment and simplification of the herbaceous community**.** The shift from a grass- to a shrub-dominated state is related to the reduction in important grassland-obligate species, forage resources for herbivore livestock and wild animals, affecting the ecological dynamics and the economy of rangelands. Conservation of these grassland ecosystems depends on rangeland management practices guided by scientific knowledge on the causes and consequences of plant community changes.

Doi: 10.1111/avsc.12230 © 2016 International Association for Vegetation Science

Introduction

The loss of natural open vegetation as a result of the encroachment of woody species is a concern of ecologists and land managers (Archer et al. 1995; Davis et al. 2000; Ravi & D'Odorico 2008; Van Auken 2009; Hirota et al. 2011; Kgosikoma et al. 2012; Cable et al. 2013; Angassa 2014). Encroachment consists of a gradual increase in the cover, density or biomass of native woody or shrubby plants (Van Auken 2000; Moleele et al. 2002; Eldridge et al. 2011). As a consequence, highly diverse open habitats, such as tropical grassland and savanna communities, are converted into rather uniform forests or shrublands. This biotic homogenization increases the similarity of initially differentiated communities (Elton 1958) and has resulted in immense costs for restoration (Daryanto & Eldridge 2011; Gray & Bond 2013).

Woody encroachment is responsible for changes in biotic and abiotic site conditions. It is used athe s a predictor of decreases in herbaceous and grass cover (Clark & Wilson 2001; Eldridge et al. 2011) and, in long term, plant species richness (Luoto et al. 2003; Knapp et al. 2008; Ratajczak et al. 2012; Alofs & Fowler 2013). Other studies have stated that encroachment may increase soil fertility and carbon, nitrogen, calcium and phosphorus stocks (Sitters et al. 2012; Grellier et al. 2013). As the encroaching plant advances, islands of fertility can be created through the accumulation of nutrients beneath the plant canopy (Maestre et al. 2009). In turn, these islands change light availability, microclimate, soil moisture and soil respiration (Browning et al. 2008; Cable et al. 2012), favouring the long-term permanence of the woody plants.

The increase in woody plant cover is seen as an undesirable process that decreases the carrying capacity of rangelands (Hongo & Masikini 2003; Van Auken 2009). Grasslands and savannas are ecologically and economically valuable biomes, largely used for livestock and wild herbivore grazing. In wetlands, encroachment is often promoted by human-induced changes, such as artificial drainage and fire suppression, producing communities of woody plants that grow on saturated to seasonally flooded soils (Bren 1992; Clark & Wilson 2001; Johnston 2003; Warren et al. 2007). The Neotropical scandent shrub *Combretum laxum* (Croat 1974; Linsingen & Cervi 2008) has potential to cover large areas and turn them into impenetrable thickets in the Pantanal wetland (Dorado-Rodrigues et al. 2015). Substantial changes in vegetation structure, e.g. from herbaceous- to shrub-dominated communities, alter the availability of plant resources, such as light and space, and as consequence, change habitat conditions of the previous herbaceous communities (Oba et al. 2000; Warren et al. 2007; Archer et al. 2011; Eldridge et al. 2011).

In this study we classified encroachment stages in seasonally flooded grasslands in the Pantanal wetland based on the cover degree of the encroaching shrub *Combretum laxum* Jacq. (Combretaceae), and changes in herbaceous community composition and structure. We also investigated the effects of the encroaching plant advance on herbaceous cover, number of species and species diversity. We hypothesize that shrub encroachment decreases the number and richness of herbaceous plants in seasonally flooded grasslands. The vegetation changes promoted by the encroaching plant might decrease the carrying capacity of grasslands as natural pastures by reducing the niche for regeneration of herbaceous species (Smit 2004; Archer et al. 2011). Our data will contribute to the guidance of wetland management, as addressed by the Ramsar Convention (Ramsar Convention Secretariat 2013), by indicating in which stage of encroachment seasonally flooded grasslands lose their economic and ecological value as natural pastures, and where removal of the encroaching plant may become a fruitless task.

Methods

Study site

This study was carried out in seasonally flooded grassland in the Pantanal wetland. The Pantanal is a Quaternary sedimentary basin in the centre of South America, composed of fluvial megafans (Assine 2010). The Pantanal wetland has a great diversity of habitats that include grasslands, savannas and forests under different flooding regimes (Nunes da Cunha et al. 2006; Nunes da Cunha & Junk 2009). The climate is Aw, marked by seasonal dry winters and rainy and warm summers, with average temperatures of 25 °C (Alvares et al. 2013). Annual flooding occurs in the rainy period, from Dec to May, following a monomodal wave pattern (Hamilton 2002; Nunes da Cunha & Junk 2004) and is driven by river overflow and rainwater trapped in poorly drained soils. Multiannual inundation cycles of approximately 10–15 yr cause extreme flood events alternating with pronounced droughts. The drought years are associated with the highest frequency of natural fires (Hamilton 2002; Nunes da Cunha & Junk 2004).

The Pantanal grasslands occur in flat geomorphologic units in low or meso relief and are subject to distinct flooding periods (Pinder & Rosso 1998; Hamilton 2002; Nunes da Cunha et al. 2006). The studied grasslands are located in a modern depositional lobe of the Cuiaba river megafan (16°34′ S, 57°01′ W; Assine 2010), an important tributary in the northern limits of Pantanal wetland. These areas are used as pasture areas in extensive grazing systems (Junk & Nunes da Cunha 2012). The maximum depth of the

Doi: 10.1111/avsc.12230 © 2016 International Association for Vegetation Science

watertables is around 0.7 m, making these natural pastures unavailable for at least 4 mo. Considering the 1863 species of phanerogams listed for the Pantanal, 1000 are herbaceous, Poaceae being the second most numerous family with 212 species (Pott et al. 2011). The aquatic phase is dominated by aquatic macrophytes and flooding-tolerant plants; the terrestrial phase is associated with the dominance of grasses, forbs and sedges (Rebellato et al. 2012). The last decades were marked by the advance of woody plants over the Pantanal grasslands, savanna species such as *Byrsonima orbygniana*, *Curatella americana,* and forest species as *Combretum lanceolatum, C. laxum* and *Vochysia divergens* (Arieira & Nunes da Cunha 2006; Nunes da Cunha et al. 2006; Santos et al. 2006). The encroachment is supposed to decrease pasture carrying capacity and force farmers to intensify cattle management through introduction of exotic species and increasing the number of animals (Nunes da Cunha & Junk 2004; Santos et al. 2006).

Sampling design and data collection

Field sampling was conducted in 2009 and 2010, during the dry season. A total of 29 transects of 100-m length each and 250 m apart were established over grasslands with various levels of *C. laxum* cover (see Appendix S1). The point quadrat method (Bullock 1996) was used to acquire data of plant cover, species richness and diversity. The method consisted of placing a vertical rod at successive 1-m intervals along each transect and counting individual plant species that touched the rod (n = 100 points per transect). The counting of plant touches using the metallic thin rod was realized by dropping the rod through shrub branches. In such a point interception method, assumptions on shrub canopy are not needed (Floyd & Anderson 1987). The cover value was the proportion of n in which the rod touched each plants species. Species richness (S) corresponded to the total number of species, and Shannon-Wiener diversity index (H') was calculated based on species richness and plant cover, here considered a measurement of species abundance (Heip et al. 2001; Magurran 2004). Specimens were identified by comparison with species illustrated in the literature (Pott & Pott 1994, 2000) and identified species at the herbarium of the Federal University of Mato Grosso (Brazil). Scientific names were updated using data from the Missouri Botanical Garden website (http://www.tropicos.org/).

Data analysis

To measure similarities among plant communities across different levels of *C. laxum* cover and identify encroachment stages, non-metric multidimensional scaling (NMDS) ordination was applied to the 29 standardized plant cover data sets using the Bray-Curtis dissimilarity index. The proximity between sample points in the NMDS biplot was used to define stages of encroachment and significant differences between encroachment stages were tested using analysis of similarity (ANOSIM). In ANOSIM, the R statistic was used to assess the level of association between groups/stages, with 999 Monte Carlo permutations to evaluate the significance of the R-value (Clarke 1993). Linear and polynomial models were fitted to the same data set to investigate changes in the herbaceous community caused by the encroachment (Chartier & Faulkner 2008). Herbaceous cover, square root of richness and Shannon-Wiener diversity index were included as response variables, and *C. laxum* cover as explanatory variable for linear models. The second-order polynomial and linear values of predictors were included as covariate in the polynomial models. The Akaike information criterion (AIC) weights were calculated to judge the quality of the models and the most parsimonious were chosen (Akaike 1974). All statistical computations were performed in the R v. 3.0.1 with the *vegan* package (R Foundation for Statistical Computing, Vienna, AT) and the functions *metaMDS*, *diversity, anosim, lm* and *extractAIC*.

Results

Stages of encroachment

The NMDS showed clear patterns of floristic variability in the study site. A total of 35 species were found belonging to 33 genera and 21 families. The two axis components of the NMDS explained 87% (stress = 0.09) of total variability of the data matrix (Fig. 1). Three encroaching stages, initial, intermediate and final, were identified in the ordination space and confirmed by ANOSIM (global R = 0.86, P = 0.001) that showed a significant difference in species composition and cover between stages. The initial or *grassland stage* was dominated by a short grass–herbaceous layer and *C. laxum* was absent (Fig. 2a). The intermediate or *shrub islands stage* was characterized by a grassland matrix with sparse or grouped *C. laxum* individuals (Fig. 2b). This stage showed the highest variability in vegetation structure and plant species composition, as indicated by the sample scores. The final and most advanced or *shrubland stage* was a monospecific, impenetrable thicket dominated by *C. laxum* and climber species <3 m in height and with a closed canopy (Fig. 2c).

Because the intermediate encroachment stage presented a larger sample size (n = 17) compared to the others (n = 6), six transects were selected randomly from this group to equal the sample size and allow comparisons of vegetation parameters between the three encroachment stages. A total of 18 species were recorded in the *grassland stage*. This initial stage was dominated by a short and dense

Doi: 10.1111/avsc.12230 © 2016 International Association for Vegetation Science

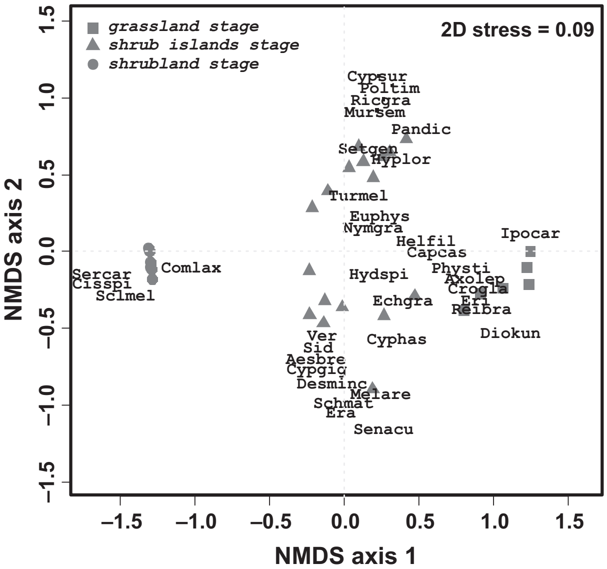

Fig. 1. Two NMDS components ($R^2 = 0.87$, stress = 0.09) showing variation in community structure and species composition across encroachment stages (squares (■), *grassland stage*; triangles (▲), *shrub islands stage*; circles (●), *shrubland stage*) in the studied seasonally flooded grasslands. Differences between encroachment stages were confirmed by ANOSIM (global $R = 0.86$, $P = 0.001$). The genus or species scores are represented by the first three letters of their taxonomic level. These are: *Aeschynomene brevipes* (Aesbre), *Axonopus leptostachyus* (Axolep), *Caperonia castaneifolia* (Capcas), *Cissus spinosa* (Cisspi), *Combretum laxum* (Comlax), *Croton glandulosus* (Crogla), *Cyperus giganteus* (Cypgig), *Cyperus haspan* (Cyphas), *Cyperus surinamensis* (Cypsur), *Desmodium incanum* (Desminc), *Diodia kuntzei* (Diokun), *Echinodorus grandiflorus* (Echgra), *Eragrostis* sp. (Era), *Eriosema* sp. (Eri), *Euphorbia hyssopifolia* (Euphys), *Heliotropium filiforme* (Helfil), *Hyptis lorentziana* (Hyplor), *Ipomoea carnea* subsp. *fistulosa* (Ipocar), *Melochia arenosa* (Melare), *Murdannia semifoliata* (Mursem), *Nymphoides grayana* (Nymgra), *Panicum dichotomiflorum* (Pandic), *Phyllanthus stipulatus* (Physti), *Polygala timoutoides* (Poltim), *Reimarochloa brasiliensis* (Reibra), *Richardia grandiflora* (Ricgra), *Senna aculeata* (Senacu), *Setaria geniculata* (Setgen), *Schizosepala matogrossensis* (Schmat), *Scleria melaleuca* (Sclmel), *Serjania caracasana* (Sercar), *Sida* sp. (Sid), *Turnera melochioides* (Turmel), *Vernona* sp. (Ver).

graminoid layer and forb species. The *shrub islands stage* was the richest encroachment stage with 22 species, five of which were exclusive. From the *grassland stage* to the *shrub islands stage* the degree of cover of Poaceae species decrease from 80% to about 62%. This decrease was substantial for two dominant species, *Reimarochloa brasiliensis* and *Axonopus leptostachyus*. In contrast, the cover of the grasses *Setaria geniculata* and *Panicum dichotomiflorum* increased, as well as cover of forb species such as *Euphorbia hyssopifolia, Hyptis lorentziana* and *Hydrolea spinosa*. The highest cover of *C. laxum* and the lowest plant richness were recorded in the *shrubland stage*, with four species. The sedge *Scleria melaleuca* and climber species, *Serjania caracasana* and *Cissus spinosa,* appeared only in the *shrubland stage,* where individuals of *C. laxum* are hard to separate since they form thickets with tangled stems above the soil surface (see Appendix S2).

Effect of encroachment on cover and richness of herbaceous species

The relation between herbaceous cover and shrub cover was represented as a linear model ($r^2 = 0.84$, $P < 0.000$; Fig. 3a), chosen due few differences in the coefficient of determination and AIC by insertion of a co-variable (Table 1). In contrast, herbaceous richness and diversity were fitted with polynomial models (Table 1), showing a non-linear relation between these variables and herbaceous cover. According to the model, the fitted curve indicates an initial increase in species richness ($r^2 = 0.69$, $P < 0.000$; Fig. 3b) and Shannon-Wiener diversity index ($r^2 = 0.76$, $P < 0.000$; Fig. 3c) up to 30% of *C. laxum* cover, and thereafter these parameters declined.

Discussion

This study is focused on the spread of a native species that behaves as an invasive species, advancing beyond its his-

Fig. 2. Encroachment stages in the seasonally flooded grasslands in the Pantanal wetland. (**a**) *Grassland stage*, the initial pre-encroachment phase, dominated by a herbaceous layer; (**b**) *Shrub islands stage*, the intermediate and ecotonal phase; (**c**) *Shrubland stage*, the final stage with high dominance of the encroaching shrub *Combretum laxum*.

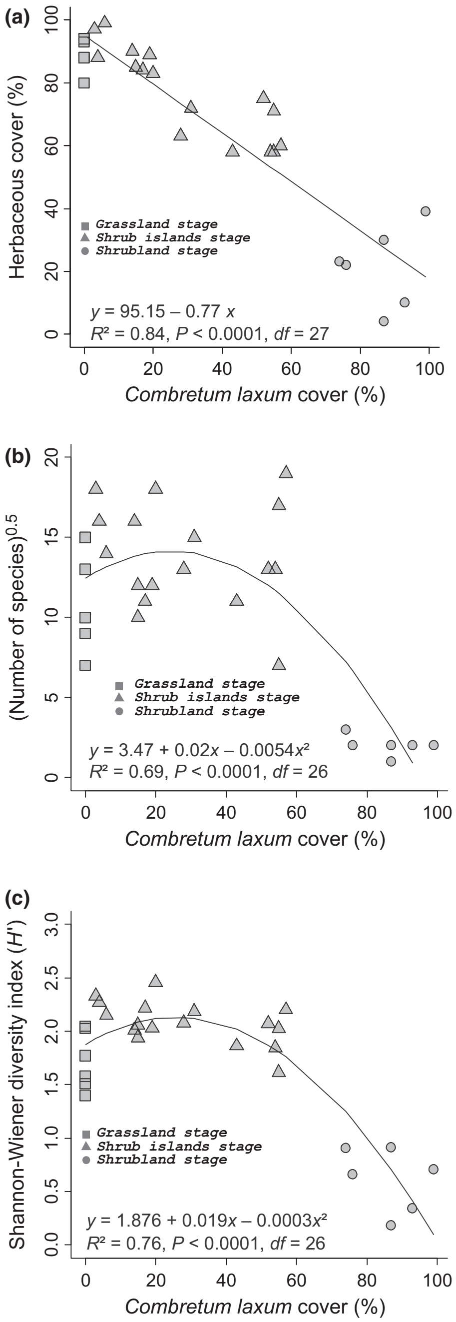

Fig. 3. Most parsimonious regression models between *C. laxum* cover and (**a**) herbaceous cover, (**b**) square root of number of species, and (**c**) Shannon-Wiener diversity index (H') in seasonally flooded grasslands in the Pantanal wetland. Parsimonious models are based on a first-order regression with 27 *df* for herbaceous cover, and on a second-order polynomial regression with 26 *df* for number of species and Shannon-Wiener diversity index, using GLM. Squares (■): *grassland stage*, triangles (▲): *shrub islands stage*, circles (●): *shrubland stage*. All regressions were statistically significant at $P < 0.05$.

Table 1. ANOVA of the linear and polynomial regression models for the relationship between *Combretum laxum* cover and herbaceous cover, square root of number of species and Shannon-Wiener index. Polynomial models are constructed by nesting as extra covariate the exponential power function of the original variable.

Models	R^2	*F*-Statistic	*df*	RSE	AIC
Herbaceous Cover					
I. Linear	0.84	156.3	27	10.82	140.04
II. Polynomial	0.85	82.28	26	10.61	139.82
Species Richness					
I. Linear	0.49	28.16	27	0.71	−17.26
II. Polynomial	0.69	33.11	26	0.55	−31.26
Shannon-Wiener Diversity Index					
I. Linear	0.50	29.01	27	0.44	−45.47
II. Polynomial	0.76	46.38	26	0.30	−66.36

R^2, coefficient of determination; RSE, residual standard error; AIC, Akaike information criterion.

torical limits and causing impacts to wetland habitats (Bren 1992; Báez & Collins 2008; Knapp et al. 2008; Archer et al. 2011; Eldridge et al. 2011; Hirota et al. 2011; Grellier et al. 2013; Angassa 2014). Despite the fact that the dynamic behaviour of woody and herbaceous species is of general interest for plant ecologists, it has received limited attention in Neotropical wetlands. We found that the shrub's encroachment is a strong predictor of the distribution, structure and diversity of the herbaceous community, resulting in landscape homogenization in areas under fluvial influence, as indicated by previous studies in wetland ecosystems in Australia (Bren 1992) and the United States (Johnston 2003; Warren et al. 2007), including Alaska (Berg et al. 2009). As the proportion of woody plants increases, the characteristics of the herbaceous community change, e.g. species composition and structural dominants. These changes have been associated with different encroachment stages, as observed by Browning et al. (2008) in semi-desert grasslands of Arizona. Browning et al. (2008) described two phases associated with encroachment: one characterized by high rates of colonization of bare spaces, and the other, called stabilization phase, where encroachment develops in association with recruitment. Our classification of encroachment stages differs from Browning's with the inclusion of the unoccupied grassland community, named *grassland stage*.

A decrease in herbaceous species is a common result of encroachment, because woody plants compete by space that was previously occupied by herbaceous plants (Laliberte et al. 2004; Velázquez & Gómez-Sal 2009; Eldridge et al. 2011; Ratajczak et al. 2012). The relation between encroaching plants and the herbaceous communities ranges from linear to exponential decline, as observed here (Báez & Collins 2008; Knapp et al. 2008; Belay et al. 2013). The initial *grassland stage* contains the highest cover of grasses (>80%) and the abundance of two forage species, *Axonopus leptostachyus* and *Reimarochloa brasiliensis* (Fig. 4), that are references of natural conditions and integrity of this ecosystem in future restoration efforts

Doi: 10.1111/avsc.12230 © 2016 International Association for Vegetation Science

(Santos et al. 2002; Desbiez et al. 2011). Non-linear relations between woody plant and species diversity reflect a transitional phase of the encroachment, as the *shrub islands stage* (Fig. 4). This is associated with the co-occurrence of shrubs, grasses and forbs, resulting in an increase in the species diversity and niches for fauna (Archer et al. 2011; Ratajczak et al. 2012; Grellier et al. 2013; Wiezik et al. 2013). For instance, a study conducted in the same study location as ours showed that the richness and abundance of anuran community were higher in open habitats in the *grassland stage* and *shrub island stage* (Dorado-Rodrigues et al. 2015).

Despite the initial gain in diversity, forage species were negatively correlated with the proportion of the encroaching plant, showing the undesirable aspect of woody encroachment for the maintenance of the low-impact extensive cattle ranching practiced in the studied site. Since encroachment is transformative (Archer et al. 2011), as the encroaching plant becomes dominant, reaching more than 30% of woody cover, substantial changes in herbaceous community are observed through the displacement of grassland-obligate plants (Warren et al. 2007; Archer et al. 2011), such as *R. brasiliensis* and *A. leptostachyus*, and anurans (Dorado-Rodrigues et al. 2015). The primary attributes of seasonally flooded grassland biodiversity, the species composition and the vegetation structure are threatened by the habitat loss and fragmentation associated with progressive changes in the dominant life form from herbaceous to shrubby (Fig. 4). Changes in light availability and soil attributes promoted by advance of the woody plant may favour a different pool of species, with different life strategies. In this study, climber species, such as *Cissus spinosa,* and *Serjana caracasana* (Fig. 4), were favoured by the tangled woody cover that serves for plant support and improves light acquisition (Ibarra-Manriquez & Martínez-Ramos 2002). Although, the final *shrubland stage* results in a species-poor community, it has its own ecological value.

The ecological behaviour of encroaching species -species is similar to the other invasive species (e.g. *Mimosa pigra*, *Tamarix ramosissima*). They show broad ecological niches and a variety of life-history strategies enabling them to expand very rapidly, such as vegetative reproduction and high seed production (Zedler & Kercher 2004). In the case of *C. laxum*, the mechanisms that guarantee its rapid expansion might be related to dispersal mechanisms and adaptations to the oscillation between terrestrial and aquatic phases (Junk 2000; Parolin 2009). *C. laxum* shows two dispersal mechanisms: producing a large amount of buoyant diaspores that are dispersed in the flood water, and horizontal spread of prostrate shoots that develop new plants wherever the shoot touches the ground (Schessl 1999; Cronk & Fennessy 2001). In wetlands, rapid stem elongation is considered a plant strategy to avoid submergence and obtain oxygen and available light close to the water surface (Cronk & Fennessy 2001). On the other hand, strategies to deal with severe drought during the terrestrial phase are also a guarantee of establishment success in wetlands such as the Pantanal (Junk 2000). Rapid resprouting after stem damage, as well as seed production are observed in *C. laxum* after fire events in rangeland management treatments (E. F. Calabria, local farmer, pers. comm.). We believe that both mechanisms are responsible for promoting the shrub encroachment.

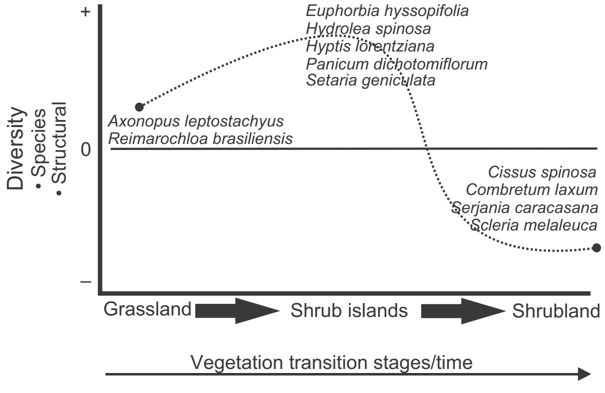

Fig. 4. Conceptual model of vegetation changes in the herbaceous community since the *grassland stage* when *C. laxum* is absent, until *shrubland stage*, when *C. laxum* is dominant. A non-linear relation with woody cover is expressed as a decrease in species diversity and richness after an initial increase in these parameters (pointed line with filled circles). This conceptual model was adapted from Archer et al. (2011).

In grasslands adjacent to woody communities, proximity acts as a catalyst favouring encroachment. *C. laxum* occurs as a liana in the border of riparian forests and forested paleo-levees (uplands). From these forests, seeds reach neighbouring flooded open habitats creating shrub islands. Later, *C. laxum* spreads horizontally in contact with the ground surface, creating a circular shape closed-canopy 10–110 m in diameter, i.e. the shrubland (Schessl 1999). The closed-canopy *shrubland stage* creates difficult accessibility to animals (Archer et al. 2011) and makes field sampling difficult. Considering the problems in counting individual touches within the *shrubland stage*, vegetation adjacent to each transect was cleared to allow such measurements.

The management of woody encroaching plants in the Pantanal has been discussed in terms of conservation of key wetland habitats, such as seasonally flooded grasslands used for grazing (Santos et al. 2006; Junk & Nunes da Cunha 2012). It seems that changes from grassland stages to woody encroachment stages may be promoted by grazing intensity. Nunes da Cunha & Junk (2004) indicated that the exclusion of cattle allows the growth of woody plants in flooded grasslands. On another hand, the preference of grazers (e.g. cattle) for herbaceous plants can lead to high amounts of vacant space available for woody colonization, promoting encroachment by non-palatable woody species (Moleele et al. 2002; Hongo & Masikini 2003; Sarmiento et al. 2004; Ravi & D'Odorico 2008; Van Auken 2009; Angassa 2014). This finding associates the low density of livestock to the maintenance of habitat and species diversity, multiple services to populations and to the environment, as a controller of encroaching plants and as a tool for grassland habitat conservation (Junk & Nunes da Cunha 2012).

Another possible cause of encroachment in wetlands is multi-annual changes in hydrological cycles (Nunes da Cunha & Junk 2004; Junk et al. 2006). Natural or man-made changes of the hydrological dynamics may cause shifts in the ecological niche and promote competitive advantages for some woody species (Bren 1992; Berg et al. 2009). The dominance of *C. laxum* in the Pantanal grasslands is more often found in grasslands subject to long-term flooding, about 5–6 mo (Nunes da Cunha & Junk 2004). This species shows strong resistance to inundation in initial stages of development due the protrusion of adventitious roots (C. Nunes da Cunha, pers. comm.) that ensure oxygen and nutrient entrance during the aquatic phase. This can be considered an adaptive advantage in wetland ecosystems (Maurenza et al. 2009), probably linked to *C. laxum* success in colonizing long-term flooded grasslands (Nunes da Cunha & Junk 2004).

According to ranchers in the Pantanal, the *C. laxum* expansion began approximately 30 yr ago, in the 1980s, coinciding with a multi-annual cycle of wet years. The traditional management of invaded grasslands includes the use of machinery designed to cut, shear, shred or crush woody plants (Santos et al. 2006). These strategies generally fail if the encroaching plant has already covered large areas, becoming the dominant life form. In this situation, restoring the native grassland community might have high management costs (Ansley et al. 2006; Ravi & D'Odorico 2008; Van Auken 2009; Archer et al. 2011), and uncertain chances of success (Clark & Wilson 2001). Solving these problems needs the development of specific management plans to restore habitats affected by encroachment and subjected to an annual flood pulse (Junk & Nunes da Cunha 2012) through cooperation between scientists, farmers and environmental agencies (Finlayson et al. 2005).

Conclusions

The wise use and maintenance of the ecological characteristics of wetland grasslands depends on understanding the causes and consequences of changes in vegetation structure and diversity. The results of our study show that woody encroachment changes the structure and species composition of grassland communities in a non-linear manner. The increase in species diversity and richness at intermediate encroachment stages may be a signal of critical changes to a poorly diverse woody-dominant community. We believe that Neotropical savanna wetlands with a rich herbaceous community composed of important forage species should be conserved, and in some situations, restored. Data on ecological and cultural conditions provide a baseline for restoration projects.

Acknowledgements

The authors are grateful to the Brazilian Governmental Agencies for continuous support. MEC/CAPES granted a Master's scholarship to F.H.B. Silva. MCTI/CNPq through INCT/INAU funded field activities. We thank Jerry Penha, Lúcia Matheus and Viviane Layme from UFMT/IB for helpful discussions on the manuscript and analysis. We also thank local ranchers Francisco Eduardo Calábria, Felício Carmélio Calábria and Osvaldo Cid Nunes da Cunha and the *Sindicato Rural de Poconé* for logistic support. This study is a contribution of the 'Núcleo de Estudos Ecológicos do Pantanal' (UFMT/IB/NEPA).

References

Akaike, H. 1974. A new look at the statistical model identification. *IEEE Transactions on Automatic Control* 19: 716–723.

Alofs, K.M. & Fowler, N.L. 2013. Loss of native herbaceous species due to woody plant encroachment facilitates the establishment of an invasive grass. *Ecology* 94: 751–760.

Alvares, C.A., Stape, J.L., Sentelhas, P.C., Gonçalves, J.L. & Sparovek, G. 2013. Köppen's climate classification map for Brazil. *Meteorologische Zeitschrift* 22: 711–728.

Angassa, A. 2014. Effects of grazing intensity and bush encroachment on herbaceous species and rangeland condition in southern Ethiopia. *Land Degradation & Development* 25: 438–451.

Ansley, R.J., Wiedemann, H.T., Castellano, M.J. & Slosser, J.E. 2006. Herbaceous restoration of Juniper-dominated grasslands with chaining and fire. *Rangeland Ecology and Management* 59: 171–178.

Archer, S., Schimel, D.S. & Holland, E.A. 1995. Mechanisms of shrubland expansion: land use, climate or CO_2? *Climatic Change* 29: 91–99.

Archer, S.R., Davies, K.W., Fulbright, T.E., McDaniel, K.C., Wilcox, B.P. & Predick, K.I. 2011. Brush management as a rangeland conservation strategy: a critical evaluation. In: Briske, D.D. (ed.) *Conservation benefits of rangeland practices: assessment, recommendations, and knowledge gaps*, pp. 105–170. USDA, Natural Resources Conservation Service, Lawrence, KS, US.

Arieira, J. & Nunes da Cunha, C. 2006. Fitossociologia de uma floresta inundável monodominante de *Vochysia divergens* Pohl (Vochysiaceae), no Pantanal norte, MT, Brasil. *Acta Botanica Brasilica* 20: 569–580.

Assine, M.L. 2010. Pantanal Mato-grossense: uma paisagem de exceção. In: Modenesi-Gauttieri, M.C., Bartorelli, A., Mantesso-Neto, V., Carneiro, C.D.R. & Lisboa, M.B.A.L. (eds.) *A obra de Aziz Nacib Ab'Saber*, pp. 464–489. Beca-BALL Edições, São Paulo, BR.

Báez, S. & Collins, S.L. 2008. Shrub invasion decreases diversity and alters community stability in northern Chihuahuan desert plant communities. *PLoS ONE* 3: e2332.

Belay, T.A., Totland, Ø. & Moe, S.R. 2013. Ecosystem responses to woody plant encroachment in a semiarid savanna rangeland. *Plant Ecology* 214: 1211–1222.

Berg, E.E., Hillman, K.M., Dial, R. & DeRuwe, A. 2009. Recent woody invasion of wetlands on the Kenai Peninsula lowlands, south-central Alaska: a major regime shift after 18000 years of wet *Sphagnum*–sedge peat recruitment. *Canadian Journal of Forest Research* 39: 2033–2046.

Bren, L.J. 1992. Tree invasion of an intermittent wetland in relation to changes in the flooding frequency of the river Murray, Australia. *Austral Ecology* 17: 395–408.

Browning, D.M., Archer, S.R., Asner, G.P., McClaran, M.P. & Wessman, C.A. 2008. Woody plants in grasslands: post-encroachment stand dynamics. *Ecological Applications* 18: 928–944.

Bullock, J. 1996. Plants. In: Sutherland, W.J. (ed.) *Ecological census techniques: a handbook*, pp. 111–138. Cambridge University Press, New York, NY, US.

Cable, J.M., Barron-Gafford, G.A., Ogle, K., Pavao-Zuckerman, M., Scott, R.L., Williams, D.G. & Huxman, T.E. 2012. Shrub encroachment alters sensitivity of soil respiration to temperature and moisture. *Journal of Geophysical Research* 117: G01001.

Cable, J.M., Ogle, K., Barron-Gafford, G.A., Bentley, L.P., Cable, W.L., Scott, R.L., Williams, D.G. & Huxman, T.E. 2013. Antecedent conditions influence soil respiration differences in shrub and grass patches. *Ecosystems* 16: 1230–1247.

Chartier, S. & Faulkner, A. 2008. General linear models: an integrated approach to statistics. *Tutorial in Quantitative Methods for Psychology* 4: 65–78.

Clark, D.L. & Wilson, M.V. 2001. Fire, mowing, and hand-removal of woody species in restoring a native wetland prairie in the Willamette Valley of Oregon. *Wetlands* 21: 135–144.

Clarke, K.R. 1993. Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* 18: 117–143.

Croat, T.B. 1974. *Combretum laxum* Jacq. var. *epiphyticum* (Combretaceae) a case of selection for water dispersal. *Phytologia* 28: 188–191.

Cronk, Julie.K. & Fennessy, M.S. 2001. *Wetland plants: biology and ecology*. Lewis, Washington, DC, US.

Daryanto, S. & Eldridge, D.J. 2011. Is shrub removal an appropriate management strategy in shrub-encroached woodlands? *WIT Transactions on Ecology and Environment* 148: 37–46.

Davis, M.A., Grime, J.P. & Thompson, K. 2000. Fluctuating resource in plant communities: a general theory of invasibility. *Journal of Ecology* 88: 528–534.

Desbiez, A.L.J., Santos, S.A., Alvarez, J.M. & Tomas, W.M. 2011. Forage use in domestic cattle (*Bos indicus*), capybara (*Hydrochoerus hydrochaeris*) and pampas deer (*Ozotoceros bezoarticus*) in a seasonal Neotropical wetland. *Mammalian Biology* 76: 351–357.

Dorado-Rodrigues, T.F., Layme, V.M.G., Silva, F.H.B., Nunes da Cunha, C. & Strussmann, C. 2015. Effects of shrub encroachment on the anuran community in periodically flooded grasslands of the largest Neotropical wetland. *Austral Ecology* 40: 547–557.

Eldridge, D.J., Bowker, M.A., Maestre, F.T., Roger, E., Reynolds, J.F. & Whitford, W.G. 2011. Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. *Ecology Letters* 14: 709–722.

Elton, C.S. 1958. *The ecology of invasions by animals and plants*. Methuen, London, UK.

Finlayson, C.M., Bellio, M.G. & Lowry, J.B. 2005. A conceptual basis for the wise use of wetlands in northern Australia — linking information needs, integrated analyses, drivers of change and human well-being. *Marine and Freshwater Research* 56: 269–277.

Floyd, D.A. & Anderson, J.E. 1987. A comparison of three methods for estimating plant cover. *Journal of Ecology* 75: 221–228.

Gray, E.F. & Bond, W.J. 2013. Will woody plant encroachment impact the visitor experience and economy of conservation areas? *Koedoe* 55: 1–9.

Grellier, S., Ward, D., Janeau, J.-L., Podwojewski, P., Lorentz, S., Abbadie, L., Valentin, C. & Barot, S. 2013. Positive versus negative environmental impacts of tree encroachment in South Africa. *Acta Oecologica* 53: 1–10.

Hamilton, S.K. 2002. Hydrological controls of ecological structure and function in the Pantanal wetland (Brazil). In: McClain, M. (ed.) *The ecohydrology of South American rivers and wetlands*, pp. 133–158. International Association of Hydrological Sciences, Manaus, BR.

Heip, C.H.R., Herman, P.M.J. & Soetaert, K. 2001. Indices of diversity and evenness. *Océanis* 2: 61–87.

Hirota, M., Holmgren, M., Van Nes, E.H. & Scheffer, M. 2011. Global resilience of tropical forest and savanna to critical transitions. *Science* 334: 232–235.

Hongo, H. & Masikini, M. 2003. Impact of immigrant pastoral herds to fringing wetlands of Lake Victoria in Magu district Mwanza region, Tanzania. *Physics and Chemistry of the Earth* 28: 1001–1007.

Ibarra-Manriquez, G. & Martínez-Ramos, M. 2002. Landscape variation of liana communities in a Neotropical rain forest. *Plant Ecology* 160: 91–112.

Johnston, C.A. 2003. Shrub species as indicators of wetland sedimentation. *Wetlands* 23: 911–920.

Doi: 10.1111/avsc.12230 © 2016 International Association for Vegetation Science

Junk, W.J. 2000. Mechanisms for development and maintenance of biodiversity in neotropical floodplains. In: Gopal, B., Junk, W.J. & Davids, J.A. (eds.) *Biodiversity in wetlands: assessment, function and conservation*, pp. 119–139. Backhuys, Leiden, NL.

Junk, W.J. & Nunes da Cunha, C. 2012. Pasture clearing from invasive woody plants in the Pantanal: a tool for sustainable management or environmental destruction? *Wetlands Ecology and Management* 20: 111–122.

Junk, W.J., Nunes da Cunha, C., Wantzen, K.M., Petermann, P., Strüssmann, C., Marques, M.I. & Adis, J. 2006. Biodiversity and its conservation in the Pantanal of Mato Grosso, Brazil. *Aquatic Science* 68: 278–309.

Kgosikoma, O.E., Harvie, B.A. & Mojeremane, W. 2012. Bush encroachment in relation to rangeland management systems and environmental conditions in Kalahari ecosystem of Botswana. *African Journal of Agricultural Resources* 7: 2312–2319.

Knapp, A.K., Briggs, J.M., Collins, S.L., Archer, S.R., Syndonia Bret-Harte, M., Ewers, B.E., Peters, D.P., Young, D.R., Shaver, G.R., Pendall, E. & Cleary, M.B. 2008. Shrub encroachment in North American grasslands: shifts in growth form dominance rapidly alter control of ecosystem carbon inputs. *Global Change Biology* 14: 615–623.

Laliberte, A.S., Rango, A., Havstad, K.M., Paris, J.F., Beck, R.F., McNeely, R. & Gonzalez, A.L. 2004. Object-oriented image analysis for mapping shrub encroachment from 1937 to 2003 in southern New Mexico. *Remote Sensing of Environment* 93: 198–210.

Linsingen, L.V. & Cervi, A.C. 2008. A família Combretaceae R. Brown nas formações de Cerrado do estado do Paraná. *Pesquisas Botânica* 59: 211–221.

Luoto, M., Pykälä, J. & Kuussaari, M. 2003. Nature conservation decline of landscape-scale habitat and species diversity after the end of cattle grazing. *Journal for Nature Conservation* 178: 171–178.

Maestre, F.T., Bowker, M.A., Puche, M.D., Belén-Hinojosa, M., Martínez, I., García-Palacios, P., Castillo, A.P., Soliveres, S., Luzuriaga, A.L., Sánchez, A.M., Carreira, J.A., Gallardo, A. & Escudero, A. 2009. Shrub encroachment can reverse desertification in semi-arid Mediterranean grasslands. *Ecology Letters* 12: 930–941.

Magurran, A.E. 2004. *Measuring ecological diversity*. Blackwell Science, Oxford, UK.

Maurenza, D., Marenco, R.A. & Piedade, M.T.F. 2009. Efeito da inundação de longa duração sob o crescimento de *Pouteria glomerata* (Sapotaceae), uma espécie arbórea de várzea da Amazônia Central. *Acta Amazônica* 39: 519–526.

Moleele, N.M., Ringrose, S., Matheson, W. & Vanderpost, C. 2002. More woody plants? The status of bush encroachment in Botswana's grazing areas. *Journal of Environmental Management* 64: 3–11.

Nunes da Cunha, C. & Junk, W.J. 2004. Year-to-year changes in water level drive the invasion of *Vochysia divergens* in Pantanal grasslands. *Applied Vegetation Science* 7: 103–110.

Nunes da Cunha, C. & Junk, W.J. 2009. A preliminary classification of habitats of the Pantanal of Mato Grosso and Mato Grosso do Sul, and its relation to national and international wetland classification systems. In Junk, W.J., Da Silva, C.J., Nunes da Cunha, C. & Wantzen, K.M. (eds.), *The pantanal: ecology, biodiversity and sustainable management of a large neotropical seasonal wetland*, pp. 127–141. Pensoft Publishers, Sofia-Moscow, RU.

Nunes da Cunha, C., Rawiel, P., Wantzen, K.M., Junk, W.J. & Lemes do Prado, A. 2006. Mapping and characterization of vegetation units by means of Landsat imagery and management recommendations for the Pantanal of Mato Grosso (Brazil), north of Poconé. *Amazoniana* 19: 1–32.

Oba, G., Post, E., Syvertsen, P.O. & Stenseth, N.C. 2000. Bush cover and range condition assessments in relation to landscape and grazing in southern Ethiopia. *Landscape Ecology* 15: 535–546.

Parolin, P. 2009. Submerged in darkness: adaptations to prolonged submergence by woody species of the Amazonian floodplains. *Annals of Botany* 103: 359–376.

Pinder, L. & Rosso, S. 1998. Classification and ordination of plant formations in the Pantanal of Brazil. *Plant Ecology* 136: 151–165.

Pott, A. & Pott, V.J. 1994. *Plantas do Pantanal*. EMBRAPA, Brasília, BR.

Pott, V.J. & Pott, A. 2000. *Plantas aquáticas do Pantanal*. EMBRAPA, Brasília, BR.

Pott, A., Oliveira, A.K.M., Damasceno-Junior, G. & Silva, J.S.V. 2011. Plant diversity of the Pantanal wetland. *Brazilian Journal of Biology* 71: 265–273.

Ramsar Convention Secretariat 2013. *The Ramsar Convention manual: a guide to the Convention on wetlands (Ramsar, Iran, 1971)*, 6th edn. Ramsar Convention Secretariat, Gland, CH.

Ratajczak, Z., Nippert, J.B. & Collins, S.L. 2012. Woody encroachment decreases diversity across North American grasslands and savannas. *Ecology* 93: 697–703.

Ravi, S. & D'Odorico, P. 2008. Post-fire resource redistribution and fertility island dynamics in shrub encroached desert grasslands: a modeling approach. *Landscape Ecology* 24: 325–335.

Rebellato, L., Nunes da Cunha, C. & Figueira, J.E.C. 2012. Respostas da comunidade herbácea ao pulso de inundação no Pantanal de Poconé, Mato Grosso. *Oecologia Australis* 16: 797–818.

Santos, S.A., Costa, C., Souza, G.S., Moraes, A.S. & Arrigoni, M.B. 2002. Qualidade da dieta selecionada por bovinos na sub-região da Nhecolândia, Pantanal. *Revista Brasileira de Zootecnia* 31: 1663–1673.

Santos, S.A., Nunes da Cunha, C., Tomas, W.M., Abreu, U.G.P. & Arieira, J. 2006. *Plantas invasoras no Pantanal: como entender o problema e soluções de manejo por meio de diagnóstico participativo*. EMBRAPA Pantanal, Corumbá, BR.

Sarmiento, G., Pinillos, M., Silva, M.P. & Acevedo, D. 2004. Effects of soil water regime and grazing on vegetation diversity and production in a hyperseasonal savanna in the Apure Llanos, Venezuela. *Journal of Tropical Ecology* 20: 209–220.

Schessl, M. 1999. Floristic composition and structure of floodplain vegetation in the Northern Pantanal of Mato Grosso, Brazil. *Phyton* 39: 303–336.

Sitters, J., Edwards, P.J. & Olde-Venterink, H. 2012. Increases of soil C, N, and P pools along an *Acacia* tree density gradient and their effects on trees and grasses. *Ecosystems* 16: 347–357.

Smit, G.N. 2004. An approach to tree thinning to structure southern African savannas for long-term restoration from bush encroachment. *Journal of Environmental Management* 71: 179–191.

Van Auken, O.W. 2000. Shrub invasions of North American semiarid grasslands. *Annual Review of Ecology and Systematics* 31: 197–215.

Van Auken, O.W. 2009. Causes and consequences of woody plant encroachment into western North American grasslands. *Journal of Environmental Management* 90: 2931–2942.

Velázquez, E. & Gómez-Sal, A. 2009. Changes in the herbaceous communities on the landslide of the Casita volcano, Nicaragua, during early succession. *Folia Geobotanica* 44: 1–18.

Warren, R.J. II, Rossell, I.M., Moorhead, K.K. & Pittillo, J.D. 2007. The influence of woody encroachment upon herbaceous vegetation in a southern Appalachian wetland complex. *American Midland Naturalist* 157: 39–51.

Wiezik, M., Svitok, M., Wieziková, A. & Dovčiak, M. 2013. Shrub encroachment alters composition and diversity of ant communities in abandoned grasslands of western Carpathians. *Biodiversity and Conservation* 22: 2305–2320.

Zedler, J.B. & Kercher, S. 2004. Causes and consequences of invasive plants in wetlands: opportunities, opportunists, and outcomes. *Critical Reviews in Plant Sciences* 23: 431–452.

Supporting Information

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

Appendix S1. Primary data.

Appendix S2. Cover measurements comparison in encroachment stages.

Applied Vegetation Science
Doi: 10.1111/avsc.12230 © 2016 International Association for Vegetation Science