Effects of exotic pastures on tadpole assemblages in Pantanal floodplains: assessing changes in species composition

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Abstract. Land use change has been identified as a major driver of amphibian decline around the world. Yet we generally lack an understanding of how conversion to exotic pastures affects freshwater communities. This study examined tadpole assemblages in areas converted to exotic pastures and native wooded grasslands in northern Pantanal wetland, Midwestern Brazil. We tested the differences in site occupancy probability and assemblage composition during a flood season. We registered thirteen tadpole species, but only five were detected at levels suitable for occupancy modelling. For most species, tadpole occupancy was higher at the beginning of the flood season. Only *Scinax fuscomarginatus* occupancy was related with vegetation cover. Occupancy probability for three species (*Dendropsophus nanus*, *Physalaemus centralis*, and *Physalaemus cuvieri*) was associated positively with species richness of fish. Multivariate analyses demonstrated that exotic pastures hosted a different tadpole assemblage than native areas. The assemblage composition gradient was associated with species richness of fish, vegetation cover and volume of herbaceous vegetation and leaf litter. These differences likely relate to specific traits of individual anuran species (dietary plasticity, reproductive mode, and habitat preference). The study showed that some generalist species were able to cope with replacement of native vegetation by exotic species. However, management practices have maintained many areas in the Pantanal at a stage of a near-pristine wetland ecosystem and replacement of native vegetation by exotic pastures should be done with caution.

Keywords: amphibians, detection probability, land use, *Urochloa*, wooded grasslands.

Introduction

Land use change is an ongoing process often associated with biodiversity loss (Wassenaar et al., 2007; Ferreira et al., 2012). In wetlands, conversion of land for agriculture or permanent pastures often involves clearing of terrestrial habitats (forests and grasslands) and changes in hydrological cycles of wetlands. Such modified habitats generally support lower amphibian diversity (e.g. Machado, Moreira and Maltchik, 2012; Alix et al., 2014). While many studies have addressed effects of forest clearance, there

are important knowledge gaps on impacts of native vegetation removal in wooded grasslands and freshwater ecosystems.

In addition, invasive species associated with agricultural practices are particularly widespread in the non-forested biomes (Ferreira et al., 2012). Impacts of exotic plants on biological community structure are well known (Levine et al., 2003; Levine, Adler and Yelenik, 2004). Exotic plants can reduce the richness of amphibians (Watling, Hickman and Orrock, 2011), and disturb tadpole development and behaviour (Watling et al., 2011).

Studies on movement of amphibians through modified landscapes have pointed to the importance of vegetation structure and individual traits of species on ease of movement (Roznik and Johnson, 2009; Youngquist and Boone, 2014). Open canopy habitats, such as wooded grasslands, tend to have higher temperatures and lower humidity, resulting in greater desiccation risk (Cosentino, Schooley and Phillips, 2010; Tingley and Shine, 2011; Nowakowski

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et al., 2013). Therefore, dispersing amphibians may be more willing to use good-quality habitats, such as forested patches. Changes in native vegetation can reduce habitat quality and heterogeneity, which have been shown to be important drivers of dispersal and population persistence in amphibians (Fahrig, 2007).

The Pantanal ecoregion lies in the centre of South America, and is characterized by a mosaic of annually flooded grasslands and savannas along the upper portion of the Paraguay river and its tributaries (Junk et al., 2006). All these habitats are under varying degrees of human impact, due to livestock activities and the replacement of native vegetation by exotic pastures (mainly *Urochloa humidicola* and *U. decumbens*) as a strategy for improving animal productivity (Junk and Nunes da Cunha, 2012). In the Neotropical savannas, effects of invasive grasses of African origin, such as *Urochloa*, are various. Exotic grasses commonly form monodominant stands that inhibit tree regeneration and exclude herbaceous species (Hoffmann and Haridasan, 2008; Rossi et al., 2014). The effect of exotic pastures on animal communities is less straightforward than on plants. In the Pantanal, studies have documented that replacement by *Urochloa* pastures did not affect aquatic invertebrates or fish assemblages (Fernandes, Machado and Penha, 2010; Santos et al., 2013). However, cattle ranchers tend to plant exotic pastures on the areas not subject to flooding, which also tend to be forested (Seidl, Silva and Moraes, 2001). By changing the environmental heterogeneity associated with the vegetation mosaic, the replacement of native vegetation by exotic pastures can potentially result in shifts in amphibian species composition.

In floodplains, amphibian assemblages are structured by both local and landscape factors, such as hydroperiod, riparian vegetation, water temperature, rainfall, and fish density (Ficetola and De Bernardi, 2004; Tockner et al., 2006; Ocock et al., 2014). Flood pulse has a major effect on several ecological processes in floodplains, being responsible for the variation between aquatic and terrestrial phases (Junk et al., 2006; Tockner et al., 2010). It is also known that flood pulse plays an important role in determining amphibian distribution and community structure (Tockner et al., 2006; Ocock et al., 2014), and individual species characteristics (e.g., dispersal ability, reproductive modes and habitat preference) are also likely to influence amphibian behaviour during the flooding.

Understanding the role of detection bias in apparent species occupancy is critical when habitat use is being studied (MacKenzie et al., 2006; Durso, Willson and Winne, 2011). Most studies of occupancy and detection probability of amphibian species have either focused on calling survey data or have concentrated on methodologically tractable segments of the community (e.g. terrestrial species caught in pitfall traps). Some characteristics of tadpoles make them good models for field inventories and aquatic monitoring studies, namely general abundance and longer presence in the aquatic habitats than adults (Andrade et al., 2007). Although surveys focusing on tadpoles also allow the confirmation of successful breeding activity (including explosive breeders that are frequently missed during calling surveys), few studies have focused on ecological aspects of larval stages (Curtis and Paton, 2010).

In this context, we evaluated the effects of conversion of native vegetation to exotic pastures in the northern Pantanal on the structure of tadpole assemblages. Specifically, we determined: (1) if detection bias-adjusted site occupancy probability was associated with vegetation cover; (2) if areas influenced by exotic pastures have a different anuran composition relative to areas of native vegetation. Based on previous results for Neotropical tadpole assemblages (Both et al., 2011; Almeida et al., 2014), we predicted that biotic variables (vegetation structure and species richness of predatory fish) would have greater influence on species occupancy probability than abiotic factors. We also predicted that, due to habitat homogenization, only a subset of the anuran species assemblage

would be able to successfully occupy exotic pastures.

Materials and methods

The study area is located in the floodplain of Cuiabá River, at a Long-Term Sampling Site (LTSS) of the Brazilian Biodiversity Research Program (PPBio) (56.3088° to 56.3554°S, 16.3293° to 16.3651°W). In the rainy season, floods are common in the region as a result of overflow waters from river and rainfall runoff. The topography is flat, formed mostly by hydromorphic soils, causing drainage problems, which partially explain the tendency for periodic and prolonged floods (Junk et al., 2011). As in the most of the non-protected areas in the Pantanal, extensive livestock farming (about 15 cows/km^2) is the major land use (Junk and Nunes da Cunha, 2012). The LTSS consists of 30 plots systematically distributed over 25 km^2. Each plot is 250 m long, and follows elevation isoclines. Plot start points are located at a distance of 1 km from each other (see Magnusson et al., 2005). Vegetation is a mosaic of flooded grasslands (native and exotic), dense arboreal savanna, seasonally flooded evergreen forest (composed mainly of *Licania parvifolia* and *Calophyllum brasiliense*), and monodominant forests composed by *Vochysia divergens*, locally known as cambarazal.

Sampling occurred three times during a flooding cycle: one sampling at flood beginning (December 2006; ten days after flood pulse), one during steady flood period (February 2007), and one during the drawdown (April 2007). Flood beginning is characterized by appearance of distinct aquatic environments (rain puddles, flooded areas, permanent and temporary ponds) that are not necessarily connected. During the steady flood period, the floodplain is almost completely covered by surface water (mean depth < 30 cm), except for scattered patches with higher elevation. These remnants of paleo-levees, which rise one meter above the mean flood level, are normally covered with forests. Three out of the 30 plots in the LTSS grade were established in such areas and were not subject to annual flooding. Seasonal shallow lakes are formed in water drainage channels during drawdown.

We sampled 27 plots (fig. 1), in areas that were flooded in December 2006. The spatial independence of the 27 sampling areas was tested using a principal coordinates of neighbour matrices (PCNM) analysis (Borcard and Legendre, 2002). We generated a set of eight spatial variables from Cartesian coordinates with the 'pcnm' function of the vegan package 2.3 (Oksanen et al., 2015). As the PCNM did not detect significant spatial structure in the tadpole assemblage composition ($F_{8,18} = 0.822$, $P = 0.8$), spatial autocorrelation was not included in the statistical analysis.
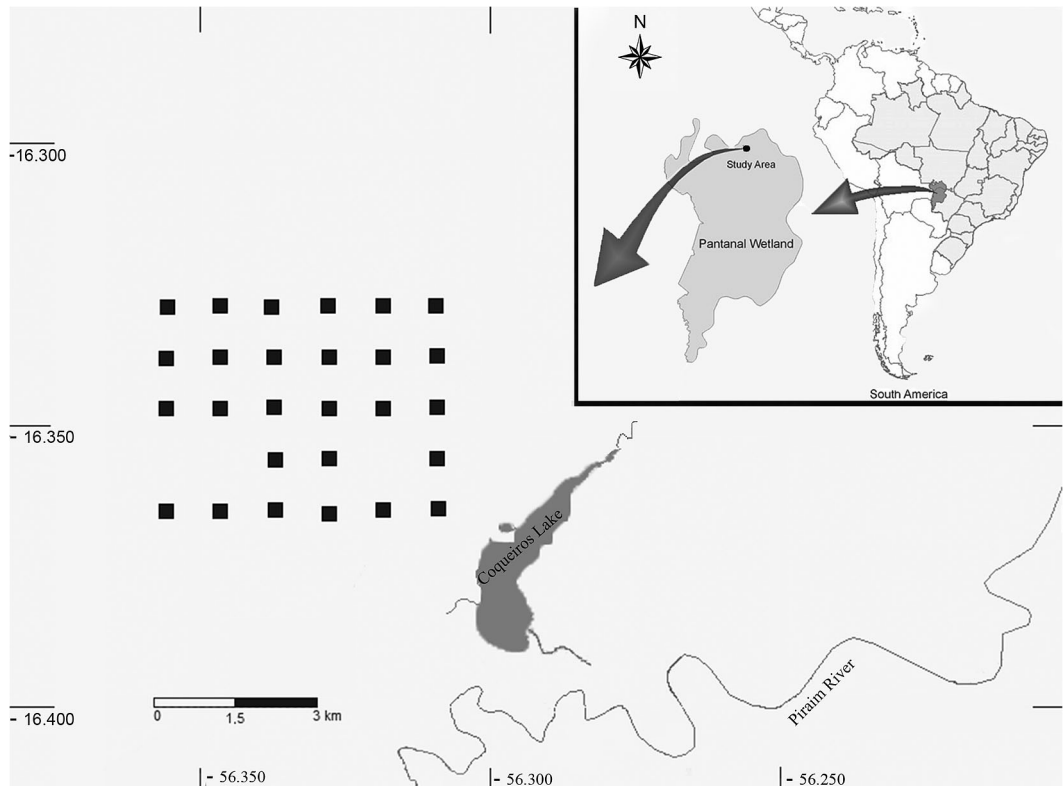
Figure 1. Geographical location of the long-term sampling site in the northern Pantanal, Brazil. Black squares indicate sampling plots.

At each plot, tadpoles and fish were collected with a throw trap (a cubic metal structure with a volume of 1 m^3, with the four sides covered by a 1.5 mm nylon mesh). Starting at point zero, we performed six throw trap launches at regular intervals of 50 m along (250 × 2 m) each plot. For each launch, the collector slowly approached the predetermined point, waited for about 1 minute and then placed the throw trap quickly in the water. All tadpoles and fish within each trap were removed with a net (10 cm width, 2.5 mm mesh). Each trap sampling ended when 10 sweeps of the net caught no more tadpoles or fish. Collected specimens were anaesthetized in a 5% solution of benzocaine, then immediately fixed in 10% formaldehyde. Samples were taken to the laboratory for further processing and identification. Voucher specimens were deposited in the Coleção Zoológica de Vertebrados of the Universidade Federal de Mato Grosso, Brazil.

Data on site-specific and survey-specific factors thought to influence occupancy and detection probabilities were collected at each trap location (Weir, Fiske and Royle, 2009). These included information on type of dominant vegetation cover, water temperature, electrical conductivity, pH, water depth, rainfall in the last 48 h, species richness of predatory fish (species considered as potential tadpole predators), and volume of leaf litter and herbaceous vegetation in the water column. Physical and chemical characteristics of surface water were measured using a portable multiparameter probe YSI, the water column depth was measured in the centre of the trap using a ruler. To estimate vegetation volume, all herbaceous stratum within the area bounded by the throw trap was cut at water level with the aid of a knife. The remaining below-water vegetation and leaf litter inside trap was transferred to a plastic measuring bucket, the contents of which was then uniformly compressed three times with a heavy wooden tamper, and post-packing volume recorded. Four vegetation cover classes were used to occupancy modelling (native grassland, exotic pastures, cambarazal, and seasonally-flooded forest). Vegetation cover data used in this study are freely available at the PPBio website (http://ppbio.inpa.gov.br). A detailed description of vegetation characteristics along each plot and sampling protocols are also available in Nunes da Cunha, Rebellato and Costa (2010).

For our analysis of site occupancy estimates, we used a multi-season occupancy model that explicitly accounts for imperfect detection (MacKenzie et al., 2006). A detection history was constructed for each species, assigning "1" to those sampling plots in which the species was detected and a "0" otherwise. The study consisted of three primary sampling periods, and within each primary period six sites (each trap launch) surveyed by plot. If a plot dried, we considered tadpole occupancy as missing value for that sampling event. We incorporated into the models the site-specific and survey-specific covariates on occupancy probability (ψ) and detection probability (p), through a logit link function. Since our main focus was how occupancy changes, we assumed that colonization probability (γ) and extinction probability rate (ε) were constant over the study period. Estimates of occupancy probability in sampling periods were obtained by a smoothing-based method (Weir,

Fiske and Royle, 2009). We used 100 bootstrap iterations to compute standard errors of derived parameter estimates, as recommended by Mackenzie et al. (2006). For vegetation volume and water temperature, both linear and quadratic effects were considered. Quadratic effects were tested in order to detect a potential peak in tadpole activity.

We followed a two step process for building occupancy models: first, we held site occupancy probability constant while modelling those covariates considered most likely to influence species detection probabilities (i.e. $\psi(.)$, p(covariate), see online supplementary table S1). Only species with a detection probability $\geqslant 0.15$ were used for occupancy probability modelling (O'Connel et al., 2006). Second, we examined four occupancy models (online supplementary table S2) where ψ was allowed to vary with vegetation cover and species richness of predatory fish, using the best model for detection probability. We used corrected Akaike's information criteria (AICc; Burnham and Anderson, 2002) to rank the candidate models for each species. Analyses were carried out using the R statistical computing environment version 3.2. (R Development Core Team, 2015), and its extension package unmarked (Fiske and Chandeler, 2011).

We used a permutational variance analysis (PERMANOVA) to assess differences in anuran assemblage composition between areas with different types of vegetation cover (native grassland, exotic pasture, cambarazal and seasonally-flooded forest), based on Bray-Curtis dissimilarity. We used a constrained redundancy analysis (RDA) to evaluate the effects of herbaceous vegetation volume, species richness of predatory fish, and type of vegetation cover on the abundance matrix of species composition. For composition analysis, we used the sum of launch traps at each plot, and tadpole data were Hellinger-transformed to reduce the influence of outliers (Legendre and Gallagher, 2001). We calculated the significance of variance explained by RDAs by performing ANOVA-like permutation tests (1000 permutations). The analyses were conducted on the vegan package 2.3. for R (Oksanen et al., 2015).

Results

We recorded 13 anuran species belonging to families Hylidae, Leptodactylidae, and Microhylidae (table 1). Some tadpoles in our sample could not be unambiguously assigned to any particular taxon from within the analysed species groups. Tadpoles classified herein as *Leptodactylus fuscus* may correspond to one or another of the two species from this group recorded at the study site – *L. elenae* and *L. fuscus*. Similarly, tadpoles referred as *Chiasmocleis albopunctata* and *Elachistocleis matogrosso* may

Table 1. Number of sites where tadpole species were encountered by sampling event, sample size, and corresponding detection probabilities for constant model (p), in northern Pantanal. SE: Standard error. [a]The Total column sums the number of sites where each species was detected at least once.

| Family Species	December 2006 Flood beginning ($n = 27$)	February 2007 Steady flood ($n = 27$)	April 2007 Drawdown ($n = 9$)	Total[a]	$p \pm SE$
Hylidae					
Dendropsophus nanus	4	9	1	13	0.16 ± 0.06
Hypsiboas raniceps	2	0	0	2	0.01 ± 0.01
Lysapsus limellum	0	1	1	2	0.02 ± 0.02
Scinax fuscomarginatus	20	13	0	21	0.27 ± 0.03
Scinax nasicus	0	7	0	7	0.06 ± 0.02
Trachycephalus typhonius	3	0	0	3	0.12 ± 0.10
Leptodactylidae					
Leptodactylus fuscus	3	0	0	3	0.02 ± 0.01
Physalaemus albonotatus	5	0	0	5	0.14 ± 0.08
Physalaemus biligonigerus	10	1	0	10	0.09 ± 0.05
Physalaemus centralis	11	3	0	11	0.18 ± 0.06
Physalaemus cuvieri	11	0	0	11	0.25 ± 0.06
Microhylidae					
Chiasmocleis albopunctata	1	0	0	1	0.01 ± 0.01
Elachistocleis matogrosso	12	0	0	12	0.29 ± 0.06

include tadpoles of congeners. The most frequently encountered species was *Scinax fuscomarginatus*, recorded in 21 of 27 plots (online supplementary table S3). Conversely, *C. albopunctata*, the least frequently encountered species, was recorded in only one plot. The majority of species were recorded in the beginning of the flood (table 1), and six species were recorded in the steady flood period. During the drawdown, *Dendropsophus nanus* and *Lysapsus limellum* were the only species recorded. We are able to model occupancy of five species: *D. nanus*, *S. fuscomarginatus*, *Physalaemus centralis*, *P. cuvieri*, and *E. matogrosso*.

During the study period, water temperature ranged from 43.5°C (December) to 22.7°C (April) and was correlated with maximum daily temperature (online supplementary fig. S1). Only nine out of 27 flooded plots in December 2006 still contained water in the drawdown period. Overall predatory fish of eight families (Acestrorhynchidae, Callichthyidae, Characidae, Cichlidae, Erythrynidae, Heptapteridae, Hypopomidae, and Pimelodidae) were recorded from 24 fish-containing plots. Vegetation cover

was entirely composed of exotic pasture in five plots.

The best detection model for *E. matogrosso* and *S. fuscomarginatus* included effect of electrical conductivity. Detection probabilities of both species were positively associated with electrical conductivity (online supplementary fig. S2). Volume of vegetation explained variation in detection probability for *P. cuvieri* and *D. nanus*. Detection probability of *P. centralis* was positively associated with water temperature. The full set of ranked candidate models is presented in tables S1 and S2.

Occupancy probability was higher at the beginning of the flood for most species (fig. 2). Only *D. nanus* tadpoles showed a constant occupancy probability throughout the entire flood period. Occupancy probability was positively associated with species richness of predatory fish for three species: *D. nanus*, *P. centralis*, and *P. cuvieri* (table 2). Only *S. fuscomarginatus* was associated with vegetation cover, and occupancy probability was highest in native grasslands and exotic pasture (fig. 3). Species showed lower occupancy probability values in seasonally-flooded forests. For *E. matogrosso*,
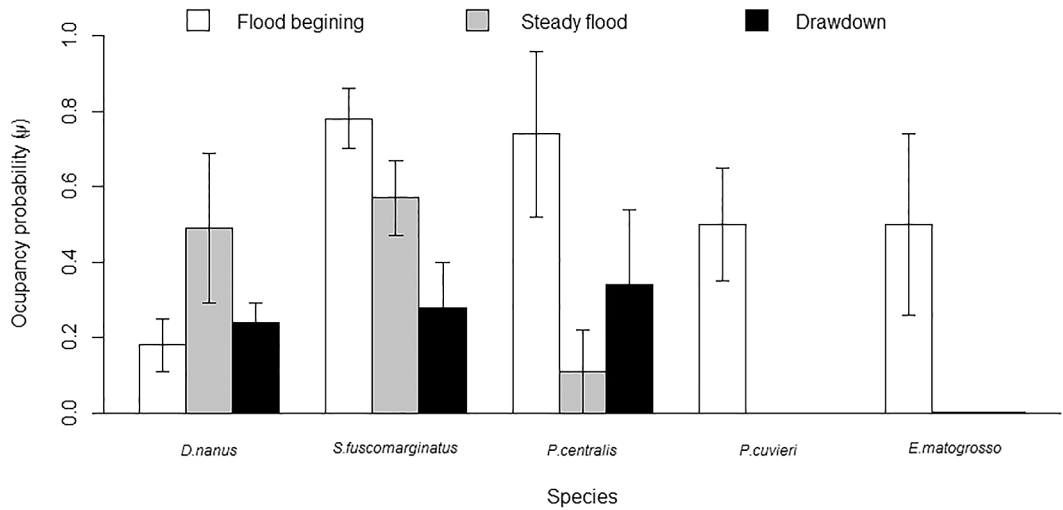
Figure 2. Estimated site occupancy across a flooding season (December 2006 to April 2007) for tadpoles of five anuran species across 27 plots in northern Pantanal, Brazil. Bars represent ± 1 standard error after 100 bootstraps. See Results for full species names.

Table 2. Parameters estimates contained in the two most supported models selected using AICc (corrected Akaike's information criterion) for plot occupancy probability. [a]The symbol Ψ indicates the occupancy portion of the model, while the symbol p denotes the detection portion of the model. (.) The parameter was constant. $-$ indicates a negative relationship. [b]w_i: model Akaike weight. [c]Evidence ratio: ratio of Akaike weights between the two best ranked models.

| Species Model[a]	ΔAICc	w_i[b]	Evidence ratio[c]
Dendropsophus nanus			
Ψ(fish), $p(-\text{vegetation volume}^2)$	0.00	0.98	98.00
Ψ(fish, vegetation cover), $p(-\text{vegetation volume}^2)$	9.72	0.01	
Scinax fuscomarginatus			
Ψ(vegetation cover), p(conductivity)	0.00	0.55	1.48
Ψ(.), p(conductivity)	0.78	0.37	
Physalaemus centralis			
Ψ(fish), p(temperature)	0.00	0.72	2.67
Ψ(.), p(temperature)	1.98	0.27	
Physalaemus cuvieri			
Ψ(fish), p(vegetation volume)	0.00	0.53	1.20
Ψ(.), p(vegetation volume)	0.39	0.44	
Elachistocleis matogrosso			
Ψ(.), p(conductivity)	0.00	0.65	3.61
Ψ(fish), p(conductivity)	2.50	0.18	

the highest ranking occupancy model included only the intercept (table 2).

Comparison of assemblages between areas showed significant differences in species composition associated with vegetation cover (PERMANOVA, $F_{3,26} = 2.036$; $P < 0.001$). However, this association was relatively weak,

explaining only 21% of the variability ($R^2 = 0.21$). The RDA corroborated the outcome of variance analysis. There was a weak but significant relationship ($P < 0.01$) between tadpole assemblages and vegetation characteristics. Type of vegetation cover, vegetation volume, species richness of predatory fish explained
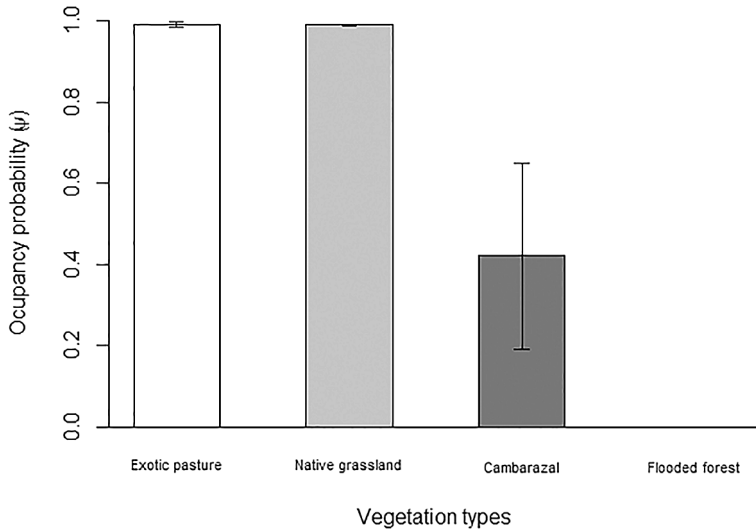
Figure 3. Estimated occupancy across different vegetation cover types for tadpoles of *Scinax fuscomarginatus*. Bars represent ±1 standard error after 100 bootstraps.
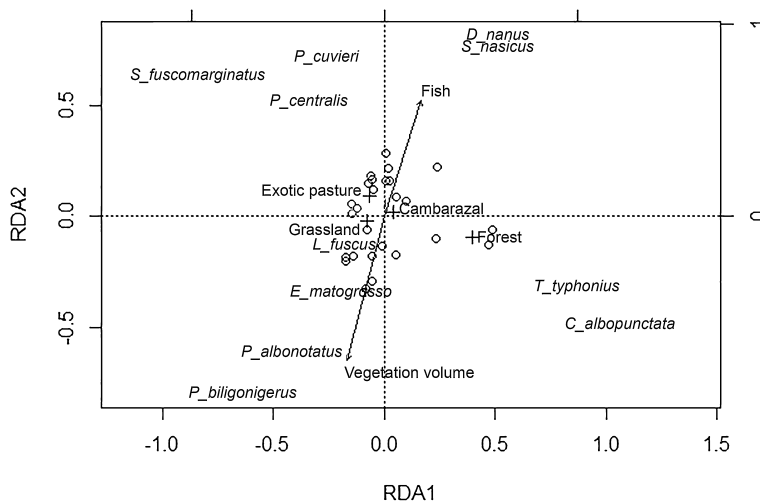
Figure 4. Redundancy analysis (RDA) ordination describing the relationships between tadpole assemblage and vegetation cover. Open circles represent sampled sites. Crosses represent centroids of levels of vegetation cover. The scores of *Hypsiboas raniceps* and *Lysapsus limellum* are close to the origin and are not labelled. See Results for full species names.

16% of the variation in assemblage structure. The first two canonical axes together explained 25% of the total variance in the data, the first axis alone explaining 16%. The RDA showed that differences in vegetation type (open or forested areas) played an important role along the first axis. Assemblages with *C. albopunctata* and *T. typhonius* were associated with forested areas; assemblages with *E. matogrosso* and *S. fuscomarginatus* were associated with open areas (fig. 4). Assemblages dominated by *P. centralis* and *P. cuvieri* were associated with exotic pastures with low vegetation volume. *Dendropsophus nanus* and *Scinax nasicus* tadpoles were registered mainly in plots with predatory fish (fig. 4).

Discussion

Tadpole assemblages differed among wetlands in different vegetation types of the Pantanal. Our results showed that tadpole composition was related to vegetation characteristics (vegetation cover type and volume of herbaceous vegetation) and species richness of predatory fish. Some species (*S. fuscomarginatus*, *P. centralis*, and *P. cuvieri*) were strongly associated with exotic pastures. In addition, tadpole occupancy probability for some species was positively associated with exotic land cover and species richness of fish. These results are in contrast to effects of exotic pasture on aquatic organisms in previous studies conducted in the same study area (Fernandes, Machado and Penha, 2010; Santos et al., 2013). Exotic plants have been found to negatively affect amphibian performance, including larval development time and foraging success of adults (Maerz, Nuzzo and Blossey, 2009; Cotten et al., 2012; Martin, Rainford and Blossey, 2015). However, the effects of changes in plant assemblages will depend on changes to habitat structure or quality, because an exotic matrix is not necessarily hostile to all species (Ficetola and De Bernardi, 2004; Dixo and Metzger, 2010).

In the Pantanal, variation of structural complexity related to vegetation cover can be affected: i) by forest and woodland clearance and the deliberate establishment of exotic pastures; ii) by expansion of exotic grasses through grasslands and replacement of native species. It has been widely demonstrated that forest clearance has detrimental effects on amphibians through habitat loss, edge effects, and reducing vertical structural heterogeneity (e.g. Vallan, 2000; Bell and Donnelly, 2006). In savannas, forested and woodland patches may provide shaded, mesic microhabitats on adjacent grasslands that would otherwise not occur.

The presence of tadpoles in ponds or pools relies, in the first instance, on the site selected by adults for egg-laying. We know that the littoral habitat complexity (in terms of vegetation cover) can influence breeding site selection by some species (Eterovick and Barata, 2006; Silva, Gibbs and Rossa-Feres, 2011). These microhabitats provide refuges for tadpoles to avoid predators, support for clutches, and calling site for adults (Kopp, Wachlevski and Eterovick, 2006; Hartel et al., 2007). Results from our study can be explained by species' different calling site requirements. Tadpoles of arboreal species (*T. typhonius*) were associated with plots in flooded forests, because bushes and trees provide suitable perches for adults (Pansonato, Mott and Strüssmann, 2011), as well as cavities and hollows in tree trunks or branches to serve as daytime retreats. Small species that call perched within herbaceous vegetation (*S. fuscomarginatus*) or in shallow water (*P. centralis* and *P. cuvieri*) were associated with exotic pastures. In addition, we found similar occupancy probability in open areas (grasslands or pastures) for *S. fuscomarginatus*. Because of the dense herbaceous cover, tussock grasses (such as *Urochloa* spp.) may constitute a suitable calling site for species that call close to the ground.

In addition to calling sites, herbaceous cover may offer shelter for recently metamorphosed tadpoles and adults of species with low vagility (Shulse et al., 2010; Watling, Hickman and Orrock, 2011). Close to the study area, there is an evidence that dense shrub encroachment favoured some anuran species (Dorado-Rodrigues et al., 2015). Although monodominant stands reduce the vegetation cover heterogeneity, the dense cover seems to provide shelter and other resources not readily available in open habitats (Cosentino, Schooley and Phillips, 2010). Therefore, a plausible hypothesis is that desiccation risk in *Urochloa* pastures is lower compared to native grasslands, due to the habitual dense herbaceous cover provided by species in that genus. This might favourably change microclimate conditions for post-metamorphic dispersal (Marsh et al., 2004).

Oviposition sites and daytime shelter are more directly associated with juvenile and adult habitat use, and connection of vegetation cover

with tadpole occurrence is indirect. Previous studies on invasive plants have reported elevated mortality of tadpoles in exotic extracts containing a greater concentration of phenolic compounds than native extracts (Brown et al., 2006; Watling et al., 2011). However, negative direct effects on tadpole development or survival were species specific. For some tadpole species, litter traits (elemental composition such as C:N) seem to be particularly important, and plant origin had no significant effect on anuran performance (Cohen, Maerz and Blossey, 2012; Martin, Rainford and Blossey, 2015). These results were attributed to species plasticity, because tadpoles vary greatly in physiology and feeding behaviour (Altig, Whiles and Taylor, 2007). *Urochloa* species are known to release allelopathic substances to the environment (Barbosa, Pivello and Meirelles, 2008), such as phenolic acids and alkaloids. It is therefore likely that tadpoles will respond negatively to compounds leached from *Urochloa* leaf litter.

In spite of presence of fish being considered an important factor in determining tadpole assemblage richness and composition (Werner et al., 2007; Both et al., 2009), our results showed that occupancy probabilities of three species were positively associated with species richness of predatory fish. Predation can be an important factor at small spatial scales (ponds), however environmental features, such as hydroperiod, can be the major factors at spatial mesoscales (Almeida et al., 2014). Hydroperiod is an important factor that influences amphibian communities, and a peak of diversity is expected in long term temporary wetlands (Babbitt, Baber and Tarr, 2003; Werner et al., 2007; Prado and Rossa-Feres, 2014). However, the availability of reproductive habitats due to hydroperiod-related constraints is not a static factor and interacts with spatial features (e.g. pond connectivity, Werner et al., 2007). In Neotropical floodplains, pond availability and connectivity are affected by the surface flooding dynamics and daily rainfall, which may result in transfer of individuals between ponds (Maltchik et al., 2008;

Almeida et al., 2014). We recognized that some tadpoles could have been washed to a certain plot from another one, but this effect should be small because: i) most species reproduce during the beginning of the rainy season, reaching the post metamorphic stage before the steady flood period (Prado et al., 2005); ii) anuran movements during the breeding season are commonly >1 km (Semlitsch, 2008). In addition to developmental constraints imposed on tadpoles, hydroperiod length influences predation-prey interactions (Wellborn, Skelly and Werner, 1996). Some reproductive modes or microhabitat choice may enable species to avoid or minimize predation by fish. For *Physalaemus* species, positive association with fish could be attributed to tadpole preference for shallow water (up to 20 cm) (Brasileiro and Martins, 2006). For *D. nanus* our results are in agreement with its reported continuous reproductive activity throughout the year (Prado et al., 2005).

While model selection did not reveal a single shared best model with which to explain species detection probability, our results are more associated with habitat characteristics than phenology of species. Similar patterns have been seen in tadpole assemblages in grasslands in southern Brazil (Moreira, Moura and Maltchik, 2016). Although seasonal phenologies may affect detection probabilities of amphibian species, mainly explosive breeders (Curtis and Paton, 2010; Moreira, Moura and Maltchik, 2016), our detection probabilities for tadpoles vary most with vegetation volume, water temperature, and electrical conductivity. We also found linear and quadratic vegetation volume effects on detection probability. It highlights that amphibians are a group with remarkable differences in life-histories strategies, thus the incorporation of species-traits is fundamental to unbiased assessment of habitat use.

From the perspective of our study developed over one rainy season, tadpole occupancy and species composition differed between natural areas and exotic pasture. Although our results showed an association of some anuran species

with exotic pasture, the idea that vegetation origin (i.e., native or exotic) is a good predictor of tadpole habitat quality is not necessarily true. In a functional context, anuran adults and larvae live in different worlds, so changes in wetland plant communities may have distinct and very different effects for each stage. It remains unclear which mechanisms are linked to plant-tadpole interactions, but the effects of exotic pastures seem to be related to individual traits each species (dietary plasticity, habitat preference, and reproductive mode of adults). Our results showed that some generalist species were able to cope with replacement of native vegetation by exotic species. However, traditional management practices have maintained many areas of Pantanal as near-pristine wetland ecosystems (Junk and Nunes da Cunha, 2012), and replacement of native vegetation by exotic pasture should be done with caution.

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